A HISTORY of LAND MAMMALS in the WESTERN HEMISPHERE

WM. BERRYMAN SCOTT

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Frontispiece. — A Pleistocene tar-pool in southern California: †Giant Wolves (*Canis †dirus*) and †Sabre-tooth Tiger (†*Smilodon californicus*) on the carcass of an elephant (*Elephas †columbi*). The elephant is hairless, as may have been true of the southern race.

A
HISTORY OF LAND MAMMALS
IN THE
WESTERN HEMISPHERE

BY

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ILLUSTRATED WITH 32 PLATES AND MORE THAN 100 DRAWINGS
BY BRUCE HORSFALL

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Dedicated

TO

MY CLASSMATES

HENRY FAIRFIELD OSBORN AND FRANCIS SPEIR

IN MEMORY OF A NOTABLE SUMMER AFTERNOON
IN 1876 AND IN TOKEN OF FORTY
YEARS' UNCLOUDED FRIENDSHIP

Speak to the earth and it shall teach thee.

—Job, xii, 8.

Can these bones live?

—Ezekiel, xxxvii, 3.

PREFACE

One afternoon in June, 1876, three Princeton undergraduates were lying under the trees on the canal bank, making a languid pretence of preparing for an examination. Suddenly, one of the trio remarked: "I have been reading an old magazine article which describes a fossil-collecting expedition in the West; why can't we get up something of the kind?" The others replied, as with one voice, "We can; let's do it." This seemingly idle talk was, for Osborn and myself, a momentous one, for it completely changed the careers which, as we then believed, had been mapped out for us. The random suggestion led directly to the first of the Princeton palæontological expeditions, that of 1877, which took us to the "Bad Lands" of the Bridger region in southwestern Wyoming. The fascination of discovering and exhuming with our own hands the remains of the curious creatures which once inhabited North America, but became extinct ages ago, has proved an enduring delight. It was the wish to extend something of this fascinating interest to a wider circle, that occasioned the preparation of this book.

The western portion of North America has preserved a marvellous series of records of the successive assemblages of animals which once dwelt in this continent, and in southernmost South America an almost equally complete record was made of the strange animals of that region. For the last half-century, or more, many workers have coöperated to bring this long-vanished world to light and to decipher and interpret the wonderful story of mammalian development in the western hemisphere. The task of making this history intelligible, not to say interesting, to the layman, has been one of formidable difficulty, for it is recorded in the successive modifications of the bones and teeth, and without some knowledge of osteology, these records are in an unknown tongue. To meet this need, Chapter III gives a sketch of the mammalian skeleton and dentition, which the reader may use as the schoolboy uses a vocabulary to translate his Latin exercise, referring to it from time to time, as may be necessary to make clear the descriptions of the various mammalian groups. Technical terms have been avoided as far as possible, but, unfortunately, it is not practicable to dispense with them altogether. The appended glossary will, it is hoped, minimize the inconvenience.

No one who has not examined it, can form any conception of the enormous mass and variety of material, illustrating the history of American mammals, which has already been gathered into the various museums. A full account of this material would require many volumes, and one of the chief problems in the preparation of this book has been that of making a proper selection of the most instructive and illuminating portions of the long and complicated story. Indeed, so rapid is the uninterrupted course of discovery, that parts of the text became antiquated while in the press and had to be rewritten. As first prepared, the work proved to be far too long and it was necessary to excise several chapters, for it seemed better to cover less ground than to make the entire history hurried and superficial. The plan of treatment adopted involves a considerable amount of repetition, but this is perhaps not a disadvantage, since the same facts are considered from different points of view.

The facts which are here brought together have been ascertained by many workers, and I have borrowed with the greatest freedom from my fellow labourers in the field of palæontology. As every compiler of a manual finds, it is not feasible to attribute the proper credit to each discoverer. Huxley has so well explained the situation in the preface to his "Anatomy of Vertebrated Animals," that I may be permitted to borrow his words: "I have intentionally refrained from burdening the text with references; and, therefore, the reader, while he is justly entitled to hold me responsible for any errors he may detect, will do well to give me no credit for what may seem original, unless his knowledge is sufficient to render him a competent judge on that head."

A book of this character is obviously not the proper place for polemical discussions of disputed questions. Whenever, therefore, the views expressed differ widely from those maintained by other palæontologists, I have attempted no more than to state, as fairly as I could, the alternative interpretations and my own choice between them. Any other course was forbidden by the limitations of space.

It is a pleasure to give expression to my sincere sense of gratitude to the many friends who have helped me in an unusually laborious undertaking. Professor Osborn and Dr. Matthew have placed at my disposal the wonderful treasures of the American Museum of Natural History in New York and in the most liberal manner have supplied me with photographs and specimens for drawings, as well as with information regarding important discoveries which have not yet been published. Dr. W. J. Holland, Director of the Carnegie Museum in Pittsburgh, has likewise generously provided many photographs from the noble collection under his charge, kindly permitting the use of material still undescribed. To Professor Charles Schuchert, of Yale University, I am also indebted for several photographs.

The figures of existing animals are almost all from photographs taken in the New York and London zoölogical gardens, and I desire to thank Director Hornaday, of the Bronx Park, and Mr. Peacock, of the London garden, for the very kind manner in which they have procured these illustrations for my use. The photographs have been modified by painting out the backgrounds of cages, houses, and the like, so as to give a less artificial appearance to the surroundings.

To my colleagues at Princeton I am under great obligations for much valuable counsel and assistance. Professor Gilbert van Ingen has prepared the maps and diagrams and Dr. W. J. Sinclair has devoted much labour and care to the illustrations and has also read the proofs. Both of these friends, as also Professors C. H. Smyth and E. G. Conklin and Drs. Farr and McComas, have read various parts of the manuscript and made many helpful suggestions in dealing with the problems of treatment and presentation.

For thirteen years past I have been engaged in the study of the great collections of fossil mammals, gathered in Patagonia by the lamented Mr. Hatcher and his colleague, Mr. Peterson, now of the Carnegie Museum. This work made it necessary for me to visit the museums of the Argentine Republic, which I did in 1901, and was there received with the greatest courtesy and kindness by Dr. F. Moreno, Director, and Dr. Santiago Roth, of the La Plata Museum, and Dr. F. Ameghino, subsequently Director of the National Museum at Buenos Aires. To all of these gentlemen the chapters on the ancient life of South America are much indebted, especially to Dr. Ameghino, whose untimely death was a great loss to science. It is earnestly to be hoped that the heroic story of his scientific career may soon be given to the world.

Finally, I desire to thank Mr. Horsfall for the infinite pains and care which he has expended upon the illustrations for the work, to which so very large a part of its value is due.

While the book is primarily intended for the lay reader, I cannot but hope that it may also be of service to many zoölogists, who have been unable to keep abreast of the flood of palæontological discovery and yet wish to learn something of its more significant results. How far I have succeeded in a most difficult task must be left to the judgment of such readers.

Princeton, N.J.,
June 1, 1913.

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CHAPTER I

METHODS OF INVESTIGATION — GEOLOGICAL

THE term *Mammal* has no exact equivalent in the true vernacular of any modern language, the word itself, like its equivalents, the French *Mammifère* and the German *Säugethier*, being entirely artificial. As a name for the class Linnæus adopted the term Mammalia, which he formed from the Latin *mamma* (*i.e.* teat) to designate those animals which suckle their young; hence the abbreviated form Mammal, which has been naturalized as an English word. "Beast," as employed in the Bible, and "Quadruped" are not quite the same as mammal, for they do not include the marine forms, such as whales, dolphins, seals, walruses, or the flying bats, and they are habitually used in contradistinction to Man, though Man and all the forms mentioned are unquestionably mammals.

In attempting to frame a definition of the term *Mammal*, it is impossible to avoid technicalities altogether, for it is the complete unity of plan and structure which justifies the inclusion of all the many forms that differ so widely in habits and appearance. *Mammals are air-breathing vertebrates, which are warm-blooded and have a 4-chambered heart; the body cavity is divided into pleural and abdominal chambers by a diaphragm; except in the lowest division of the class, the young are brought forth alive and are always suckled, the milk glands being universal throughout the class. In the great majority of mammals the body* *is clothed with hair; a character found in no other animals. In a few mammals the skin is naked, and in still fewer there is a partial covering of scales.* The list of characters common to all mammals, which distinguish them from other animals, might be indefinitely extended, for it includes all the organs and tissues of the body, the skeletal, muscular, digestive, nervous, circulatory, and reproductive systems, but the two or three more obvious or significant features above selected will suffice for the purposes of definition.

While the structural plan is the same throughout the entire class, there is among mammals a wonderful variety of form, size, appearance, and adaptation to special habits. It is as though a musician had taken a single theme and developed it into endless variations, preserving an unmistakable unity through all the changes. Most mammals are *terrestrial,* living, that is to say, not only on the land, but on the ground, and are herbivorous in habit, subsisting chiefly or exclusively upon vegetable substances, but there are many departures from this mode of life. It should be explained, however, that the term *terrestrial* is frequently used in a more comprehensive sense for all land mammals, as distinguished from those that are aquatic or marine. Monkeys, Squirrels, Sloths and Opossums are examples of the numerous *arboreal* mammals, whose structure is modified to fit them for living and sleeping in the trees, and in some, such as the Sloths, the modification is carried so far that the creature is almost helpless on the ground. Another mode of existence is the burrowing or *fossorial,* the animal living partly or mostly, or even entirely underground, a typical instance of which is the Mole. The Beaver, Muskrat and Otter, to mention only a few forms, are *aquatic* and spend most of their life in fresh waters, though perfectly able to move about on the land. *Marine* mammals, such as the Seals and Whales, have a greatly modified structure which adapts them to life in the sea.

Within the limits of each of these categories we may note that there are many degrees of specialization or adaptation to particular modes of life. Thus, for example, among the marine mammals, the Whales and their allies, Porpoises, etc., are so completely adapted to a life in the seas that they cannot come upon the land, and even stranding is fatal to them, while the Seals frequently land and move about upon the shore. It should further be observed that mammals of the most diverse groups are adapted to similar modes of existence. Thus in one natural group or *order* of related forms, occur terrestrial, burrowing, arboreal and aquatic members, and the converse statement is of course equally true, that animals of similar life-habits are not necessarily related to one another, and very frequently, in fact, are not so related. Among the typically marine mammals, for example, there are at least three and probably four distinct series, which have independently become adapted to life in the sea.

Before attempting to set forth an outline of what has been learned regarding the history of mammalian life in the western hemisphere, it is essential to give the reader some conception of the manner in which that knowledge has been obtained. Without such an understanding of the methods employed in the investigation the reader can only blindly accept or as blindly reject what purports to be the logical inference from well-established evidence. How is that evidence to be discovered? and how may trustworthy conclusions be derived from it?

The first and most obvious step is to gather all possible information concerning the mammals of the present day, their structure (comparative anatomy), functions (physiology), and their geographical arrangement. This latter domain, of the geographical distribution of mammals, is one of peculiar significance. Not only do the animals of North America differ radically from those of Central and South America, but within the limits of each continent are more or less well-defined areas, the animals of which differ in a subordinate degree from those of other areas. The study of the modern world, however, would not of itself carry us very far toward the goal of our inquiries, which is an *explanation*, not merely a statement, of the facts. The present order of things is the outcome of an illimitably long sequence of events and can be understood only in proportion to our knowledge of the past. In other words, it is necessary to treat the problems involved in our inquiry *historically;* to trace the evolution of the different mammalian groups from their simpler beginnings to the more complex and highly specialized modern forms; to determine, so far as that may be done, the place of origin of each group and to follow out their migrations from continent to continent.

While we shall deal chiefly, almost exclusively, with the mammals of the New World, something must be said regarding those of other continents, for, as will be shown in the sequel, both North and South America have, at one time or another, been connected with various land-masses of the eastern hemisphere. By means of those land-connections, there has been an interchange of mammals between the different continents, and each great land-area of the recent world contains a more or less heterogeneous assemblage of forms of very diverse places of origin. Indeed, migration from one region to another has played a most important part in bringing about the present distribution of living things. From what has already been learned as to the past life of the various continents and their shifting connections with one another, it is now feasible to analyze the mammalian faunas of most of them and to separate the indigenous from the immigrant elements. Among the latter may be distinguished those forms which are the much modified descendants of ancient migrants from those which arrived at a much later date and have undergone but little change. To take a few examples from North America, it may be said that the Bears, Moose, Caribou and Bison are late migrants from the Old World; that the Virginia and Black-tailed Deer and the Prong-horned Antelope are of Old World origin, but their ancestors came in at a far earlier period and the modern species are greatly changed from the ancestral migrants. The Armadillo of Texas and the Canada Porcupine are almost the only survivors, north of Mexico, of the great migration of South American mammals which once invaded the northern continent. On the other hand, the raccoons and several families of rodents are instances of indigenous types which may be traced through a long American ancestry.

Fully to comprehend the march of mammalian development, it thus becomes necessary to reconstruct, at least in outline, the geography of the successive epochs through which the developmental changes have taken place, the connections and separations of land-masses, the rise of mountain ranges, river and lake systems and the like. Equally significant factors in the problem are climatic changes, which have had a profound and far-reaching effect upon the evolution and geographical spread of animals and plants, and the changes in the vegetable world must not be ignored, for, directly or indirectly, animals are dependent upon plants. To one who has paid no attention to questions of this kind, it might well seem an utterly hopeless task to reconstruct the long vanished past, and he would naturally conclude that, at best, only fanciful speculations, with no foundation of real knowledge, could be within our reach. Happily, such is by no means the case. Geology offers the means of a successful attack upon these problems and, although very much remains to be done, much has already been accomplished in elucidating the history, especially in its later periods, with which the story of the mammals is more particularly concerned.

It is manifestly impossible to present here a treatise upon the science of Geology, even in outline sketch. Considerations of space are sufficient to forbid any such attempt. Certain things must be taken for granted, the evidence for which may be found in any modern text-book of Geology. For example, it is entirely feasible to establish the mode of formation of almost any rock (aside from certain problematical rocks, which do not enter into our discussion) and to determine whether it was laid down in the sea, or on the land, or in some body of water not directly connected with the sea, such as a lake or river. With the aid of the microscope, it is easy to discriminate volcanic material from the ordinary water-borne and wind-borne sediments and, in the case of the rocks which have solidified from the molten state, to distinguish those masses which have cooled upon the surface from those which have solidified deep within the earth.

While the nature and mode of formation of the rocks may thus be postulated, it will be needful to explain at some length the character of the evidence from which the history of the earth may be deciphered. First of all, must be made clear the method by which the events of the earth's history may be arranged in chronological order, for a history without chronology is unintelligible. The events which are most significant for our purpose are recorded in the rocks which are called *stratified, bedded or sedimentary,* synonymous terms. Such rocks were made mostly from the débris of older rocks, in the form of gravel, sand or mud, and were laid down under water, or, less extensively, spread by the action of the wind upon a land-surface. Important members of this group of rocks are those formed, more or less completely, from the finer fragments given out in volcanic eruptions, carried and sorted by the wind and finally deposited, it may be at great distances from their point of origin, upon a land-surface, or on the bottom of some body of water. Stratified or bedded rocks, as their name implies, are divided into more or less parallel layers or beds, which may be many feet or only a minute fraction of an inch in thickness. Such a division means a pause in the process of deposition or a change in the character of the material deposited over a given area. Owing to the operation of gravity, the layers of sediment are spread out in a horizontal attitude, which disregard the minor irregularities of the bottom, just as a deep snow buries the objects which lie upon the surface.

A moment's consideration will show that, in any series of stratified rocks which have not been greatly disturbed from their original horizontal position, *the order of succession or superposition of the beds must necessarily be the chronological order of their formation.* (Fig. 1.) Obviously, the lowest beds must have been deposited first and therefore are the oldest of the series, while those at the top must be the newest or youngest and the beds intermediate in position are intermediate in age. This inference depends upon the simple principle that each bed must have been laid down before the next succeeding one can have been deposited upon it. While this is so clear as to be almost self-evident, it is plain that such a mode of determining the chronological order of the rocks of the earth's crust can be of only local applicability and so far as the beds may be traced in unbroken continuity. It is of no direct assistance in correlating the events in the history of one continent with those of another and it fails even in comparing the distinctly separated parts of the same continent. Some method of universal applicability must be devised before the histories of scattered regions can be combined to form a history of the earth. Such a universal method is to be found in the *succession of the forms of life,* so far as that is recorded in the shape of *fossils,* or the recognizable remains of animal and vegetable organisms preserved in the rocks.

This principle was first enunciated by William Smith, an English engineer, near the close of the eighteenth century, who thus laid the foundations of Historical Geology. In the diagram, Fig. 2, is reproduced Smith's section across England from Wales to near London, which shows the successive strata or beds, very much tilted from their original horizontal position by the upheaval of the sea-bed upon which they were laid down. The section pictures the side of an imaginary gigantic trench cut across the island and was constructed by a

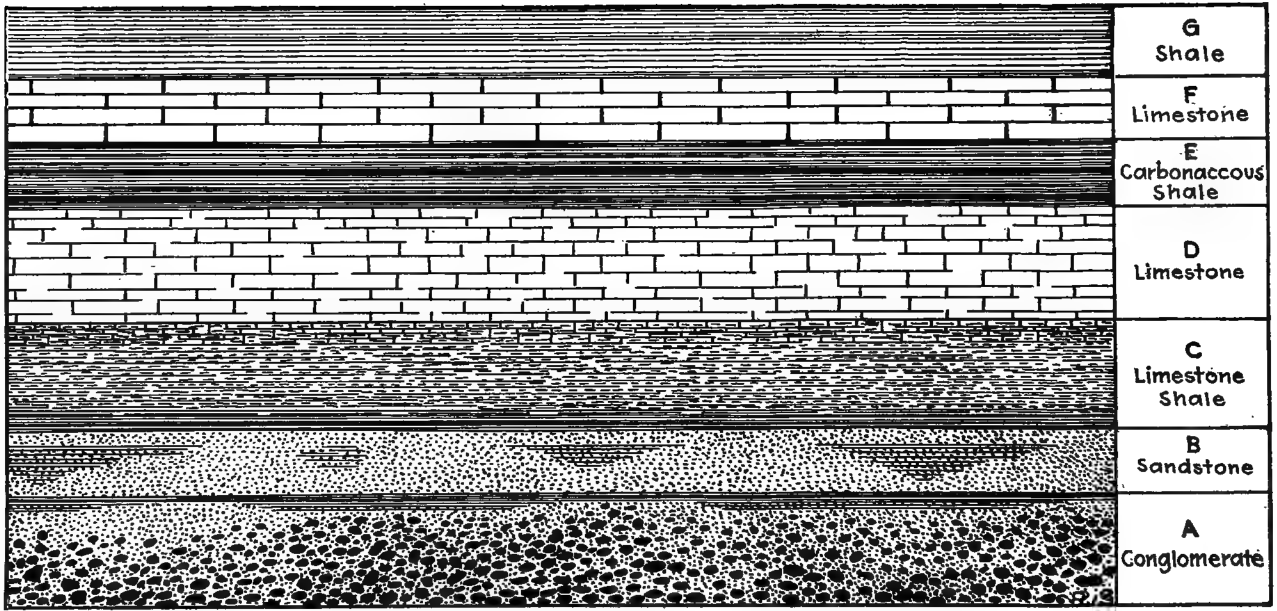

FIG. 1.—Diagram section of a series of beds, illustrating superposition. A is the oldest, B, C, D, etc., succeeding in ascending order.

simple geometrical method from the surface exposures of the beds, such as mining engineers continually employ to map the underground extension of economically important rocks, and shows how an enormous thickness of strata may be studied from the surface. The older beds are exposed at the western end of the section in Wales and, passing eastward, successively later and later beds are encountered, the newest appearing at the eastern end. Very many of the strata are richly fossiliferous, and thus a long succession of fossils was obtained in the *order of their appearance,* and this order has been found to hold good, not only in England, but throughout the world. The order of succession of the fossils was thus in the first instance actually ascertained from the succession of the strata in which they are found and has been verified in innumerable sections in many lands and is thus a matter of observed and verifiable fact, not merely a postulate or working hypothesis. Once ascertained, however, the order of succession of living things upon the earth may be then employed as an independent and indispensable means of geologically dating the rocks in which they occur.

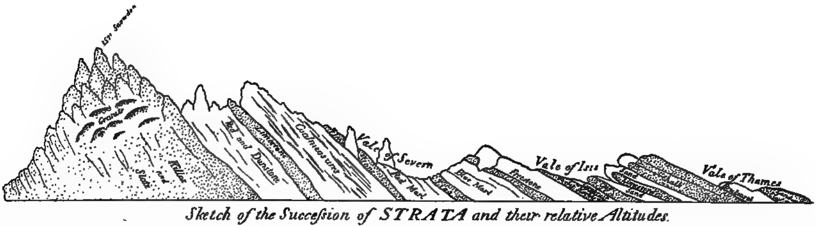

FIG. 2.— William Smith's section across the south of England. The vertical scale is exaggerated, which makes the inclination of the beds appear too steep.

N. B. The original drawing is in colors, which are not indicated by the dotted strata.

This is the *palæontological method,* which finds analogies in many other branches of learned inquiry. The student of manuscripts discovers that there is a development, or regular series of successive changes, in handwriting, and from the handwriting alone can make a very close approximation to the date of a manuscript. The order in which those changes came about was ascertained from the comparative study of manuscripts, the date of which could be ascertained from other evidence, but, when once established, the changes in handwriting are used to fix the period of undated manuscripts. Just so, the succession of fossils, when learned from a series of superposed beds, may then be employed to fix the geological date of strata in another region. Similarly, the archæologist has observed that there is an evolution or development in every sort of the work of men's hands and therefore makes use of coins, inscriptions, objects of art, building materials and methods, etc., to date ancient structures. In the German town of Trier (or Trèves) on the Moselle, the cathedral has as a nucleus a Roman structure, the date and purpose of which had long been matters of dispute, though the general belief was that the building had been erected under Constantine the Great. In the course of some repairs made not very long ago, it became necessary to cut deep into the Roman brickwork, and there, embedded in the undisturbed mortar, was a coin of the emperor Valentinian II, evidently dropped from the pocket of some Roman bricklayer. That coin fixed a date older than which the building cannot be, though it may be slightly later, and it well illustrates the service rendered by fossils in determining geological chronology.

Other methods of making out the chronology of the earth's history have been proposed from time to time and all of them have their value, though none of them renders us independent of the use of fossils, which have the pre-eminent advantage of not recurring or repeating themselves at widely separated intervals of time, as all physical processes and changes do. An organism, animal or plant, that has become extinct never returns and is not reproduced in the evolutionary process.

Great and well founded as is our confidence in fossils as fixing the geological date of the rocks in which they occur, it must not be forgotten that the succession of the different kinds of fossils in time was first determined from the superposition of the containing strata. Hence, it is always a welcome confirmation of the chronological inferences drawn from the study of fossils, when those inferences can be unequivocally established by the succession of the beds themselves. For example, in the Tertiary deposits of the West are two formations or groups of strata, called respectively the Uinta and the White River, which had never been known to occur in the same region and whose relative age therefore could not be determined by the method of superposition. Each of the formations, however, has yielded a large number of well-preserved fossil mammals, and the comparative study of these mammals made it clear that the Uinta must be older than the White River and that no very great lapse of time, geologically speaking, occurred between the end of the former and the beginning of the latter. Only two or three years ago an expedition from the American Museum of Natural History discovered a place in Wyoming where the White River beds lie directly upon those of the Uinta, thus fully confirming the inference as to the relative age of these two formations which had long ago been drawn from the comparative study of their fossil mammals.

The palæontological method of determining the geological date of the stratified rocks is thus an indispensable means of correlating the scattered exposures of the strata in widely separated regions and in different continents, it may be with thousands of miles of intervening ocean. The general principle employed is that *close similarity of fossils in the rocks of the regions compared points to an approximately contemporaneous date of formation of those rocks.* This principle must not, however, be applied in an offhand or uncritical manner, or it will lead to serious error. In the first place, the evolutionary process is a very slow one and geological time is inconceivably long, so that deposits which differ by some thousands of years may yet have the same or nearly the same fossils. The method is not one of sufficient refinement to detect such relatively small differences. To recur to the illustration of the develop-

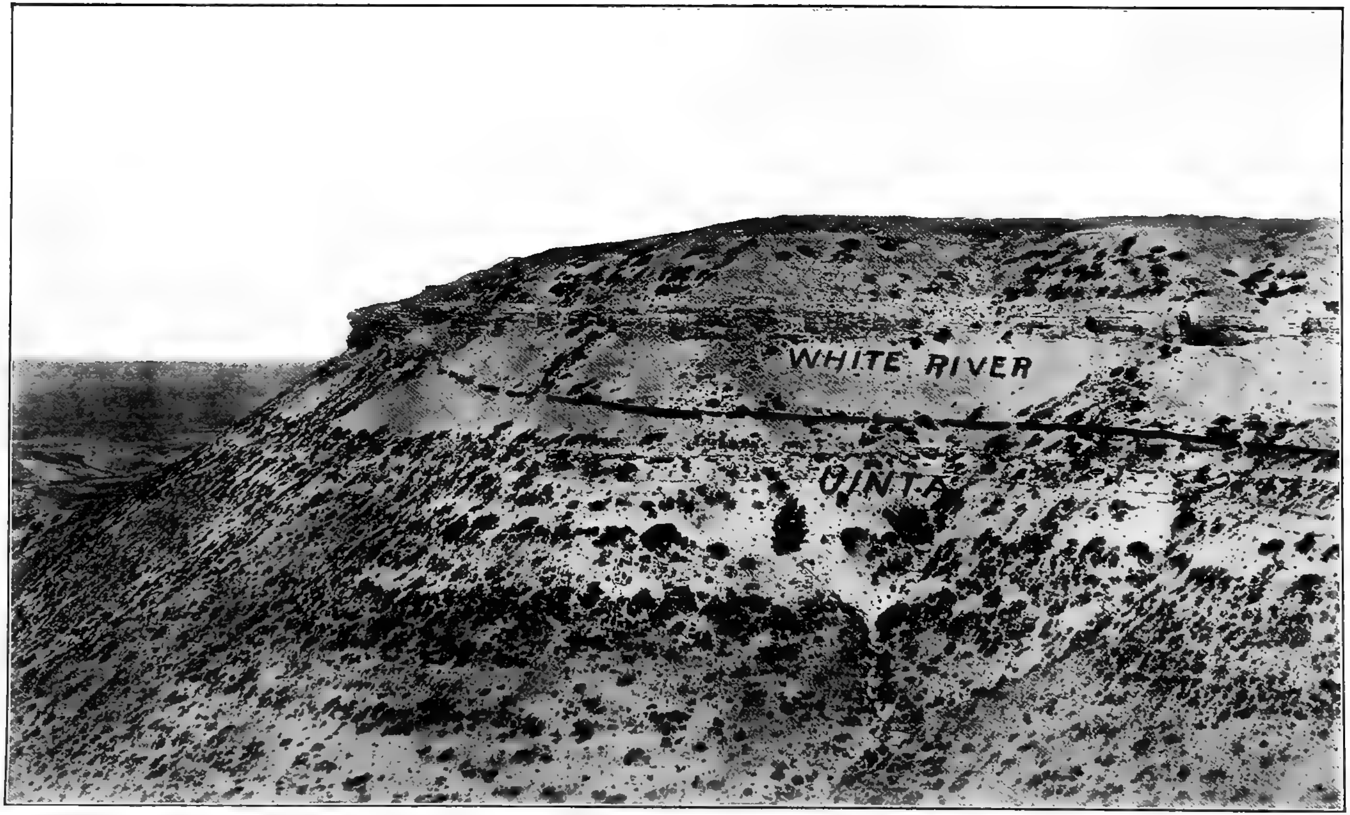

Fig. 3. — Bluff on Beaver Creek, Fremont Co., Wyoming. The White River beds were deposited on the worn and weathered surface of the Uinta, the heavy, broken line marking the separation between them. The valley was carved out long after the deposition of the White River strata.

ment in handwriting, the palæographer can hardly do more than determine the decade in which a manuscript was written; no one would expect him to fix upon the exact year, still less the month, from the study of handwriting alone. As is the month in recorded human history, so is the millennium in the long course of the earth's development.

In the second place, there are great differences in the contemporary life of separate regions and such geographical differences there have always been, so far as we can trace back the history of animals and plants. A new organism does not originate simultaneously all over the world but, normally at least, in a single area and spreads from that centre until it encounters insuperable obstacles. Such spreading is a slow process and hence it is that new forms often appear in one region much earlier than in others and in the very process of extending their range, the advancing species may themselves be considerably modified and reach their new and distant homes as different species from those which originated the movement. Extinction, likewise, seldom occurs simultaneously over the range of a group, but now here and now there in a way that to our ignorance appears to be arbitrary and capricious. The process may go on until extinction is total, or may merely result in a great restriction of the range of a given group, or may break up that range into two or more distinct areas.

Of such incomplete extinctions many instances might be given, but one must suffice. The camel-tribe, strange as it may appear, originated in North America and was long confined to that continent, while at the present day it is represented only by the llamas of South America and the true camels of Asia, having completely vanished from its early home. These facts and a host of similar ones make plain how necessary it is to take geographical considerations into account in all problems that deal with the synchronizing of the rocks of separate areas and continents.

Properly to estimate the significance of a difference in the fossils of two regions and to determine how far it is geographical, due to a separation in space, or geological and caused by separation in time, is often a very difficult matter and requires a vast amount of minute and detailed study. Once more, the principle involved is illustrated by the study of manuscripts. Down to the time when the printing press superseded the copyist, each of the nations of Europe had its own traditions and its more or less independent course of handwriting development. A great monastery, in which the work of copying manuscripts went on century after century, became an independent geographical centre with its particular styles. Thus the palæographer, like the geologist, is confronted by geographical problems as well as by those of change and development in general.

In addition to the method of geologically dating the rocks by means of the fossils which they contain, there are other ways which may give a greater precision to the result. Climatic changes, when demonstrable, are of this character, for they may speedily and simultaneously affect vast areas of the earth's surface or even the entire world. From time to time in the past, glacial conditions have prevailed over immense regions, several continents at once, it may be, as in one instance in which India, South Africa, Australia, South America were involved. The characteristic accumulations made by the glaciers in these widely separated regions must be contemporaneous in a sense that can rarely be predicated of the ordinary stratified rocks. Such climatic changes as the formation and disappearance of the ice-fields give a sharper and more definite standard of time comparisons than do the fossils alone, and yet the fossils are in turn needed to show which of several possible glacial periods are actually being compared.

Again, great movements of the earth's crust, which involve vast and widely separated regions and bring the sea in over great areas of land, or raise great areas into land, which had been submerged, may also yield more precise time-measurements, because occurring within shorter periods than do notable changes in the system of living things. Such changes in animals and plants may be compared to the almost imperceptible movement of the hour-hand of a clock, while the recorded climatic revolutions and crustal movements often supply the place of the minute-hand. It is obvious, however, that if the hour-hand be wanting, the minute-hand alone can be of very limited use. There have been a great many vast submergences and emergences of land in the history of the earth, and only the fossils can give us the assurance that we are comparing the same movement in distant continents, and not two similar movements separated by an enormous interval of time.

It may thus fairly be admitted that it is possible to arrange the rocks which compose the accessible parts of the earth's crust in chronological order and to correlate in one system the rocks of the various continents. The terms used for the more important divisions of geological time are, in descending order of magnitude, era, period, epoch, age or stage, and the general scheme of the eras and periods, which is in almost uniform use throughout the world, is given in the table, which is arranged so as to give the succession graphically, with the most ancient rocks at the bottom and the latest at the top.

Cenozoic era	Quaternary period
	Tertiary period
Mesozoic era	Cretaceous period
	Jurassic period
	Triassic period
Palæozoic era	Permian period
	Carboniferous period
	Devonian period
	Silurian period
	Ordovician period
	Cambrian period
Pre-Cambrian eras	Algonkian period
	Archæan period

It must not be supposed that all the divisions of similar rank, such as the eras, for example, were of equal length, as measured by the thickness of the rocks assigned to those divisions. On the contrary, they must have been of very unequal length and are of very different divisibility. The Pre-Cambrian eras, with only two periods, were probably far longer than all subsequent time, and all that the major divisions imply is that they represent changes in the system of life of approximately equivalent importance. It is impossible to give any trustworthy estimate of the actual lengths of these divisions in years, though many attempts to do so have been made. All that can be confidently affirmed is that geological time, like astronomical distances, is of inconceivable vastness and its years can be counted only in hundreds of millions.

To discuss in any intelligible manner the history of mammals, it will be necessary to go much farther than the above table in the subdivision of that part of geological time in which mammalian evolution ran its course. As mammals represent the highest stage of development yet attained in the animal world, it is only the latter part of the earth's history which is concerned with them; the earlier and incomparably longer portion of that history may be passed over. Mammals are first recorded in the later Triassic, the first of the three periods which make up the Mesozoic era. They have also been found, though very scantily, in the other Mesozoic periods, the Jurassic and Cretaceous, but it was the Cenozoic era that witnessed most of the amazing course of mammalian development and diversification, and hence the relatively minute subdivisions necessary for the understanding of this history deal only with the Cenozoic, the latest of the great eras.

In the subjoined table the periods and epochs are those which are in general use throughout the world, the ages and stages are those which apply to the western interior of North America, each region, even of the same continent, requiring a different classification. The South American formations are given in a separate table, as it is desirable to avoid the appearance of an exactitude in correlation which cannot yet be attained.

CENOZOIC ERA

Quaternary period	Recent epoch Pleistocene epoch = Glacial and Interglacial stages.
Tertiary period	Pliocene epoch Miocene epoch Oligocene epoch Eocene epoch Paleocene epoch

Continuing the subdivision of the Tertiary period still farther, we have the following arrangement:

TERTIARY PERIOD (North America)

Pliocene	Upper	Wanting	
	Middle	Blanco age	
	Lower	Thousand Creek age Snake Creek age Republican River age	
Miocene	Upper	Loup Fork age	
	Middle	Deep River age	
	Lower	Arikaree age	
Oligocene	Upper	John Day age	
	Lower	White River age	
Eocene	Upper	Uinta age	
	Middle	Bridger age	
	Lower	Wind River age Wasatch age	
Paleocene	Upper	Torrejon age	Fort Union
	Lower	Puerco age	

This is a representative series of the wide-spread and manifold non-marine Tertiary deposits of the Great Plains, but a much more extensive and subdivided scheme would be needed to show with any degree of fullness the wonderfully complete record of that portion of the continent during the Tertiary period. A much more elaborate table will be found in Professor Osborn's "Age of Mammals," p. 41. There are some differences of practice among geologists as to this scheme of classification, though the differences are not those of principle. No question arises concerning the reality of the divisions, or their order of succession in time, but merely as to the rank or relative importance which should be attributed to some of them, and that is a very minor consideration.

Much greater difficulty and, consequently, much more radical differences of interpretation arise when the attempt is made to correlate or synchronize the smaller subdivisions, as found in the various continents, with one another, because of the geographical differences in contemporary life. Between Europe and North America there has always been a certain proportion of mammalian forms in common, a proportion that was at one time greater, at another less, and this community renders the correlation of the larger divisions of the Tertiary in the two continents comparatively easy, and even in the minor subdivisions very satisfactory progress has been made, so that it is possible to trace in some detail the migrations of mammals from the eastern to the western hemisphere and *vice versa.* Such intermigrations were made possible by the land-bridges connecting America with Europe across the Atlantic, perhaps on the line of Greenland and Iceland, and with Asia where now is Bering Strait. These connections were repeatedly made and repeatedly broken during the Mesozoic and Cenozoic eras down to the latest epoch, the Pleistocene. By comparing the fossil mammals of Europe with those of North America for any particular division of geological time, it is practicable to determine whether the way of intermigration was open or closed, because separation always led to greater differences between the faunas of the two continents through divergent evolution.

Correlation with South America is exceedingly difficult and it is in dealing with this problem that the widest differences of opinion have arisen among geologists. Through nearly all the earlier half of the Tertiary period the two Americas were separated and, because of this separation, their land mammals were utterly different. Hence, the lack of elements common to both continents puts great obstacles in the way of establishing definite time-relations between their geological divisions. Only the marine mammals, whales and dolphins, were so far alike as to offer some satisfactory basis of comparison. When, in the later Tertiary, a land-connection was established between the two continents, migrations of mammals from each to the other began, and thenceforward there were always certain elements common to both, as there are to-day. In spite of the continuous land between them, the present faunas of North and South America are very strikingly different, South America being, with the exception of Australia, zoölogically the most peculiar region of the earth.

In the following table of the South American Cenozoic, the assignment of the ages to their epochs is largely tentative, especially as regards the more ancient divisions, and represents the views generally held by the geologists of Europe and the United States; those of South America, on the contrary, give an earlier date to the ages and stages and refer the older ones to the Cretaceous instead of the Tertiary.

CENOZOIC ERA (South America)

Quaternary period	Recent epoch
	Pleistocene epoch — Pampean Beds, Brazilian caverns

Tertiary period	Pliocene epoch	Monte Hermoso age
		Catamarca age
		Paraná age
	Miocene epoch	Santa Cruz age
		Patagonian age
	Oligocene epoch	Deseado age (*Pyrotherium* Beds)
		Astraponotus Beds
	Eocene epoch	Casa Mayor age (*Notostylops* Beds)

The Pleistocene and Pliocene deposits are most widely distributed over the Pampas of Argentina, but the former occur also in Ecuador, Brazil, Chili, and Bolivia. The other formations cover extensive areas in Patagonia, and some extend into Tierra del Fuego.

We have next to consider the methods by which past geographical conditions may be ascertained, a task which, though beset with difficulties, is very far from being a hopeless undertaking. As has already been pointed out, it is perfectly possible for the geologist to determine the circumstances of formation of the various kinds of rocks, to distinguish terrestrial from aquatic accumulations and, among the latter, to identify those which were laid down in the sea and those which were formed in some other body of water. By platting on a map all the marine rocks of a given geological date, an approximate estimate may be formed as to the extension of the sea over the present land for that particular epoch. It is obvious, however, that for those areas which then were land and now are covered by the sea, no such direct evidence can be obtained, and only indirect means of ascertaining the former land-connections can be employed. It is in the treatment of this indirect evidence that the greatest differences of opinion arise and, if two maps of the same continent for the same epoch, by separate authors, be compared, it will be seen that the greatest discrepancies between them are concerning former land-connections and extensions.

The only kind of indirect evidence bearing upon ancient land-connections, now broken by the sea, that need be considered here is that derived from the study of animals and plants, both recent and fossil. All-important in this connection is the principle that the same or closely similar species do not arise independently in areas between which there is no connection. It is not impossible that such an independent origin of organisms which the naturalist would class as belonging to the same species may have occasionally taken place, but, if so, it must be the rare exception to the normal process. This principle leads necessarily to the conclusion that the more recently and broadly two land-areas, now separated by the sea, have been connected, the more nearly alike will be their animals and plants. Such islands as Great Britain, Sumatra and Java must have been connected with the adjacent mainland within a geologically recent period, while the extreme zoölogical peculiarity of Australia can be explained only on the assumption that its present isolation is of very long standing. The principle applies to the case of fossils as well as to that of modern animals, and has already been made use of, in a preceding section, in dealing with the ancient land-connections of North America. It was there shown that the connection of this continent with the Old World and the interruptions of that connection are reflected and recorded in the greater or less degree of likeness in the fossil mammals at any particular epoch. Conversely, the very radical differences between the fossil mammals of the two Americas imply a long-continued separation of those two continents, and their junction in the latter half of the Tertiary period is proved by the appearance of southern groups of mammals in the northern continent, and of northern groups in South America.

Inasmuch as the connection between North and South America still persists, the geology of the Isthmus of Panama should afford testimony in confirmation of the inferences drawn from a study of the mammals. Of course, the separating sea did not necessarily cross the site of the present isthmus; it might have cut through some part of Central America, but a glance at the map immediately suggests the isthmus as the place of separation and subsequent connection. As a matter of fact, isthmian geology is in complete accord with the evidence derived from the mammals. Even near the summit of the hills which form the watershed between the Atlantic and the Pacific and through which the great Culebra Cut passes, are beds of marine Tertiary shells, showing that at that time the land was completely submerged. This does not at all preclude the possibility of other transverse seas at the same period; indeed, much of Central America was probably under the sea also, but the geology of that region is still too imperfectly known to permit positive statements.

When several different kinds of testimony, each independent of the other, can be secured and all are found to be in harmony, the strength of the conclusion is thereby greatly increased. Many distinct lines of evidence support the inference that North and South America were completely severed for a great part of the Tertiary period. This is indicated in the clearest manner, not only by the geological structure of the Isthmus and by the mammals, living and extinct, as already described, but also by the freshwater fishes, the land-shells, the reptiles and many other groups of animals and plants.

The distribution of marine fossils may render the same sort of service in elucidating the history of the sea as land-mammals do for the continents, demonstrating the opening and closing of connections between land-areas and between oceans. The sea, it is true, is one and undivided, the continental masses being great islands in it, but, nevertheless, the sea is divisible into zoölogical provinces, just as is the land. Temperature, depth of water, character of the bottom, etc., are factors that limit the range of marine organisms, as climate and physical barriers circumscribe the spread of terrestrial animals. Professor Perrin Smith has shown that in the Mesozoic era Bering Strait was repeatedly opened and closed, and that each opening and closing was indicated by the geographical relationships of the successive assemblages of marine animals that are found in the Mesozoic rocks of California and Nevada. When the Strait was open, the coast-line between North America and Asia was interrupted and the North Pacific was cooled by the influx of water from the Arctic Sea. At such times, sea-animals from the Russian and Siberian coasts extended their range along the American side as far south as Mexico, and no forms from the eastern and southern shores of Asia accompanied them. On the other hand, when the Strait was closed, the Arctic forms were shut out and the continuous coast-line and warmer water enabled the Japanese, Indian, and even Mediterranean animals to extend their range to the Pacific coast of North America. A comparison of the marine fishes of the two sides of the Isthmus of Panama shows an amount and degree of difference between the two series as might be expected from the length of time that they have been separated by the upheaval of the land.

In working out the geographical conditions for any particular epoch of the earth's history, it is possible to go much farther than merely gaining an approximate estimate of the distribution of land and sea; many other important facts may be gathered from a minute examination of the rocks in combination with a genetic study of topographical forms. By this physiographical method, as it is called, the history of several of the great mountain-ranges has been elaborated in great detail. It is quite practicable to give a geological date for the initial upheaval and to determine whether one or many such series of movements have been involved in bringing about the present state of things. Similarly, the history of plains and plateaus, hills and valleys, lake and river systems, may be ascertained, and for the earth's later ages, at least, a great deal may be learned regarding the successive forms of the land-surfaces in the various continents. It would be very desirable to explain the methods by which these results are reached, but this could hardly be done without writing a treatise on physiography, for which there is no room in this chapter. We must be permitted to make use of the results of that science without being called upon to prove their accuracy.

No factor has a more profound effect in determining the character and distribution of living things than climate, of which the most important elements, for our purpose, are temperature and moisture. One of the most surprising results of geological study is the clear proof that almost all parts of the earth have been subjected to great vicissitudes of climate, and a brief account of the evidence which has led to this unlooked for result will not be out of place here.

The evidence of climatic changes is of two principal kinds, (1) that derived from a study of the rocks themselves, and (2) that given by the fossils of the various epochs. So far as the rocks laid down in the sea are concerned, little has yet been ascertained regarding the climatic conditions of their formation, but the strata which were deposited on the land, or in some body of water other than the sea, often give the most positive and significant information concerning the circumstances of climate which prevailed at the time of their formation. Certain deposits, such as gypsum and rock-salt, are accumulated only in salt lakes, which, in turn, are demonstrative proof of an arid climate. A salt lake could not exist in a region of normal rainfall and, from the geographical distribution of such salt-lake deposits, it may be shown that arid conditions have prevailed in each of the continents and, not only once, but many times. As a rule, such aridity of climate was relatively local in extent, but sometimes it covered vast areas. For example, in the Permian, the last of the Palæozoic, and the Triassic, the first of the Mesozoic periods (see Table, p. 15) nearly all the land-areas of the northern hemisphere were affected, either simultaneously or in rapid succession.

Until a comparatively short time ago, it was very generally believed that the Glacial or Pleistocene epoch, which was so remarkable and conspicuous a feature of the Quaternary period, was an isolated phenomenon, unique in the entire history of the earth. Now, however, it has been conclusively shown that such epochs of cold have been recurrent and that no less than five of these have left unmistakable records in as many widely separated periods of time.

When the hypothesis of a great "Ice Age" in the Pleistocene was first propounded by the elder Agassiz, it was naturally received with general incredulity, but the gradual accumulation of proofs has resulted in such an overwhelming weight of testimony, that the glacial hypothesis is now accepted as one of the commonplaces of Geology. The proofs consist chiefly in the characteristic glacial accumulations, moraines and drift-sheets, which cover such enormous areas in Europe and North America and, on a much smaller scale, in Patagonia, and in the equally characteristic marks of glacial wear left upon the rocks over which the ice-sheets moved. Many years later it was proved that the Permian period had been a time of gigantic glaciation, chiefly in the southern hemisphere, when vast ice-caps moved slowly over parts of South America, South Africa, Australia and even of India. The evidence is of precisely the same nature as in the case of the Pleistocene glaciation. In not less than three more ancient periods, the Devonian, Cambrian, and Algonkian, proofs of glacial action have been obtained.

While the rocks themselves thus afford valuable testimony as to the climatic conditions which prevailed at the time and place of their formation, this testimony is fragmentary, missing for very long periods, and must be supplemented from the information presented by the fossils. As in all matters where fossils are involved, the evidence must be cautiously used, for hasty inferences have often led to contradictory and absurd conclusions. When properly employed, the fossils give a more continuous and complete history of climatic changes than can, in the present state of knowledge, be drawn from a study of the rocks alone. For this purpose plants are particularly useful, because the great groups of the vegetable kingdom are more definitely restricted in their range by the conditions of temperature and moisture than are most of the correspondingly large groups of animals. Not that fossil animals are of no service in this connection; quite the contrary is true, but the evidence from them must be treated more carefully and critically. To illustrate the use of fossils as recording climatic changes in the past, one or two examples may be given.

In the Cretaceous period a mild and genial climate prevailed over all that portion of the earth whose history we know, and was, no doubt, equally the case in the areas whose geology remains to be determined. The same conditions extended far into the Arctic regions, and abundant remains of a warm-temperate vegetation have been found in Greenland, Alaska and other Arctic lands. Where now only scanty and minute dwarf willows and birches can exist, was then a luxuriant forest growth comprising almost all of the familiar trees of our own latitudes, a most decisive proof that in the Cretaceous the climate of the Arctic regions must have been much warmer than at present and that there can have been no great accumulation of ice in the Polar seas. Conditions of similar mildness obtained through the earlier part of the Tertiary. In the Eocene epoch large palm-trees were growing in Wyoming and Idaho, while great crocodiles and other warm-country reptiles abounded in the waters of the same region.

It is of particular interest to inquire how far the fossils of Glacial times confirm the inferences as to a great climatic change which are derived from a study of the rocks, for this may be taken as a test-case. Any marked discrepancy between the two would necessarily cast grave doubt upon the value of the testimony of fossils as to climatic conditions. The problem is one of great complexity, for the Pleistocene was not one long epoch of unbroken cold, but was made up of Glacial and Interglacial ages, alternations of colder and milder conditions, and some, at least, of the Interglacial ages had a climate warmer than that of modern times. Such great changes of temperature led to repeated migrations of the mammals, which were driven southward before the advancing ice-sheets and returned again when the glaciers withdrew under the influence of ameliorating climates. Any adequate discussion of these complex conditions is quite out of the question in this place and the facts must be stated in simplified form, as dealing only with the times of lowered temperature and encroaching glaciers.

The plants largely fail us here, for little is known of Glacial vegetation, but, on the other hand, a great abundance of the fossil remains of animal life of that date has been collected, and its testimony is quite in harmony with that afforded by the ice-markings and the ice-made deposits. Arctic shells in the marine deposits of England, the valley of the Ottawa River and of Lake Champlain, Walruses on the coast of New Jersey, Reindeer in the south of France, and Caribou in southern New England, Musk-oxen in Kentucky and Arkansas, are only a few examples of the copious evidence that the climate of the regions named in Glacial times was far colder than it is to-day.

I have thus endeavored to sketch, necessarily in very meagre outlines, the nature of the methods employed to reconstruct the past history of the various continents and the character of the evidence upon which we must depend. Should the reader be unconvinced and remain sceptical as to the possibility of any such reconstruction, he must be referred to the numerous manuals of Geology, in which these methods are set forth with a fulness which cannot be imitated within the limits of a single chapter. The methods are sound, consisting as they do merely in the application of "systematized common sense" (in Huxley's phrase) to observed facts, but by no means all applications of them are to be trusted. Not to mention ill-considered and uncritical work, or inverted pyramids of hypothesis balanced upon a tiny point of fact, it should be borne in mind that such a complicated and difficult problem as the reconstruction of past conditions can be solved only by successive approximations to the truth, each one partial and incomplete, but less so than the one which preceded it.

CHAPTER II

METHODS OF INVESTIGATION — PALÆONTOLOGICAL

PALÆONTOLOGY is the science of ancient life, animal and vegetable, the Zoölogy and Botany of the past, and deals with fossils. Fossils are the recognizable remains or traces of animals or plants, which were buried in the rocks at the time of the formation of those rocks. In a geological sense, the term *rock* includes loose and uncompacted materials, such as sand and gravel, as well as solid stone. Granting the possibility of so determining the relative dates of formation of the rocks, that the order of succession of the fossils in time may be ascertained in general terms, the question remains: What use, other than geological, can be made of the fossils? In dealing with this question, attention will be directed almost exclusively to the mammals, the group with which this book is concerned.

As a preliminary to the discussion, something should be said of the ways in which mammals became entombed in the rocks in which we find them. In this connection it should be remembered that, however firm and solid those rocks may be now, they were originally layers of loose and uncompacted material, deposited by wind or water, and that each layer *formed in its turn the surface of the earth, until buried by fresh accumulations upon it,* it may be to enormous depths.

One method of the entombing of land-mammals, which has frequently been of great importance, is burial in volcanic dust and so-called ash, which has been compacted into firm rock. During a great volcanic eruption enormous quantities of such finely divided material are ejected from the crater and are spread out over the surrounding country, it may be for distances of hundreds of miles. Thus will be buried the scattered bones, skeletons, carcasses, that happen to be lying on the surface; and if the fine fragments are falling rapidly, many animals will be buried alive and their skeletons preserved intact. A modern instance of this is given by the numerous skeletons of men and domestic animals buried in the volcanic ash which overwhelmed Pompeii in 79 A.D. Pliny the Younger, who witnessed that first recorded eruption of Vesuvius, tells us in a letter written to Tacitus, that far away at Misenum, west of Naples, it was often necessary to rise and shake off the falling ashes, for fear of being buried in them. In the Santa Cruz formation of Patagonia (see p. 124), which has yielded such a wonderful number and variety of well-preserved fossils, the bones are all found in volcanic dust and ash compacted into a rock, which is usually quite soft, but may become locally very hard. The Bridger formation of Wyoming (p. 110) and the John Day of eastern Oregon (p. 116) are principally made up of volcanic deposits; and no doubt there are several others among the Tertiary stages which were formed in the same way, but have not yet received the microscopic study necessary to determine this.

Much information concerning the mammalian life of the Pleistocene, more especially in Europe and in Brazil (p. 211), has been derived from the exploration of caverns. Some of these caves were the dens of carnivorous beasts and contain multitudes of the bones of their victims, as well as those of the destroyers themselves. Others, such as the Port Kennedy Cave, on the Schuylkill River above Philadelphia, the Frankstown Cave in central Pennsylvania, the Conard Fissure in Arkansas, are hardly caverns in the ordinary sense of the word, but rather narrow fissures, into which bones and carcasses were washed by floods, or living animals fell from above and died without being able to escape. The bones are mostly buried in the earth which partially or completely fills many caverns and may be covered by a layer of stalagmite, derived from the solution and re-deposition of the limestone of the cavern-walls, by the agency of percolating waters.

A mode of preservation which is unfortunately rare is exemplified by the asphaltic deposits near Los Angeles, at Rancho La Brea, which have been very fully described by Professor J. C. Merriam of the University of California. The asphalt has been formed by the oxidation and solidification of petroleum, which has risen up through the Pleistocene rocks from the oil-bearing shales below. At one stage in the conversion of petroleum into asphalt, tar-pools of extremely viscid and adhesive character were, and still are, formed on the surface of the ground; and these pools were veritable traps for mammals and birds and for the beasts and birds of prey which came to devour the struggling victims.

"The manner in which tar or asphalt pools may catch unsuspecting animals of all kinds is abundantly illustrated at the present time in many places in California, but nowhere more strikingly than at Rancho La Brea itself, where animals of many kinds have frequently been so firmly entrapped that they died before being discovered, or if found alive were extricated only with the greatest difficulty. As seen at this locality, the tar issuing from springs or seepages is an exceedingly sticky, tenacious substance which is removed only with the greatest difficulty from the body of any animal with which it may come in contact. Small mammals, birds, or insects running into the soft tar are very quickly rendered helpless by the gummy mass, which binds their feet, and in their struggles soon reaches every part of the body. Around the borders of the pools the tar slowly hardens by the evaporation of the lighter constituents until it becomes as solid as an asphalt pavement. Between the hard and soft portions of the mass there is a very indefinite boundary, the location of which can often be determined only by experiment, and large mammals in many cases run into very tenacious material in this intermediate zone, from which they are unable to extricate themselves."

The foregoing account refers to what may actually be observed at the present time; in regard to the Pleistocene, Professor Merriam says: "In the natural accumulation of remains at the tar pools through accidental entangling of animals of all kinds, it is to be presumed that a relatively large percentage of the individuals entombed would consist of young animals with insufficient experience to keep them away from the most dangerous places, or with insufficient strength to extricate themselves. There would also be a relatively large percentage of old, diseased, or maimed individuals that lacked strength to escape when once entangled. In the census of remains that have been obtained up to the present time the percentages of quite young, diseased, maimed, and very old individuals are certainly exceptionally large. . . . In addition to the natural accumulation of animal remains through the entangling of creatures of all kinds by accidental encountering of the tar, it is apparent from a study of the collections obtained that some extraordinary influence must have brought carnivorous animals of all kinds into contact with the asphalt with relatively greater frequency than other kinds of animals. In all the collections that have been examined the number of carnivorous mammals and birds represented is much greater than that of the other groups. . . . Whenever an animal of any kind is caught in the tar, its struggles and cries naturally attract the attention of carnivorous mammals and birds in the immediate vicinity, and the trapped creature acts as a most efficient lure to bring these predaceous animals into the soft tar with it. It is not improbable that a single small bird or mammal struggling in the tar might be the means of entrapping several carnivores, which in turn would naturally serve to attract still others. . . . In the first excavations carried on by the University of California a bed of bones was encountered in which the number of saber-tooth and wolf skulls together averaged twenty per cubic yard." [1]

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[1] Memoirs of the University of California, Vol. I, pp. 209–211.

As the animals were thus entombed alive, it would be expected that a large number of complete skeletons would be preserved, but this is not the case: "connected skeletons are not common." This scattering and mingling of the bones were due partly to the trampling of the heavier animals in their struggles to escape, but, in more important degree, to the movements within the tar and asphalt.

In arid and semi-arid regions great quantities of sand and dust are transported by the wind and deposited where the winds fail, or where vegetation entangles and holds the dust. Any bones, skeletons or carcasses which are lying on the surface will thus be buried, and even living animals may be suffocated and buried by the clouds of dust. An example of such wind-made accumulations is the Sheridan formation (Equus Beds, see p. 131), which covers vast areas of the Great Plains from Nebraska to Mexico and contains innumerable bones, especially of horses. In this formation in northwestern Kansas, Professor Williston found nine skeletons of the large peccary (†*Platygonus leptorhinus*), lying huddled together, with their heads all pointing in the same direction, and in the upper Miocene (p. 121) of South Dakota Mr. Gidley discovered six skeletons of three-toed horses (†*Neohipparion whitneyi*) crowded together, killed and buried probably by a sandstorm. Similar illustrations might be gathered from many other parts of the world.

Swamps and bogs may, especially under certain conditions, become the burial places of great numbers of animals, which venture into them, become buried and are unable to extricate themselves. Especially is this true in times of great drought, when animals are not only crazed with thirst, but very much weakened as well, and so unable to climb out of the clinging mud. In an oft-quoted passage, Darwin gives a vivid description of the effects of a long drought in Argentina between the years 1827 and 1830. "During this time so little

† Extinct.

rain fell, that the vegetation, even to the thistles, failed; the brooks were dried up, and the whole country assumed the appearance of a dusty high road." "I was informed by an eyewitness that the cattle in herds of thousands rushed into the Parana, and being exhausted by hunger they were unable to crawl up the muddy banks, and thus were drowned. The arm of the river which runs by San Pedro was so full of putrid carcasses, that the master of a vessel told me that the smell rendered it quite impassable. Without doubt several hundred thousand animals thus perished in the river; their bodies when putrid were seen floating down the stream; and many in all probability were deposited in the estuary of the Plata. All the small rivers became highly saline, and this caused the death of vast numbers in particular spots; for when an animal drinks of such water it does not recover. Azara describes the fury of the wild horses on a similar occasion, rushing into the marshes, those which arrived first being overwhelmed and crushed by those which followed. He adds that more than once he has seen the carcasses of upwards of a thousand wild horses thus destroyed. . . . Subsequently to the drought of 1827 to 1832, a very rainy season followed, which caused great floods. Hence it is almost certain that some thousands of the skeletons were buried by the deposits of the very next year." [1]

In the arid and desolate regions of the interior of South Australia is a series of immense dry lakes, which only occasionally contain water and ordinarily "are shallow, mud-bottomed or salt-encrusted claypans only." One of these, Lake Callabonna, is of great interest as having preserved in its soft mud many remains of ancient life, of creatures which were mired in the clay and destroyed, as has been described by Dr. E. C. Stirling. "There is, however, compensation for the unpromising physical features of Lake Callabonna in the fact that its bed proves to be a veritable necropolis of gigantic extinct

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[1] Voyage of a Naturalist, Amer. ed., pp. 133–134.

marsupials and birds which have apparently died where they lie, literally, in hundreds. The facts that the bones of individuals are often unbroken, close together, and, frequently, in their proper relative positions, the attitude of many of the bodies and the character of the matrix in which they are embedded, negative any theory that they have been carried thither by floods. The probability is, rather, that they met their deaths by being entombed in the effort to reach food or water, just as even now happens in dry seasons, to hundreds of cattle which, exhausted by thirst and starvation, are unable to extricate themselves from the boggy places that they have entered in pursuit either of water or of the little green herbage due to its presence. The accumulation of so many bodies in one locality points to the fact of their assemblage around one of the last remaining oases in the region of desiccation which succeeded an antecedent condition of plenteous rains and abundant waters."

It is a very general experience in collecting fossil mammals to find that they are not evenly or uniformly distributed through the beds, but rather occur in "pockets," where great numbers of individuals are crowded together, while between the "pockets" are long stretches of barren ground. It is equally common to find the bones thickly distributed in certain layers, or beds, and the layers above and below entirely wanting in fossils. The reasons for this mode of occurrence have been partially explained in the foregoing paragraphs, but the reason differs for each particular mode of entombment. The important part played by drought in causing such accumulation of closely crowded bodies in swamps and mud-holes is indicated in the quotations from Darwin and Stirling; but similar accumulations may take place on hard ground, as was observed in central Africa by Gregory. "Here and there around a water hole we found acres of ground white with the bones of rhinoceroses and zebra, gazelle and antelope, jackal and hyena. . . . These animals had crowded around the dwindling pools and fought for the last drops of water."[1] Even in normal seasons springs and water holes and the drinking places in streams are the lurking places of beasts of prey and crocodiles, so that great accumulations of bones are made around these spots. A succession of unusually severe winters frequently leads to great mortality among mammals, as happened in Patagonia in the winter of 1899, when enormous numbers of Guanaco perished of starvation on the shore of Lake Argentine, where they came to drink.

Bones which are exposed on the surface of the ground decay and crumble to pieces in the course of a very few years; and if they are to be preserved as fossils, it is necessary that they should be buried under sedimentary or volcanic deposits. Several such modes of burial have been described in the foregoing paragraphs, but there are other and equally important methods, which remain to be considered.

The deposits made by rivers are often extremely rich in fossils, and most of the Tertiary formations of the Great Plains are now ascribed to the agency of rivers. The flood-plain of a stream, or that part of its basin which is periodically overflowed, is gradually built up by the layers of clay and silt thrown down by the relatively still waters of the flooded area, and scattered bones, skeletons or carcasses that may have been lying on the ground before the freshet are buried in the deposits. Bones covered up in this manner frequently show the marks of teeth of rodents or carnivores which have gnawed them when lying exposed. Deposits made in the stream-channels, where the current was swiftest, are of coarser materials such as gravel and sand, and these often contain the skeletons of animals which were drowned and swept downward by the flooded stream. When the Bison (the mistakenly so-called Buffalo) still roamed in countless herds over the western plains, immense numbers of them were drowned in the upper Missouri

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[1] J. W. Gregory, The Great Rift Valley, p. 268.

River by breaking through the ice, when they attempted to cross at times when the ice had not attained its winter thickness, or was weakened by melting in the spring. No doubt, the bed of that river contains innumerable bones of the Bison. Frequently, too, animals are caught in quicksands and, unable to escape, are buried in the soft mass; fossil skeletons which are preserved in sandstones in an erect or standing position are usually to be interpreted in this manner.

The sedimentary accumulations formed in lakes and ponds sometimes yield fossil bones or skeletons in considerable numbers, which have, for the most part, been derived from the carcasses of animals carried into the lake by streams. A newly drowned mammal sinks to the bottom and, if sufficient sediment be quickly deposited upon it, it may be anchored there and fossilized as a complete skeleton. Otherwise, when distended by the gases of putrefaction, the body will rise and float on the surface, where it will be attacked and pulled about by crocodiles, fishes and other predaceous creatures. As the bones are loosened in the course of decomposition, they will drop to the bottom and be scattered, now here, now there, over a wide area.

Land mammals are rarely found in marine rocks, or such deposits as were made on the sea-bottom; but the remains of marine mammals, whales, porpoises, dolphins, seals, etc. are often found in large numbers. In principle, the method of entombment is the same as in the case of lakes, but currents may drift to some bay or cove multitudes of carcasses of these marine mammals. At Antwerp, in Belgium, incredible quantities of such remains have been exposed in excavations and in all probability were drifted by currents into a quiet and shallow bay, which was subsequently converted into land.

While the foregoing account by no means exhausts the various methods of accumulation and burial of the skeletons and scattered bones of mammals, it covers the more important of these methods sufficiently for a general understanding of the different processes. In whatever manner the preservation may have been effected, there is great difference in the relative abundance and completeness among the fossils of the various kinds of mammals which were living at the same time and in the same area. It need hardly be said, that the more abundant any species was, the better was the chance of its being represented among the fossils; hence, gregarious species, living in large herds, were more likely to be preserved than those which led a solitary existence, or were individually rare. Most of the hoofed mammals are and apparently always have been gregarious, and are therefore much better represented among the fossils, and are, in consequence, better known than the beasts of prey, which, of necessity, were individually less numerous and generally solitary in habits. Not only this, but large and medium-sized mammals, with strong and heavy bones, were better fitted to withstand the accidents of entombment and subsequent preservation than small creatures with delicate and fragile skeletons. The mere dead weight of overlying sediments often crushes and distorts the bones, and the movements of uplift, compression, folding and fracture, to which so many strata have been subjected, did still further damage to the fossils. The percolating waters, which for ages have traversed the porous rocks, often attack and dissolve the bones, completely destroying the minute ones and greatly injuring those which are massive and strong. In consequence of all those accidents it frequently happens that only the teeth, the hardest and most resistant of animal structures, and it may be the dense and solid jaw-bones, are all that remain to testify of the former existence of some creature that long ago vanished from the earth. Very many fossil mammals are known exclusively from the teeth, and it is this fact which makes the exact study of teeth so peculiarly important to the palæontologist.

In view of all these facts, it is not surprising that concerning the history of many mammalian groups we have but scanty information, or none at all, while in the case of others the story is wonderfully full and detailed. The latter are, very generally, the groups which were not only numerically abundant at all stages of their history, but also had skeletons that were strong enough to resist destruction; while the groups as to which there is little or no information are chiefly of small and fragile animals, or such as were always rare. For example, a great deal has been learned regarding the development of horses and rhinoceroses in North America, but the history of the tapirs is very unsatisfactorily known, because, while horses and rhinoceroses were common, tapirs were solitary and rare. In Europe bats have been found in the Eocene, Oligocene and Miocene, and there is no reason to suppose that they were not equally ancient and equally abundant in America; but none have been found in the western hemisphere in any formation older than the Pleistocene. All things considered, the extraordinary fact is, not that so many forms have irretrievably perished, but that so much has been preserved, escaping all the chances of destruction.

As to the degree of preservation in fossil mammals, we have to do almost entirely with bones and teeth. With very rare exceptions, and those all of late geological date, the viscera, muscles, skin, hair, horns, hoofs and claws have been completely destroyed and have vanished without leaving a trace. In northern Siberia the gravel soil is permanently frozen to a depth of several hundred feet and contains the intact carcasses of elephants and rhinoceroses of Pleistocene date and notably different from any species of these animals now in existence. Sometimes such a carcass is disinterred from a bluff by the cutting action of a stream and is in a state of nearly complete preservation, with hide, hair and flesh almost as in an animal freshly killed. From these remains it has been learned that the †Mammoth was an elephant densely covered with hair and wool, just as he was depicted in the carvings and cave-paintings

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† Extinct.

of Pleistocene Man in Europe, where †Mammoth bones have been abundantly found, and also that there were Siberian rhinoceroses similarly protected against the cold. †Mammoth remains with hide and flesh, but much less complete, have likewise been found in Alaska.

In a cavern in southern Patagonia an expedition from the La Plata Museum discovered, with the remains of a gigantic, extinct †ground-sloth, large pieces of the skin still covered with hair and affording most welcome information as to the colouration of these most curious animals. The skin had been preserved from decay by deep burial in dry dust. Mummies of Pleistocene rodents have been found in the dry caves of Portugal, whereas in the ordinary caves which are damp or wet, only bones are preserved. Unfortunately, as has been said, such instances of complete preservation are very rare, and none are known of mammals more ancient than those of the Pleistocene epoch.

In general, it may be said that the higher the geological antiquity of a skeleton is, the greater is the chemical alteration which it has undergone. Bones of Pleistocene or later date have, as a rule, suffered little change beyond the loss of more or less of their animal matter, the amount of such loss depending chiefly upon exposure to the air. Bones which, for thousands or tens of thousands of years, have been buried in dense cave-earth, in an antiseptic peat-bog, or in asphalt, are often perfectly sound and fresh when taken up. Skeletons of the antecedent (Tertiary) period are, on the other hand, very frequently *petrified;* that is to say, the original substance of the bones has been completely removed and replaced by some stony material, most commonly lime or flint. This substitution took place very gradually, molecule by molecule, so that not only is the form of the bone or tooth most accurately reproduced, but the internal, microscopic structure is perfectly retained and may be studied to as great advantage as in the case of modern animals.

† Extinct.

While, save in the rarest instances, only the hard parts of fossil mammals remain to testify of their structure, very important information as to the size, form and external character of the brain may be secured from "brain-casts," which may be natural or artificial. The pressure of the mud, sand or other material, in which the fossil was embedded, filled up all openings in the skeleton and, as the brain decayed and disappeared, its place was taken by this material, which subsequently hardened and solidified and quite accurately reproduces the external form and character of the brain. When a fossil skull is exposed and shattered by weathering, the natural brain-cast often remains intact, and a great many such specimens are in the collections. An artificial cast is made by sawing open the cranial cavity, cleaning out the stony matrix which fills it and then pouring liquid gelatine or plaster of Paris into the cavity. These artificial casts are often quite as satisfactory as the natural ones.

As has been shown above, the history of the mammals is recorded, save in a very few instances, in terms of bones and teeth and, to the uninitiated, it might well seem that little could be accomplished with such materials. However, it is the task, and the perfectly feasible task, of palæontology to make these dry bones live. It is a current and exceedingly mischievous notion that the palæontologist can reconstruct a vanished animal from a single bone or tooth and, in spite of repeated slayings, this delusion still flourishes and meets one in modern literature at every turn. No doubt, much of the scepticism with which attempts to restore extinct animals are met by many intelligent people is traceable to the widespread belief that such off-hand and easy-going methods are used in the work. So far from being able to make a trustworthy reconstruction from a few scattered bones, competent palæontologists have been sometimes led completely astray in associating the separated parts of the same skeleton. More than once it has happened that the dissociated skull and feet of one and the same animal have been assigned to entirely different groups, just because no one could have ventured, in advance of experience, to suppose that such a skull and teeth could belong to a creature with such feet. In all these cases (and they are few) the error has been finally corrected by the discovery of the skeleton with all its essential parts in their natural connection.

While the number of complete skeletons of Tertiary mammals as yet collected is comparatively small, it is often possible to construct a nearly complete specimen from several imperfect ones, all of which can be positively shown to belong to the same species. Such composite skeletons are almost as useful as those in which all the parts pertain to a single individual, though in making the drawings it is not easy to avoid slight errors of proportion. It must not be supposed that no successful restoration of missing bones is practicable; on the contrary, this can often be done very easily, but only when all the essential parts of the skeleton are known.

Even if an unlimited number of perfect skeletons were available, of what use would they be? A skeleton is a very different looking object from a living animal, and how is it possible to infer the latter from the former? Do the many restorations of extinct mammals which this book owes to the skill of Mr. Horsfall and Mr. Knight deserve any other consideration than that due to pleasing, graceful or grotesque fancies, with no foundation of solid fact? To answer these questions, it is necessary first to consider the relations of the bony structure to the entire organism and then to discuss the principles in accordance with which the restorations have been made.

The skeleton is far from being merely the mechanical framework of the animal. Such a frame-work it is, of course, but it is much more than that; it is the living and growing expression of the entire organism and is modified, not only by age, but by the conditions of the environment and accidental circumstances as well. The bones of the same individual differ very materially in early youth, maturity and old age; so long as the animal lives, its bones are perpetually changing, slowly it is true, but with ready response to needs. Not only that, but dislocated bones may and frequently do develop entirely new joints, and their internal structure is remodelled to meet the requirements of stresses differing in character or direction from those of normal, uninjured bones. The general form and proportions of any mammal are determined chiefly by its muscular system and this may be directly and confidently inferred from its skeleton, for the muscles which are of importance in this connection are attached to the bones and leave their indelible and unmistakable mark upon them. In any good text-book of anatomy this extremely intimate relation of bone and muscle is made clear; and it is shown how each attachment of muscle, tendon and ligament is plainly indicated by rough lines, ridges, projections or depressions, which speak a language intelligible enough to those who have learned to interpret it. Given the skeleton, it is no very difficult task to reconstruct the muscular system in sufficient detail. Further, the teeth afford valuable information as to the food, habits and appearance of the animal, for the bulk of the viscera, a significant element in the general form, is principally conditioned by the character of the diet.

Beasts of prey, which live by catching and devouring other animals, have a certain likeness to one another, even though they are in no wise related, except as all mammals are. The Thylacine, or so-called "Tasmanian Wolf" (*Thylacynus cynocephalus*), a marsupial and related to the opossums, is deceptively like the true wolves in appearance, although belonging to an order (Marsupialia) almost as widely separated from that to which the wolves belong (Carnivora) as two mammalian groups well can be. This resemblance is as clearly indicated by the skeletons as by the living animals themselves, though the fundamental differences of structure which distinguish the marsupial from the carnivore are no less clearly displayed. Large herbivorous mammals too, though referable to very different orders, bear a strong resemblance to one another, the characteristic differences, so far as the living animal is concerned, appearing chiefly in the head. It was this general likeness that induced Cuvier to form his order, "Pachydermata," which comprised elephants, rhinoceroses, hippopotamuses, tapirs, etc., animals that are now distributed into no less than three separate orders; aside from the head, all of these forms are quite distinctly similar in appearance.

Of course, the external features, such as ears, tail, skin and hair, are most important factors in the general make-up of any mammal; and, as to these matters, the fossils leave us largely in the lurch, save in the all too rare cases, like the Siberian †Mammoth, in which these external features are actually preserved. Two artists may so restore the same animal as to result in two very different pictures, and no one can positively decide between them; just as two modern mammals, which are closely related and have very similar skeletons, may yet differ markedly in outward appearance, because of the different character of the skin, as do, for example, the Bornean and Indian rhinoceroses. Yet even in dealing with purely external features, we are not left altogether to conjecture. Ears of unusual size or form frequently leave some indication of this on the skull, and the presence or absence of a proboscis can nearly always be inferred with confidence from the character of the bones of the nose and muzzle. The length and thickness of the tail may be generally directly deduced from the caudal vertebræ, but whether it was close-haired and cylindrical, or bushy, or tufted at the end, or flat and trowel-shaped, as in the Beaver, is not determinable from the bones alone.

Most uncertain of all the characters which determine outward appearance are the hair and the pattern of colouration; the Horse and Zebra differ much more decidedly in the living form than their skeletons would lead one to expect, as do also the Lion, the Tiger and the Leopard. The curious and exceptional colour-pattern of the Okapi, that remarkable giraffe-like animal but lately discovered in the equatorial forests of western Africa, could never have been inferred from a study of the skeleton alone. However, even in the problem of colour-patterns there is more to go upon than sheer guess-work, for certain definite principles of animal colouration have been ascertained; the great difficulty lies in the application of these principles to a particular case. It is quite certain that the naked, hairless skin is never primitive, but always a comparatively late acquisition and, in many mammalian orders, is not found at all. Aside from a few domesticated animals, this type of skin occurs only in very large herbivorous mammals living in warm climates, such as elephants, rhinoceroses and hippopotamuses, in a few burrowers, and in marine mammals, like the walruses, whales, porpoises, etc. Useful hints as to the colouring of ancient and extinct forms may be gathered from

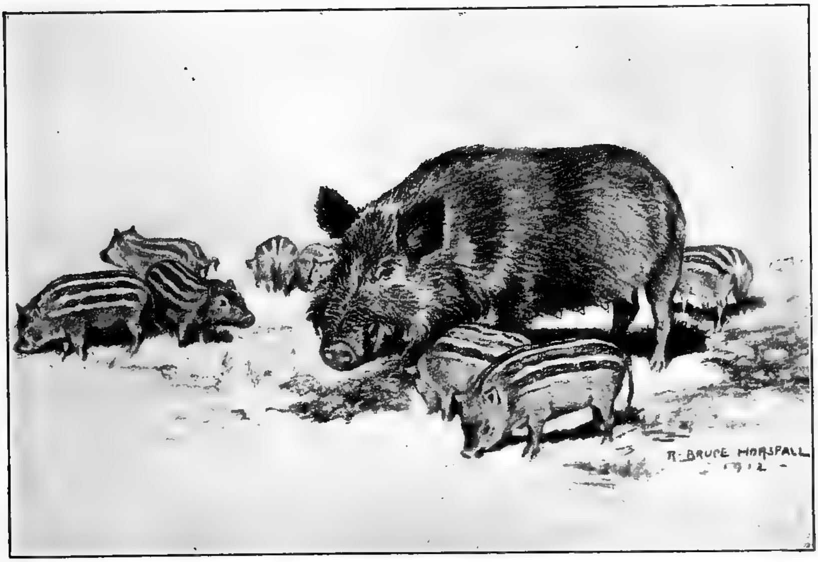

FIG. 4. — Wild sow and pigs, showing the uniform colour of the adult and stripes of the young.

a study of series of living animals, such as lizards and butterflies, in which the development of a definite scheme of colouration may be followed step by step. Young animals very frequently retain more or less distinct traces of the ancestral colouration, which disappear in the adult, for the development of the individual is, in some respects at least, an abbreviated and condensed recapitulation of the history of the species. In many mammals which, in the adult condition, have a solid body-colour, the young are striped or spotted, a strong indication that these mammals were derived from striped or spotted ancestors. Thus, the Wild Boar has a uniform body-colour in the full-grown stage, but the pigs are longitudinally striped; many deer are spotted throughout life, as in the Fallow Deer, the Axis Deer of India and others, but the great majority of the species, including all the American forms, have uniform colouration, while the fawns are always spotted. Lion cubs are also spotted and the adults have a uniform tawny colour, and many such examples might be given.

FIG. 5. — Fawns of the Mule Deer (*Odocoileus hemionus*). Compare with Fig. 83, p. 167. (By permission of the N. Y. Zoölog. Society.)

The study of colouration among existing animals has led to the conclusion that in mammals the primitive colour-pattern was that of stripes, either longitudinal or transverse and more probably the former. In the second stage these bands break up into spots, which still show the longitudinal arrangement and may be either light on a dark ground, or dark on a light ground. In a third stage the spots may again coalesce into stripes, the course of which is at right angles to that of the original stripes, or the spots may disappear, leaving a uniform body-colour, lighter or white on the belly. These changes of colour-pattern have not proceeded at a uniform rate in the various mammalian groups, or even within the same group, for an all-important factor is the mode of life of the particular animal. In general, it may be said that the scheme of colour is such as to render its possessor inconspicuous, or even invisible, and many a creature that seems to be very conspicuous and striking in a museum case can hardly be seen at all when in its natural surroundings. Thus, Arctic mammals and birds, in their winter dress, are white; desert animals are tawny or sandy-brown; forest animals are frequently striped or spotted; while those that live on open plains are more commonly of uniform colouration. There are exceptions to these rules, but they hold good for the most part. From careful comparative study of the teeth and skeletons a clew may be gained as to the habits of animals and from the habits something may be inferred as to the colouration.

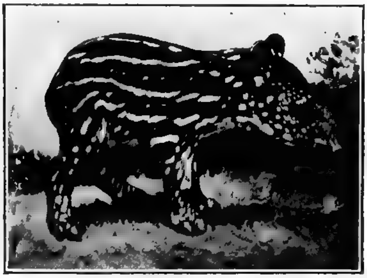

FIG. 6. — *Tapirus terrestris*, 3 days old. Compare with Fig. 137, p. 320. (By permission of W. S. Berridge, London.)

It would, however, be misleading to claim a greater authority for these attempts at restoring a long-vanished life than can fairly be ascribed to them. The general form and proportions of the head, neck, body, tail, limbs and feet may be deduced with a high degree of accuracy from the skeleton, while the external characters of skin, hair and colouration are largely conjectural, but not altogether imaginary. It cannot be doubted that among the extinct mammals were many which, owing to some uncommon growth of subcutaneous fat, or some unusual local development of hair, were much more curious and bizarre in appearance than we can venture to represent them. If, for example, the Camel, the Horse, the Lion and the Right Whale were extinct and known only from their skeletons, such restorations as we could make of them would assuredly go astray in some particulars. The Camel would be pictured without his hump, for there is nothing in the skeleton to suggest it; the forelock, mane and characteristic tail of the Horse and the Lion's mane would certainly not be recognized; while the immense development of blubber in the head of the Whale gives to it a very different appearance from that which the skull would seem to indicate. Such cases are, however, exceptional and restorations made by competent hands from complete skeletons probably give a fair notion of the appearance of those animals when alive.

It will thus be sufficiently plain that the work of restoration is beset with difficulties, but that there is no good ground for the uncritical scepticism which summarily rejects the results as being purely fanciful, or for the equally uncritical credulity which unhesitatingly accepts them as fully and incontestably accurate. It is altogether likely that one of the main sources of error consists in making the extinct animal too closely resemble some existing species which is selected as a model.

Too much space has perhaps been devoted to the problem of restoring the external form of these extinct mammals, a problem which, after all, is of distinctly subordinate importance. The most valuable results which may be gained from a study of these fossil mammals are the answers which they afford to the great questions of relationship, classification and genetic descent, and the light which they throw upon the processes of evolution and the course of geographical arrangement. The bones and teeth afford admirable means of tracing the gradual steps of modification by which the modern mammals have arisen from very different ancestors and of following their wanderings from region to region and continent to continent. It is to these questions that most of the subsequent chapters are devoted.

CHAPTER III

THE CLASSIFICATION OF THE MAMMALIA

THE terminology and nomenclature of science form a great barrier, which only too often shuts out the educated layman from following the course of investigation and keeping abreast of the discoveries in which he may be particularly interested. No more frequent and heartfelt complaint is uttered than that which decries the "scientific jargon," and one might be tempted to think that this jargon was a superfluous nuisance, deliberately adopted to exclude the uninitiated and guard the secrets of the temple from the curious intruder. As a matter of fact, however, this terminology, though an unquestionable evil from one point of view, is an indispensable implement of investigation and description. Ordinary language has far too few words for the purpose and most of the words that might be used lack the all-important quality of precision. The vernacular names of animals and plants are notoriously inexact and, even when not inaccurately employed, are not sufficiently refined and destinctive for scientific use. This is pre-eminently true of the New World, where the European settlers gave the names of the creatures with which they had been familiar at home to the new animals which they found in the western hemisphere. Some of these names, such as deer, wolf, fox, bear, are accurate enough for ordinary purposes, while others are ludicrously wrong. The bird that we call the Robin is altogether different from his European namesake, and the great stag, or Wapiti, is commonly called "Elk," a name which properly belongs to the Moose. In short, it is impossible to gain the necessary accuracy and abundance of vocabulary without devising an artificial terminology, drawn chiefly from Greek and Latin.

In dealing with fossils, the difficulty of nomenclature becomes formidable indeed. The larger and more conspicuous mammals of the modern world are more or less familiar to all educated people, and such names as rhinoceros, hippopotamus, elephant, kangaroo, will call up a definite and fairly accurate image of the animal in question. For the strange creatures that vanished from the earth ages before the appearance of Man *there are no vernacular names* and it serves no good purpose to coin such terms. To the layman names like *Uintatherium* or *Smilodon* convey no idea whatever, and all that can be done is to attempt to give them a meaning by illustration and description, using the name merely as a peg upon which to hang the description.

The system of zoölogical classification which is still in use was largely the invention of the Swedish naturalist Linnæus, who published it shortly after the middle of the eighteenth century. As devised by Linnæus, the scheme was intended to express ideal relationships, whereas now it is employed to express real genetic affinities, so far as these can be ascertained. The Linnæan system is an organized hierarchy of groups, arranged in ascending order of comprehensiveness. In this scheme, what may be regarded as the unit is the *species*, a concept around which many battles have been waged and concerning which there is still much difference of opinion and usage. Originally a term in logic, it first received a definite meaning in Zoölogy and Botany from John Ray (1628–1705) who applied it to indicate a group of animals, or plants, with marked common characters and freely interbreeding. Linnæus, though not always consistent in his expressions on the subject, regarded species as objective realities, concrete and actual things, which it was the naturalist's business to discover and name, and held that they were fixed entities which had been separately created. This belief in the fixity and objective reality of species was almost universally held, until the publication of Darwin's "Origin of Species" (1859) converted the biological world to the evolutionary faith, which declares that the only objective reality among living things is the individual animal or plant.

According to this modern conception, a species may be defined as signifying a "grade or rank assigned by systematists to an assemblage of organic forms which they judge to be more closely interrelated by common descent than they are related to forms judged to be outside the species" (P. Chalmers Mitchell). The technical name of a species, which is either in Latin, or in latinized form, is in two words, one of which designates the genus (see below) and the other the particular species of that genus, as, for example, *Equus caballus*, the species Horse, *E. przewalskii*, the Asiatic Wild Horse, *E. asinus*, the species Ass, etc. In order to identify a species, the genus to which it belongs must be stated, hence the term, *binomial system* of nomenclature, which Linnæus introduced, becoming *trinomial* when the name of a subspecies is added, a modern refinement on the older method. A very large species (*i.e.* one which is represented by great numbers of individuals), extending over a very large area, is often divisible into groups of minor rank, as *varieties*, *geographical races* or *subspecies*. Taking the species as the unit in the scheme of classification, the varieties and subspecies may be considered as fractions.

There is great difference of usage among writers on systematic zoölogy in the manner of applying the generally accepted concept of species, some making their groups very much more comprehensive than others, according as they are "lumpers" or "splitters," to employ the slang phrase. The difficulty lies in the fact that there are no fixed and definite criteria, by which a given series of individuals can be surely distinguished as a variety, a species or a genus; it is a matter for the judgment and experience of the systematist himself. The individuals of a species may differ quite widely among themselves, provided that they are all connected by intergradations, and the more or less constant varieties or subspecies are to be distinguished from the individual variants, which are inconstant and fluctuating. No two specimens agree exactly in every particular, but if a very large suite of them be compared, it will be found that the great majority depart but little from the average or norm of the species, and the wider the departure from the norm, the fewer the individuals which are so aberrant. Taking so easily measured a character as size, for example, and measuring several hundred or a thousand representatives of some species, we see that a large majority are of average size, a little more or a little less, while very large or very small individuals are rare in proportion to the amount by which they exceed or fall short of the norm. Subspecies or varieties are marked by differences which are relatively constant, but not of sufficient importance to entitle them to rank as species.

A group of the second rank is called a *genus*, which may contain few or many species, or only a single one. In the latter case the species is so isolated in character that it cannot properly be included in the same genus with any other species. A large genus, one containing numerous species, is frequently divisible into several *subgenera*, each comprising a group of species which are more similar to one another than they are to the other species of the genus.

The third of the main groups in ascending order is the *family*, which ordinarily consists of a number of genera united by the possession of certain common characters, which, at the same time, distinguish them from other genera, though a single isolated genus may require a separate family for its reception. Just as it is often convenient to divide a genus into subgenera, so families containing many genera are usually divisible into *subfamilies*, as indicative of closer relationships within the family. The name of the family is formed from that of the genus first described or best known, with the termination *-idæ*, while that for the subfamily is *-inæ*. To take an example, all the genera of cats, living and extinct, are assembled in the family Felidæ (from the genus *Felis*) which falls naturally into two subfamilies. One of these, the Felinæ, includes the true cats, a very homogeneous group, both the existing and the extinct genera; the other subfamily, that of the highly interesting series of the "Sabre-tooth Tigers," called the †Machairodontinæ, comprises only extinct forms.

The fourth principal rank or grade is the *order*, distinguished by some fundamental peculiarity of structure and usually including a large number of families. Some of the orders, however, contain but a single family, a single genus, or even, it may be, a single species, because that species is in important structural characters so unlike any other that it cannot properly be put into the same order with anything else. Such isolation invariably implies that the species or genus in question is the sole survivor of what was once an extensive series. As in the case of the family and the genus, it is often necessary to recognize the degrees of closer and more remote affinity by the use of *suborders*. Existing Artiodactyla, or even-toed hoofed animals, an enormous assemblage, may conveniently be divided into four suborders: (1) Suina, swine and the Hippopotamus; (2) Tylopoda, the Camel and Llama; (3) Tragulina, "mouse-deer," or chevrotains; (4) Pecora, or true ruminants, deer, giraffes, antelopes, sheep, goats, oxen, etc. In nearly all of the orders such subordinal divisions are desirable and it is frequently useful to employ still further subdivisions, like *superfamilies*, which are groups of allied families within the suborder, *sections* and the like.

In the Linnæan scheme, the next group in ascending rank is the *class*, which includes all mammals whatsoever, but the advance of knowledge has made it necessary to interpolate several intermediate grades between the class and the order, which, in the descending scale, are *subclass*, *infraclass*, *cohort*,

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† Extinct.

superorder and others, while above the class comes the *subkingdom* of Vertebrata, or animals with internal skeletons, which includes mammals, birds, reptiles, amphibians and fishes.

A word should be said as to the conventions of printing technical names. The names of all species are, in American practice, printed in small letters, but many Europeans write specific terms which are proper nouns or adjectives with a capital. Generic, family and all groups of higher rank are always written with a capital, unless used in vernacular form, *e.g.* Artiodactyla and artiodactyls. It is also a very general custom to give capitals to vernacular names of species, as the Mammoth, the Coyote, the Black Bear. Genus and species are almost invariably in italics, groups of higher rank in roman.

Such a scheme of classification as is outlined above has a decidedly artificial air about it and yet it serves a highly useful purpose in enabling us to express in brief and condensed form what is known or surmised as to the mutual relationships of the great and diversified assemblage of mammals. The scheme has been compared to the organization of an army into company, battalion, regiment, brigade, division, army corps, etc., and there is a certain obvious likeness; but the differences go deeper, for an army is an assemblage of similar units, mechanically grouped into bodies of equal size. A much closer analogy is the genealogical or family tree, which graphically expresses the relationships and ramifications of an ancient and wide-spread family, though even this analogy may easily be pushed too far. Blood-relationship is, in short, the underlying principle of all schemes of classification which postulate the theory of evolution.

The system of Linnæus, as expanded and improved by modern zoölogists, has proved itself to be admirably adapted to the study of the living world; but it is much more difficult to apply it to the fossils, for they introduce a third dimension, so to speak, for which the system was not designed. This third dimension is the successive modification in time of a genetically connected series. The cumulative effect of such modifications is so great that only very elastic definitions will include the earlier and later members of an unbroken series. In attempting to apply the Linnæan system to the successive *faunas* (*i.e.* assemblages of animals) which have inhabited the earth, palæontologists have employed various devices. One such method is to classify each fauna without reference to those which precede and follow it, but this has the great drawback of obscuring and ignoring the relationships, to express which is the very object of classification. Another and more logical method is to treat species and genera as though they belonged to the present order of things, for these groups, particularly species, were relatively short-lived, when regarded from the standpoint of geological time, and either became so modified as to require recognition as new species and genera, or died out without leaving descendants. Groups of higher rank, families, orders, etc., are treated as *genetic series* and include the principal line or stock and such side-branches as did not ramify too widely or depart too far from the main stem. Under the first arrangement, the horses, a long history of which has been deciphered, would be divided into several families; under the second, they are all included in a single family.

One of the most interesting results of palæontological study is the discovery that in many families, such as the horses, rhinoceroses and camels, there are distinct series which independently passed through parallel courses of development, the series of each family keeping a remarkably even pace in the degree of progressive modification. Such a minor genetic series within a family is called a *phylum*, not a very happy selection, for the same term had been previously employed in a much wider sense, as equivalent to the subkingdom. In both uses of the term the underlying principle, that of genetic series, is the same; the difference is in the comprehensiveness of meaning.

It must be admitted that no method, yet devised, of applying the Linnæan scheme to the fossils is altogether satisfactory, and indeed it is only the breaks and gaps in the palæontological record which makes possible any use of the scheme. Could we obtain approximately complete series of all the animals that have ever lived upon the earth, it would be necessary to invent some entirely new scheme of classification in order to express their mutual relationships.

In the present state of knowledge, classification can be made only in a preliminary and tentative sort of way and no doubt differs widely from that which will eventually be reached. So far as the mammals are concerned, part of the problem would seem to be quite easy and part altogether uncertain. Some mammalian groups appear to be well defined and entirely natural assemblages of related forms, while others are plainly heterogeneous and artificial, yet there is no better way of dealing with them until their history has been ascertained. The mutual relations of the grand groups, or orders, are still very largely obscure.

The class Mammalia is first of all divided into two subclasses of very unequal size. Of these, the first, PROTOTHERIA, is represented in the modern world by few forms, the so-called Duck-billed Mole (*Ornithorhynchus paradoxus*) and Spiny Anteaters (*Echidna*) of Australia. They are the lowest and most primitive of the mammals and retain several structural characters of the lower vertebrates. Their most striking characteristic is that the young are not brought forth alive, but are hatched from eggs, as in the reptiles, birds and lower vertebrates generally.

The second subclass, EUTHERIA, which includes all other mammals, is again divided into two very unequal groups or infraclasses. One of these, DIDELPHIA, contains but a single order, the Marsupialia, or pouched mammals, now in existence, and is also very primitive in many respects, though far more advanced than the Prototheria. The young, though born alive, are brought forth in a very immature state and, with the exception of one genus (*Perameles*) the fœtus is not attached by a special structure, the placenta, to the womb of the mother. Like the Prototheria, the Marsupials, which were once spread all over the world, are at present almost entirely confined to Australia and the adjoining islands, the Opossums of North and South America, and one small genus (*Cœnolestes*) in the latter continent being the exceptions to this rule of distribution. The second and vastly larger infraclass, the MONODELPHIA, is characterized by the *placenta*, a special growth, partly of fœtal and partly of maternal origin, by means of which the unborn young are attached to the mother and nourished during the fœtal period; they are born in a relatively mature state and are generally able to walk immediately after birth and resemble their parents in nearly all respects.

The vast assemblage of placental mammals, which range over all the continents, are divided into numerous orders, most of which appear to be natural groups of truly related forms, while some are but doubtfully so and others again are clearly unnatural and arbitrary. As has already been pointed out, the mutual relationships of these orders, as expressed in groups of higher than ordinal rank, offer a much more difficult problem, chiefly because our knowledge of the history of mammals is most deficient just where that history is most important and significant, namely, in its earlier portion. In many instances, the evolution of genera and families may be followed out within the limits of the order in a very convincing way, but very rarely can the origin of an order be demonstrated. When the history began to be full and detailed,the orders had nearly all been established, and, until the steps of their divergence and differentiation can be followed out, their mutual relationships can be discussed only from the standpoint of their likenesses and differences. In the valuation of these, there is much room for difference of opinion, and such difference is not lacking. On the other hand, concerning the number and limits of the orders themselves there is very general agreement.

In the following table only the major groups are included and those which are extinct are marked with a dagger (†). The scheme is almost identical with that given in Professor Osborn's "Age of Mammals," the few points in which I should prefer a somewhat different arrangement being waived in the interests of uniformity and avoidance of confusion. A few changes are, however, made in matters which I regard as too important to ignore.

I. SUBCLASS PROTOTHERIA. Egg-laying Mammals.
  1. ORDER † **PROTODONTA.**
  2. ORDER **MONOTREMATA,** *e.g.* the Duck-billed Mole and Spiny Anteaters.
II. SUBCLASS EUTHERIA. Viviparous Mammals.
  A. INFRACLASS DIDELPHIA. Pouched Mammals.
    1. ORDER † **TRICONODONTA.**
    2. ORDER **MARSUPIALIA.**
      a. SUBORDER **Polyprotodonta.** Opossums, carnivorous and insectivorous Marsupials.
      b. SUBORDER **Diprotodonta.** Herbivorous Marsupials; Kangaroos, etc.
      c. SUBORDER † **Allotheria.**
  B. INFRACLASS MONODELPHIA. Placental Mammals.
    AA. COHORT UNGUICULATA. Clawed Mammals.
      1. ORDER † **TRITUBERCULATA.**
      2. ORDER **INSECTIVORA.** Insect-eating Mammals.
        a. SUBORDER **Lipotyphla,** *e.g.* Moles, Hedgehogs, Shrews, etc.
        b. SUBORDER † **Hyopsodonta.**
        c. SUBORDER † **Proglires.**
        d. SUBORDER **Menotyphla,** *e.g.* Tree and Jumping Shrews.
      3. ORDER † **TILLODONTIA.**
      4. ORDER **DERMOPTERA.** The Flying Lemur.
      5. ORDER **CHIROPTERA.** Bats.
      6. ORDER **CARNIVORA.** Beasts of Prey.
        a. SUBORDER † **Creodonta.** Primitive Flesh-eaters.
        b. SUBORDER **Fissipedia.** Wolves, Bears, Weasels, Cats, etc.
        c. SUBORDER **Pinnipedia.** Marine Carnivores — Seals and Walruses.
      7. ORDER **RODENTIA.** Gnawing Mammals.
        a. SUBORDER **Duplicidentata,** *e.g.* Hares, Rabbits, Pikas.

- *b.* Suborder **Simplicidentata**, *e.g.* Squirrels, Marmots, Beavers, Rats, Mice, Porcupines, etc.

8. Order † **TÆNIODONTIA.**
9. Order **EDENTATA.**
   - *a.* Suborder **Pilosa.** Hairy Edentates, *e.g.* Sloths, Anteaters, etc.
   - *b.* Suborder **Loricata.** Armoured Edentates, *e.g.* Armadillos, † Glyptodonts.
10. Order **PHOLIDOTA.** Scaly Anteaters or Pangolins.
11. Order **TUBULIDENTATA.** The Aard Vark.

BB. Cohort PRIMATES. Mammals with nails.

12. Order **PRIMATES.**
    - *a.* Suborder **Lemuroidea.** Lemurs.
    - *b.* Suborder **Anthropoidea.** Monkeys, Apes, Man.

CC. Cohort UNGULATA. Hoofed Mammals.

13. Order † **CONDYLARTHRA.**
14. Order † **AMBLYPODA.**
15. Order **ARTIODACTYLA.** Even-toed Hoofed Mammals.
    - *a.* Suborder † **Artiodactyla Primitiva.**
    - *b.* Suborder **Suina.** Swine, Peccary, Hippopotamus.
    - *c.* Suborder **Tylopoda.** Camels, Llama, Guanaco.
    - *d.* Suborder **Tragulina.** Mouse-deer or Chevrotains.
    - *e.* Suborder **Pecora,** *e.g.* Deer, Antelopes, Sheep, Oxen, etc.
16. Order **PERISSODACTYLA.** Odd-toed Hoofed Mammals.
    - *a.* Suborder **Chelodactyla,** *e.g.* Horses, Tapirs, Rhinoceroses, etc.
    - *b.* Suborder † **Ancylopoda.** † Chalicotheres.
17. Order **PROBOSCIDEA.** Elephants and † Mastodons.
18. Order † **BARYTHERIA.**
19. Order † **EMBRITHOPODA.**
20. Order **SIRENIA.** Sea-cows and Dugongs.
21. Order **HYRACOIDEA.** Conies.
22. Order † **TOXODONTIA.**
    - *a.* Suborder † **Toxodonta.**
    - *b.* Suborder † **Typotheria.**
    - *c.* Suborder † **Entelonychia.**
    - *d.* Suborder † **Pyrotheria.**
23. Order † **ASTRAPOTHERIA.**
24. Order † **LITOPTERNA.**

DD. Cohort CETACEA. Whales, Dolphins, Porpoises.

25. Order † **ZEUGLODONTIA.**
26. Order **ODONTOCETI.** Toothed Whales, Dolphins, Porpoises.
27. Order **MYSTACOCETI.** Whalebone Whales.

CHAPTER IV

THE SKELETON AND TEETH OF MAMMALS

WITH very rare exceptions, and those only of the latest geological period (Quaternary), the fossil remains of mammals consist only of bones and teeth. The evolutionary changes, so far as these are preserved, are recorded therefore in terms of dental and skeletal modifications. To render these changes intelligible, it is necessary to give some account of the mammalian skeleton and teeth, with no more use of technical language than is unavoidable; ordinary speech does not furnish a sufficient number of terms, nor are most of these sufficiently precise. With the aid of the figures, the reader may easily gain a knowledge of the skeleton which is quite adequate for the discussion of fossil series, which will follow in the subsequent chapters.

I. THE SKELETON

I. The most obvious distinction of the skeletal parts is into *axial* and *appendicular* portions, the former comprising the skull, backbone or *vertebral column,* ribs and breastbone or *sternum,* and the latter including the limb-girdles, limbs and feet. In the axial skeleton only the ribs and certain bones of the skull are paired, but in the appendicular all the bones are in pairs, for the right and left sides respectively.

The *skull* is a highly complex structure, made up of many parts, most of which are immovably fixed together, and performing many functions of supreme importance. In the first place, it affords secure lodgement and protection for the brain and higher organs of sense, those of smell, sight and hearing, and second, it carries the teeth and, by its movable jaws, enables these to bite, to take in and masticate food. The portion of the skull which carries the brain, eyes and ears, is called the *cranium*, and the portion in front of this is the face, the boundary between the two being an oblique line drawn immediately in front of the eye-socket (Fig. 7). A great deal of the endless variety in the form of the skull of different mammals depends upon the differing proportions of cranium and face. In the human skull, for example, the cranium is enormously developed and forms a great dome, while the face is shortened almost to the limit of possibility; the skull of the Horse, on the other hand, goes to nearly the opposite extreme of elongation of the facial and shortening of the cranial region. The posterior surface of the skull, or *occiput*, is made up of four bones, which in most adult mammals are fused into a single *occipital* bone. At the base of the occiput is a large opening, the *foramen magnum*, through which the spinal cord passes to its junction with the brain; and on each side of the opening is a large, smooth, oval prominence, the *occipital condyles*, by means of which the skull is articulated with the

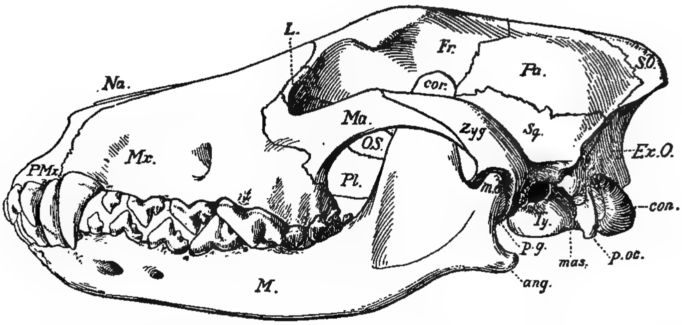

FIG. 7.—Skull of Wolf (*Canis occidentalis*). *P.Mx.*, premaxillary. *Mx.*, maxillary. *Na.*, nasal. *L.*, lachrymal. *Ma.*, malar or jugal. *Fr.*, frontal. *Pa.*, parietal. *Sq.*, squamosal. *Zyg.*, zygomatic process of squamosal. *O.S.*, orbitosphenoid. *Pl.*, palatine. *M.*, mandible. *cor.*, coronoid process of mandible. *m.c.*, condyle of mandible. *ang.*, angular process of mandible. *p.g.*, postglenoid process of squamosal. *Ty.*, tympanic (auditory bulla). *mas.*, mastoid. *p.oc.*, paroccipital process. *con.*, occipital condyle. *Ex.O.*, exoccipital. *S.O.*, supraoccipital.

neck. The *paroccipital processes* are bony styles of varying length, which are given off, one on each side external to the condyles. The boundary of the occiput is marked by a ridge, the *occipital crest*, which varies greatly in prominence, but is very well marked in the more primitive forms and tends to disappear in the more highly specialized ones. The roof and much of the sides of the cranium are formed by two pairs of large bones, the *parietals* behind and the *frontals* in advance; along the median line of the cranial roof, where the two parietals meet, is usually another ridge, the *sagittal crest*, which joins the occipital crest behind. The sagittal crest also varies greatly in prominence, being in some mammals very high and in others entirely absent, and, like the occipital crest, is a primitive character; as a rule, it is longest and highest in those mammals which have the smallest brain-capacity. As pointed out by Professor Leche, the development of the sagittal crest is conditioned by the relative proportions of the brain-case and the jaws. Powerful jaws and a small brain-case necessitate the presence of the crest, in order to provide sufficient surface of attachment for the temporal muscles, which are important in mastication, while with large brain-case and weak jaws the crest is superfluous. Though the brain-case proper may be quite small, yet it may have its surface enormously increased by great thickening of the cranial bones, as is true of elephants and rhinoceroses, and in them sufficient surface for attachment is afforded to the muscles without the development of a crest.

The structure of these cranial bones, more particularly of the parietals, is subject to important changes; in most mammals they are of moderate thickness and have dense layers, or "tables," forming the outer and inner surfaces and, between these, a layer of spongy bone. In many large mammals, however, especially those which have heavy horns or tusks, the cranial bones become enormously thick and the spongy layer is converted into a series of communicating chambers, or *sinuses*, the partitions between which serve as braces, thus making the bone very strong in proportion to its weight. Sinuses are very generally present in the frontals and communicate by small openings with the nasal passage, even in genera of moderate size and without horns or tusks. The frontals form the roof of the eye-sockets, or *orbits*, and usually there is a projection from each frontal, which marks the hinder border of the orbit and is therefore called the *postorbital process*. The roof of the facial region is made by the *nasals*, which are commonly long and narrow bones, but vary greatly in form and

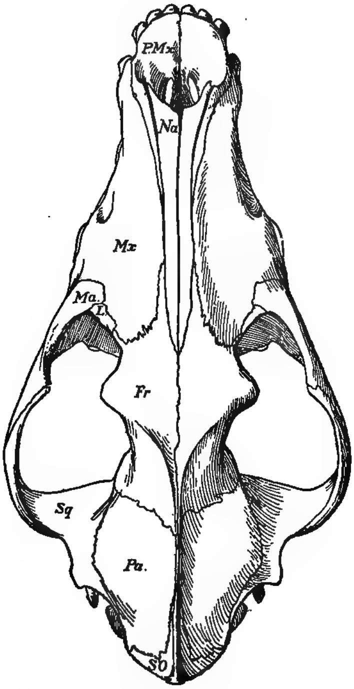

FIG. 8. — Skull of Wolf, top view. *P.Mx.*, premaxillary. *Na.*, nasal. *Ma.*, malar or jugal. *L.*, lachrymal. *Fr.*, frontal. *Sq.*, squamosal. *Pa.*, parietal. *S.O.*, supraoccipital.

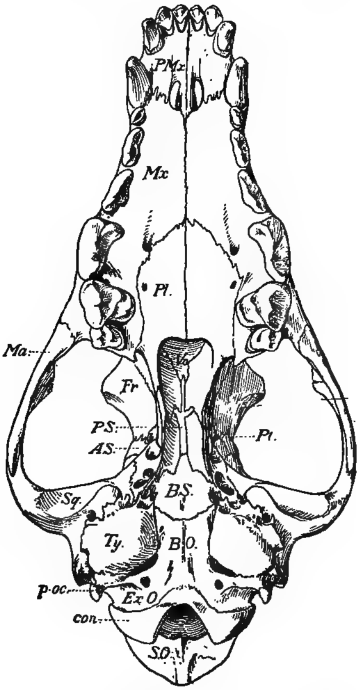

FIG. 9. — Skull of Wolf, view of base. *P.Mx.*, premaxillary. *Mx.*, palatine process of maxillary. *Pl.*, palatine. *Fr.*, frontal. *Pt.*, parietal. *Ma.*, malar or jugal. *Sq.*, glenoid cavity of squamosal. *B.S.*, basisphenoid. *B.O.*, basioccipital. *Ty.*, tympanic (auditory bulla). *p.oc.*, paroccipital process. *con.*, occipital condyle. *S.O.*, supraoccipital.

proportions in different mammals; in those which have a proboscis, like tapirs and elephants, or a much inflated snout, such as the Moose (*Alce*) or the Saiga Antelope (*Saiga tatarica*) the nasals are always very much shortened and otherwise modified in form.

The anterior end of the skull is formed by a pair of rather small bones, the *premaxillaries*, which carry the incisor teeth; they bound the sides of the nasal opening, or *anterior nares*, reaching to the nasals, when the latter are of ordinary length; they also form the front end of the hard or bony palate, which divides the nasal passage from the mouth. The *maxillaries*, or upper jaw-bones, make up nearly all of the facial region on each side and send inward to the median line from each side a bony plate which together constitute the greater part of the hard palate; the remainder of the upper teeth are implanted in the maxillaries. A varying proportion of the hinder part of the hard palate is formed by the *palatines*, which also enclose the *posterior nares*, the opening by which the nasal passage enters the back part of the mouth. The maxillary of each side extends back to the orbit, which it bounds anteriorly and in the antero-superior border of which is the usually small *lachrymal*. The inferior, and more or less of the anterior, border of the orbit is made by the cheek-bone (*malar* or *jugal*) which may or may not have a postorbital process extending up toward that of the frontal; when the two processes meet, the orbit is completely encircled by bone, but only in monkeys, apes and Man is there a bony plate given off from the inner side of the postorbital processes, which extends to the cranial wall and converts the orbit into a funnel-shaped cavity. For most of its length, the jugal projects freely outward from the side of the skull and extends posteriorly beneath a similar bar of bone, the *zygomatic process* of the *squamosal*. This process and the jugal together constitute the *zygomatic arch*, which on each side of the skull stands out more or less boldly, and the size and thickness of which are subject to great variation in different mammals, the massiveness of the arch being proportional to the power of the jaws. One of the principal muscles of mastication (the *masseter*) is attached to the zygomatic arch.

The squamosal itself is a large plate, which makes up a great part of the side-wall of the cranium and articulates above with the frontal and parietal; it also supports the lower jaw, the articular surface for which is called the *glenoid cavity.* The lower jaw is held in place by the *postglenoid process,* which is a projection, usually a transverse ridge, behind the cavity. Back of the postglenoid process is the entrance to the middle ear, the *auditory meatus,* which may be merely an irregular hole, or a more or less elongated tube. The meatus is an opening into the *tympanic,* a bone which at birth is a mere ring and in some mammals remains permanently in that condition, but as a rule develops into a swollen, olive-shaped *auditory bulla,* which sometimes reaches enormous proportions, especially in nocturnal mammals. The labyrinth of the internal ear is contained in the *periotic,* a very dense bone which is concealed in the interior of the cranium, but in many mammals a portion of it, the *mastoid,* is exposed on the surface between the squamosal and occipital.

The lower jaw-bone (*inferior maxillary,* or *mandible*) is the only freely movable element of the skull; it consists of two halves which meet anteriorly at the chin in a contact of greater or less length, called the *symphysis.* In nearly all young mammals and in many adult forms the two halves of the lower jaw are separate and are held together at the symphysis only by ligaments, while in others, as in Man, they are indistinguishably fused to form a single bone. Each half consists of two portions, a horizontal part or *ramus* and an *ascending ramus* or vertical part; the former supports all of the lower teeth, and its length, depth and thickness are very largely conditioned by the number and size of those teeth. The ascending ramus is a broad, rather thin plate, divided at the upper end into two portions, the hinder one of which terminates in the *condyle,* a rounded, usually semicylindrical projection, which fits into the glenoid cavity of the squamosal. The anterior portion of the ascending ramus ends above in the *coronoid process,* which serves for the insertion of the temporal muscle, the upper portion of which is attached to the walls of the cranium and thus, when the muscle is contracted, the jaws are firmly closed; the coronoid process passes inside of the zygomatic arch. The lower jaw is therefore a lever of the third order, in which the power is applied between the weight (*i.e.* the food, the resistance of which is to be overcome) and the fulcrum, which is the condyle. At the postero-inferior end of the ascending ramus is the *angle,* the form of which is characteristically modified in the various mammalian orders and is thus employed for purposes of classification.

The *hyoid arch* is a U-shaped series of small and slender bones, with an unpaired element closing the arch below; each vertical arm of the U is attached to the tympanic of its own side and the whole forms a flexible support for the tongue, but with no freely movable joint like that between the lower jaw and the squamosal.

The mammalian skull in its primitive form may be thought of as a tube divided into two parts, of which the hinder one is the brain-chamber, or cranial cavity, and the forward one the nasal chamber or passage. With the growth of the brain and consequent enlargement of the cranium, this tubular character is lost; and various modifications of the teeth, jaws and facial region, the development of horns and tusks, bring about the many changes which the skull has undergone.

This brief sketch of the skull-structure is very incomplete, several of its elements having been altogether omitted and only those parts described which are needful in working out the history and descent of the various mammalian groups.

The second portion of the axial skeleton is the backbone, or *vertebral column,* which is made up of a number of separate bones called *vertebræ.* These are so articulated together as to permit the necessary amount of flexibility and yet retain the indispensable degree of strength. The function of the backbone is a twofold one: (1) to afford a firm support to the body and give points of attachment to the limbs, and (2) to carry the spinal cord, or great central axis of the nervous system, in such a manner that it shall be protected against injury, a matter of absolutely vital necessity.

While the vertebræ differ greatly in form and appearance in the various regions of the neck, body and tail, in adaptation to the various degrees of mobility and strength which are required of them, yet they are all constituted upon the same easily recognizable plan. The principal mass of bone in each vertebra is the body, or *centrum,* which is typically a cylinder, or modification of that form, and the two ends of the cylinder are the *faces,* by which the successive vertebræ are in contact with one another. In the living animal, however, the successive centra are not in actual contact, but are separated by disks of *cartilage* (gristle) which greatly add to the elasticity of the column. From the upper surface of the centrum arises an arch of bone, the *neural arch,* enclosing with the centrum the *neural canal,* through which runs the spinal cord. As already mentioned, the protection of the spinal cord is essential to the life of the animal, yet this protection must be combined with a certain flexibility, both lateral and vertical. Mere contact of the centra, even though these be held in place by ligaments, would not give the column strength to endure, without dislocation, the great muscular stresses which are put upon it. Additional means of articulation between the successive vertebræ are therefore provided, and these vary in size, form and position in different regions of the backbone, in nice adjustment to the amount of motion and degree of strength needed at any particular part of the column. Of these additional means of articulation, which are called the *zygapophyses,* each vertebra has two pairs, an anterior and a posterior pair, placed upon the neural arch. From the summit of the arch arises the *neural spine*, a more or less nearly straight rod or plate of bone, which may be enormously long or extremely short, massive or slender, in accordance with the muscular attachments which must be provided for. Finally, should be mentioned the *transverse processes*, rod-like or plate-like projections of bone, which arise, one on each side of the vertebra, usually from the centrum, less commonly from the neural arch; these also differ greatly in form and size in the various regions of the column. Anatomists distinguish several other processes of the vertebra, but for our purpose it is not necessary to take these into consideration.

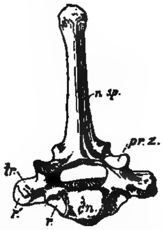

FIG. 10.—First dorsal vertebra of Wolf from the front. *cn.*, centrum. *r.*, facet for the head of the rib. *r'.*, facet for the tubercle of the rib. *tr.*, transverse process. *pr.z.*, anterior zygapophyses. *n.sp.*, neural spine.

Five different regions of the backbone may be distinguished, in each of which the vertebræ are modified in a characteristic way. There is (1) the *cervical* region, or neck, the vertebræ of which, among mammals (with only one or two exceptions) are always seven in number, however long or short the neck may be; the immoderately long neck of the Giraffe has no more and the almost invisible neck of the Whale has no less, and thus the elongation of the neck is accomplished by lengthening the individual vertebræ and not by increasing their number. (2) Those vertebræ to which ribs are attached are named *dorsal* or *thoracic* and can always be recognized by the pits or articular facets which receive the heads of the ribs. (3) Behind the dorsal is the *lumbar* region, or that of the loins, made up of a number of vertebræ which carry no ribs. The dorso-lumbars are known collectively as the *trunk-vertebræ* and are generally quite constant in number for a given group of mammals, though often differently divided between the two regions in different members of the same group. In the Artiodactyla, for example, there are very constantly 19 trunk-vertebræ, but the Hippopotamus has 15 dorsals and 4 lumbars, the Reindeer (*Rangifer*) 14 D., 5 L., the Ox (*Bos taurus*) 13 D., 6 L., the Camel (*Camelus dromedarius*) 12 D. and 7 L. (4) Next follows the *sacrum*, which consists of a varying number of coalesced vertebræ. The number of sacral vertebræ varies from 2 to 13, but is usually from 3 to 5. (5) Finally, there are the *caudal* vertebræ, or those of the tail, which are extremely variable in number and size, depending upon the length and thickness of the tail.

We must next consider briefly some of the structural features which characterize the vertebræ of the different regions. (1) The length of the neck varies greatly in different mammals and, up to a certain point, flexibility increases with length, but, as the number of 7 cervicals is almost universally constant among mammals and the lengthening of the neck is accomplished by an elongation of the individual vertebræ, a point is eventually reached, where greater length is accompanied by a diminution of mobility. For instance, in the Giraffe the movements of the neck are rather stiff and awkward, in striking contrast to the graceful flexibility of the Swan's neck, which has 23 vertebræ, more than three times as many.

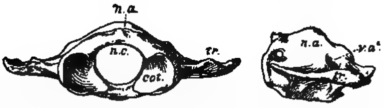

FIG. 11. — Atlas of Wolf, anterior end and left side. *cot.*, anterior cotyles. *n.c.*, neural canal. *n.a.*, neural arch. *tr.*, transverse process. *v.a.*, posterior opening of the canal for the vertebral artery.

The first two cervical vertebræ are especially and peculiarly modified, in order to support the skull and give to it the necessary degree of mobility upon the neck. The first vertebra, or *atlas*, is hardly more than a ring of bone with a pair of oval, cuplike depressions (*anterior cotyles*) upon the anterior face (superior in Man) into which are fitted the occipital condyles of the skull. By the rolling of the condyles upon the atlas is effected the nodding movement of the head, upward and downward, but not from side to side; this latter movement is accomplished by the partial rotation of skull and atlas together upon the second vertebra in a manner presently to be explained. On the hinder aspect are two articular surfaces (*posterior cotyles*) in shape like the anterior pair, but very much less concave, which are in contact with corresponding surfaces on the second vertebra. The neural arch of the atlas is broad and low and the neural canal is apparently much too large for the spinal cord, but, in fact, only a part of the circular opening belongs to the neural canal. In life, the opening is divided by a transverse ligament into an upper portion, the true neural canal, and a lower portion, which lodges a projection from the second vertebra. The atlas usually has no neural spine and never a prominent one; the transverse processes are broad, wing-like plates and each is perforated by a small canal, which transmits the vertebral artery.

The second vertebra, or *axis*, is a little more like the ordinary vertebra, having a definite and usually elongate centrum, on the anterior end of which are the two articular surfaces for the atlas. Between these is a prominent projection, the *odontoid process*, which fits into the ring of the atlas and has a special articulation with the lower bar of that ring. In most mammals the odontoid process is a bluntly conical peg, varying merely in length and thickness, but in many long-necked forms the peg is converted into a semicylindrical spout, convex on the lower side and concave above. The neural spine of the axis is almost always a relatively large, hatchet-shaped plate, which is most developed in the carnivorous forms, and the transverse processes are commonly slender rods.

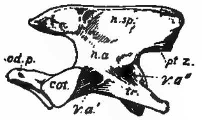

Fig. 12. — Axis of Wolf, left side. *od.p.* odontoid process. *cot.*, anterior cotyles. *n.a.*, neural arch. *n.sp.*, neural spine. *pt.z.*, posterior zygapophyses. *tr.*, transverse process. *v.a′.*, anterior opening of canal for the vertebral artery. *v.a″.*, posterior opening of the same.

The five succeeding cervical vertebræ are much alike, though each one has a certain individuality, by which its place in the series may readily be determined. The centrum has a convex anterior and concave posterior face, which in long-necked animals form regular "ball and socket" joints; neural spines are frequently wanting and, when present, are almost always short and slender; the zygapophyses are very prominent and are carried on projections which extend before and behind the neural arch; the transverse processes are long, thin plates and, except in the seventh cervical, are usually pierced by the canal for the vertebral artery, but in a few forms (*e.g.* the camels) this canal pierces the neural arch.

FIG. 13. — Fifth cervical vertebra of Wolf, left side. *tr.*, transverse process. *v.a''.*, posterior opening of canal for the vertebral artery. *pr.z.* and *pt.z.*, anterior and posterior zygapophyses. *n.sp.*, neural spine.

(2) The dorsal or thoracic vertebræ have more or less cylindrical centra, with nearly flat faces, and on the centra, for the most part at their ends, are the concave facets for the rib-heads. The transverse processes are short and rod-like and most of them articulate with the tubercles of the ribs. The zygapophyses are smaller than in the cervical region, less prominent and less oblique; the anterior pair, on the front of the neural arch, face upward and the posterior pair downward. The neural spines are very much longer than those of the neck and those of the anterior dorsals are often of relatively enormous length, diminishing toward the hinder part of the region.

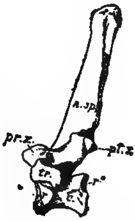

FIG. 14. — First dorsal vertebra of Wolf, left side. *c.*, centrum. *r.*, anterior rib-facet. *r''.*, posterior rib-facet. *tr.*, transverse process. *pr.z.* *pt.z.*, anterior and posterior zygapophyses. *n.sp.*, neural spine.

(3) The lumbar vertebræ are almost always heavier and larger than those of the dorsal region; they carry no ribs and their neural spines and transverse processes are broad and plate-like and the latter are far larger and more prominent than those of the dorsals. As an especial degree of strength is frequently called for in the loins, together with a greater flexibility than is needed in the dorsal region, the modes of articulation between the successive vertebræ are more complex, sometimes, as in the Edentata, most elabo-

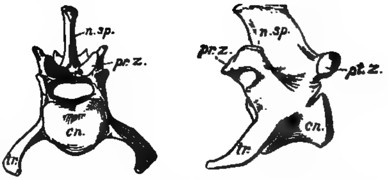

Fig. 15. — Third lumbar vertebra of Wolf, front end and left side. *tr.*, transverse process. *cn.*, centrum. *pr.z.* and *pt.z.*, anterior and posterior zygapophyses. *n.sp.*, neural spine.

rately so. Taking the dorso-lumbars, or trunk-vertebræ, as a single series, we may note that in a few mammals (*e.g.* the elephants) all the neural spines have a backward slope, but in the great majority of forms this backward inclination ceases near the hinder end of the dorsal region, where there is one vertebra with erect spine, while behind this point the spines slope forward.

(4) The sacral vertebræ, varying from 2 to 13 in number, are fused together solidly into one piece, the combined centra forming a heavy mass and the neural canals a continuous tube, while the neural spines are united into a ridge. As a rule, only the first two vertebræ of the sacrum are in contact with the hip-bones, to support which they have developed special processes, the remainder of the mass projecting freely backward.

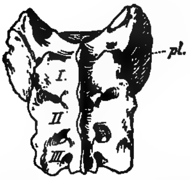

Fig. 16. — Sacrum of Wolf, upper side. *I*, *II*, *III*, first, second and third sacral vertebræ. *pl.*, surface for attachment to hip-bone.

(5) The caudal vertebræ vary greatly, in accordance with the length and thickness of the tail. In an animal with well-developed tail several of the anterior caudals have the parts and processes of a typical vertebra, centrum, neural arch and spine, zygapophyses and transverse processes. Posteriorly, these gradually diminish, until only the centrum is left, with low knobs or ridges, which are the remnants of the various processes. A varying number of long, cylindrical centra, diminishing backward in length and diameter, complete the caudal region and the vertebral column. In some mammals, *chevron bones* are attached to the under side of the anterior and middle caudals; these are forked, Y-shaped bones,

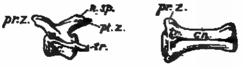

Fig. 17. — Caudal vertebræ of Wolf, from anterior and middle parts of the tail. Letters as in Fig. 15.

which form a canal for the transmission of the great blood-vessels of the tail.

The *ribs*, which are movably attached to the backbone, together with the dorsal vertebræ and breast-bone, compose the *thorax*, or chest. The articulation with the vertebræ is by means of a rounded head; in most cases the head has two distinct facets, the pit being formed half on the hinder border of one dorsal vertebra and half on the front border of the next succeeding one, but posteriorly the pit is often shifted, so as to be on a single vertebra. A second articulation is by means of the *tubercle*, a smooth projecting facet on the convexity of the rib's curvature and near the head; the tubercle articulates with the transverse process of its vertebra. The ribs, in general, are curved bars of bone, which in small mammals generally and in the clawed orders are slender and rod-like, while in the hoofed mammals they are broader, thinner and more plate-like, especially the anterior ones. The number of pairs of ribs is most commonly 13, but ranges among existing mammals from 9 in certain whales to 24 in the Two-toed Sloth (*Cholœpus didactylus*). The complex curvature of the ribs, outward and backward, is such that, when they are drawn forward (in Man upward) by muscular action, the cavity of the thorax is enlarged and air is drawn into the lungs, and when they are allowed to fall back, the cavity is diminished and the air expelled.

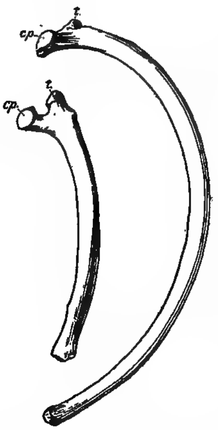

Fig. 18. — Ribs of Wolf from anterior and middle parts of the thorax. *cp.*, head. *t.*, tubercle.

Below, a varying number of the ribs are connected by the cartilages in which they terminate with the breast-bone (*sternum*); sometimes these cartilages are ossified and then form the *sternal ribs*, but there is always a flexible joint between the latter and the true ribs. In certain edentates, notably the anteaters and the extinct †ground-sloths, these sternal ribs, at their lower ends, are provided with head and tubercle, for articulation with the sternum.

The *sternum*, or breast-bone, is made up of a number of distinct segments, usually broad and flat, but often cylindrical, which may unite, but far more commonly remain separate throughout life. The number, size and form of these segments often give useful characters in classification. The first segment, or *manubrium*, has quite a different shape from the succeeding ones and is considerably longer.

II. The appendicular skeleton consists of the limb-girdles and the bones of the limbs and feet. The limb-girdles are the means of attaching the movable limbs to the body, so as to combine the necessary mobility with strength. The anterior, or *shoulder-girdle*, has no direct articulation with the vertebral column, but is held in place by muscles; it is made up of the shoulder-blade and collar-bone, though very many mammals have lost the latter.

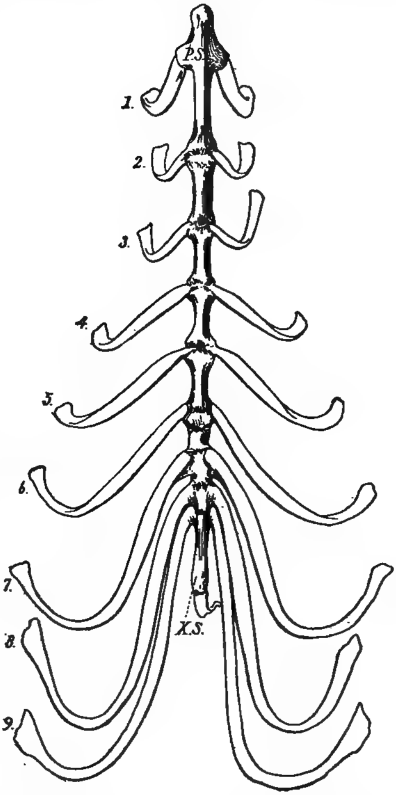

Fig. 19. — Sternum and rib-cartilages of Wolf, lower side. *P.S.*, manubrium. *X.S.*, xiphisternum.

The shoulder-blade, or *scapula*, is a broad, thin, plate-like bone, which contracts below to a much narrower neck, ending in a concave articular surface, the *glenoid cavity*, for the head of the upper arm-bone, the two together making the shoulder-joint. On the outer side the blade is divided into two parts by a prominent ridge, the *spine*, which typically ends below in a more or less conspicuous projection, the *acromion*, which may, however, be absent, its prominence being, generally speaking, correlated with the presence of the collar bone. A hook-like process, the *coracoid*, rises from the antero-internal side of the glenoid cavity and varies greatly in size in the different groups of mammals; though it usually appears to be merely a process of the scapula, with which it is indistinguishably fused, yet its development shows it to be a separate element and in the lowest mammals (Prototheria), as in the rep-

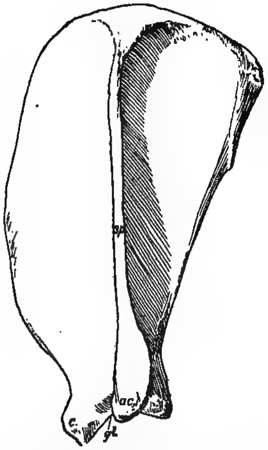

Fig. 20. — Left scapula of Wolf. *gl.*, glenoid cavity. *c.*, coracoid. *ac.*, acromion. *sp.* spine.

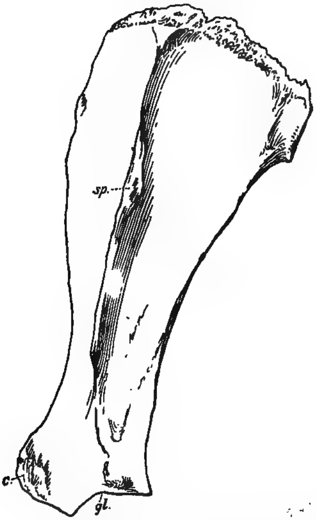

Fig. 21. — Left scapula of Horse. This figure is much more reduced than Fig. 20.

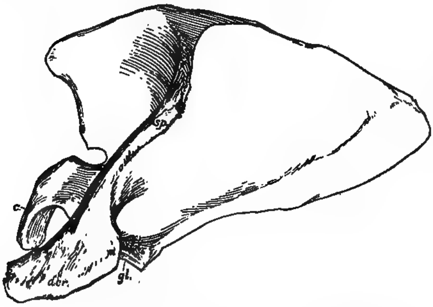

Fig. 22. — Left scapula of Man in position of walking on all fours. Letters as in Fig. 20.

tiles and lower vertebrates generally, it is a large and important part of the shoulder-girdle and articulates with the sternum.

The collar-bone, or *clavicle*, is a complexly curved bar, which, when present and fully developed, extends from the forward end of the sternum to the acromion, the projecting lower end of the scapular spine, supporting and strengthening the shoulder-joint. In many mammalian orders, notably all existing hoofed animals, the clavicle has become superfluous and is lost more or less completely; it may be said, in general, that the clavicle is developed in proportion to the freedom of motion of the shoulder-joint and to the power of rotation of the hand upon the arm. In arboreal animals, such as monkeys, in which the hand rotates freely and the arm moves in any direction on the shoulder, the clavicle is large and fully developed, as it also is in Man. Many burrowing mammals (*e.g.* the moles) have very stout clavicles.

FIG. 23. — Left clavicle of Man, front side.

The posterior, or *pelvic*, girdle is composed on each side of a very large, irregularly shaped bone, which is firmly attached to one or more of the coalesced vertebræ which form the sacrum and thus affords a solid support to the hind leg. Each half of the *pelvis*, or hip-bone, is made up of three elements, called respectively the *ilium*, *ischium* and *pubis*, which are separate in the very young animal, indistinguishably fused in the adult. The three elements unite in a deep, hemispherical pit, the *acetabulum*, which receives the head of the thigh-bone, a perfect ex-

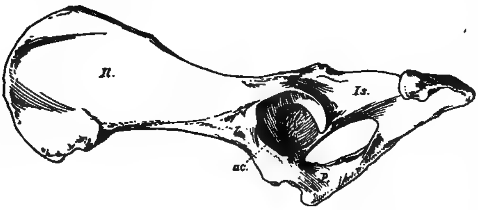

FIG. 24. — Left hip-bone of Wolf. *Il.*, ilium. *Is.*, ischium. *P.*, pubis. *ac.*, acetabulum.

ample of the "ball and socket joint." In the inferior median line the two pubes meet and may become coalesced, in a *symphysis*, the length of which differs in various mammals. The pelvis and sacrum together form a short, wide tube, the diameter of which is normally greater in the female skeleton than in the male.

The limbs are each divided into three segments, which in the anterior extremity are the arm, fore-arm and hand (or fore foot) and in the posterior extremity are the thigh, leg and foot (or hind foot), and there is a general correspondence between the structure of these segments in the fore and hind legs, however great the superficial difference. The bones of the limbs, as distinguished from those of the feet, are the *long bones* and, except in a few very large and heavy mammals, are essentially hollow cylinders, thus affording the maximum strength for a given weight of bone; the cavity of a long bone contains the marrow and hence is called the *medullary cavity*. In the young mammal each of the long bones consists of three parts, the *shaft*, which makes up much the greater part of the length, and at each end a bony cap, the *epiphysis*. Growth takes place by the intercalation of new material between the shaft and the epiphyses; when the three parts unite, growth ceases and the animal is adult.

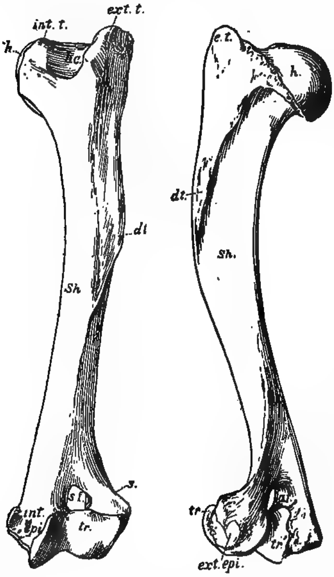

FIG. 25. — Left humerus of Wolf, from the front and outer sides, the latter somewhat oblique. *h.*, head. *int.t.*, internal tuberosity. *ext.t.*, external tuberosity. *bc.*, bicipital groove. *dt.*, deltoid ridge. *sh.*, shaft. *s.*, supinator ridge. *int. epi.* internal epicondyle. *s.f.* anconeal foramen. *tr.*, trochlea. *tr'.*, trochlea, posterior side. *ext. epi.* external epicondyle. *a.f.* anconeal fossa.

The superior segment of the fore limb has a single bone, the *humerus*, the upper end of which is the rounded, convex *head*, which fits into the glenoid cavity of the shoulder-blade, forming the joint of the shoulder; in front of the head are two prominent and sometimes very large projections for muscular attachment, the *external* and *internal tuberosities*, separated by a groove, in which play the two tendons of the biceps muscle and is therefore called the *bicipital groove*. In a few mammals, such as the Horse, Camel and Giraffe, the groove is divided into two by a median tubercle or ridge. From the external tuberosity there generally passes down the front face of the shaft a rough and sometimes very prominent ridge, the *deltoid crest*, to which is attached the powerful *deltoid* muscle. At the lower end of the humerus is the *trochlea*, an irregular half-cylinder, for articulation with the two bones of the fore-arm and varying in form according to the relative sizes of those bones. On each side of the trochlea is frequently a rough prominence, the *epicondyle*, and above the inner one is, in many mammals, a perforation, the *epicondylar foramen*, for the passage of a nerve. Extending up the shaft from the outer epicondyle is a rough crest, the *supinator ridge*, to which is attached one of the muscles that rotate the hand and is conspicuously developed in those mammals which have the power of more or less free rotation and especially in burrowers. On the posterior face of the humerus,

FIG. 26. — Left humerus of Horse, front side. *i.t.*, internal tuberosity. *ex.t.*, external tuberosity. *bc.*, outer part of bicipital groove. *dt.*, deltoid ridge. *s.*, supinator ridge. *tr.*, trochlea.

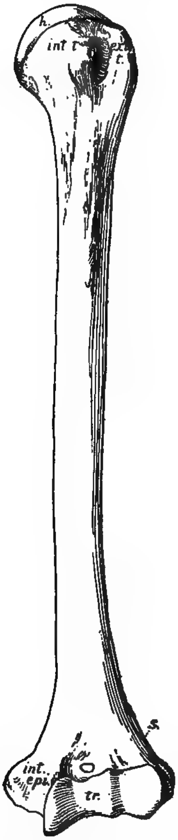

FIG. 27. — Left humerus of Man, front side. Letters as in Fig. 25.

just above the trochlea, is a large, deep pit, the *anconeal fossa.*

The two bones of the fore-arm, the *radius* and *ulna,* are, in most mammals, entirely separate from each other, but in certain of the more highly specialized hoofed animals are immovably coössified. Primitively, the two bones were of nearly equal size, but in most of the mammalian orders there is a more or less well-defined tendency for the radius to enlarge at the expense of the ulna. These bones are normally crossed, the radius being external at the upper end and passing in front of the ulna to the inner side of the arm. The radius varies considerably in form in accordance with the uses to which the

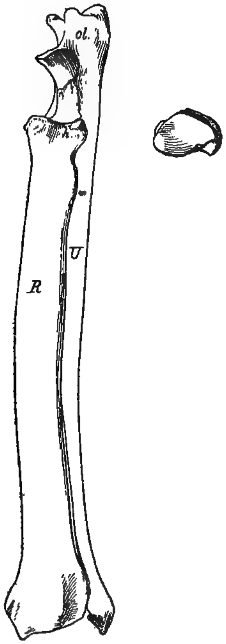

FIG. 28. — Left fore-arm bones of Wolf, front side. *R.*, radius. *U.*, ulna. *ol.*, olecranon. *h.*, head of radius.

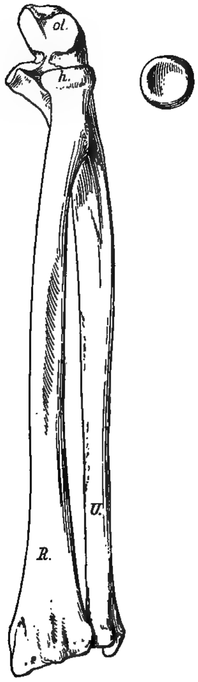

FIG. 29. — Left fore-arm bones of Man, front side. Letters as in Fig. 28. The small object at the right of each figure is the head of the radius, seen from above.

hand is put; if the capacity of rotation is retained, the upper end, or head, of the radius is small, circular or disk-like, covering little of the humeral trochlea, but when the head of the radius is broadened to cover the whole width of the humerus, then all power of rotation is lost. (Cf. Figs. 28 and 29.) As a rule, the radius broadens downward and covers two-thirds or more of the breadth of the wrist-bones.

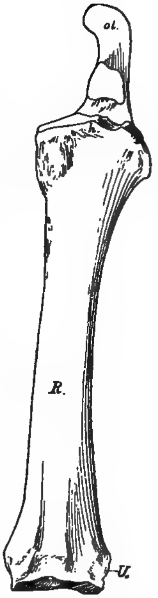

FIG. 30. — Coössified bones of left fore-arm of Horse, front side. For most of its length, the ulna is concealed by the radius.

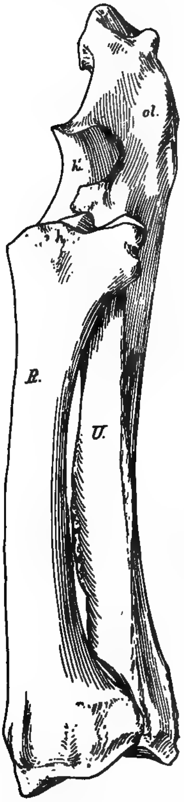

FIG. 31. — Left fore-arm bones of the Tapir (*Tapirus terrestris*). *R.*, radius. *U.*, ulna. *h.*, head of radius. *h'.*, sigmoid notch of ulna. *ol.*, olecranon. N.B. This figure is on a much larger scale than Fig. 30.

The ulna is longer than the radius, its upper end being extended into a heavy process, the *olecranon*, or *anconeal process*, into which is inserted the tendon of the great triceps muscle, the contraction of which straightens the arm; this process is the bony projection at the back of the elbow-joint. Below the olecranon is a semicircular articular concavity, which embraces the humeral trochlea and its upper angle fits into the anconeal fossa of the humerus. The ulna contracts and grows more slender downwards and its lower end covers but one of the wrist-bones. While in the more primitive mammals, and in those which retain the power of rotating the hand, the ulna has nearly or quite the same thickness as the radius, it is often much more slender and in the more highly specialized of the hoofed animals, such as the horses, camels and true ruminants, the radius carries the entire weight and the ulna has become very slender, more or less of its middle portion is lost and the two ends are coössified with the radius, so that the fore-arm appears to have but a single bone. The reverse process of enlarging the ulna and reducing the radius is very rare and practically confined to the elephant tribe.

The fore foot, or hand, for which the term *manus* may be conveniently employed, is divisible into three parts, corresponding in ourselves to the wrist, back and palm of the hand, and the fingers. The bones of the wrist constitute the *carpus*, those of the back and palm the *metacarpus*, and those of the fingers the *phalanges*.

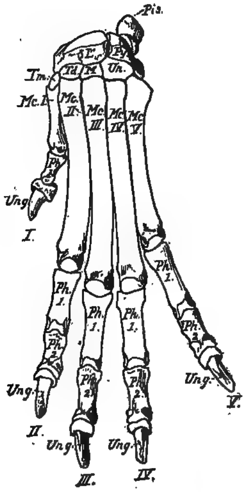

FIG. 32.—Left manus of Wolf, front side. *SL.*, scapho-lunar. *Py.*, pyramidal. *Pis.*, pisiform. *Tm.*, trapezium. *Td.*, trapezoid. *M.*, magnum. *U.*, unciform. *Mc.I–V*, first to fifth metacarpals. *Ph.1*, first phalanx. *Ph.2*, second phalanx. *Ung.*, ungual phalanx. *I*, first digit, or pollex. *II–V*, second to fifth digits.

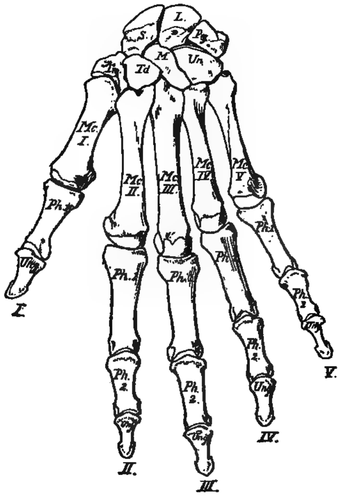

FIG. 33.—Left manus of Man. *S.*, scaphoid. *L.*, lunar. *Py.*, pyramidal (pisiform not shown). *Tm.*, trapezium. *Td.*, trapezoid. *M.*, magnum. *Un.*, unciform. Other letters as in Fig. 32.

The carpus consists primitively of nine distinct bones, though one of these, as will be shown later, is not a true carpal. These bones are of a rounded, subangular shape, closely appressed together, with very little movement between them, and are arranged in two transverse rows. The upper row contains four bones, which enumerating from the inner side are the *scaphoid*, *lunar*, *pyramidal* (or cuneiform) and *pisiform*. The scaphoid and lunar support the radius, while the ulna rests upon the pyramidal. The pisiform, though very constantly present, is not a true carpal, but an ossification in the tendon of one of the flexor muscles, which close the fingers; it projects more or less prominently backward and articulates with the ulna and pyramidal. The second row is also made up of four bones, which, from within outward, are the *trapezium*, *trapezoid*, *magnum* and *unciform*. The relations of the two rows vary much in different mammals and the arrangement may be serial or alternating; thus, the scaphoid rests upon the trapezium and trapezoid and usually covers part of the magnum; the lunar may rest upon the magnum only, but very much more frequently is equally supported by the magnum and unciform and the pyramidal by the latter only. The ninth carpal is the *central*, which, when present and distinct, is a small bone, wedged in between the two rows. Few existing mammals have a separate central, which, though present in the embryo, has coalesced with the scaphoid in the great majority of forms. In the more advanced and differentiated mammals the number of carpals may be considerably reduced by the coössification of certain elements or the complete suppression and loss of others. In all existing Carnivora and a few other mammals the scaphoid and lunar are united in a compound element, the *scapho-lunar* (or, more accurately, the scapho-lunar-central); hoofed animals with a diminished number of toes generally lose the trapezium, and other combinations occur. The second row of carpals carries the metacarpals, and primitively the trapezium, trapezoid and magnum are attached each to one metacarpal and the unciform has two.

The metacarpus consists typically of five members, a number which is never exceeded in any normal terrestrial mammal; the members are numbered from the inner side, beginning with the thumb or *pollex*, from I to V. Many mammals have fewer than five metacarpals, which may number four, three, two or only one; the third is never lost, but any or all of the others may be suppressed, and functionless rudiments of them may long persist as splints or nodules. The metacarpals are elongate, relatively slender and of more or less cylindrical shape; but the form varies considerably in different groups, according to the way in which the hand is used. When employed for grasping, as in many arboreal animals and preeminently in Man, the pollex is frequently opposable to the other fingers and enjoys much freedom of motion. In the camels and true ruminants the third and fourth metacarpals are coössified to form a *cannon-bone* (*see* Fig. 43, p. 91), but the marrow cavities and the joints for the phalanges remain separate.

The phalanges in land mammals never exceed three in each digit, except the pollex, which, when present and fully developed, has but two. The phalanges are usually slender in proportion to their length, but in very heavy hoofed animals they are short and massive. The terminal joint is the *ungual phalanx*, which carries the nail, claw, or hoof, its shape varying accordingly.

The hind leg is constituted in very much the same manner as the fore, but with certain well-marked and constant differences. The thigh-bone, or *femur*, is usually the longest and stoutest of the limb-bones and in very large animals may be extremely massive. At the upper end is the hemispherical *head*, which is set upon a distinct *neck* and projects inward and upward, fitting into the acetabulum of the hip-bone. Nearly all land mammals have a small pit on the head of the femur, in which is inserted one end of the *round ligament*, while the other end is attached in a corresponding depression in the floor of the acetabulum. This ligament helps to hold the thigh-bone firmly in place and yet allows the necessary freedom of movement. On the outer side of the upper end of the femur is a large, roughened protuberance, which often rises higher

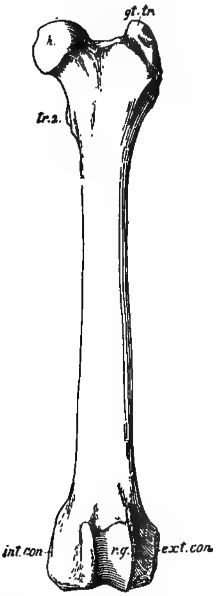

FIG. 34. — Left femur of Wolf, front side. *h.*, head. *gt.tr.*, great trochanter. *tr. 2*, second trochanter. *int. con.*, internal condyle. *r.g.*, rotular groove. *ext. con.*, external condyle.

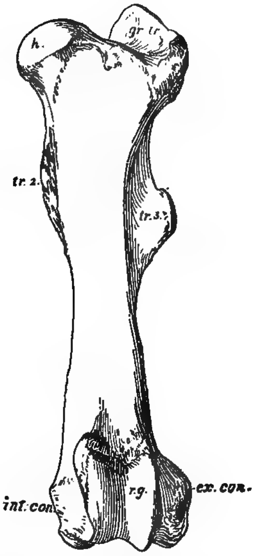

FIG. 35. — Left femur of Horse. *tr .3*, third trochanter. Other letters as in Fig. 34, than which this drawing is very much more reduced.

than the head and is called the *great trochanter;* another, the *second* or *lesser trochanter*, is a small, more or less conical prominence on the inner side of the shaft, below the head. These two processes are well-nigh universal among land mammals; and in a few of the orders occurs the *third trochanter*, which arises from the outer side of the shaft, usually at or above the middle of its length. Though comparatively rare in the modern world, the third trochanter is an important feature, and the early members of most, if not all, of the mammalian orders possessed it. The shaft of the femur is elongate and, except in certain very bulky mammals, of nearly cylindrical shape. The lower end of the bone is thick and heavy and bears on the posterior side two large, rounded prominences, the *condyles*, which articulate with the shin-bone to form the knee-joint. On the anterior side is a broad, shallow groove, the *rotular groove*, in which glides the *patella*, or knee-cap. The patella is a large ossification, of varying shape, in the tendon common to the four great extensor muscles of the thigh, the action of which is to straighten the leg.

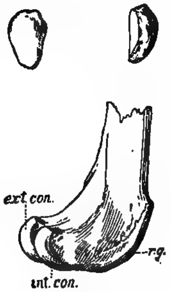

FIG. 36. — Left femur of Wolf, inside of lower end. *ext. con.*, external condyle. *int. con.*, internal condyle. *r.g.*, rotular groove. Above, are two views of the left patella, anterior and internal sides.

The lower leg, like the fore-arm, has two bones, which, however, are always parallel, never crossed, and have no power of rotation. Of these, the inner one is the shin-bone, or *tibia*, which is always the larger and alone enters into the knee-joint. The external bone is the *fibula*, which is almost entirely suppressed in certain highly specialized forms, such as the horses and ruminants, the tibia carrying the whole weight. The upper end of the tibia is enlarged and extends over that of the fibula; it has two slightly concave surfaces for articulation with the condyles of the femur, the approximate edges of which are raised into a bifid *spine*. The upper part of the shaft is triangular, with one edge directed forward, and the superior end of this edge is roughened and thickened to form the *cnemial crest*, to which is attached the patellar ligament. The middle portion of the shaft is rounded and the lower end broad and usually divided by a ridge into two grooves or concavities for the ankle-bone; from the inner side of this end projects downward a tongue-like process, the *internal malleolus*, which prevents inward dislocation of the ankle.

The fibula is relatively stoutest in the less advanced mammals and is usually straight and slender, with enlarged ends, the lower one forming the *external malleolus*, which serves to prevent outward dislocation of the ankle. In many forms the fibula is coössified with the tibia at both ends, and in the most highly specialized hoofed animals, such as the horses, camels and true ruminants, the bone has apparently disappeared. The young animal, however, shows that the ends of the fibula have been retained and the shaft completely lost; the upper end is in the adult firmly fused with the tibia and, in the horses, the lower end is also, but this remains separate in the ruminants and camels, forming the *malleolar bone,* which is wedged in between the tibia and the heel-bone. Because of its importance in holding the ankle-bone in place, this lower end of the fibula is never lost in any land mammal.

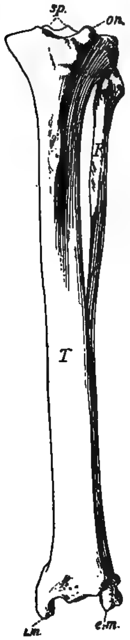

Fig. 37. — Bones of left lower leg of Wolf, front side. *T.*, tibia. *F.*, fibula. *sp.* spine of tibia. *cn.* cnemial crest. *i.m.*, internal malleolus. *e.m.*, external malleolus.

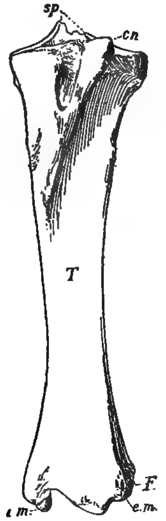

Fig. 38. — Bones of left lower leg of Horse (much more reduced). *cn.* cnemial crest. *F.*, lower end of fibula, coössified with tibia. Other letters as in Fig. 37.

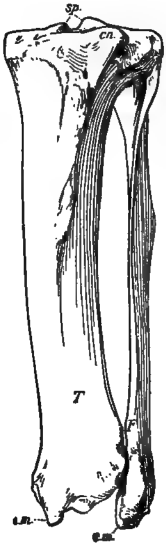

Fig. 39. — Bones of lower leg, left side, of Tapir. *T.*, tibia. *F.*, fibula. *sp.*, spine of tibia. *cn.*, cnemial crest. *i.m.*, internal malleolus. *e.m.*, external malleolus. N.B. This figure is on a much larger scale than Fig. 38.

The hind foot, or *pes,* like the manus, is clearly divisible

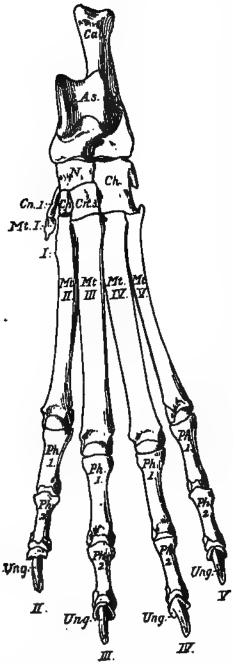

Fig. 40. — Left pes of Wolf, front side. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Ch.*, cuboid. *Cn. 1*, *Cn. 2*, *Cn. 3*, internal, middle and external cuneiforms. *Mt.I*, rudimentary first metatarsal. *Mt. II–V*, second to fifth metatarsals. *Ph. 1*, first phalanx. *Ph. 2*, second phalanx. *Ung.*, ungual phalanx. *I*, rudimentary hallux. *II–V*, second to fifth digits.

into three parts, the bones of which are called respectively the *tarsus*, *metatarsus* and *phalanges*, and the correspondence in structure between manus and pes is close and obvious. The tarsus consists typically of seven bones, which are tightly packed and rarely permit any movement between them. The upper row of the tarsus consists of two bones, which are peculiarly modified to form the ankle-joint and heel; on the inner side is the ankle-bone, or *astragalus*, the shape of which is highly characteristic of the various mammalian orders. The upper or posterior portion of the astragalus, according to the position of the foot, is a pulley which glides upon the lower end of the tibia and is held firmly in place by the internal and the external malleolus. Below the pulley-like surface the astragalus usually contracts to a narrow neck, which ends in a flat or convex head. The astragalus is supported behind (or beneath) by the heel-bone, or *calcaneum*, which is elongate and extends well above (or behind) the remainder of the tarsus; it frequently has a distinct articulation with the fibula, but more commonly is not in contact with that bone. The astragalus rests upon the *navicular*, which

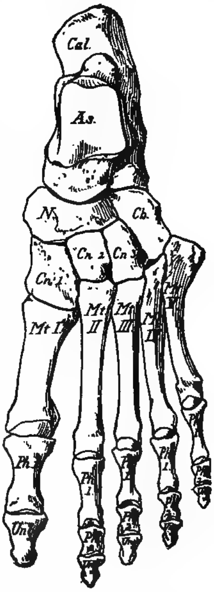

Fig. 41. — Left pes of Man. Note the large size of *Mt. I*, the metatarsal of the first digit, or hallux. Letters as in Fig. 40, except *Cb.*, cuboid.

is moulded to fit its head and corresponds in position to the central of the carpus, but, unlike that carpal, it is a very important element and is never suppressed or lost in any land mammal. The navicular, in turn, rests upon three bones of the second row, which are called respectively the *internal, middle* and *external cuneiform,* which correspond to the trapezium, trapezoid and magnum of the carpus and to which are attached the three inner metatarsals, one to each. Finally, the *cuboid,* the external element of the second row, is a large bone, which supports the calcaneum and often part of the astragalus and to which the fourth and fifth metatarsals are attached; it is the equivalent of the unciform in the manus. The number of tarsals is more constant than that of the carpals, but some suppressions and coössifications do occur.

The long bones of the pes constitute the metatarsus, which is the counterpart of the metacarpus. There are never more than five metatarsals in any normal mammal, but there may be any number less than five, down to a single one. In form and size the metatarsals of any given mammal are usually so like the metacarpals, that it requires some experience to distinguish them, but when either manus or pes is especially adapted to some particular kind of work, there may be very decided differences between metatarsals and metacarpals. For example, the burrowing forefoot of the moles is very different from the hind foot, which has undergone but little modification, and even more striking is the difference between the wing of a bat and its foot. Many other instances of a less extreme divergence might be enumerated, but when manus and pes are used only for locomotion, as in nearly all hoofed animals and many other mammals, the metacarpals and metatarsals are very similar. When there is a difference in number, it is the general rule that there are fewer metatarsals; an instance of this is found in the tapirs, which have four toes in the front foot and three in the hind. Forms which have a cannon-bone in the manus have it also in the pes, and some, like the peccaries and the jumping rodents called jerboas, have it only in the pes. The first (or inner) metatarsal, that of the great toe, or *hallux*, is sometimes opposable to the others, as in the monkeys, apes and lemurs.

The word *metapodial* is a useful general term which includes both metacarpals and metatarsals. A metapodial with its phalanges is a *digit*, a term often employed because of the ambiguity which arises in the use of the words "fingers" and "toes," and is applicable to both fore and hind feet.

Normally, the phalanges of the pes are so like those of the manus as to require no particular description; and only when the two pairs of extremities are specialized for entirely different functions, is there any notable divergence between the phalanges of manus and pes.

Before leaving the subject of the skeleton, it will be well to explain the terms used in describing the gait and manner of using the feet. When the entire sole of the foot is in contact with the ground and weight is thrown upon the heel-bone, or calcaneum, the gait is said to be *plantigrade* and is exemplified in Man, bears, raccoons and many other mammals. The Dog is *digitigrade*, that is to say, the feet in the standing position are nearly erect and the wrist and heel are raised high above the ground; the weight is borne upon ball-like pads, one under the phalanges of each functional digit and one under the metapodials. The digitigrade gait is found not only in all the dogs and cats, but in many other Carnivora and in the camels and llamas, as well. Transitions between the plantigrade and digitigrade gait are so numerous and gradual, that such terms as *semi-plantigrade* and *semi-digitigrade* are sometimes necessary.

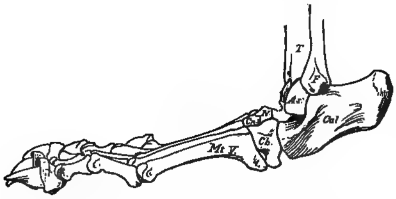

FIG. 42.—Left pes of Black Bear (*Ursus americanus*), showing the plantigrade gait. *T.*, tibia. *F.*, fibia. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn.3*, external cuneiform. *Cb.*, cuboid. *Mt.V*, fifth metatarsal.

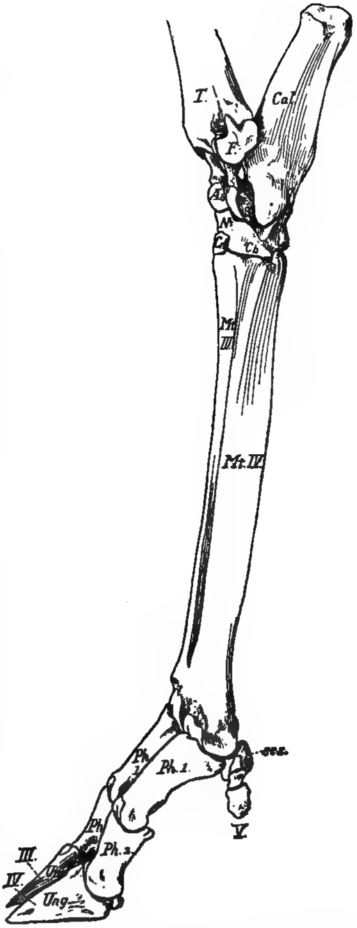

FIG. 43. — Left pes of Patagonian Deer (*Hippocamelus bisulcus*), showing the unguligrade gait. *T.*, tibia. *F.*, lower end of fibula (malleolar bone). *Cal.*, calcaneum. *As.*, astragalus. *N.Cb.*, coössified cuboid and navicular. *Mt. III*, *Mt. IV*, cannon-bone, formed by the coössification of the third and fourth metatarsals. *V.*, Rudimentary fifth digit.

An animal is said to be *unguligrade* when the weight is carried entirely upon the hoofs and is used only of hoofed animals; examples are the horses, pigs, deer, antelopes, oxen, etc. The so-called "knee" of a horse is really his wrist and the "hock" is the heel, so that the feet make nearly half the apparent length of the legs. Certain very large and massive animals, such as the rhinoceroses and elephants, are unguligrade in a modified sense; the foot is a heavy column, seemingly a part of the leg, and the weight is borne upon a great pad of elastic tissue, with the hoofs disposed around its periphery. A very peculiar mode of locomotion is exemplified by certain of the Edentata, in the forefoot of the existing Ant Bear (*Myrmecophaga jubata*) and in both extremities of some of the later representatives of the extinct †ground-sloths, or †Gravigrada. Here the weight is carried upon the outer edge of the foot, the palm and sole being turned inward. No term has been suggested for this very exceptional gait, which is a modified form of plantigradism.

II. The Teeth

It was pointed out in Chapter II (p. 38) that very often the teeth are all that remains to us of extinct genera and species of mammals, and it may be further noted that the teeth are very characteristic and often suffice to fix the systematic position of a genus. Since, therefore, the teeth play such an uncommonly important part as fossils and are so pre-eminently useful to the palæontologist, it is necessary to give some general account of them.

Among the mammals the teeth display a very great variety of size and form in accordance with the manner in which they are used. Primarily, the function of the teeth is to seize and masticate food, and the kind of food habitually eaten by any animal is well indicated by the form of its teeth. The beasts of prey have teeth adapted for shearing flesh and crushing bones; plant-feeders have teeth fitted for cropping plants and triturating vegetable tissues; insect-eaters have teeth with numerous sharp-pointed cusps, or it may be, no teeth at all, swallowing without mastication the insects which they capture, etc. Among animals that have similar diet there is very great difference in the form and elaborateness of the grinding apparatus and it is often possible to follow out the steps of evolutionary change, by which, from simple beginnings, a high degree of complexity has been attained. In addition to the uses of the teeth as organs of mastication, they frequently serve as weapons of offence or defence. In the flesh-eaters which capture living prey they are formidable offensive weapons, and the fangs of the Lion or the Wolf are instances familiar to every one; but the tusks of the elephants or the hippopotamuses have nothing to do with the taking of prey. Several Old World deer, which have no antlers or very small ones, possess scimitar-like upper tusks, with which they are able to defend themselves very effectually.

In the lower vertebrates, such as reptiles and fishes, the number of teeth is usually indefinite and they continue to be shed and replaced, as needed, throughout life; but in each species of mammal, aside from abnormalities, the number is fixed and constant. Mammalian teeth are very generally divisible into four categories · (1) the *incisors*, or front teeth, which in the upper jaw are inserted in the premaxillary bones, (2) the *canines*, or eye-teeth, which are never more than one on each side of each jaw, or four in all, (3) the *premolars*, called in Man the bicuspids, the anterior grinding teeth which have predecessors in the milk-series and (4) the *molars*, the posterior grinding teeth which have no such predecessors.

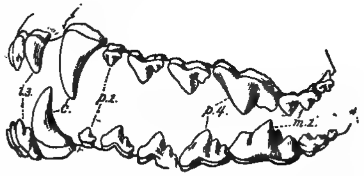

FIG. 44. — Dentition of Wolf, left side. *i. 3*, third incisor. *C.*, canine. *p. 1*, first premolar. *p. 4*, fourth premolar. *m. 1*, first molar.

It is customary and convenient to express the numbers and kinds of teeth of a given mammalian species by means of a "dental formula"; for example, in Man the formula is: $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $p\,\frac{2}{2}$, $m\,\frac{3}{3}$, $\times 2 = 32$; the reason for the multiplication by two is that the figures deal only with one side of the mouth and must be doubled to give the sum total. Just because, however, the two sides are alike, it is usual to take the doubling for granted. Written out in full, the formula means that Man has two incisors, one canine, two premolars and three molars on each side of each jaw, the horizontal line indicating the division between upper and lower teeth. The number of teeth is frequently not the same in the upper and lower jaws; for instance, the formula for the Sheep is: $i\,\frac{0}{3}$, $c\,\frac{0}{1}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 32$; the total is the same as in Man, but the arrangement is entirely different. The meaning is that in the Sheep there are no upper incisors or canines, but three incisors and a canine are present in each half of the lower jaw, with three premolars and three molars on each side above and below. The Dog gives still another formula: $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{2}{3}$, $\times 2 = 42$. What is called the typical formula for the higher terrestrial mammals above the grade of the marsupials and which is but rarely exceeded, is $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 44$, though most existing mammals have fewer teeth than this. Compared with the typical formula, the Dog has lost but two teeth, the third upper molar on each side, while Man and the Sheep have each lost twelve.

As every one knows from his own experience, mammals normally have two sets of teeth, the first, temporary, or milk-dentition, in the young animal, and the second, or permanent dentition, in the adult. The milk-dentition, when fully developed, consists of incisors, canines and premolars, which usually agree in number, though often not in form, with the permanent teeth which replace them in the adult. The milk-teeth are frequently more conservative than the permanent ones and retain ancestral characters which have disappeared in the adult series, thus affording welcome information as to lines of descent and steps of evolutionary change. While there can be little doubt that the development of more than one dentition, or set of teeth, is the primitive condition among mammals and was derived by inheritance from their lower vertebrate ancestors, in which there was an indefinite succession of teeth; yet there are many mammals in which the milk-dentition is greatly reduced or altogether lost. In some, the milk-teeth are shed and replaced before birth, in others only the germs of the milk-teeth are formed and never cut the gum, while in others again all traces of the temporary series have vanished. This complete loss of the milk-teeth, like the presence of a great number of simple and similar teeth in the dolphins and porpoises, or the total absence of teeth, as in the anteaters and whalebone whales, is a secondary and derivative condition, never a primitive one.

The structure of mammalian teeth varies greatly, from the simplest slender cones to enormous and highly complicated apparatus, and, in order to comprehend the significance of these differences, we must look a little more closely into the materials of which the teeth are constructed and the manner in which those materials are combined. In all primitive mammals and in many of the higher and more advanced ones (including Man) a tooth is composed of the *crown*, or portion which is exposed above the gum, and the *roots,** one or more in number, by means of which the tooth is firmly inserted in the jaw-bone; the roots are at least partly formed before the tooth comes into use. Such a tooth is said to be short or low-crowned, or *brachyodont.* In many plant-feeders, such as horses, cattle, elephants, beavers, etc., the teeth continue to grow in height for a long time and do not form roots until late in life, or perhaps not at all. Such teeth are said to be long- or high-crowned, or *hypsodont,* and in very many instances the development of brachyodont into hypsodont teeth may be followed through every step of the change. The advantage of the change is obvious in lengthening the animal's life, especially in those which feed upon abrasive substances, like grass, for the growth of the teeth long continues to make up for the loss through wear. Serious trouble has often been caused for captive elephants by giving them too soft food, so that the growth of the teeth is not properly balanced by abrasion. Still another category of teeth is

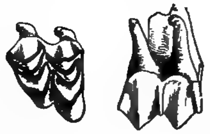

FIG. 44*a.* — First upper molar, right side of Deer (*Odocoileus*). On the left, the masticating surface; heavy black line, enamel. On the right, external side, showing crown and roots. *Brachyodont.*

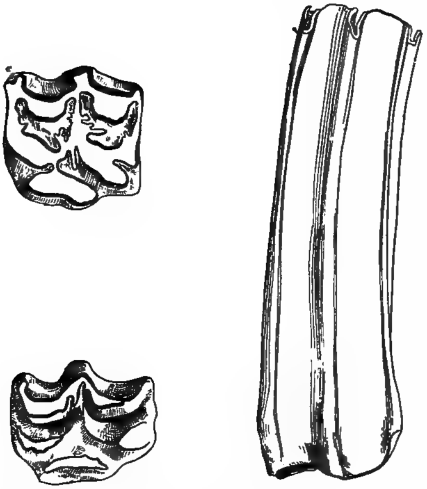

FIG. 45. — First upper molar, left side, of a fossil horse (*Equus sp.*). On the right, external side. On the left, the grinding surface, showing two stages of wear. Heavy black line, enamel; white, dentine; shaded, cement. *Hypsodont,* roots not yet formed.

the *rootless*, which are of simple form, like those of an armadillo, and grow throughout life, never forming roots. The chisel-like, or *scalpriform* incisors of the rodents do not cease to grow while the animal lives; they are kept of constant length by continual use, and the arrangement of harder and softer tissue is such that the sharp edge is maintained; through accident or malformation it sometimes happens that the upper and lower teeth fail to meet, then the continued growth causes them to form curved hoops in the mouth, locking the jaws and bringing death by starvation to the unfortunate animal.

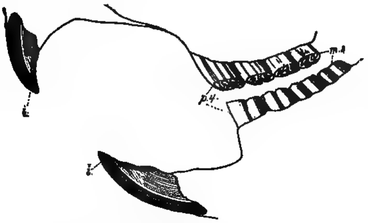

FIG. 46.—Dentition of Beaver (*Castor canadensis*). *m. 3*, last molar. *p. 4*, last premolar. *i.*, scalpriform incisors; enamel face black, dentine in vertical lines.

The typical mammalian tooth is composed of three kinds of tissue, all differing in structure and hardness and called respectively (1) dentine, (2) enamel, (3) cement. (1) The *dentine*, or ivory, is the indispensable tissue of the tooth; the other kinds may be absent, but never the dentine. Chemically, it is like bone, but the microscope shows that its structure is quite different from that of true bone, being composed of an immense number of fine tubules, which radiate from the "pulp-cavity," or chamber which contains the blood-vessels and nerves, these entering the tooth through the canals of the roots. The tubules of the dentine lodge excessively fine fibrillæ of the nerve and that is why the cutting into a live tooth is so painful an operation. (2) The *enamel*, which is the hardest of all animal tissues, has a polished and shining appearance and is arranged in a mosaic of microscopic prisms, closely packed together, which in most mammals are solid, but in the marsupials, with some exceptions, are tubular. The enamel normally covers the entire crown of the tooth, but does not extend upon the roots, where its superior hardness would be of no advantage. In several instances, always as a secondary specialization, the enamel does not cover the whole crown, but is arranged in vertical bands, it may be on one side only, or at intervals around the tooth. The scalpriform incisors of the rodents, already alluded to, have the enamel band on the front face of the tooth; the softer dentine behind wears away more rapidly, keeping the cutting surface bevelled, like the edge of a chisel, while the hard enamel forms the sharp edge. In some instances the enamel is absent altogether and the teeth are composed entirely of dentine, as in the elephant tusk. In all the Edentata, such as sloths and armadillos, both living and extinct, that have any teeth at all, the teeth have no enamel, but in some of the fossil forms the place of the missing enamel is taken by a harder dentine and thus the effect of differential hardness is secured.

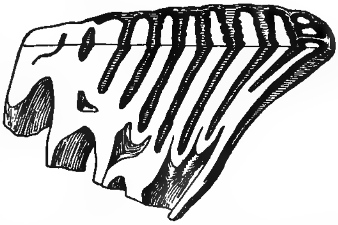
FIG. 47.—Section through a lower molar of the Indian Elephant (*Elephas maximus*). Enamel, heavy black; dentine, white; cement, horizontal lines.

(3) The *cement* is simply bone, both chemically and in microscopic structure; it is not quite so hard as dentine, but it is less affected by the fluids of the mouth and the juices of the food. In the brachyodont or low-crowned tooth, such as a human molar, the cement merely forms a sheath over the roots and does not appear upon the crown, but in many hypsodont teeth, those of horses and elephants, for example, the cement completely encases the entire tooth in a thick layer, filling up all the depressions and irregularities of the enamel surface and making a freshly erupted and unworn tooth look like a shapeless lump. When the cement and the enamel covering are partially worn through, the masticating surface is made up of three distinct substances, each having a different degree of hardness and thus, through unequal wear,

the grinding surface is always kept rough and therefore efficient. Not all hypsodont teeth have the cement covering, but in such teeth the differing degrees of hardness of enamel and dentine suffice to keep a rough surface, though not so effectively.

CHAPTER V

THE GEOGRAPHICAL DEVELOPMENT OF THE AMERICAS IN CENOZOIC TIMES

I. TERTIARY PERIOD

In the interior regions of western North America the transition from the Mesozoic to the Cenozoic was so gradual that there is great difficulty in drawing the line between them and therefore, as might be expected, there is much difference of opinion as to just where that line should be drawn. From one point of view, the matter is of no great consequence; but from another, it is of the utmost importance, for, unless the events in different continents can be approximately synchronized, it will often prove a hopeless undertaking to trace the course of migration of the various mammalian groups and determine their place of origin and primary home. Until a definitive answer can be given to the question as to when the Cenozoic era began, many significant points must be left in doubt, and much remains to be done in the geology of the Far West before that definitive solution can be reached.

1. *Paleocene Epoch*

So far as North America is concerned, the best available evidence points to the conclusion that we should regard the Fort Union, Puerco and Torrejon as the most ancient of the Cenozoic formations (see Table, p. 17), though retaining so many features of Mesozoic life that a separate division of the Tertiary, the Paleocene epoch, is made for them. Such a separation is not the common practice in this country, where it is more usual to employ the terms "Lowest" or "Basal" Eocene.

In my judgment, however, the balance of advantage is in favour of giving to this so-called Basal Eocene a rank equivalent to that of the four other universally recognized and admitted epochs of the Tertiary period. No marine rocks of Paleocene date have yet been found in North America, which indicates that the continent was at least as extensive as it is now. The very scanty development of deposits representing this epoch in Europe renders the comparison with the fossils of the Old World unsatisfactory and hence leads to uncertainty, when it is attempted to determine the land-connections of the time. During the Mesozoic era the shallow Bering Sea had repeatedly been elevated into a land joining North America with Asia and had as often been depressed, so as to separate the continents and allow the waters of the Arctic Ocean to mingle with those of the Pacific. A like alternation of junction and separation went on during the Tertiary and Quaternary periods and, by a comparison of the fossil mammals of Europe and America for any particular division of geological time, it is almost always feasible to say whether the two continents were connected, or altogether separated. This statement does not imply that the proportion of common elements in the two faunas during epochs of continental connection was a constant one at all times, for that was by no means true. Mere land-connections or separations are not the only factors which limit the spread of terrestrial animals; if they were, the community of forms between North and South America would be much greater than it actually is. Climatic barriers are of almost equal importance in determining animal distribution, and changes of climate may greatly alter the conditions of migration between connected continents. As the connections between North America and the Old World were probably in high latitudes, where the seas are narrow, changes of climate produced a greater effect upon migration than they could have done had the land-bridges been in the tropical or warm temperate zones. That these vicissitudes of climate really did occur and are not mere guesses to bolster up a tottering hypothesis, there is abundant evidence to prove.

In the Paleocene, or most ancient epoch of the Tertiary period, the geographical condition of North America was approximately as follows: The continent had attained nearly its modern outlines and on the Atlantic and Pacific coasts probably extended farther seaward than it does to-day. Florida, however, and perhaps a narrow strip of the northern Gulf coast were still submerged, the Gulf of Mexico opening broadly into the Atlantic. It is very probable that the continent was connected with the Old World by a land occupying the site of Bering Sea and perhaps also by way of Greenland and the North Atlantic; and there is some evidence, though not altogether convincing, that it was also joined to South America. The great mountain ranges were largely what they now are, though subsequent upheavals greatly modified the Rocky Mountains, Sierra Nevada and the ranges of the Pacific coast, while the lofty St. Elias Alps of Alaska were not in existence. The region of high plateaus, between the Rockies and the Sierras, was much less elevated than it is now. The Appalachians, which were of far more ancient date than the western ranges, had been worn down by ages of weathering and stream-erosion into a low-lying, almost featureless plain, with some scattered peaks rising from it here and there, of which the mountains of western North Carolina were the highest. In general, it may be said that while the *average* height of the continent above the sea-level may have been as great or greater than at present, yet the inequalities of surface appear to have been less marked, and both along the Atlantic coast and in the interior were vast stretches of plains.

The Paleocene formations of the western interior are of non-marine or continental origin. In northwestern New Mexico is the typical area of the *Puerco* and *Torrejon*, a series of beds 800 to 1000 feet in thickness and for the most part quite barren of fossils, but there are two horizons, one near the top and the other near the bottom of the series, which have yielded a very considerable number of fossil mammals, and of these the lower is the Puerco, the upper the Torrejon. The *Fort Union* is quite different in character and is composed of great areas of sandstone and clay rocks, with a maximum thickness of 2000 feet, in eastern Wyoming, South Dakota, Montana and the adjoining parts of Canada. The modes of formation of these beds have not yet been fully determined; that they may have been partly laid down in shallow lakes is indicated by the masses of fresh-water shells in certain localities. In others are preserved multitudes of leaves, which have given a very full conception of the plants of the time, and great swamps and bogs have left the traces of their presence in beds of lignite, or imperfectly formed coal. Deposits made on the flood-plains of rivers and wind accumulations are probably also represented. "Vast stretches of subtropical and more hardy trees were interspersed with swamps where the vegetation was rank and accumulated rapidly enough to form great beds of lignite. Here were bogs in which bog iron was formed. Amid the glades of these forests there wandered swamp turtles, alligators, and large lizards of the characteristic genus *Champsosaurus*" (Osborn, p. 100).

Fort Union mammals are relatively rare and most of those that have been found are very fragmentary; they are amply sufficient, however, to demonstrate the Paleocene date of the beds and to make it probable that they include both the Puerco and the Torrejon faunas.

The climate, as shown by the plants, was much milder and more uniform than that of the Recent epoch, though some indication of climatic zones may already be noted. The vegetation was essentially modern in character; nearly all our modern types of forest-trees, such as willows, poplars, sycamores, oaks, elms, maples, walnuts and many others, were abundantly represented in the vast forests which would seem to have covered nearly the entire continent from ocean to ocean and extended north into Alaska and Greenland, where no such vegetation is possible under present conditions. Numerous conifers were mingled with the deciduous trees, but we do not find exclusively coniferous forests. Palms, though not extending into Greenland, flourished magnificently far to the north of their present range. On the other hand, the Paleocene flora of England points to a merely temperate climate, while that of the succeeding Eocene was subtropical.

South America. — Nothing is definitely known concerning the condition of Central America and the West Indies and very little as to South America. As no marine rocks of Paleocene date have been found in any of these regions, it may be inferred that all the existing land areas were then above the sea, and there is some evidence that South America was much more extended in certain directions than now. From the character and distribution of modern plants, fresh-water fishes, land and fresh-water shells, there is strong reason to believe that in late Mesozoic times a land-bridge connected Brazil with equatorial Africa and this connection may have continued into the Paleocene, though it is only fair to observe that some highly competent authorities deny the reality of this bridge. There is also evidence, though incomplete, of a connection between South America and Australia by way of the Antarctic continent, and it is clear that that polar region could not have had the rigorous climate of the present time. In the upper part of the Cretaceous, the last of the Mesozoic periods, there was a possibility of migration, however indirect, between every continent and every other, for the huge land reptiles called Dinosaurs have been found in the non-marine Cretaceous rocks of every continent, which could not have been the case, had any of the great land areas been isolated. There is no known reason to assume that the land-bridges were essentially different in the Paleocene.

2. *Eocene Epoch*

North America. — The Eocene witnessed quite extensive geographical changes, though but little is known of it in Central or South America, or the West Indies. Along the Atlantic and Gulf coasts of the United States there was an extensive submergence of the coastal plain, the sea covering the southern half of New Jersey and extending thence to the southwestward in an ever broadening band, through the South Atlantic and Gulf states. Northern Florida was under water and the Gulf extended as a narrow sound, known as the "Mississippi Embayment," up the valley of that river to southern Illinois and westward into Texas. The Embayment was present in the Cretaceous and again in the Eocene, but it is not known whether it persisted through the Paleocene; probably it did not, as the whole Atlantic coast region appears to have stood at a higher level then than now. While the condition of Mexico and Central America during the Eocene is not known in any save the vaguest manner, it is evident that there was then a broad communication between the Atlantic and the Pacific, completely severing North and South America, though the place of this transverse sea has not been fixed. On the Pacific side, a long, narrow arm of the sea occupied what is now the great valley of California, extending north into Oregon and Washington. It will be noted that in North America the Eocene sea was almost confined to the neighbourhood of the present coast-lines, nowhere penetrating very far inland, except in the Mississippi Embayment, and thus differing widely from the condition of Europe at that epoch, where much of what is now land was submerged. The greatly expanded Mediterranean covered most of southern Europe, where the great mountain ranges, the Pyrenees, Alps, etc., had not yet been formed. Very important, from the point of view of American geography, is the fact that Europe was completely separated from Asia by a narrow strait or sea, which ran down the eastern

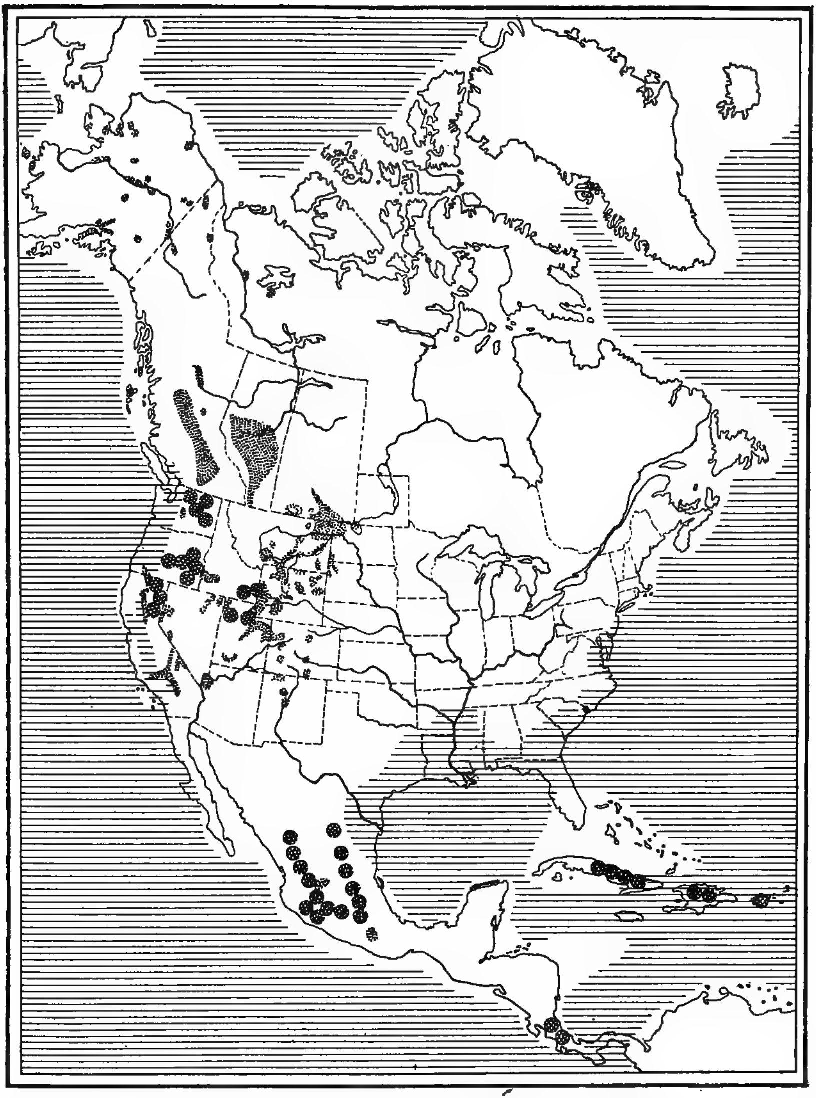

FIG. 48. — Map of North America during the Eocene epoch. The present limits of the continent are shown in outline; white areas = land; horizontal lines = sea; dotted areas = non-marine deposits; black circles with white dots = active volcanoes. (After Schuchert.)

side of the Ural Mountains from the Arctic Ocean and joined the enlarged Mediterranean. During the existence of this Ural Sea any land connection of North America with Europe must necessarily have been by means of a North Atlantic bridge, or by one across the Arctic Sea, since communication with Asia by way of Alaska would not have reached eastern Europe.

Any such general statement of geographical conditions during the Eocene as the foregoing sketch, cannot but be to some extent misleading, because it brings together, as contemporary, arrangements which were, in some cases at least, separated by considerable intervals of time and which were subject to continual change. Along nearly all coasts the position of the sea was quite different in the latter part of the epoch from what it had been in the earlier portion. On the north side of the Gulf of Mexico, for example, the sea retreated from time to time, and the successive divisions of the Eocene rocks are so arranged that the later ones are farther to the south. Limitations of space, however, forbid the attempt to follow out these minor changes.

In the western interior are found extensive non-marine or continental deposits of Eocene date, which must be considered more in detail, because of the highly important bearing which they have upon mammalian history. With the exception of a few small areas in Colorado, these deposits are all situated in the plateau region west of the Rocky Mountains, and were made of the débris of older rocks washed down by rain and rivers and deposited in broad basins. Some of them are the sediments of shallow or temporary lakes, and one series, at least, is made up of volcanic ash and dust showered upon the land, or into water of no great depth. The oldest of these Eocene stages, known as the *Wasatch* (see Table, p. 17) covers a very large region, though in a discontinuous manner; the principal area begins in New Mexico, where it lies over the Torrejon, of the Paleocene, and extends far to the north through

FIG. 49. — Bad Lands of the lower Eocene, Wasatch stage. Big Horn Basin, Wyo. (Photograph by Sinclair.)

western Colorado and eastern Utah to the Uinta Mountains, around the eastern end of which it passes in a narrow band and then expands again over southwestern Wyoming. A second area is in the Big Horn Basin of northwestern Wyoming and southern Montana, and probably two small areas in southern Colorado are of the same date. The Wasatch beds are richly fossiliferous and have yielded a most interesting and important series of mammals, which were far more advanced than those of the Paleocene; and, at first sight, the student is tempted to believe that they must be of very much later date. A more critical examination shows that this appearance of a great lapse of time between the Paleocene and the Wasatch is deceptive; the more advanced and characteristic of the Wasatch mammals were obviously not the descendants of ancestors in the North American Paleocene, but were altogether newcomers to this continent, immigrants from some region which cannot yet be identified. On the other hand, a considerable number of the old, indigenous types still persisted, and these, when compared with their Paleocene ancestors, are found not to have changed so much as to require a very great length of time, geologically speaking, for the degree of development involved. This is the earliest recorded one of the great waves of mammalian migration which invaded North America down almost to our own time.

The same wave of migration extended to Europe, and that there was a broad and easy way of communication between that continent and North America is plain, for the similarity between the Wasatch mammals and those of the corresponding formation in France, the *Sparnacian,* is remarkably close. At no subsequent time were the mammalian faunas of North America and Europe so nearly identical as during the Wasatch-Sparnacian age, which is especially remarkable when the discrepancy is noted between the vast stretches of the Wasatch (150,000 square miles) and the very limited areas in France.

If, as is probable, the Ural Sea was in existence at that time, the land-connection with Europe must have been across the North Atlantic, most likely from Greenland eastward. At the present time a land-bridge in such high latitudes would be of little service in bringing about a similarity of mammals in the two continents, for the severity of the Arctic climate would be as effective a barrier against the intermigration of all save the Arctic mammals as the ocean itself; but in the mild and genial Eocene climate the latitude of the bridge was of small consequence.

The second of the Eocene stages, the *Wind River — Green River*, is found in two very different phases. The Wind River phase occupies the basin of that stream, north of the Wind River Mountains in central Wyoming, and in the Big Horn Basin of the same state it very extensively overlies the Wasatch, and in this phase the sediments are very like those of the latter, flood-plain and wind accumulations. A widely distant area of this stage occurs in the Huerfano Cañon in Colorado. The Wind River beds contain numerous mammals which were clearly sequential to those of the Wasatch, of which they were the more or less modified descendants. With two possible exceptions, there were no new immigrants and the connection with the Old World may have been already severed, as it assuredly was in the succeeding age, the Bridger, though divergent development had not yet had time to produce the very striking differences in the mammals of North America from those of Europe, which characterized the Bridger.

The Green River phase is a thick body of finely laminated "paper shales," which seem to have been deposited in a very shallow lake and occupy some 5000 square miles of the Green River valley in southern Wyoming and northern Utah, where they overlie the Wasatch, just as do the Wind River beds in the Big Horn Basin. These fine-grained and thinly laminated shales have preserved, often in beautiful perfection, countless remains of plants, insects and fishes, but no traces of mammals, other than footprints, have been found.

The third of the Eocene stages of the interior is the *Bridger* of southern Wyoming and northeastern Utah, where it lies upon the Green River shales, but overlaps these shales both eastward and westward, extending out upon the Wasatch. The Bridger beds are largely made up of volcanic ash and dust deposited partly upon the land and partly in shallow or temporary lakes. The frequency with which the remains of fishes, crocodiles and fresh-water shells are found indicates deposition in water, and the large crystals of gypsum which are abundant in certain localities show that the water became salt, at least occasionally. From the immense mass of volcanic débris, it is evident that volcanic activity broke out at this time on a much greater scale than had been known in that region since the Cretaceous period. Two different horizons, or substages, are distinguishable in the Bridger, lower and upper, each of which has its distinct mammalian fauna, though the two are very closely allied. Their difference from the contemporary mammals of Europe is very great, hardly any genera being common to the two continents. So striking a difference indubitably points to a severance of the land-connection, a severance which, as was shown above, probably took place during the Wind River stage, for its effects would not be immediately apparent; time would be required for the operation of divergent evolution, the fauna of each continent developing along its own lines, to make itself so strongly felt. Had the connection never been renewed, North America, on the one hand, and Eurasia on the other, would to-day be utterly different from the zoölogical point of view, instead of containing, as they do, a great many identical or closely similar animals of all classes, a likeness due to subsequent migrations.

The fourth and last of the stages referred to the Eocene is the *Uinta*, the geological position of which is the subject of much debate; almost as good reasons can be brought forward for placing it in the Oligocene as in the Eocene, so nearly is it on the boundary line between those two epochs.

The Uinta is found in the Green River valley of northeastern Utah and northwestern Colorado, where it lies upon the upper Bridger and is the latest of the important Tertiary formations to be found in the plateau region west of the Rocky Mountains. It is probable that the separation of North America from the Old World still continued, for, as a whole, the Uinta fauna is totally different from that of the upper Eocene of Europe. There were, however, a few doubtful forms, which may prove to be the outposts of a renewed invasion.

The Eocene climate was decidedly warmer than the present one, and subtropical conditions extended over the whole United States and perhaps far into Canada. On the other hand, signs of increasing aridity in the western part of the continent are not wanting, and that must have resulted in a great shrinkage of the forests and increase of the open plains. The vegetation was essentially the same as in the Paleocene, when it had already attained a modern character, the differences from the present being chiefly in regard to geographical distribution. Large palms were then flourishing in Wyoming and Idaho, and another indication of a warm climate is furnished by the large crocodiles which abounded in all of the Eocene stages.

So far as North America was concerned, the Eocene epoch was brought to a close by extensive movements of the earth's crust, which more or less affected the entire continent and were registered both on the sea-coasts and in the mountain ranges of the interior. Upheaval added a narrow belt of land along the Atlantic and Gulf coasts and the Mississippi Embayment was nearly closed. On the Pacific side the sea withdrew from the great valley of California and Oregon, and in the interior the plateau region was elevated by a great disturbance, which also increased the height of the western mountains.

Our knowledge of Eocene land-mammals in North America is almost wholly derived from the formations of the western United States, but it may be inferred from the uniform climatic conditions that there were no very great geographical differences among the animals. This inference is confirmed by the discovery of a Bridger genus, very fragmentary but identifiable, in the marine Eocene of New Jersey.

South America. — No Eocene rocks, marine or continental, are known in the West Indies or Central America, but the latter region has been so imperfectly explored that no great importance can be attached to this fact. North and South America were separated completely, as is proved by the entire dissimilarity of their mammalian faunas, but the position of the transverse sea or strait cannot be determined. There is much reason to believe that the Greater Antilles were connected into a single large land, which has been called "Antillia" and may have been joined to the mainland of Central America. Certain marine rocks in Patagonia and Chili have been referred to the Eocene by South American geologists, but the reference is almost certainly erroneous, the rocks in question being much more probably Miocene. The Andes, probably throughout their length and certainly in their southern half, stood at a much lower level than they do now, and, no doubt, were rising, either slowly and steadily, or periodically and more rapidly, throughout the whole Tertiary period. At all events, their present height in the south is due to movements in the Pliocene or later. Continental deposits of Eocene date have been discovered only in northern Patagonia (Casa Mayor) where they occupy depressions in the worn and eroded surfaces of the Cretaceous rocks; the mode of their formation has not been carefully studied.

There is great uncertainty as to the status of the land-bridge which, it is believed, in the Cretaceous period connected South America with Africa. Some of the evidence goes to show that the connection persisted throughout the Eocene epoch, but the testimony is that of fragmentary and therefore imperfectly understood fossils and is far from being unequivocal. The connection with Antarctica probably continued.

3. *Oligocene Epoch*

North America. — The Oligocene, or third of the Tertiary epochs, was a time of great significance in the history of the American mammals and of great geographical changes in the West Indian and Central American regions, but in North America proper the changes were not so widespread. On the Atlantic coast the marine Oligocene is but scantily displayed except in the Florida peninsula, where it is found in a thickness of some 2000 feet, but it is well developed along the north shore of the Gulf of Mexico, where the coast-line followed that of the Eocene, only a little farther to the south, marking the retreat of the sea at the end of the Eocene. The Gulf Stream entered the Atlantic over the site of northern Florida and flowed northward nearer the coast than it does to-day, in consequence of which warm-water conditions extended far to the north and West Indian shells flourished on the New Jersey coast. In the middle Oligocene part of northern Florida was elevated into an island and the water over much of the remainder of the peninsula became shallower, but this did not greatly alter the course of the Gulf Stream. The Pacific encroached upon the western shore of Oregon and British Columbia and very extensively upon that of Alaska, where strata no less than 10,000 feet thick are assigned to this epoch.

In the western interior Oligocene formations are among the most important and widely spread of the continental Tertiaries and are divisible into two principal stages and each of these again into three substages. Of these, the older or *White River* stage covers a vast region in northeastern Colorado, western Nebraska, eastern Wyoming and southern South Dakota, with separate areas in the Black Hills, North Dakota and the Northwest Territory of Canada. The deposits are believed to be chiefly of fluviatile origin, and many of the ancient stream-channels, some of great size, may still

FIG. 50.—Map of North America in the upper Oligocene. Explanation as in Fig. 48. (After Schuchert.)

be traced, filled with the consolidated sands and gravels of the old rivers. The country was very flat and the divides between the streams very low, so that in seasons of flood great regions were converted into shallow, temporary lakes, in which were deposited the finer silt and mud, but were dry for most of the year. The volcanic activity which had gone on so impressively in the Bridger Eocene was renewed in White River times, as is proved by thick beds of pure volcanic ash, which must have been carried long distances by the wind, for they occur far from any volcanic vent.

The White River fauna is more completely known than that of any other Tertiary formation of this continent. The first discovery of these fossils was made more than 70 years ago and since then oft-repeated expeditions have brought to light an astonishing number and variety of mammals. Not only are these beds remarkable for the immense quantity of material which they have yielded, but also for its completeness and beauty of preservation, a most unusual number of skeletons having been obtained. The mammals demonstrate that the land-connection with the Old World had been reestablished, for many European genera, which could not have been derived from an American ancestry, are found in the White River beds. At the same time, there was no such proportion of forms common to both continents as there had been in the Wasatch-Sparnacian stage of the lower Eocene, each having many genera and even families which did not extend their range into the other. The reason for this remarkable and, at first sight, inexplicable difference between the lower Eocene and the lower Oligocene is probably to be found in climatic changes, in consequence of which relatively fewer genera were able to take advantage of the reopened connection, which lay far to the north. The White River mammals, like those of the Recent epoch, are thus divisible into two groups or elements, one set indigenous and descended from ancestors which are found in the American Eocene, and the other composed of late immigrants from the Old World. Migrants from North America likewise made their way to Europe.

The upper continental Oligocene of the interior has received the peculiar appellation of the *John Day*, from the river of that name in eastern Oregon, a large part of which was buried to a depth of 3000 or 4000 feet in stratified volcanic ash and tuff. This great mass of finely divided volcanic material was derived from the craters of the Cascade Mountains to the westward; a long-continued series of eruptions would be needed to form such thick accumulations at such a distance from the sources of supply. The John Day evidently succeeded the White River very closely in time, but is marked by the disappearance of almost all the European migrants. This fact, together with the absence of any new immigrant genera, is evidence that the connection had again been broken and it was not renewed until after a considerable lapse of time.

There are many reasons for believing that the Oligocene climate marked the beginning of the very long and gradual process of refrigeration which culminated in the glacial conditions of the Pleistocene epoch, but the change was slight and probably chiefly affected the far north. The climate, however, remained notably warmer than the present one of the same extra-tropical latitudes, as is abundantly proved by the fossils. The Atlantic coast, as noted above, was bathed in warm waters, the plants of the Alaskan Oligocene point to temperate conditions and the vegetation of Europe was subtropical, palms growing in the north of Germany. The change which was distinctly to be noted in the Great Plains region of North America was probably due rather to the elevation and increased altitude of the western interior than to general climatic alteration. Crocodiles are very rare indeed in the White River beds and those that have been found all belong to dwarf species, while none are known from the John Day. Unfortunately, hardly anything has been ascertained concerning the Oligocene vegetation of the region, but the reptiles indicate diminished warmth.

South America.—Marine Oligocene strata have great extent around the Gulf of Mexico and the Caribbean Sea, and the distribution of these shows that Antillia was broken up by great submergences, the islands of the Greater Antilles being much smaller than they are to-day. The greater part of Central America and the Isthmus were under water, a broad sea, broken only by scattered islands, separating North and South America. Very little is known of the Oligocene in the latter continent save a non-marine formation in northern Patagonia, the *Deseado* stage (or Pyrotherium Beds), which, like the Eocene of the same region, occupies depressions in the worn and irregular surface of the Cretaceous rocks. The attribution of the Deseado to the Oligocene is open to some doubt, because of the entire absence in its mammalian fauna of any elements which are also found in the northern hemisphere. Hence, there are no means of direct comparison.

4. *Miocene Epoch*

North America. — The Atlantic and Gulf coasts, which had been raised in the Oligocene, were again depressed, almost restoring the Eocene coast-line, the chief differences being the presence of the Florida islands and the nearly complete closing of the Mississippi Embayment. There was a remarkable change in the marine fauna from that of Oligocene times; a cool current flowed southward along the coast and entered the Gulf of Mexico through the strait between the Florida island and the mainland, bringing the northern animals with it and driving out the tropical forms. This complete faunal change, which might fairly be called a revolution, was the most sudden and striking in the Tertiary history of the continent.

On the Pacific coast also there was a depression, which caused a renewed transgression of the sea. The Coast Range formed a chain of reefs and islands in the Miocene sea, which again filled the great valley of California, except in the northern part of what is now the Sacramento Valley, where there was an accumulation of continental deposits. The immense thickness (5000 to 7000 feet) of the California Miocene is largely made up of volcanic material, which testifies to the great activity of the vents. In the Sierras, the height of which was increased in the upper Miocene, there was also a great display of vulcanism, recorded in the lava-flows and tuffs of the time. In the region of Lower California and northwestern Mexico considerable changes of the coast-line took place during the Miocene; in the earlier half of the epoch the Gulf of California was much shorter and narrower than it is to-day and the peninsula was broadly united with the mainland to the east as well as to the north. A wide submergence marked the upper Miocene, reducing the peninsula to a long, narrow island and enlarging the gulf considerably beyond its present limits, flooding an extensive area in northwestern Mexico and sending a small bay into southeastern California. There were great disturbances in the course of the epoch, for in the Santa Cruz Mountains near San Francisco the lower Miocene strata were crumpled into folds, before those of the upper Miocene were deposited upon them. British Columbia, Washington and Oregon were invaded by the sea, which extended up the valley of the Columbia River and its southern tributary, the Willamette, though here the beds are far thinner than those of California. Much of Alaska, both on the north and west coasts and in the valley of the Yukon, was submerged, and the land-connection with Asia appears to have been broken. This is made probable not only by the submergence of the Alaskan coast, but also by the fact that the marine animals of the California coasts and shoal waters, which could not migrate across the ocean, were quite unlike the contemporary forms of the eastern Asiatic shore, which would hardly have been the case, had a continuous coast-line united the two continents. On the other hand, there was a renewed connection with Europe, as

FIG. 51. — Map of North America in the upper Miocene. Explanation as in Fig. 48. (Modified from Schuchert.)

is shown by the appearance of Old World land-mammals, beginning scantily in the lower and becoming numerous in the middle Miocene. This connection, it will be remembered, had been interrupted during the upper Oligocene. Many students of the problem have maintained that the land-bridge was by way of the West Indies and the Mediterranean lands, but such a bridge would not account for the facts of mammalian distribution, which would seem to require its location in the far north.

Several distinct lines of evidence go to prove that the junction of the Americas dates from the Miocene, possibly from the beginning of it. The absence of Atlantic species from the Pacific Miocene is an indication that the passage from ocean to ocean had been closed, and this is confirmed by the geology of the Central American and Isthmian region. In the middle Miocene of Oregon and Nebraska have been found remains, which are unfortunately too incomplete for altogether convincing identification, but which can be interpreted only as belonging to the extinct and most characteristically South American group of edentates, the †ground-sloths or †Gravigrada; if this reference is correct, the fact of the junction cannot be questioned.

Continental deposits of Miocene date, chiefly accumulations made by rivers and the wind, cover vast areas of the western interior, though but rarely to any considerable depth. These have been divided into several stages and have received various names; the lower Miocene, known as the *Arikaree, Harrison* or *Rosebud,* overlies the White River in South Dakota, western Nebraska and eastern Wyoming, with smaller areas in Montana and Colorado. In the deposits of this stage there are no mammals of indisputably Old World type, though a few which I consider to be such are a probable indication of renewed connection with Europe. The middle Miocene is found typically in central Montana, where it is called the

† Extinct.

Deep River (or *Smith River*) stage, but occurs also in numerous small, scattered and widely separated areas in Oregon, Wyoming, Colorado and Texas, with local names in these different states. It is most likely that these middle Miocene formations are not strictly contemporaneous in the geological sense, but rather form a closely connected and successive series. The mammals of the Deep River stage leave no doubt that the way of migration from the Old World was again open.

The *Loup Fork*, or upper Miocene, itself susceptible of further subdivision, is by far the most extensive of the Miocene formations and covers much of the Great Plains region, in separate areas, from South Dakota far into Mexico. Perhaps also referable to the upper Miocene is a small, but very interesting formation, the *Florissant*, which is in the South Park of Colorado; it was made by very fine volcanic material showered into a small and shallow lake. The finely laminated papery shales of the Florissant have preserved countless plants and insects and many fishes, and these throw very welcome light upon the vegetation and climatic conditions of the epoch and afford an interesting contrast to the fauna and flora of the Green River shales of the lower or middle Eocene. That the Florissant shales are Miocene, no one questions, but their isolated position and the fact that they have yielded no mammals make it somewhat doubtful whether they belong in the middle or later part of the epoch.

In the western portion of the continent vulcanism was displayed on a grand scale during the Miocene. Mention has already been made of the quantity of volcanic material in the marine Miocene of California and also in the lavas and tuffs of the Sierras. The magnificent cones, such as Mts. Hood and Tacoma, which are the glory of the Cascades, are believed to date from this time. In Idaho and eastern Oregon and Washington are the immense lava-fields of the Columbia River, which are, partly at least, of Miocene date and were chiefly extruded through great fissures, the lava flooding the valleys and plains in a fiery sea of molten rock. In Oregon these lavas rest upon the upper Oligocene (John Day stage) and middle Miocene beds are deposited upon them, which fixes their date sufficiently. In the Yellowstone Park was piled up a huge mass of volcanic products, lava-flows and beds of ash and tuff, to a thickness of several thousand feet. The ash-beds have preserved the petrified forests, with their tree-trunks still standing one above another; one locality in the Park shows seven such forests, each one killed and buried by a great discharge of ash and then a new forest established and growing upon the surface of the accumulation. In the tuffs are leaf-impressions which permit identification of the plants.

In the latter part of the Miocene and at its close there were important crustal movements, which affected all the Pacific coast mountain ranges, though this epoch was no such time of mountain making in America as it was in the Old World. The principal elevation of the Coast Range in California and Oregon was due to these movements, and the Sierras and the plateaus of Utah and Arizona were increased in height. On the Atlantic side the Florida island was joined to the mainland and thus the present shape of the continent was almost exactly gained.

The Miocene climate of North America, as indicated by the plants of Florissant, the Yellowstone Park and Oregon, was distinctly milder than at present, a southern vegetation of warm-temperate character extending to Montana and perhaps much farther north, but it was not so warm as it had been in the Eocene, and palms are not found in any of the localities mentioned, nor do crocodiles occur in any of the northern Miocene formations. In Europe the climate of the early Miocene was considerably warmer than in North America, the vegetation of central and western Europe being very much like that of modern India. This difference between the two sides of the Atlantic was probably due, in large part, to the manner in which Europe was broken and intersected by arms and gulfs of the warm southern sea. In the latter half of the epoch, however, the climate became colder, the subtropical flora giving way to a distinctly temperate one.

South America. — In Central America, where marine Oligocene beds are of great extent, no Miocene is known, and on the Isthmus Oligocene is the latest marine formation, except a narrow fringe of Pleistocene on the Caribbean coast. These facts and others already cited lead to the conclusion that in the Miocene the connection of the Americas was complete and that the Isthmus was considerably broader than at present, extending nearly to Jamaica. The condition of the Greater Antilles is but vaguely understood, but they were involved in the general elevation of the Caribbean region and were at least as large as they are now and may have been considerably larger, and Cuba was perhaps joined to Central America, as Hayti probably was.

In South America proper nearly the whole of Patagonia was submerged by the transgression of a shallow, epicontinental sea, in which were accumulated the beds of the *Patagonian* stage, containing an exceedingly rich and varied assemblage of marine fossils, an assemblage which has very little in common with the contemporary formations of the northern hemisphere. It is this lack of elements common to the northern faunas which has led to the long debate concerning the geological date of the Patagonian formation, the South American geologists very generally referring it to the Eocene. However, the occurrence of genera of Cetaceans (whales and dolphins), which are also found in the Miocene of Maryland and Virginia, is very strong evidence that the proper date of the Patagonian is Miocene. A continuous coast-line, or at least an unbroken continuity of shoal-water conditions, seems necessary to account for the similarity of the Patagonian fossils with those of New Zealand and Australia, and that this connection was by way of the Antarctic continent is indicated by the occurrence of similar fossils in the South Shetland Islands, an Antarctic group. On the Chilian coast the *Navidad* formation, which is believed to be approximately contemporaneous with the Patagonian, has so different a fauna as to point to some kind of a barrier between the Atlantic and the Pacific, and this barrier, Dr. von Ihering holds, was the land-extension from South America to Antarctica.

After some oscillations of retreat and advance, the sea withdrew from Patagonia and the terrestrial accumulations of the *Santa Cruz* stage were formed. These beds are partly composed of river-deposits, but chiefly of more or less consolidated volcanic ash or tuff, and have yielded a surprising number of beautifully preserved mammals. No other assemblage of South American Tertiary Mammalia is so well known and understood as the Santa Cruz fauna, and the very large number of all but complete skeletons which have been found strongly suggests that many of the animals were buried alive in the showers of volcanic ash. The Santa Cruz fauna is completely and radically different from any of the North American assemblages, and at that time no immigrant from the north had penetrated so far as Patagonia.

In the upper Miocene the Andes stood at a much lower level than they do now; fossil plants, some of them collected at a great height in the mountains, are the remains of a luxuriant and purely tropical flora nearly identical with the vegetation of the modern forests of Bolivia and Brazil. Such a vegetation could not exist at the altitudes where the fossils occur and these demonstrate a great elevation of the mountains since those leaves were embedded. The same mild climatic conditions which prevailed in the northern hemisphere during the Miocene must also have characterized Patagonia, subtropical shells extending far to the south of their present range.

Whatever may have been true of the land-bridge connecting South America with Africa during the early Tertiary epochs, it must have been submerged in the Miocene, otherwise there would not have been the open pathway for the Cetacea of Patagonia to reach the Atlantic coast of North America and *vice versa.*

5. *Pliocene Epoch*

North America. — The Pliocene of North America is not nearly so well displayed or so satisfactorily known as the preceding Tertiary epochs, and only of comparatively late years has it been recognized at all upon the Atlantic coast. The Atlantic and Gulf shores had very nearly their present outlines, but with some notable differences. It would seem that the northeastern portion of the continent stood at a higher level than it does now, north Greenland being joined with the islands of the Arctic archipelago and Newfoundland with Labrador, the Gulf of St. Lawrence then being land. From Nova Scotia to southern New Jersey the coast-line was many miles to the east and south of its present position, but the sea encroached here and there upon the shores of Virginia, the Carolinas and Georgia, and southern Florida was mostly under water, as was also a narrow strip of the Gulf coast from Florida to Texas and along the east of Mexico. On the Pacific side of the continent the marine Pliocene is far thicker and more important than on the east coast and in California is largely made up of volcanic materials. Quite extensive disturbances in this region had marked the close of the Miocene, the strata of which in the Coast Range had been violently compressed and folded. An elevation of the land had caused the sea to withdraw from the central valley of California and had restored Lower California to its peninsular conditions, reducing the gulf to the narrow limits which it had had in the lower Miocene and extending southern Mexico to the west and south. British Columbia and southeastern Alaska stood at higher than their present levels and the countless islands of that region were part of the mainland. Bering Strait was closed, for at least a great part of the epoch, and, as a continuous shore-line was

FIG. 52. — Map of North America during the Pliocene epoch, Bering Strait open. Explanation as in Fig. 48. (Modified from Schuchert.)

thus formed and a way of migration opened, the marine fauna of California and Japan became closely similar.

In the interior, the Pliocene continental formations and faunas followed so gradually upon those of the Miocene, that there is great doubt as to where the line between them should be drawn. These interior formations are mostly of small extent and are very widely scattered, and much remains to be learned regarding the mammals of the epoch. In northern Kansas are the *Republican River* beds, which are so doubtfully Pliocene, that they may almost equally well be called uppermost Miocene. Other lower Pliocene stages, representing various divisions of time, are the *Alachua* of northern Florida, the *Snake Creek* of western Nebraska, the *Thousand Creek* and *Virgin Valley* of northwestern Nevada and the *Rattlesnake* of Oregon. Probably middle Pliocene is the *Blanco* of northwestern Texas, a valley cut in the middle and lower Miocene rocks and filled in with Pliocene deposits. Possibly upper Pliocene, or, it may be, lowest Pleistocene, are the *Peace Creek* of southwestern Florida and the so-called "*Loup River*" (not Loup Fork) of western Nebraska.

The volcanic activity of the Rocky Mountain and Pacific coast regions, which was so remarkable in the Miocene, continued into and perhaps through the Pliocene. The great outflow of light-coloured lava which built up the central plateau of the Yellowstone Park is referred to the Pliocene, and some of the enormous fissure-eruptions which formed the vast Columbia River fields of black basaltic lava were probably Pliocene, as some were demonstrably Miocene. Both of these epochs were remarkable for volcanic activity in the western part of the continent.

The Pliocene climate, as may be inferred from the plants and marine shells, was colder than that of the Miocene, and refrigeration was progressive, as is shown by the proportion of Arctic shells in the Pliocene beds of the east coast of England, rising from 5 per cent in the oldest to more than 60 per cent in the latest beds. In the Arctic regions the cold must have been severe, at least during the latter half of the epoch, for in the succeeding Pleistocene we find an Arctic fauna already fully adapted to the extreme severity of present day polar conditions and time was necessary for such an adaptation. In the western interior the climate was not only colder, but also drier than it had been in the Miocene, the desiccation which had begun in the latter epoch becoming progressively more and more marked.

South America. — The Greater Antilles were larger than at present and Cuba was much extended, especially to the southeastward, and was probably connected with the mainland, not as one would naturally expect, with Yucatan, but with Central America; this island, it is most likely, was cut off from Hayti. The Isthmian region was considerably broader than it is now and afforded a more convenient highway of intermigration. Costa Rica was invaded by a Pliocene gulf, but it is not yet clear whether this persisted for the whole or only a part of the epoch. In the Argentine province of Entrerios is a formation, the *Paraná*, which is most probably Pliocene, though it may be upper Miocene. This formation is largely marine and shows that the present Rio de la Plata was then a gulf from the Atlantic. A few northern hemisphere mammals in the Paraná beds show that the migration had advanced far into South America. A large part of Patagonia was again submerged beneath the sea, which extended to the Andes in places, but just how general the submergence was, it is impossible to say, for the *Cape Fairweather* formation has been largely carried away by erosion and only fragments of it remain. Along the foothills of the Andes these beds are upturned and raised several thousand feet above the sea-level, a proof that the final upheaval of the southern mountains took place at some time later than the early Pliocene. Continental formations of Pliocene date are largely developed in Argentina; the *Araucanian* stage is in two substages, one in the province of Catamarca, where the beds are much indurated and were involved in the Andean uplift, the other, of unconsolidated materials, is at Monte Hermoso near Bahia Blanca on the Atlantic coast. The very small proportion of northern animals in the Araucanian beds is surprising, but not more so than the almost complete absence of South American types in the upper Miocene and lower Pliocene of the United States. Intermigration between the two Americas would seem to have been a much slower and more difficult process than between North America and the Old World, and the reason for the difference is probably the greater climatic barriers involved in a migration along the lines of longitude. Upper Pliocene is found in the Tarija Valley of Bolivia and probably also in Ecuador, in both of which areas the proportion of northern animals was very greatly increased.

II. QUATERNARY PERIOD

The Quaternary period was a time of remarkable geographical and climatic changes, which had the profoundest and most far-reaching effects, partly by migration and partly by extinction, upon the distribution of animals and plants, effects which are naturally more obvious than those of earlier geological events, just because they were the latest. It is customary to divide the period into two epochs, (1) the *Pleistocene* or *Glacial*, and (2) the *Recent*, which continues to the present day.

1. *Pleistocene Epoch*

When Louis Agassiz first suggested (1840) the idea of a time, comparatively recent in the geological sense, when northern and central Europe was buried under immense sheets of slowly moving ice, like the "ice-cap" of modern Greenland, the conception was received with incredulity. Nearly thirty years passed before this startling theory gained the general acceptance of geologists, but now it is one of the commonplaces of the science, for no other hypothesis so well explains the complicated phenomena of Pleistocene geology. One great obstacle to the acceptance of the glacial theory was the supposed fact that the Pleistocene glaciation was something quite unique in the history of the earth, a violent aberration in the development of climates. Now, however, we have every reason to believe that at least three other and very ancient periods had witnessed similar climatic changes and that "ice-ages" were recurrent phenomena. This is not the place to discuss or even to summarize the evidence which has convinced nearly all geologists of the reality of Pleistocene glacial conditions on a vast scale in Asia, Europe and, above all, in North America. The reader who may wish to examine this evidence will find an admirable presentation of it in Vol. III of the "Geology" of Professors Chamberlin and Salisbury.

North America. — There has long been a difference of opinion among students of the Pleistocene as to whether the glaciation was single, or several times renewed. That there were many advances and retreats of the ice, is not denied; the question is, whether there were truly interglacial stages, when the ice altogether disappeared from the continent and the climate was greatly ameliorated. The present tendency among American and European geologists is decidedly in favour of accepting several distinct glacial stages (Chamberlin and Salisbury admit six of these) separated by interglacial stages, and for this there are very strong reasons. While it is out of the question to present the evidence for this conclusion here, one or two significant facts may be noted. On the north shore of Lake Ontario, near Toronto, are certain water-made deposits, which rest upon one sheet of glacial drift and are overlaid by another. The fossils of the aqueous sediments are in two series, upper and lower, of which the older and lower contains plants and insects indicative of a climate considerably warmer than that of the same region to-day and corresponding to the temperature of modern Virginia. In the upper and newer beds the fossils show the return of cold conditions, much like those of southern Labrador, and this was followed by the reëstablishment of the ice, as recorded in the upper sheet of drift. Even far to the north, on the Hudson's Bay slope, an interglacial forest is embedded between two glacial drift-sheets. In Iowa and South Dakota numerous mammals of temperate character occur in interglacial beds.

At the time of their greatest extension, the glaciers covered North America down to latitude 40° N., though the great terminal moraine, which marks the ice-front and has been traced across the continent from Nantucket to British Columbia, describes a very sinuous line. The ice was not a homogeneous sheet, moving southward as a whole, but flowed in all directions away from several, probably four, centres of accumulation and dispersal. At the same time, the western mountain ranges had a far greater snow-supply than at present, and great glaciers flowed down all the valleys of the Rocky Mountains as far south as New Mexico and in the Sierras to southern California, while the Wasatch, Uinta and Cascade ranges and those of British Columbia and Alaska were heavily glaciated, but, strange to say, the lowlands of Alaska were free from ice. During the periods of greatest cold the rain-belt was displaced far to the south of its normal position, bringing a heavy precipitation to regions which are now extremely arid. In the Great Basin were formed two very large lakes; on the east side, rising high upon the flanks of the Wasatch Mountains, was Lake Bonneville, the shrunken and pygmy remnant of which is the Salt Lake of Utah, and on the west side, in Nevada, was Lake Lahontan. Lake Bonneville, which was nearly two-thirds the size of Lake Superior, discharged northward into the Snake River, a tributary of the Columbia, but Lahontan had no outlet. Each of these lakes had two periods of expansion, with a time of complete desiccation between them.

Over the Great Plains the principal Pleistocene formation is that known as the *Sheridan*, or, from the abundance of horse-remains which are entombed in it, the *Equus Beds*.

These beds extend as a mantle of wind-drifted and compacted dust from South Dakota to Texas and in places contain multitudes of fossil bones; they correspond to one of the early interglacial stages and in South Dakota pass underneath a glacial moraine.

The upheaval which came at or near the end of the Pliocene had raised the continent, or at least its northeastern portion, to a height considerably greater than it has at present, and this must have facilitated the gathering of great masses of snow; but before the end of the Pleistocene a subsidence of the same region brought about important geographical changes. The depression, which lowered the coast at the mouth of the Hudson about 70 feet below its present level, increased northward to 600 feet or more in the St. Lawrence Valley and allowed the sea to invade that valley and enter Lake Ontario. From this gulf ran two long, narrow bays, one far up the valley of the Ottawa and the other into the basin of Lake Champlain. The raised beaches, containing marine shells and the bones of whales, seals and walruses, give eloquent testimony of those vanished seas. The recovery from this depression and the rise of the continent to its present level inaugurated the Recent epoch.

When the ice had finally disappeared, it left behind it great sheets of drift, which completely changed the surface of the country and revolutionized the systems of drainage by filling up the old valleys, only the largest streams being able to regain their former courses. Hundreds of buried valleys have been disclosed by the borings for oil and gas in the Middle West, and these, when mapped, show a system of drainage very different from that of modern times. Innumerable lakes, large and small, were formed in depressions and rock-basins and behind morainic dams, the contrast between the glaciated and non-glaciated regions in regard to the number of lakes in each being very striking.

On the west coast events were quite different; marine Pleistocene beds in two stages are found in southern California. The upheavals late in the Pleistocene, or at its close, were far greater than on the Atlantic side, 4000 feet in southeastern Alaska, 200 feet on the coast of Oregon and rising again to 3000 feet in southern California; all the western mountain ranges and plateaus were increased in height by these movements. The volcanoes continued to be very active, as may be seen from the lava-sheets and streams in Alaska, all the Pacific states, Arizona and New Mexico.

South America. — No such vast ice-sheets were formed in the southern hemisphere as in the northern. Patagonia was the only part of South America to be extensively covered with ice and there traces of three glaciations have been observed, of which the first was the greatest and reached to the Atlantic coast, and there were great ice-masses on the coast of southern Chili. Mountain glaciers existed throughout the length of the Andes across the Equator to 11° N. lat., the elevation increasing northward to the tropics. The surface of the great Argentine plain of the Pampas between 30° and 40° S. lat. is covered with a vast mantle, largely of wind-accumulated dust, the *Pampean,* which is the sepulchre of an astonishing number of great and strange beasts. The Pampean formation corresponds in a general way to the Sheridan or Equus Beds of North America, but involves a much greater lapse of time, beginning earlier, possibly in the late Pliocene, and apparently lasting through the entire Pleistocene. While largely of æolian origin, the Pampean seems to be in part made of delta deposits laid down by rivers. One striking difference between the Pampean, on the one hand, and the Sheridan and the loess of the Mississippi Valley and of Europe, on the other, is that the former is in many places much more consolidated and stony, which gives it a false appearance of antiquity. Another and very rich source of Pleistocene mammals is found in the limestone caves of eastern Brazil, which have yielded an incredible quantity of such material, but not in such a remarkably perfect state of preservation as the skeletons of the Pampean.

Very little is known of the Pleistocene in the West Indies, though probably to this date should be assigned the notable oscillations of level which are recorded in the raised sea-terraces of Cuba and other islands. The Windward groups were joined, at least in part, to the continent and large extinct rodents reached Antigua, which would not be possible under present conditions. The Isthmus of Panama was 200 feet or more higher than it is now and correspondingly wider, but was depressed to a lower than the present level, and finally raised to the height it now has. Marine beds, of presumably Pleistocene date and certainly not older, extend from the Caribbean shore to Gatun, some seven miles, and are nowhere more than a few feet above sea-level.

The question of Pleistocene climates is a very vexed one and is far from having received a definitive answer. Limitations of space forbid a discussion of the problem here and I shall therefore merely state the conclusions which seem best supported by the evidence so far available. Such immense accumulations of ice might be due either to greatly increased snow-fall, or to a general lowering of the temperature. The balance of testimony is in favour of the latter factor and no great refrigeration is required. Professor Penck has calculated that a reduction of 6° or 7° in the average yearly temperature would restore glacial conditions in Europe. Even the tropics were affected by the change, as is shown not only by the glaciation of the Andes, but also by Mt. Kenya, which is almost on the Equator in eastern Africa and still has glaciers. The presumably Pleistocene ice covered the whole mountain like a cap, descending 5400 feet below the present glacier limit. It was pointed out above that the interglacial stages had greatly ameliorated climatic conditions and that, in some of them at least, the climate was warmer than it is to-day in the same localities. The cause of these astonishing fluctuations and of the climatic changes in general, to which Geology bears witness, still remains an altogether insoluble mystery.

CHAPTER VI

THE GEOGRAPHICAL DISTRIBUTION OF MAMMALS

To every one who has paid the slightest attention to the subject, it is a familiar fact that different parts of the earth have different animals; school-children learn from their geographies that kangaroos are found in Australia, the Hippopotamus in Africa, the Tiger in southern Asia, armadillos and llamas in South America. These examples are all taken from distant lands, yet the zoölogical difference between two given land-areas is by no means proportional to the distance between them. An Englishman landing in Japan finds himself surrounded by animals and plants very like and often identical with those which he left at home, while the narrow Strait of Lombok, east of Java, separates two profoundly different regions. In crossing Mexico from east to west, the traveller meets very different animals in closely adjacent areas; and, at first sight, the arrangement of animals appears to be so capricious as to admit of no formulation in general laws.

In pre-Darwinian times, when it was the almost universal belief that each species had been separately created and was exactly fitted to the region which it inhabits, no explanation of the geographical arrangement of animals was possible, but the acceptance of the theory of evolution demanded that such an explanation should be found. A failure to devise any rational and satisfactory account of the geography of animal life would be a fatal weakness in the evolutionary theory, hence the facts of distribution were subjected to a renewed and searching analysis as one of the best means of critically testing the new doctrine. Not that the subject had received no attention before the publication of Darwin's book; on the contrary, it had attracted much interest as a study of facts, and this study was one of the principal avenues by which Darwin approached his great generalization. In his autobiographical fragment he tells us: "I had been deeply impressed by discovering in the Pampean formation great fossil animals covered with armour like that on the existing armadillos; secondly, by the manner in which closely allied animals replace one another in proceeding southward over the Continent; and third, by the South American character of most of the productions of the Galapagos archipelago and more especially by the manner in which they differ slightly in each island of the group."

Obviously, before attempting to explain the facts of the geographical distribution of mammals, we must first ascertain what those facts are. The following brief sketch of the terms used in describing geographical arrangement is summarized from Mr. Wallace's "Island Life."

Though with fluctuating boundaries and subject to slow secular changes, a mammalian species is limited to a fairly definite area, which may be of immense or very restricted extent, and throughout which it may be found in greater or less abundance. Many species, however, are not distributed continuously over the areas which they inhabit, but occur only in suitable *stations* adapted to their habits and mode of life. Thus, some will be found only where there are trees, others in the neighbourhood of water, others only on open plains, etc. A *specific area* is then the whole extent of country within which the species may be found, while the *stations* are the limited districts contained in the area which are exactly suited to the habits of the species in question; these stations may be hundreds of miles apart, as in the case of mountain-tops, or they may be close together. A marsh-living species, for example, will occur in all the marshes throughout its area, whether these be many or few, near together or widely scattered; for such a species marshes are its stations.

Generic areas differ in character according as the genus is large, that is, comprising many species, or small and having but few species, or, it may be, a single one. The species, as a rule, occupy each its own area, and the areas may be entirely distinct, or they may be contiguous and more or less extensively overlapping, though it seldom happens that two or more species of the same genus inhabit exactly the same area. Often some physical feature, such as a range of high mountains, a great river, the edge of a forest, plain or desert, exactly defines the limits of species of the same genus. The Amazon, for example, acts as such a boundary to many species. It was to this change of related species from one area to another that Darwin referred in the passage quoted above, saying that he had been deeply impressed "by the manner in which closely allied animals replace one another in proceeding southward over the Continent [*i.e.* South America]." On the other hand, the overlapping of areas may be very extensive, and one species of great range may cover the whole area of another and much more besides.

A remarkable example of the widely separated areas of species belonging to the same genus is that of the tapirs. Of this genus there are two or three species in Central and South America and one inhabiting the Malay Peninsula and Borneo, almost as wide a separation as the size of the earth permits. Discontinuous distribution of this character can be explained in terms of the evolutionary theory only in one of two ways. Either (1) the American and Asiatic species developed independently of one another from different ancestors, or (2) the regions intervening between these widely separated areas once formed a continuous land, occupied by species of the genus which have become extinct. From all that we know concerning the operation of the evolutionary process, the first alternative may be set aside as altogether improbable, and, even had we no information concerning the history of the tapirs and their former distribution, the second explanation would be chosen as incomparably the more likely. As a matter of fact, we have definite knowledge that tapirs once ranged all over Europe and North America and doubtless over northern Asia, as well, and, further, that North America was joined to Asia by a land occupying the place of the shallow Bering Sea, at a time when the tapirs were able to take advantage of this means of passing from one continent to the other. Such appears to be the invariable explanation of discontinuous distribution, though we may not always be able to give so clear a proof of it.

The genera of a family are distributed in much the same fashion as the species of a genus, but, as a rule, much more widely. While no genus of terrestrial mammals is cosmopolitan (*i.e.* universally distributed), at least as genera are defined and limited by most modern systematists, certain families are represented in every continent. If the extremely peculiar and isolated Australian continent be excepted, the number of such cosmopolitan families is considerable and wide separation between the genera is frequent. Of the camel family, for instance, one genus, that of the true Camel (*Camelus*), is confined to the northern hemisphere and the Old World, the other (*Lama*), comprising the Llama, Guanaco, etc., is found only in the southern hemisphere and the New World. Less extreme instances of the discontinuous distribution of a family are common enough.

The principles of distribution are the same when applied to families and orders. Most of the mammalian orders are very widely distributed and many are cosmopolitan, except for Australia, though some are confined to one or two continents. The monotremes are limited to Australia and Tasmania, the marsupials to Australia and the Americas, the edentates to the latter, the elephants and hyracoids to Africa and Asia. Carnivores and rodents, on the contrary, are found in every continent, even Australia.

We have next to inquire what is the nature of the obstacles or barriers that prevent the indefinite spread of terrestrial mammals, so that the mammalian fauna of the whole earth, and even of a single continent, is not uniform, but highly variegated. The rate of multiplication of animals is so rapid that, under normal conditions, the animal population is always pressing hard upon the means of subsistence and every species that is increasing in numbers must constantly extend its range in search of food. Every species would increase indefinitely, if there were no countervailing checks. Were all the young to survive and breed in their turn, "even large and slow-breeding mammals, which only have one at a birth, but continue to breed from eight to ten successive years, may increase from a single pair to 10,000,000 in forty years" (Wallace). Evidently, a species must spread from its place of origin until stopped by insuperable obstacles, the most obvious of which are wide seas. A few land mammals are not only excellent swimmers, but will cross straits without hesitation, as the Guanaco has been seen to swim the Straits of Magellan; for the great majority, however, a very few miles of sea form an impassable barrier. As was shown above, a broad or deep river is sufficient to limit many species, as the Santa Cruz River in Patagonia marks the southern boundary of the armadillos.

Important geographical changes, such as the joining of lands that before were separate, or the dividing of continuous lands by transgressions and incursions of the sea, must necessarily have a profound effect upon the distribution of land mammals. Separated land-areas, however similar may have been their faunas at the time of separation, will, through the operation of the divergent evolutionary process, grow more unlike in proportion to the length of time that the separation continues. Regions which have been severed within a short time (in the geological sense of a short time) are zoölogically very similar or even identical, while those that have long been isolated are correspondingly peculiar. Attention has already been called, in another connection, to the contrasted cases of such great continental islands as Great Britain, Java, Sumatra, etc., on the one hand, and Australia, on the other. The continental islands, which have but lately been detached from the neighbouring main lands, are hardly more peculiar zoölogically than equal areas of the adjoining continents, while the long-continued isolation of Australia has made it the most peculiar region of the earth. Climatic changes, which, as we saw in Chapter I, have indubitably taken place many times, have also had a great effect in shifting the distribution of mammals, which in its present form is the outcome of a very long series of geographical and climatic changes, on the one hand, and of adaptive changes in the animals themselves, on the other.

Of almost equal importance as a barrier is climate and especially temperature. Not that similar climates can produce similar forms in separate areas. Regions of almost exactly similar climate in Australia, Africa and South America have totally different faunas, but, *within continuous land-areas*, the most effective of barriers is temperature. This acts differently in the case of limiting the northward spread of southern forms and the southward spread of northern species. Dr. Merriam's long study of this problem has led him to the conclusion that southern species are bounded on the north by the temperature of the breeding season, in which the total quantity of heat must reach a certain minimum, while "animals and plants are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year." On the Pacific coast there is a remarkable mingling in the same areas of species which, east of the high mountains, are distributed in sharply separated zones. This is explained by the mild and equable climate of the coastal belt, where the hottest season of the year does not reach the limiting maximum for the northern species, while the total quantity of heat in the breeding season is sufficient to enable southern species to thrive and maintain themselves.

Dr. Merriam thus sums up the effects of climatic factors upon distribution: "Humidity and other secondary causes determine the presence or absence of particular species in particular localities within their appropriate zones, but temperature pre-determines the possibilities of distribution; it fixes the limits beyond which species cannot pass." "Concurrently with these changes in vegetation from the south northward occur equally marked differences in the mammals, birds, reptiles, and insects. Among mammals the tapirs, monkeys, armadillos, nasuas, peccaries, and opossums of Central America and Mexico are replaced to the northward by wood-rats, marmots, chipmunks, foxes, rabbits, short-tailed field-mice of several genera, shrews, wild-cats, lynxes, short-tailed porcupines, elk, moose, reindeer, sables, fishers, wolverines, lemmings, musk-oxen, and polar bears."

Dr. J. A. Allen has reached closely similar conclusions. "Of strictly climatic influences, temperature is by far the most important, although moisture plays an influential part. Where a low temperature prevails life, both animal and vegetable, is represented by comparatively few forms; under a high temperature it is characterized by great diversity and luxuriance. Within the Arctic Circle the species of both animals and plants are not only few, but they are widely distributed, being for the most part everywhere the same. Under the tropics they are a hundred fold more numerous and of comparatively restricted distribution." "The influence of temperature is perhaps most strikingly displayed in the distribution of life upon the slopes of a high mountain, especially if situated near the tropics. While its base may be clothed with palms and luxuriant tropical vegetation, its summit may be snow-capped and barren. . . . The animal life becomes likewise correspondingly changed, tropical forms of mammals, birds, and insects of the lower slopes gradually giving place to such as are characteristic of arctic latitudes." "The effect of humidity upon plant life is thus obvious, but it is equally potent, though less evident, upon animal life. Many animals . . . are so fitted for a forest life, as regards both food and shelter, that their very existence depends upon such surroundings. . . . Thus moisture alone may determine the character of life over extensive regions."

While climate is thus the most important of the barriers which determine distribution in continuous land-areas, the absence of any particular species from a given region is no proof that the climate is unsuitable to that species. This is sufficiently shown by the manner in which animals introduced into a new country often run wild and multiply to an incredible extent, as the rabbits have done in Australia, the Mongoose in Jamaica, horses on our western plains, horses and cattle on the Pampas of Argentina, etc.

Topographical features, such as great mountain-ranges and plateaus, also limit many species, not only by the difficulty of crossing them, but also by the effect which they have upon temperature and moisture. For this reason long ranges of mountains and table-lands may carry a northern fauna very far to the south of its ordinary range, as do the mountain-systems of North America in a very conspicuous manner. The great Mexican plateau is zoölogically a part of North America, while the low coastal lands as far as southeastern Texas have Central American affinities.

A different kind of obstacle to the spread of a species into a new area may be the pre-occupation of that area by another species. The pre-occupier may be one that plays so similar a part in the economy of nature as to leave no opportunity for the newcomer to establish itself. On the other hand, the obstructing form may be an active enemy and of a totally different character from the intruder, as in the case of the Tse-tse Fly in parts of Africa. The bite of the fly is fatal to horses and oxen, so that these mammals are unable to enter the fly-infested regions. Many times in the course of the Tertiary period various mammals reached North America from the south or from the Old World, which were unable to gain a permanent foothold and speedily died out. At this distance of time it is seldom, if ever, possible to explain why a species which succeeded in reaching this continent could not maintain itself, though the most probable assumption is that the forms already in possession of the land were an insuperable obstacle to the intruders.

The rate of dispersal of a species into new areas may be fast or slow, according as the conditions are more or less favourable. Newly introduced insect-pests, like the Gypsy and the Brown-tailed Moths in New England, often spread with portentous rapidity; and introduced mammals have frequently taken possession of vast areas in a surprisingly short time. One of the most remarkable of these cases is cited by Darwin. "In the time of Sarmiento (1580) these Indians had bows and arrows, now long since disused; they then also possessed some horses. This is a very curious fact, showing the extraordinarily rapid multiplication of horses in South America. The horse was first landed at Buenos Ayres in 1537 and the colony being then for a time deserted, the horse ran wild; in 1580, only forty-three years afterwards, we hear of them at the Strait of Magellan!" ("Voyage of a Naturalist," pp. 232–233.) In this example, something must be allowed for human agency, but even so, it is very surprising.

In the case of lands newly raised above the sea and connecting formerly separated areas, it is necessary that they should first be taken possession of by vegetation, before they can become passable by animals, for the migration of mammals from continent to continent is an entirely distinct phenomenon from the annual migration of birds. The latter, though a fact familiar to every one, is an unexplained mystery, and it is somewhat unfortunate that the same term should be used for the completely different process of the spread of mammals into newly opened land. This spread is purely unconscious and is due to the pressure of increasing numbers upon the means of subsistence, each new generation ranging farther and farther from the original home of the species and continuing so to extend until some insuperable obstacle is encountered. When a sea-barrier is removed by upheaval and the newly formed land rendered habitable for mammals through the invasion of plants, the interrupted process is resumed and an interchange of species between the areas thus connected is brought about. The interchange is, however, always an incomplete one, certain forms not being able so to extend their range, because of climatic differences, pre-occupation or some such barrier.

It is customary to give a graphic expression to the facts of animal distribution by dividing the land surface of the earth into districts which are characterized by their faunas. It is not possible to construct a geographical scheme which will be equally satisfactory for all classes of animals, because the geological date of most rapid development and diffusion was so different in the various classes. The geographical and climatic conditions which favoured a particular geographical arrangement of one class had been so completely altered that the class coming in later could not attain a similar distribution. For this reason, land mammals are chosen as affording the best criteria; their adaptability is such that they are found all over the earth, their dispersal is primarily dependent upon the arrangement and connections of the continental land-masses, modified by the topographical and climatic conditions, and they, with the birds, are the latest of the vertebrate classes to assume a dominating importance. Their history is the most fully known and falls within the best understood portion of the earth's history, making it possible to follow their migrations with a precision which is seldom feasible for the other classes of animals, and thus to correlate the successive physical and organic changes. A particularly great advantage which mammals possess for this purpose is that the mutual relationships of the various kinds are better understood than in the case of most other groups of animals. It is true that we shall find a great many unsolved problems, upon which the most divergent opinions are held, but the main outlines of the scheme are quite generally agreed upon.

Many plans for the zoölogical division of the continental areas have been proposed by various writers on the subject, some differing very radically from others. It would be useless and tedious to review even the more important of the many proposals and suggestions which have been made in the last half-century; and we may, with advantage, adopt an eclectic scheme which has been slowly reached by successive approximations to a satisfactory arrangement.

Just as in political geography it is found necessary to recognize divisions of different rank and scope, like nation, state, county, township, the facts of zoölogical geography require divisions of different orders of importance. Thus, in descending order, the terms *realm*, *region*, *subregion*, *province*, etc. are commonly employed, but unfortunately they are often used loosely and even interchangeably; yet it is desirable to attach a more or less precise significance to each and more terms are needed for an accurate expression of the many complex facts.

The extreme zoölogical peculiarity of Australia is recognized by making that continent and its adjoining islands one of the great primary divisions, of which the other includes all the rest of the world; the former is characterized by its almost exclusively marsupial fauna, while the other continents are inhabited by the Monodelphia or placental mammals. Aside from Australia, by far the most isolated and peculiar region of the earth is South America, and this fact is expressed by constituting it into a *realm*, or division of the second order, and to this realm is given the name *Neogœa.* The remaining continents, North America, Europe, Asia and Africa, make up the other realm, *Arctogœa,* in which there is an unmistakable general likeness among the mammals. The three continents of the Old World form a vast, connected land-mass, and the final separation of North America from this great complex is an event of geologically recent date. For reasons that will be made clear in the course of the history, the junction of the two Americas has had comparatively little effect upon the zoölogy of the northern continent, except in its tropical portion. It is obvious from a glance at the map, that the great zoölogical divisions are of very unequal size, but the arrangement is made on the basis of degrees of difference in the mammalian faunas. These degrees of difference are, in turn, an expression of length of separation or of the difficulty of communication between connected lands.

The following table gives the major divisions of the earth apart from Australia:

I. Neogæic Realm. *Neotropical Region.* — South and Central America, lowlands of Mexico, the West Indies.

II. Arctogæic Realm.
  1. *Malagasy Region.* — Madagascar.
  2. *Ethiopian Region.* — Africa south of the Sahara Desert.
  3. *Oriental Region.* — Southern peninsulas of Asia, Malay Archipelago.
  4. *Holarctic Region.* — N. Africa, Europe, Asia, (except southern part), boreal N. America.
  5. *Sonoran Region.* — Remainder of N. America (except lowlands of Mexico).

North America, as is expressed by this scheme, is zoölogically composite; the northern half, including nearly all of Canada, belongs to the vast Holarctic Region, which also comprises Europe, Africa north of the Sahara and Asia north of the Himalaya Mountains. The remainder of the continent, exclusive of the Mexican coastal lowlands, is set off as the Sonoran Region. Inasmuch as we have here to do with broadly continuous land-areas, not demarcated by great physical features, and as the genera and species of mammals differ greatly in regard to their ability to withstand a wide range of climatic variations, it is not to be expected that the boundaries between the regions which make up North America should be very sharply drawn. It is not surprising, therefore, to find a transition zone, extending all across the continent, in which the Holarctic and Sonoran faunas mingle, or that Central America should, in considerable measure, be transitional to South America, though zoölogically a part of the latter.

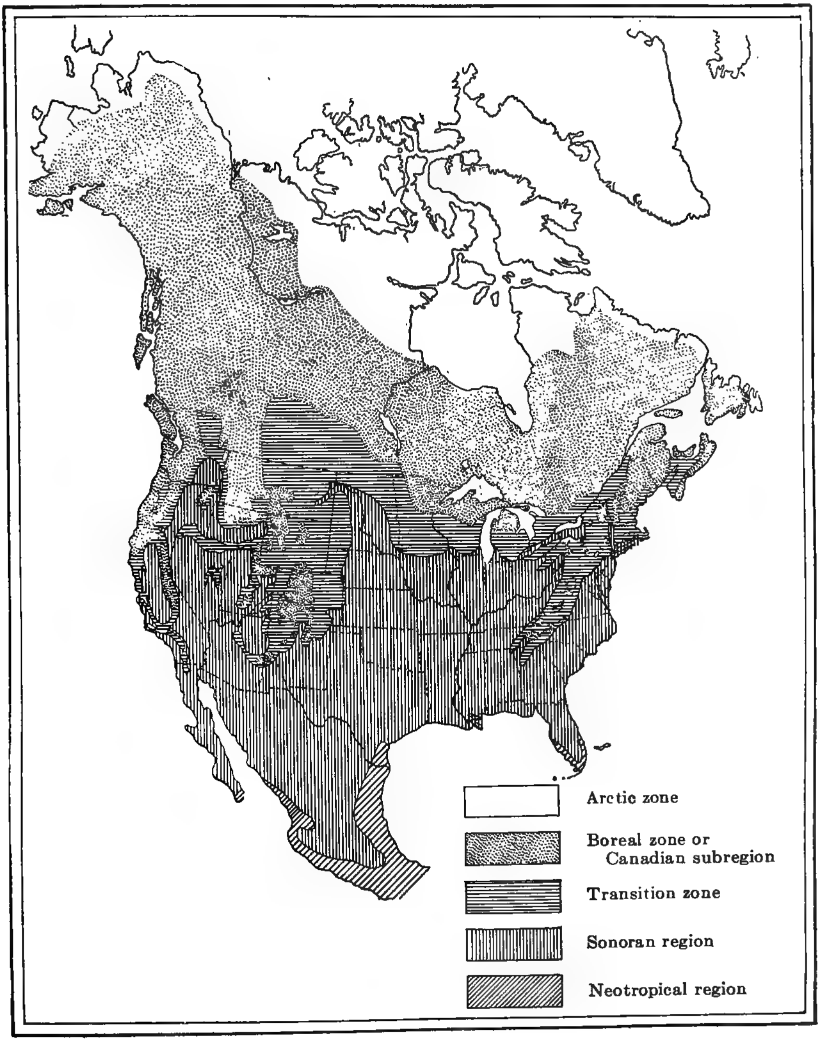

FIG. 53. — Zoölogical Divisions of North America. (After Merriam.)

Dr. Merriam's arrangement, which deals only with North America without reference to the Old World, divides the land into a series of transcontinental zones, which he calls the Arctic, Boreal, Upper and Lower Sonoran and Tropical. These zones have very irregular and sinuous boundaries, which follow lines of equal temperature (isothermal lines) during the breeding season, May, June and July, the tortuous boundaries being conditioned by topographical features, which deflect the isothermal lines.

Fig. 54. — Polar Bear (*Thalarctus maritimus*). — By permission of the N.Y. Zoölog. Soc.

The Arctic zone is part of a circumpolar area, which is very much the same in North America, Asia and Europe; and in any of these continents the fauna differs much more from that of the contiguous zone to the south than from the Arctic fauna of another continent. There are some local differences, but the characteristic mammals of this Arctic zone are the Polar Bear, Arctic Fox, Musk Ox, Barren-ground Caribou, Lemming,

FIG. 55. — Musk Ox (*Ovibos wardi*) female; the males have much larger horns. — By permission of the N.Y. Zoölog. Soc.

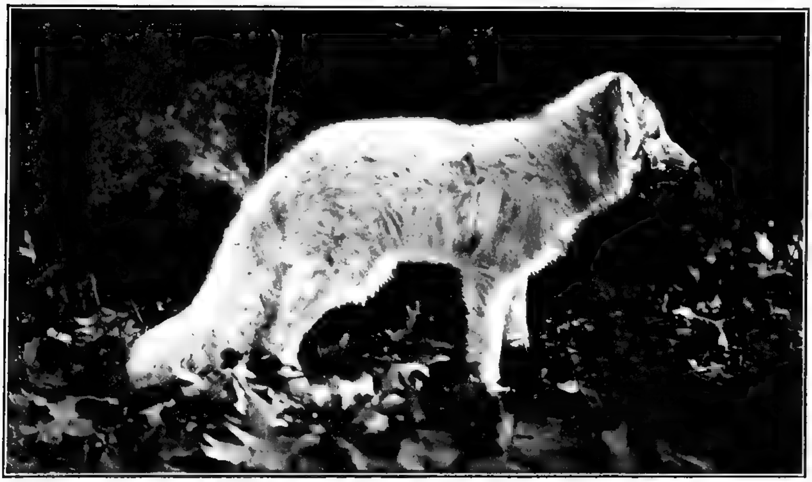

FIG. 56. — Arctic Fox (*Vulpes lagopus*) in winter dress. — By permission of the N.Y. Zoölog. Soc.

Arctic Hare, and a marmot. Most, if not all, of these forms are of Old World origin.

The American portion of the great Holarctic region is called by Mr. Lydekker, who uses Wallace's term, the "Canadian subregion," and by Dr. Merriam the "Boreal region." Not that there is any difference of principle involved in this varying nomenclature, for Dr. Merriam says: "It so happens that the Boreal element in America resembles that of Eurasia so closely that in the judgment of many eminent authorities the two constitute a single primary region — a view in which I heartily concur." The Canadian or Boreal subregion of the Holarctic is the great belt of coniferous forest, which extends obliquely across North America from Alaska to New England; its frontier with the Arctic zone is the northern limit of trees and it is divided from the Transition zone approximately by the line of latitude 45° N., though with a sinuous course, and it is carried far to the south by the wooded heights of the Appalachian, Rocky and Sierra Nevada Mountains, and along the Pacific coast, the mixed character of which has already been explained; it extends almost to San Francisco. The sub-

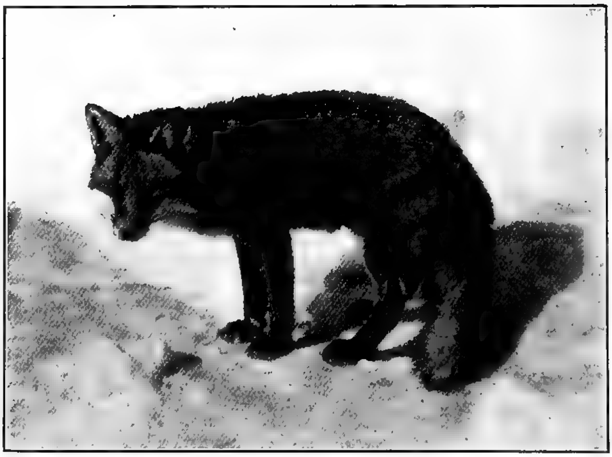

Fig. 57. — Arctic Fox in summer dress. — By permission of the N.Y. Zoölog. Soc.

region is further divisible into northern and southern belts, called the Hudsonian and Canadian faunas, the limit between them approximately following the isothermal line of 57° F. The mammals of this subregion are largely of Old World origin, many of them coming in with the great immigrations of the Pliocene and Pleistocene epochs; but there are also native American elements and even one genus of South American origin, the Short-tailed or Canada Porcupine (*Erethizon*).

In considering the mammals of this subregion, it should be remembered that they are not uniformly distributed throughout even one subdivision, but in a scattering way and in accordance with their habits and stations, and also in accordance with a gradual change to the south, following the changing temperature. The Muskrat will not be found far from water or the Porcupine from woods. Especially characteristic of the Canadian subregion are the Old World types of deer, none of which range farther south than the Transition zone. The Wapiti, erroneously called the Elk (*Cervus canadensis*), is very closely allied to the European Stag (*C. elaphus*) and still more closely to the Stag of the Thian Shan in Central Asia (*C. eustephanus*). So great is the resemblance, that some naturalists would refer all three forms to a single species. The Moose (*Alce americanus*), which should be called the Elk, is so near to the Scandinavian Elk (*A. machlis*) that it is hardly distinguishable as a separate

Fig. 58. — Canada Porcupine (*Erethizon dorsatus*). — By permission of the N.Y. Zoölog. Soc.

species, and the Woodland Caribou (*Rangifer caribou*) is the American representative of the Lapland Reindeer (*R. tarandus*). The so-called Rocky Mountain Goat (*Oreamnos montanus*), a peculiar and aberrant form of the Chamois subfamily of the Antelopes, is confined to the subregion. The Mountain Sheep (*Ovis montana, O. dalli*) are represented by three or four species, one of which extends into the Sonoran region, as does also the Bison, wrongly called Buffalo (*Bison bison*), which is nearly allied to the European *B. bonasus.* In Cæsar's time the European Bison (German, Wisent) ranged through Germany and is described in his account of the Hercynian Forest; but the advance of civilization has almost exterminated it, only a few small herds being maintained by the most rigid protection in Russia and in the Carpathian Mountains. Of the Carnivora, the weasels, martens, Fisher, Mink and Ermine are Boreal, as are the Wolverene (*Gulo*) and the Grey Wolf (*Canis*), the three last-named extending also into the Arctic zone. Essentially Boreal, though reaching and entering the Sonoran, are the bears (*Ursus*), the red foxes (*Vulpes*), the otters (*Lutra*) and the Old World shrews (*Sorex*), while the Star-nose Mole (*Condylura*) and

FIG. 59. — Woodchuck or Marmot (*Marmota monax*). — By permission of the N.Y. Zoölog. Soc.

FIG. 60. — Mink (*Lutreola vison*). — By permission of the N.Y. Zoölog. Soc.

the mole-shrews (*Urotrichus*) do not extend south of the Transition zone. Probable intruders from the south into the Boreal subregion are the pumas, or "mountain lions," which just enter the subregion, the Canada Lynx (*Lynx rufus*) and one species of skunks (*Mephitis*), the Raccoon (*Procyon lotor*), Badger (*Taxidea americana*) and the American deer (*Odocoileus*). A large number of rodents are characteristically Boreal: marmots, or woodchucks (*Marmota*), the Sewellel (*Aplodontia rufa*), lemmings (*Myodes*), Jumping Mouse (*Zapus*), the Canada Porcupine (*Erethizon dorsatus*) and the pikas, "tailless or whistling hares" (*Ochotona*). Boreal rodents that enter the Sonoran are the chipmunks (*Tamias*), beavers (*Castor*), meadow-mice (*Microtus*), the Muskrat (*Fiber zibethicus*). The white-footed mice (*Sitomys*) and the wood-rats (*Neotoma*) are southern rodents that reach or enter the Boreal.

Between the Boreal subregion and the Sonoran region is the Transition zone, which follows all the complex windings of the boundary lines. It covers most of New England, New York, Pennsylvania and southern Ontario; passing through southern Michigan and Wisconsin, it bends northward over Minnesota and covers most of North Dakota, Manitoba and the plains of the Saskatchewan, then turns abruptly southward and includes eastern Montana and parts of South Dakota and Nebraska. Crossing Wyoming, it follows around the northern edge of the Great Basin to the plains of the Columbia. The three great mountain-systems carry the zone far to the south and arms of it extend along the Appalachians to northern Georgia, along the Rockies to New Mexico, and it follows the Sierras to southern California. "The Transition zone, as its name indicates, is a zone of overlapping Boreal and Sonoran types. Many Boreal genera and species here reach the extreme southern limits of their distribution and many Sonoran genera and species their northern limits. But a single mammalian genus (*Synaptomys*) [one of the field mice] is restricted

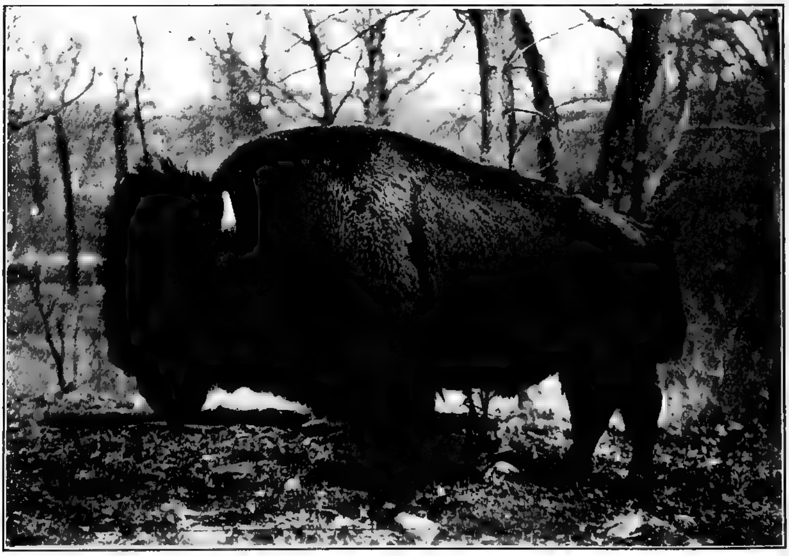

FIG. 61. — Upper figure, European Bison (*Bison bonasus*). Lower figure, American Bison (*B. bison*). — By permission of the N.Y. Zoölog. Soc.

FIG. 62. — Wolverene (*Gulo luscus*). — By permission of the N.Y. Zoölog. Soc.

FIG. 63. — Wapiti or "Elk" (*Cervus canadensis*). — By permission of the N.Y. Zoölog. Soc.

FIG. 64. — Alaska Brown Bear (*Ursus middendorfi*). — By permission of the N.Y. Zoölog. Soc.

FIG. 65. — Moose (*Alce americanus*). Young male with undeveloped antlers. — By permission of the N.Y. Zoölog. Soc.

FIG. 66. — Beaver (*Castor canadensis*). — By permission of the N.Y. Zoölog. Soc.

FIG. 67.— Woodland Caribou (*Rangifer caribou*). — By permission of the N.Y. Zoölog. Soc.

FIG. 68.—Red Fox (*Vulpes fulvus*).—By permission of the N.Y. Zoölog. Soc.

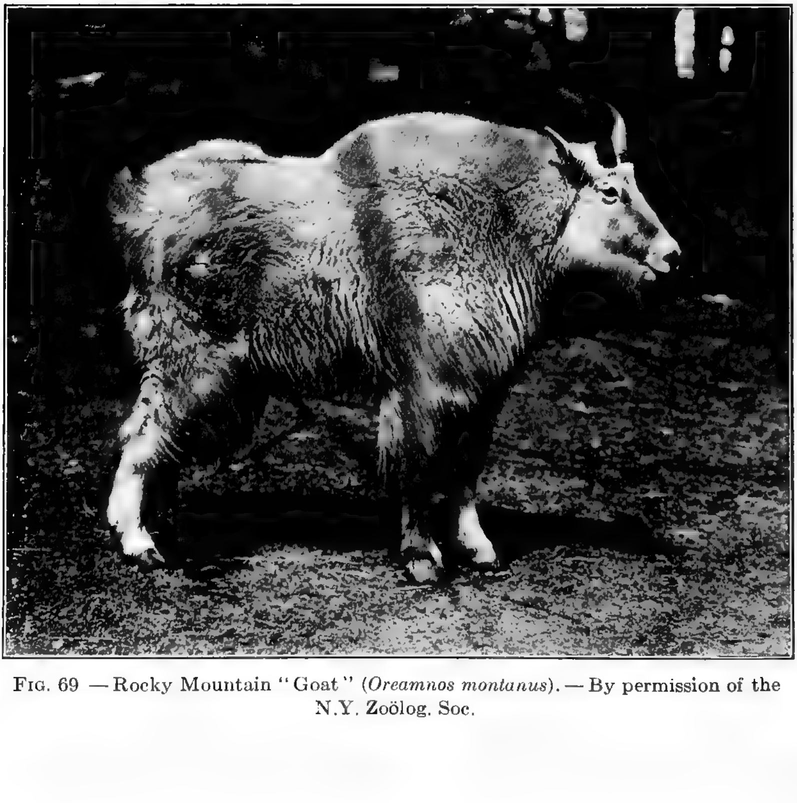

FIG. 69 —Rocky Mountain "Goat" (*Oreamnos montanus*).—By permission of the N.Y. Zoölog. Soc.

FIG. 70.— Ermine (*Mustela erminea*). —By permission of the N.Y. Zoölog. Soc.

FIG. 71.—Timber or Grey Wolf (*Canis nubilis*).—By permission of the N.Y. Zoölog. Soc.

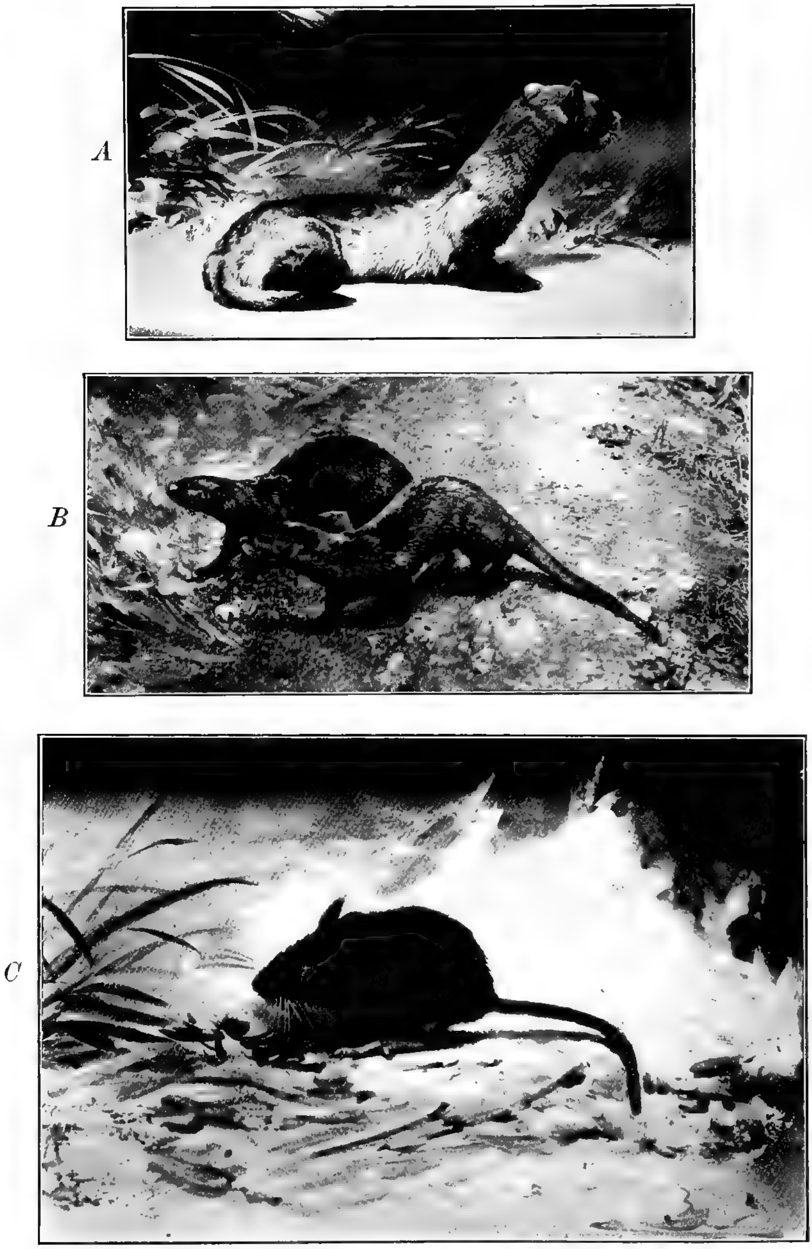

Fig. 72.—Boreal Mammals. *A*. Black-footed Ferret (*Mustela nigripes*). *B*. Otter (*Lutra canadensis*). *C*. Jumping Mouse (*Zapus hudsonius*).—*A* and *B* by permission of the N.Y. Zoölog. Soc. *C*, by permission of W. S. Berridge, London.

to the Transition zone. . . . A number of species, however, seem to be nearly or quite confined to this zone" (Merriam).

The most characteristic portion of North America, zoölogically speaking, is the Sonoran region of Dr. Merriam, the Warm Temperate of Dr. Allen. It crosses the continent from ocean to ocean, its northern boundary following for most of the way the 43d parallel of latitude, but over the Great Plains and Great Basin, on each side of the Rocky Mountains and the high plateaus, it extends to lat. 48°. On the south, it takes in the greater part of Mexico, covering all of the table-land of that country, the lowlands of which belong to the South American or Neotropical region. The Sonoran is invaded from the north by the long branches from the Boreal and Transition zones, which follow the three great mountain-systems in the manner already explained, and the Mexican plateau permits the similar invasion of Neotropical territory by the Sonoran fauna. Characteristic Sonoran genera, none of which extend into the Boreal, are the opossums (*Didelphis*), in the southern part a peccary (*Tagassu*) or "Wild Texas Pig," representative of a family of swine quite different from the true pigs of the Old

FIG. 73. — Opossum (*Didelphis marsupialis*). — By permission of the N.Y. Zoölog. Soc.

World, and an armadillo (*Tatu*). A very isolated form is the Prong-horned Antelope (*Antilocapra americana*); there are several species of the typically American deer (*Odocoileus*) which differ in important respects from those of the eastern hemisphere, and the Bison was very abundant until exterminated by Man. Bison, antelope and deer also reach or extend into the Boreal zone, but the former, or Wood Bison, is probably a different species from the plains animal.

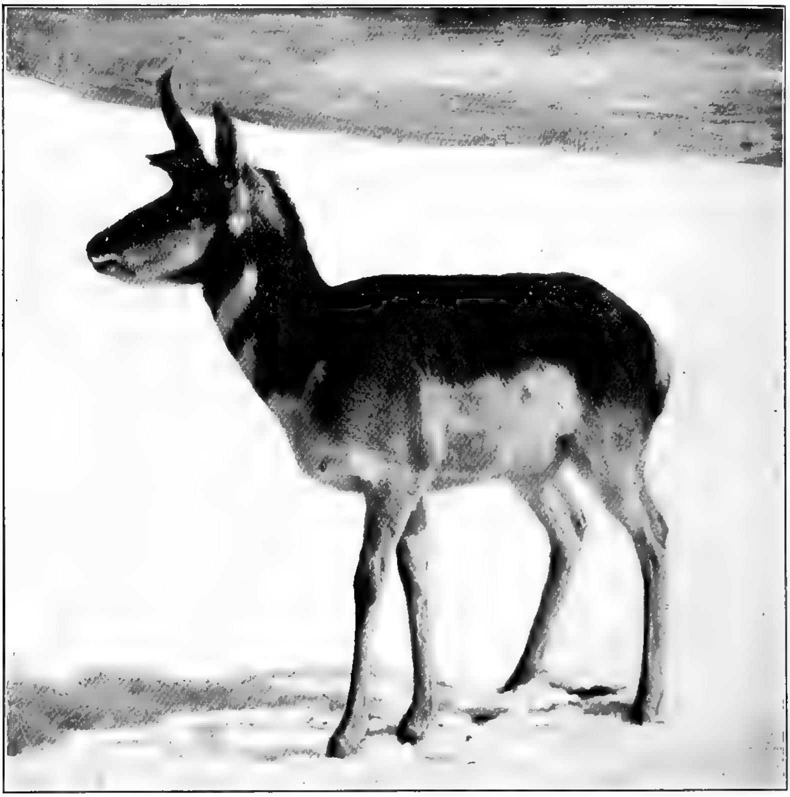

FIG. 74. — Prong-horned Antelope (*Antilocapra americana*). — By permission of the N.Y. Zoölog. Soc.

The grey foxes (*Urocyon*), Coyote (*Canis latrans*), large Timber Wolf (*Canis occidentalis*), the Caxomistle (*Bassariscus*), the Coati (*Nasua*), Raccoon (*Procyon*), Badger (*Taxi-*

dea), three genera of skunks, pumas, several species of lynx and some bears (*Ursus*) represent the Carnivora, though one species each of raccoon, skunk, badger, puma and lynx range into the Boreal. The American types of shrews (*Blarina*) and moles (*Scalops* and *Scapanus*) are characteristic of the Sonoran, though partially shared with the Boreal. A great many peculiar rodents inhabit the Sonoran; cotton-rats (*Sigmodon*), pocket-gophers (*Geomys*, etc.), several genera of the beautiful little kangaroo-rats (*Dipodomys*, etc.); while the

FIG. 75. — Kangaroo-Rat (*Dipodomys philippii*). — By permission of the N.Y. Zoölog. Soc.

FIG. 76. — Thirteen-lined Spermophile (*Spermophilus tredecimlineatus*). — By permission of the N.Y. Zoölog. Soc.

prairie-dogs (*Cynomys*), the white-footed mice (*Sitomys*), wood-rats (*Neotoma*) and one genus of pocket-gophers (*Thomomys*) are chiefly Sonoran, but have Boreal representatives. The flying squirrels (*Sciuropterus*), true squirrels (*Sciurus*), ground-squirrels (*Spermophilus*), rabbits (*Lepus*), wolves (*Canis*) and otters (*Lutra*) have a very wide range through both the Boreal and Sonoran, but have many more species in the latter region.

Fig. 77. — Grey Squirrel (*Sciurus carolinensis*). — By permission of the N.Y. Zoölog. Soc.

The Sonoran region may be divided into the upper and lower Sonoran zones, which are demarcated by temperature and are of transcontinental extent. Each of these zones may, in turn, be subdivided into *arid* and *humid* provinces, but our purpose does not necessitate entering into such refinements.

The Neotropical, which is the only region of the Neogæic realm, comprises the West Indian islands, all of Central and South America and the lowlands of Mexico, extending a short distance into southeastern Texas. Of its four subregions, the most typical is (1) the *Brazilian*, which includes not only Brazil, but all of South America east of the Andes and as far south as Paraguay, and is a vast area of tropical forests. (2) The *Chilian* subregion takes in the west coast, the high Andes and the southern end of the continent, south of the Brazilian subregion; it is a country chiefly of open plains and high mountains, and a few deserts, of which South America has less than any other continent, except Europe, which has none. (3) The *Central American* subregion reaches from the

FIG. 78. — Grey Fox (*Urocyon virginianus*). — By permission of the N.Y. Zoölog. Soc.

FIG. 79. — Prairie Wolf or Coyote (*Canis latrans*). — By permission of the N.Y. Zoölog. Soc.

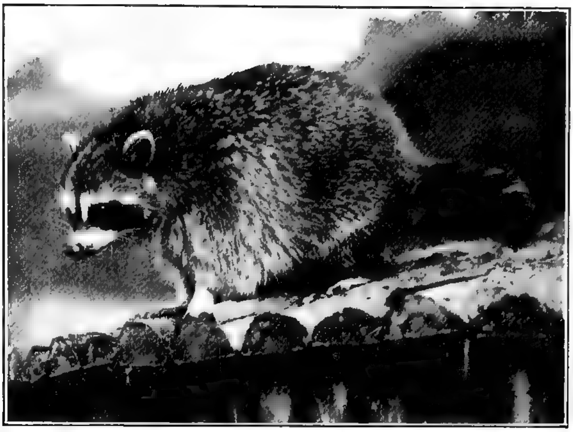

FIG. 80. — Raccoon (*Procyon lotor*). — By permission of the N.Y. Zoölog. Soc.

FIG. 81. — Virginia Deer (*Odocoileus virginianus*). — By permission of the N.Y. Zoölog. Soc.

FIG. 82. — Skunk (*Mephitis mephitis*). — By permission of the N.Y. Zoölog. Soc.

FIG. 83. — Mule Deer (*Odocoileus hemionus*). — By permission of the N.Y. Zoölog. Soc.

Fig. 84. — Badger (*Taxidea americana*). — By permission of the N.Y. Zoölog. Soc.

Fig. 85. — Puma or Mountain Lion (*Felis concolor*). — By permission of the N.Y. Zoölog. Soc.

FIG. 86. — Lynx (*Lynx rufus*). — By permission of the N.Y. Zoölog. Soc.

FIG. 87. — Prairie-Dog (*Cynomys ludovicianus*). — By permission of the N.Y. Zoölog. Soc.

FIG. 88. — Map of the Neotropical region. (After Wallace.) Mexico inaccurate; cf. Fig. 53, p. 147.

Isthmus of Panama to Mexico, the lowlands of which are included and even a small portion of southeastern Texas. (4) The *West Indian* subregion includes all the islands of that archipelago, except Trinidad, which is a fragment of the continent, detached at a comparatively recent date; the southern extremity of Florida also belongs to this subregion.

The two subregions into which continental South America is divided are not altogether satisfactory and will doubtless require change when the distribution of South American mammals has been more accurately determined.

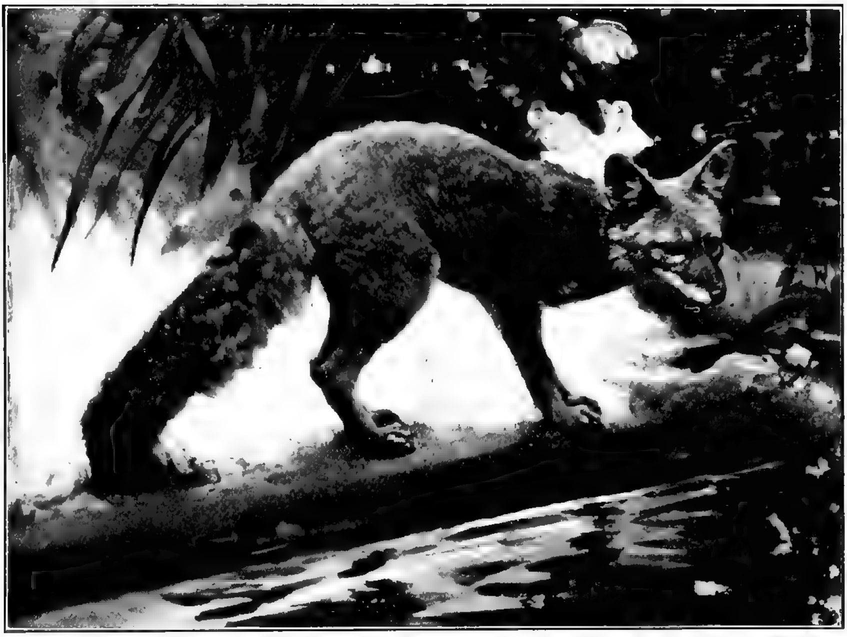

FIG. 89. — Fox-like Wolf (*Cerdocyon gracilis*). — By permission of W. S. Berridge, London.

"Richness combined with isolation is the predominant feature of Neotropical Zoölogy, and no other region can approach it in the number of its peculiar family and generic types" (Wallace). Just as North America has received many immigrants from the Old World, so it has sent many migrants into South America, materially changing the character of the Neotropical mammalian fauna, but these intruders may be readily identified and almost seem to be out of place in their new surroundings. Not all of these northern migrants were able to maintain their footing in the southern continent and several became extinct during and at the close of the Pleistocene epoch, as was even more markedly the case with the southern forms which invaded the northern continent.

FIG. 90.—Spectacled Bear (*Tremarctos ornatus*).—By permission of the N.Y. Zoölog. Soc.

There are two families of monkeys in the forested areas of South America, both very different from those of the Old World. One of these families, the marmosets (Hapalidæ), differs from all other monkeys in several particulars, most obvious of which are the long claws on the feet and the non-opposable thumb. The second family (Cebidæ) comprises forms which are superficially much more like those of the eastern hemisphere, but many of them have prehensile tails, which are used as efficient grasping organs.

Insectivora are entirely absent from the South American continent, but some shrews (*Blarina*) have entered Central America from the north and a very curious genus is represented by one species in Cuba (*Solenodon cubanus*) and another in Hayti (*S. paradoxus*). These remarkable animals are, strange to relate, most nearly allied to the tenrecs (*Centetes*) of Madagascar and by some authorities are placed in the same family.

Fig. 91. — *Solenodon cubanus.* — By permission of the N.Y. Zoölog. Soc.

The Carnivora are quite numerous and varied and rather peculiar, but they all belong to northern families and are the more or less modified descendants of northern immigrants. The dogs (Canidæ) belong to genera not represented elsewhere and form a considerable assemblage of interesting types. There are no true wolves or foxes, but several species of fox-like

Fig. 92. — Argentine Skunk (*Conepatus gibsoni*). — By permission of W. S. Berridge, London.

wolves (*Cerdocyon*), with bushy tails, are common, especially in the plains regions. The Bush-Dog (*Icticyon venaticus*), a small, short-legged animal, is very peculiar. The musteline or weasel family (Mustelidæ) is rather scantily represented. There are no badgers and but few skunks (*Spilogale* and *Conepatus*);

Fig. 93. — Little Skunk (*Spilogale putorius*). — By permission of W. S. Berridge, London.

FIG. 94.—Tayra (*Tayra tayra*).—By permission of W. S. Berridge, London.

weasels are absent, but their place is taken by the Grison (*Galera vittata*) and Tayra (*Tayra tayra*) and in the far south *Lyncodon patagonicus*. These animals are peculiar in having a lighter colouration on the back than on the belly. There are two or three species of otter (*Lutra*). The raccoons (*Procyon*) have a very wide range in South America, as in the

FIG. 95.—Kinkajou (*Potos caudivolvulus*), Central America.—By permission of W. S. Berridge, London.

northern continent, and the curious, long-snouted coatis (*Nasua*), which just enter the Sonoran region, are typically Neotropical. The Spectacled Bear (*Tremarctos ornatus*) is the only member of the family that occurs in South America and is confined to the highlands of Peru and Chili. The cat family is quite numerously represented; the Jaguar (*Felis onca*), which ranges from Texas to Patagonia, is a large spotted cat, rivalling the Leopard in size and ferocity; the Ocelot (*F. pardalis*, Arkansas to Paraguay) is smaller and streaked and blotched rather than spotted. The pumas differ little from those of North America, and there are many small cats, spotted, clouded and of solid colour, but no lynxes, which are essentially northern types.

FIG. 96. — Ocelot (*Felis pardalis*). — By permission of the N.Y. Zoölog. Soc.

Hoofed animals are not numerously represented in South America. The only existing Perissodactyla of the western hemisphere are the tapirs (*Tapirus*) of Central and tropical South America, a very remarkable contrast to the ancient faunas, especially of the northern continent, as will be shown in the sequel. The Artiodactyla are more varied, though very scanty in comparison with those of the Old World; even North America, which has but a poor representation of these animals,

FIG. 97.—Jaguar (*Felis onca*).—By permission of the N.Y. Zoölog. Soc.

FIG. 98.—Collared Peccary (*Tagassu tajacu*).—By permission of the N.Y. Zoölog. Soc.

is much richer than the southern continent, where, indeed, all the hoofed animals are the descendants of comparatively recent immigrants from the north and none are truly autochthonous. Members of three different artiodactyl suborders occur in the Neotropical region; the peccaries (*Tagassu*) extend through Central and South America to Paraguay, though also entering the Sonoran region in Texas. Most interesting are the members of the camel family, which are very distinct from the true Camel of Asia. Tierra del Fuego and the Patagonian plains support great herds of the Guanaco (*Lama huanacus*), which extends along the Andes to Ecuador and Peru, where it is associated with the Vicuña (*L. vicunia*), a smaller and more slenderly built species. The Vicuña does not range south of Bolivia. Just as the mountain systems of North America carry the Boreal and Transition faunas through nearly the whole breadth of the Sonoran region, so the high

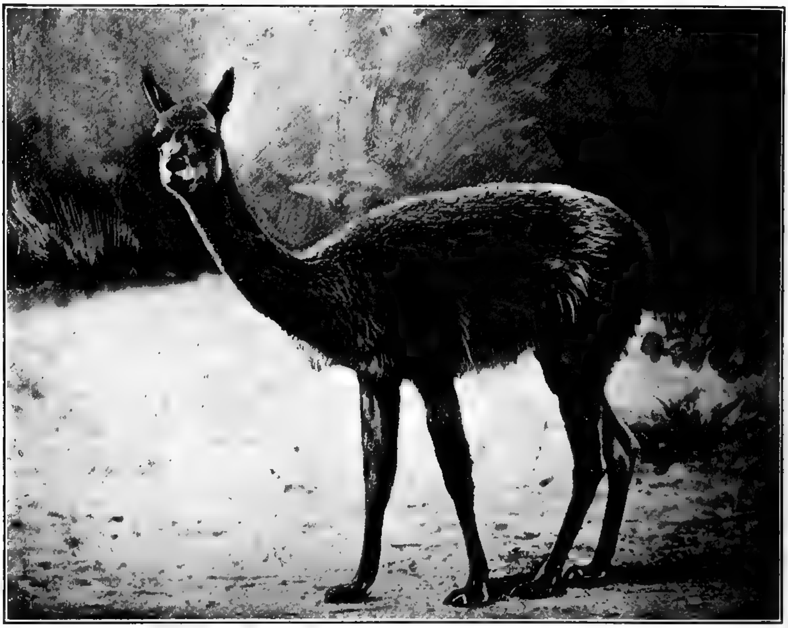

FIG. 99. — Vicuña (*Lama vicunia*). — By permission of the N.Y. Zoölog. Soc.

Andes afford a pathway by which the mammals of the south temperate zone extend their range to the equator.

The suborder Pecora of the Artiodactyla is represented in the Neotropical region only by the deer family (*Cervidæ*), of which there are several genera (or subgenera), all of them North American as distinguished from the Old World type, but some are so peculiar that they must have had a relatively long South American ancestry. The Virginia Deer (*Odocoileus virginianus*) of the northern United States is a comparatively large animal, becoming much smaller in Florida and the Southwest. The type extends through Mexico and Central America to Guiana and Peru, the Neotropical forms being so small and having such weak antlers that they are referred to separate species. Another type is the Marsh Deer

FIG. 100. — Florida Deer (*Odocoileus virginianus osceola*). — By permission of the N.Y. Zoölog. Soc.

(*Blastoceros paludosus*) of eastern South America, which has short, stout antlers, each beam with two double bifurcations; there are other species of the same genus, such as the Pampas Deer of Argentina (*B. bezoarticus*). In the Andes of Peru and Chili and the forests of western Patagonia are two species of a genus which bears the preposterous name of *Hippocamelus* and in which the antlers are simply forked. The vernacular name of these animals is "Huemul." Peculiarly Neotropical are the little brockets, which hardly exceed a height of two feet at the shoulder, with simple spike-like antlers not more than three inches long; the genus, *Mazama*, has several species, one of which occurs as far north as the state of Puebla in Mexico. "The smallest of all deer is the Chilian pudu (*Pudua pudu*),

Fig. 101. — Marsh Deer (*Blastoceros paludosus*), female. — By permission of the N.Y. Zoölog. Soc.

a creature not much larger than a hare, with almost rudimentary antlers" (Lydekker). Old World types of deer, such as the Wapiti, Moose and Caribou, of the Boreal and Transition zones of North America, are entirely absent from the Neotropical region.

South America has an astonishingly rich and varied assemblage of rodents, both indigenous and immigrant, but the former are much the more important, varied and abundant. Of the four divisions of the order, all of which are represented, three are immigrants from the north and the fourth is autochthonous, but this far outnumbers the other three combined. The hares and rabbits have but very few species, one of which occurs in Brazil and is separated by a very wide interval from the one in Costa Rica, while the pikas are absent. Of the squirrel division, only the true squirrels are found, and of these there are many species, the ground-squirrels, marmots, prairie-dogs

FIG. 102. —Wood Brocket (*Mazama nemorivagus*). —By permission of W. S. Berridge, London.

and beavers all being lacking. In the same way the rat and mouse division is represented by a single family. The vesper or white-footed mice (*Sitomys*) have invaded the southern continent and a number of peculiar genera have arisen there, but all of northern ancestry, such as the groove-toothed mice (*Rheithrodon*) and the fish-eating rats (*Ichthyomys*). The voles, or meadow-mice, the muskrats, jumping mice, kangaroo-rats and pocket-gophers of the northern continent are all absent. While the immigrant suborders have thus but one family each in South America, the case is very different with the fourth or porcupine group, of which that continent is to-day, as it has been for ages past, the headquarters. No less than six families and twenty-nine genera are known, all of the genera and four of the families being restricted to the Neotropical region. Contrast this assemblage with the extreme scantiness of this group in North America, where but a single genus, the Short-tailed or Canada Porcupine (*Ere-*

FIG. 103. — Brazilian Tree Porcupine (*Coendou prehensilis*). — By permission of the N.Y. Zoölog. Soc.

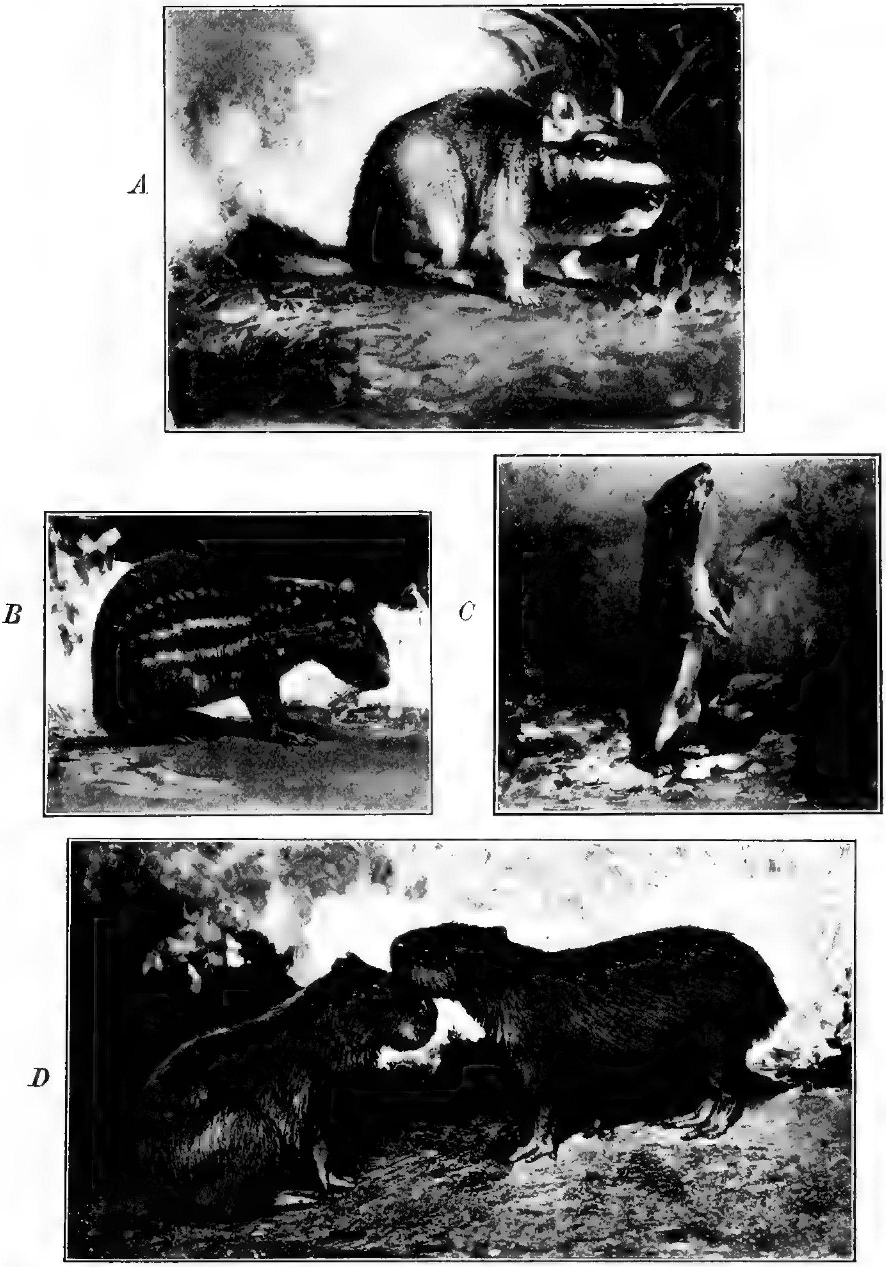

Fig. 104. — Neotropical rodents. *A*. Vizcacha (*Viscaccia*). *B*. Paca (*Agouti paca*). *C*. Rock Cavy (*Cavia rupestris*). *D*. Water-Hog, or Carpincho (*Hydrochærus*). *D*, by permission of the N.Y. Zoölog. Soc. *A*, *B*, *C*, by permission of W. S. Berridge, London.

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thizon) represents it, and that is a late immigrant from the south.

It would lead us too far to attempt a description of this horde of curious and interesting rodents, so only a few of the more striking and characteristic forms can be mentioned. There are two genera of porcupines (*Coendou* and *Chætomys*), both arboreal, which belong in the same family as the North American *Erethizon*, but are distinguished by their long, prehensile tails, which they use, as monkeys and opossums do, for grasping and climbing. The very large family of the Octodontidæ has 17 Neotropical genera and four others are found in Africa. The Degu (*Octodon*) of Chili, Bolivia and Peru has the appearance of a large rat with tufted tail; the tuco-tucos (*Ctenomys*) are extremely abundant burrowers in Patagonia, where they honeycomb the ground over wide areas. The spiny rats (*Echimys* and *Loncheres*) are so called from their appearance, not because they are related to the true rats; they have numerous horny spikes through the fur of the back. The Coypu (*Myocastor*) is a large, aquatic animal, remotely like the northern Muskrat, and the Hutias (*Capromys* and

Fig. 105. — Chinchilla (*Chinchilla laniger*). — By permission of W. S. Berridge, London.

Plagiodontia) are arboreal and found only in Cuba, Hayti and Jamaica. The chinchillas (*Chinchilla* and *Lagidium*) of the Andes and the Vizcacha (*Viscaccia*) of the Argentine plains have somewhat the appearance of hares, but with long and bushy tails. The cavies, to which the familiar, misnamed Guinea-Pig (*Cavia porcellus*) belongs, are a very characteristic family; besides the true cavies, it includes the Patagonian Mara (*Dolichotis*), a large, long-legged, long-eared, short-tailed creature, and the Water-Hog, or Carpincho (*Hydrochœrus*), an aquatic animal, as its name implies, and much the largest of existing rodents; it occurs in the warmer regions, south to Argentina. The heavy Paca (*Agouti*) and the slender-limbed Agouti (*Dasyprocta*) make up another family. Altogether, this assemblage of the porcupine-like suborder of rodents is a very remarkable one and in no other region of the earth is anything like it to be found.

Fig. 106. — Hairy-rumped Agouti (*Dasyprocta prymnolopha*). — By permission of W. S. Berridge, London.

With the exception of one genus of armadillos, which has invaded Texas, the entire order of the Edentata is at present confined to the Neotropical region, the so-called edentates of the Old World now being removed to other orders. The

Edentata, which were once far more varied and abundant than they now are, comprise three groups of animals so bizarre and strange that they seem more like fabulous creatures than actual, living mammals. One group, or suborder, is that of the sloths (Tardigrada), arboreal, shaggy animals, with short, almost monkey-like head and no tail; their very long legs and hook-like feet make them nearly helpless on the ground, but are very useful for hanging from the branches of the trees, in which the creatures live. Indeed, the sloths are the only mammals which habitually hang in a suspended position.

Fig. 107. — Three-toed Sloth (*Bradypus tridactylus*). — By permission of the N.Y. Zoölog. Soc.

Two genera of sloths inhabit the tropical forests, between which the most obvious difference is that in one (*Bradypus*) the forefoot has three toes, and in the other (*Cholœpus*) two.

The suborder of the anteaters (Vermilingua) is more varied, and is the only one of the order to which the term "edentate" applies strictly, for they alone in the order are altogether toothless. The great Ant-Bear (*Myrmecophaga jubata*), which may reach a total length of seven feet, has an extravagantly long, slender and nearly cylindrical head, long, shaggy, black and white hair and an immense, bushy tail; the forefeet are armed with huge, sharp-pointed claws, which are used for tearing open ant-hills, and when occasion arises, as formidable weapons of defence, for the Ant-Bear can successfully repulse even the Jaguar. In walking, the claws are curved inward and the preposterous beast rests his weight upon the outside edges of the forefeet, while the hind feet apply the sole to the ground, as does a bear or raccoon. The Collared Anteater (*Tamandua*) is much smaller and mainly arboreal in habits. It has a short-haired, black body, with a white stripe down the

Fig. 108. — Two-toed Sloth (*Cholœpus didactylus*). — By permission of W. S. Berridge, London.

Fig. 109. — Ant-Bear (*Myrmecophaga jubata*). — By permission of the N.Y. Zoölog. Soc.

back, white neck and limbs, a colour-pattern which gives to the animal the appearance of wearing a close-fitting black jacket; the long tail, which has some cross bars, is short-haired, very different from the extremely bushy tail of the Ant-Bear. The little Two-toed Anteater (*Cyclopes didactylus*),

Fig. 110. — Collared Anteater (*Tamandua tetradactyla*). — By permission of the N.Y. Zoölog. Soc.

hardly larger than a rat, is exclusively arboreal and has a prehensile tail, like so many other South American mammals. Sloths and anteaters are forest animals and are not found west of the Andes or south of Paraguay.

The third existing suborder of edentates is that of the armadillos (Dasypoda), which have a very complete armour of bony scutes, ossifications in the skin, covered with scales of horn. They are all more or less burrowers in habit and omnivorous in diet, eating roots, insects, worms, etc.; the extraordinary rapidity with which they burrow into the ground is almost their only way of escape from pursuit, but in one genus, *Tolypeutes*, the animal can roll itself into a ball, completely protected by mail all around. The armadillos are much more varied than the anteaters or sloths and have a wider geographical range, extending from Texas to Patagonia. The head, which is long-snouted, is protected by a shield made up of numerous horn-covered plates of bone, and the tail is encased in a tubular sheath of more or less regular rings, each ring of bony plates and horny scales. The body-shield, or carapace, which covers the back and sides, consists of an anterior and posterior buckler, in which the plates are immovably

Fig. 111. — Six-banded Armadillo (*Dasypus sexcinctus*). — By permission of the N.Y. Zoölog. Soc.

attached to one another by their edges, and between the two is a series of movable, overlapping bands, the number of which varies in the different genera. In the little Pichiciago (*Chlamydophorus truncatus*) the head and back are covered with four-sided plates of horn, the bony scutes being small and thin and much reduced. The carapace has no bucklers, but about 20 transverse rows of plates, and is attached along only the middle line of the back and beneath it the body is covered with silky, white fur; the rump is covered with a solid shield of bone, placed nearly vertically and covered with thin scales, and is notched below for the tail, altogether a most exceptional arrangement. Seven or more distinct genera of armadillos are found in the Neotropical region and they display a great range in size; the Giant Armadillo of Brazil (*Priodontes*) is a yard or more in length, while the little *Zaëdyus* of Patagonia is smaller than a rabbit and, least of all, the Pichiciago is but five inches long.

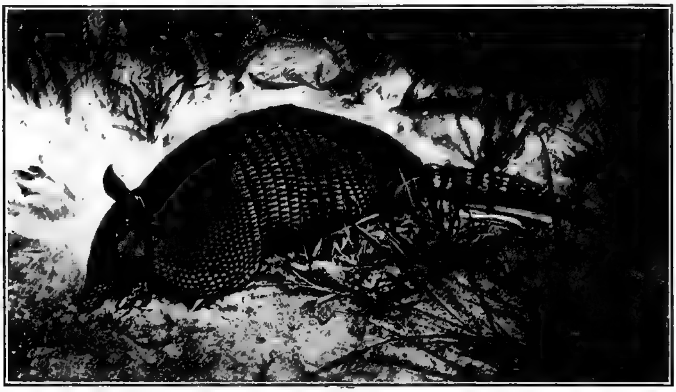

FIG. 112.—Nine-banded Armadillo (*Tatu novemcinctus*).—By permission of the N.Y. Zoölog. Soc.

Two families of marsupials occur in South America. The opossums are much more numerous and varied than in North America; three genera and a large number of species, some not larger than mice, range through the forested parts of the continent. Of particular interest is the little *Cœnolestes*, which has two species, with two enlarged lower front teeth, the sole survivors of a group which is abundantly represented in the Tertiary deposits of Patagonia.

The fauna of the Central American subregion is less rich and characteristic than that of the Brazilian and is, to a certain extent, transitional to that of the Sonoran region of North America, several genera proper to the latter region extending into it, which are not known to pass the Isthmus of Panama, such as shrews, a fox and one of the pocket-mice. The West Indian islands are exceedingly poor in mammals, a great contrast to the East Indian, or Malay, Archipelago; only a few rodents, insectivores and bats occur in them.

CHAPTER VII

THE SUCCESSIVE MAMMALIAN FAUNAS OF NORTH AND SOUTH AMERICA

THE natural method of telling a story is to begin at the beginning and go on to the end, but to deal in that manner with the many different assemblages of mammals which have in turn inhabited the western hemisphere has the great drawback of beginning with a time when everything was utterly strange to the modern eye. Could the reader be carried back to the far distant days of the Paleocene epoch, he would find himself in a completely unfamiliar world; and there is therefore a real practical advantage in reversing the story and starting with the end and thus proceeding gradually from the more to the less familiar. The foregoing chapter gave a sketch of the more striking and characteristic mammals which inhabit the Americas to-day, and we may now take a step backward to the epoch immediately preceding our own, the Pleistocene.

As was shown in Chapter V, the Pleistocene was a time of many and great climatic vicissitudes, periods of cold, when the northern part of the continent was buried under great ice-sheets, alternating with far milder periods, when the climate was much as at present, or even warmer. These climatic changes necessitated many changes in the distribution of animals and plants, increasing cold driving them southward, while the return of more genial conditions permitted the northward migration of southern forms. The effects of these changes of climate are still plainly visible in the geographical arrangement of living beings in the northern continents and many anomalies of distribution, otherwise inexplicable, are thus made clear.

Attention was long ago directed to the fact that the tops of high mountains support a flora and fauna which, on the lowlands, will be found only hundreds, or even thousands, of miles to the northward. The plants which grow on the summits of the White Mountains of New Hampshire recur in Labrador, but not in the intervening area; the vegetation and animals of the high Alps are those of the Arctic regions, and many similar instances might be cited. Hooker and Darwin were the first to find a highly probable explanation of this curious phenomenon by referring it to the climatic changes of the Pleistocene epoch. During the last period of cold and glaciation, the northern plants and animals were driven far to the south and occupied the lowlands along the ice-front and well beyond it; when milder conditions gradually returned, the northern forms not only retreated northward, but also ascended the mountains, as the latter were freed from ice, and thus became cut off as isolated colonies. The general explanation of "discontinuous distribution" (see p. 138) is thus always the same, viz., that the intervening regions were once occupied by the forms now so widely separated, which, for one reason or another, have vanished from the connecting areas.

I. QUATERNARY FAUNAS

North America. — The Quaternary faunas of North America are extremely difficult to correlate and place in chronological order, because, for the most part, they are found in locally restricted areas, such as tar-pools, bogs, caverns and similar places. Professor Osborn has, however, succeeded in making an admirable arrangement, which, though it will doubtless be corrected and expanded by future research, represents a most important advance. Of the general problem he says: "The study of the mammals of the Quaternary has by no means progressed so far in America as in Europe; it will be many years before the faunistic succession can be worked out with such chronologic accuracy and precision as has at last been attained by European geologists and palæontologists." According to Osborn's arrangement, there are three principal successive Pleistocene faunas, two of which appear to have coincided with interglacial stages, and the third with the last reëstablishment of glacial conditions on a grand scale. Regarding the details of these faunas, there still remains much uncertainty, and consequently there will be no attempt made here to do more than discriminate between the general Pleistocene assemblage, on the one hand, and that of the last cold period, on the other. It must be emphasized that we are as yet unable to assert that all of the animals listed together were actually living at the same time.

It is probable that the Pleistocene fossils already obtained give us a fairly adequate conception of the larger and more conspicuous mammals of the time, but no doubt represent very incompletely the small and fragile forms. With all its gaps, however, the record is very impressive; "the early and mid-Pleistocene life of North America is the grandest and most varied assemblage of the entire Cenozoic Period [*i.e.* era] of our continent" (Osborn). There is the further advantage that the fossils have been gathered over a very great area, extending from ocean to ocean and from Alaska to Central America. Thus, their wide geographical range represents nearly all parts of the continent and gives us information concerning the mammals of the great forests, as well as of the great plains.

Those divisions of the early and middle Pleistocene which enjoyed milder climatic conditions had an assemblage of mammals which, from one point of view, seems very modern, for most of the genera, and even many of the species, which now inhabit North America, date back to that time. From the geographical standpoint, however, this is a very strange fauna, for it contains so many animals now utterly foreign to North America, to find near relatives of which we should have to go to Asia or South America. Some of these animals which

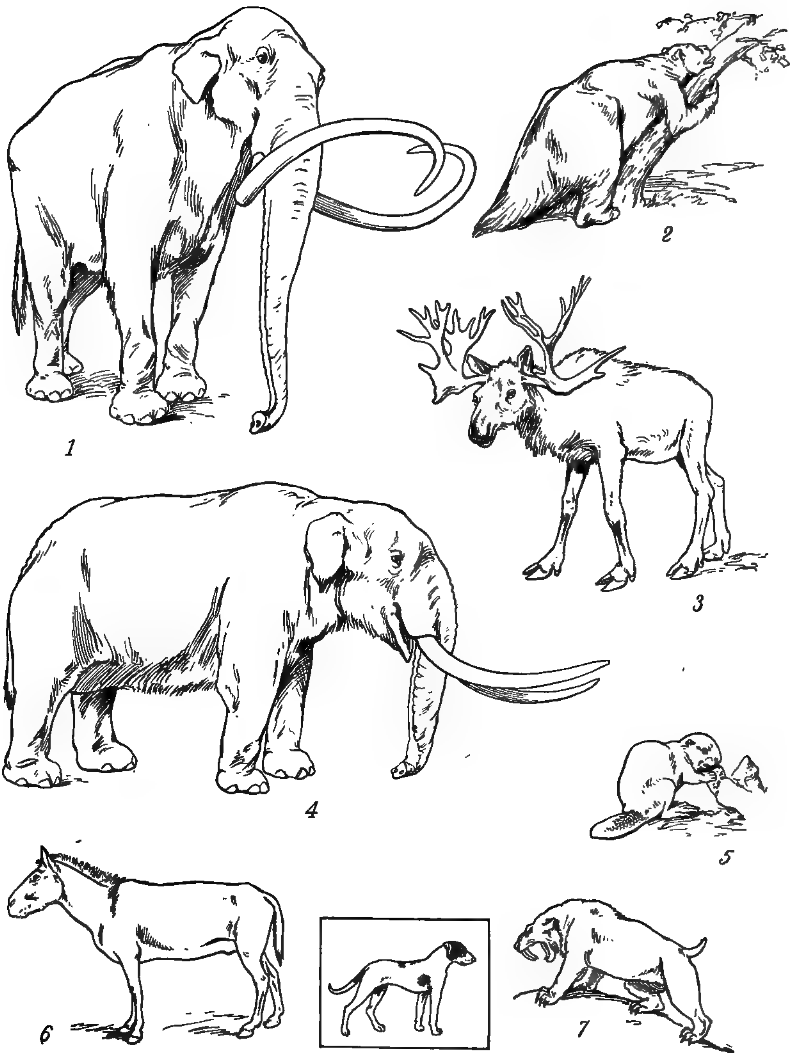

FIG. 113. — Some of the more characteristic Pleistocene mammals, reduced to a uniform scale, with a pointer dog (in the frame) to show relative sizes. — 1. † Columbian Elephant (*Elephas* † *columbi*). 2. Giant † Ground-Sloth († *Megalonyx jeffersoni*). 3. † Stag-Moose († *Cervalces scotti*). 4. †American Mastodon († *Mastodon americanus*). 5. † Giant Beaver († *Castoroides ohioensis*). 6. † Texas Horse (*Equus* † *scotti*). 7. † Sabre-tooth Tiger († *Smilodon californicus*).

now seem so exotic, such as the llamas, camels and horses, were yet truly indigenous and were derived from a long line of ancestors which dwelt in this continent, but are now scattered abroad and extinct in their original home, while others were migrants that for some unknown reason failed to maintain themselves. Others again are everywhere extinct.

Most surprising, perhaps, in a North American landscape, is the presence of the Proboscidea, of which two very distinct kinds, the †mastodons and the true elephants, are found together. Over nearly the whole of the United States and southern Canada, and even with sporadic occurrence in Alaska, ranged the †American Mastodon (†*Mastodon americanus*) which was rare in the plains, but very abundant in the forested regions, where it persisted till a very late period and was probably known to the early Indians. This animal, while nearly related to the true elephants, was yet quite different from them in appearance, as will be immediately seen on comparing 1 and 4, Fig. 113, p. 195. The most obvious external difference was the comparative shortness of the legs in the †Mastodon, which did not exceed and seldom attained a height of 9 ft. 6 in. at the shoulder; the head also was lower and more flattened. The teeth were very different from those of the elephants; the grinding teeth were much smaller and simpler, being low-crowned and rooted and having three or four high, transverse, enamel-covered crests, without cement. The tusks were elephant-like except that in the male there was a single small tusk in the lower jaw, which cannot have been visible externally; this is a remnant of an earlier stage of development, when there were two large tusks in the lower as well as the upper jaw. The creature was covered with long, coarse, dun-coloured hair; such hair has been found with some of the skeletons.

Of true elephants, the North American Pleistocene had three species. Most interesting of these is the northern or Siberian †Mammoth (*Elephas* †*primigenius*), a late immigrant from northern Asia, which came in by way of Alaska, where Bering Land (as we may call the raised bed of Bering Sea) connected it with Asia. The †Mammoth was abundant in Alaska, British Columbia and all across the northern United States to the Atlantic coast. Hardly any fossil mammal is so well known as this, for the carcasses entombed in the frozen gravels of northern Siberia have preserved every detail of structure. It is thus definitely known that the †Mammoth was well adapted to a cold climate and was covered with a dense coat of wool beneath an outer coating of long, coarse hair, while the contents of the stomach and the partially masticated food found in the mouth show that the animal fed upon the same vegetation as grows in northern Siberia to-day. The grinding teeth were very high, cement-covered, and composed of many thin plates of enamel, dentine and cement, and were closely similar to those of the existing Indian Elephant (*E. maximus*). In size this is the smallest of the three Pleistocene species, 9 feet at the shoulder. The †Mammoth was not peculiar to Siberia and North America, but extended also into Europe, where it was familiar to Palæolithic Man, as is attested by the spirited and lifelike carvings and cave-paintings of that date. Thus, during some part of the Pleistocene, this species ranged around the entire northern hemisphere.

Closely related to the †Mammoth and in some cases hardly distinguishable from it, is the †Columbian Elephant (*E. †columbi*) which, however, attained a considerably larger size, as much as 11 feet, rivalling the largest African elephants of the present time. The head was very high and had a curiously peaked appearance, and the tusks in old males curved inward, overlapping at the tips. From the likeness in teeth and skeleton to the †Mammoth, it may be inferred, though somewhat doubtfully, that the †Columbian Elephant was clothed with hair, but not so heavily as the †Mammoth, which was a northern species, the Columbian form replacing it southward, and ranging over the whole United States, including Florida

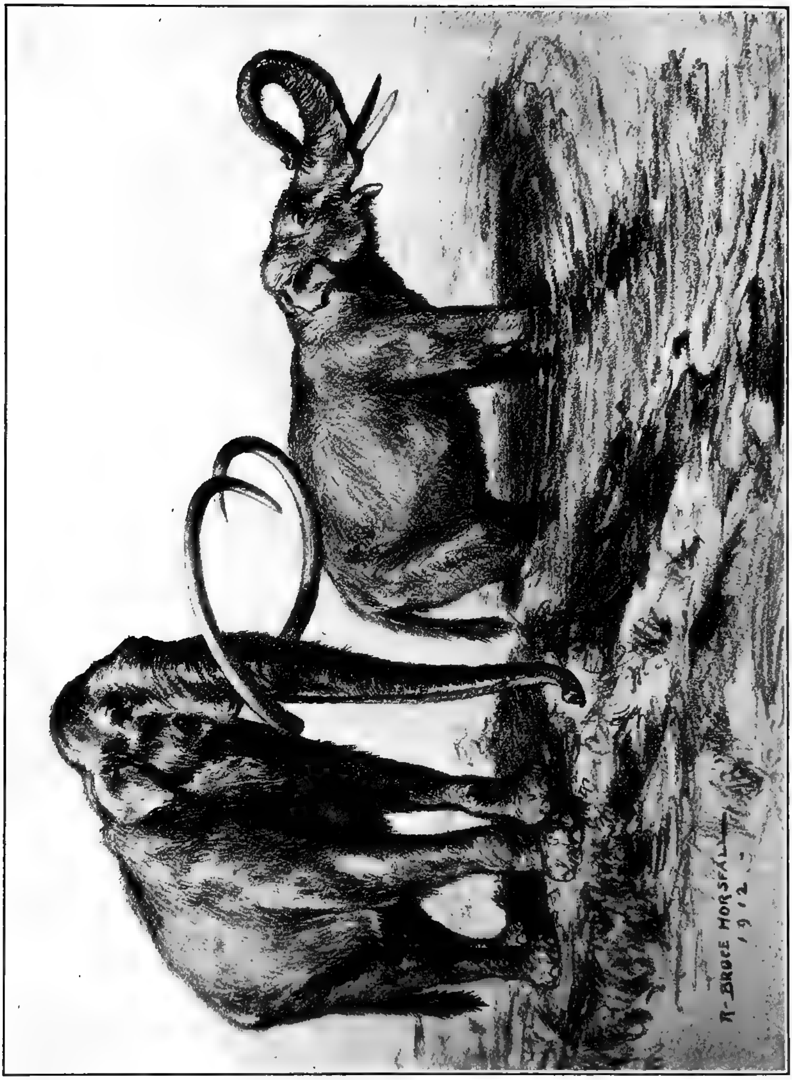

FIG. 114. — Restoration of the †Columbian Elephant (*Elephas* †*columbi*) from a skeleton in the American Museum of Natural History.

and even throughout the table-land of Mexico. The areas of the two species overlapped along the northernmost United States, but are elsewhere distinct.

A third species was the huge †Imperial Elephant (*E.* †*imperator*), the largest of American forms, to which Osborn's calculations give the almost incredible height of 13 ft. 6 in. This great creature was characterized not only by its enormous stature, but also by the proportionately very large size of its grinding teeth, and was a survivor from the preceding Pliocene epoch; it is not known to have passed beyond the middle Pleistocene and was thus the first of the species to become extinct. In geographical range, the †Imperial Elephant was a western form, extending from the Pacific coast almost to the Mississippi River, east of which it has never been found, and from Nebraska southward to the City of Mexico. The meaning of this distribution is probably that this elephant shunned the forests and was especially adapted to a life on the open plains. Over most of its area the winters were severe, and this fact makes it likely that the animal was clothed with hair, but nothing is definitely known on this point.

Many other hoofed animals, far more than now inhabit North America, are found in this Pleistocene fauna. The Perissodactyla were represented by horses and tapirs, but not by rhinoceroses; it might seem superfluous to say that there were no rhinoceroses, but, as a matter of fact, that family had a long and varied American history and became extinct only during or at the end of the Pliocene epoch. The horses were extremely numerous, both individually and specifically, and ranged, apparently in great herds, all over Mexico and the United States and even into Alaska. All the known species (at least ten in number) belong to the genus *Equus*, but the True Horse (*E. caballus*), to which all the domestic breeds are referred, is not represented. The smallest known member of the genus is the pygmy *E.* †*tau* of Mexico. *E.* †*fraternus*, likewise a very small species, is found especially in the southeast, but extended as far north as Pennsylvania and west to Nebraska. On the other hand, *E.*†*giganteus* of Texas exceeded the heaviest modern draught-horses in size and was the largest of the American species; of other Texan forms, one (*E.*†*scotti*) resembled Burchell's Zebra (*E.burchelli*) in the proportions of head and neck, body and limbs, while another (*E.*†*semiplicatus*) was more ass-like. The forest horse of the eastern states has been named *E.*†*pectinatus*, an animal of moderate size. The Great Plains must have been fairly covered with enormous herds of horses, the countless bones and teeth of which, entombed in the Sheridan formation, have given to it the name of "Equus beds." The most abundant of the plains species is *E.*†*complicatus*, a horse of about 14½ hands in height (*i.e.* 4 feet 10 inches at the shoulder) which also ranged down the Mississippi Valley nearly or quite to the Gulf of Mexico. In California was *E.*†*occidentalis*, equalling *E.*†*complicatus* in size, but with much more simple teeth, and associated with

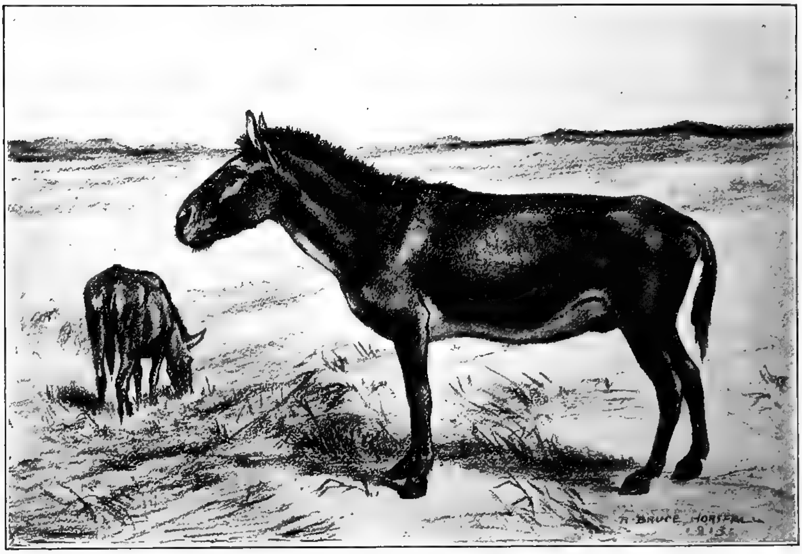

FIG. 115. — A Horse (*Equus* †*scotti*) from the older Pleistocene of Texas. Restored from a skeleton in the American Museum of Natural History.

it the much larger *E.*†*pacificus*, which was inferior only to *E.*†*giganteus* and therefore the second largest of the American Pleistocene horses.

To one who knows nothing of the geological history of North America it would be natural to suppose that the Pleistocene horses must have been immigrants from the Old World, which failed to establish themselves permanently here, since they completely disappeared before the discovery of the continent by Europeans. This would, however, be a mistaken inference, for North America was for long ages the chief area of development of the equine family, which may here be traced in almost unbroken continuity from the lower Eocene to the Pliocene. On the other hand, it is quite possible that some of the species were immigrants.

Tapirs, which are now confined to southern Asia, Central and South America, were not uncommon in the forested parts of eastern North America as far north as Pennsylvania, but they have not been found west of the Mississippi in the plains region. Two species are known, a larger and heavier one, *Tapirus*†*haysii*, and a smaller one which seems to be identical with the living *T. terrestris* of Central and South America. Like the horses, the tapirs had a long history of development in North America and may well have originated here, but they withdrew from the continent in the Pleistocene, probably yielding to the last of the glacial advances.

There was likewise a much greater variety of Artiodactyla than North America can boast at the present day; some were autochthonous, but, for the most part, they were migrants from the eastern hemisphere, where the great group of the true ruminants (Pecora) passed through the greater part of its development and where its headquarters still are. Indigenous were the peccaries, or American swine, which still occur from Texas south to Brazil. In Pleistocene time they ranged over nearly all of the United States, as far northward as Pennsylvania, and across the plains to the Pacific coast; they were represented by two genera, now extinct, one of which (†*Platygonus*) had crested grinding teeth and much longer legs than the modern peccaries. Another indigenous group, strange as that may seem, is the suborder (Tylopoda) of the camels and llamas, both of which are represented in the North American Pleistocene, the descendants of a very long American ancestry. Some of these tylopodans were far larger than existing forms, and at least one species extended its range to Alaska.

Of ultimately Old World origin, but through a considerable line of descent in America, were the typically American deer (*Odocoileus*) of which the Virginian and Black-tailed species are familiar modern instances. Whether or not the Old World types, the Caribou (*Rangifer*) and Wapiti (*Cervus canadensis*) had reached the western hemisphere, is a matter of some doubt; if present at all, they must have been comparatively rare. The Moose (*Alce americanus*), on the other hand, had already appeared, but seems to have been confined to the western half of the continent, its presence in the east being questionable. The mistakenly named "Rocky Mountain Goat" (*Oreamnos montanus*), which is an antelope of the chamois group, was an apparently late arrival in the Pleistocene, while the peculiar Prong-Buck (*Antilocapra americana*), which is very different from any of the Old World antelopes, was present in the early part of the epoch. The descent of this remarkable animal is still a problem, but not improbably it was derived from the "deer-antelopes" of the Miocene and Pliocene, the last of which occurred in the early Pleistocene. Mr. Gidley has announced the surprising discovery in Maryland of a large antelope hardly distinguishable from the African Eland (*Taurotragus*). Other late arrivals from the Old World were several forms allied to the existing Musk Ox (*Ovibos*), at least two genera of which (†*Preptoceras* and †*Euceratherium*) have been found in California. A surprising number of species of *Bison* occurred in the Pleistocene, no less than seven of which are recognized as distinct, ranging from Florida to Alaska. It is not likely that all these species coexisted at the same time, but we cannot yet determine their order of succession, though the modern species, *B. bison*, was probably the latest to arise. Most of these species were much larger than *B. bison*, and some were gigantic, such as *B.†latifrons*, which had a spread of horns of 6 feet and is found through the Mississippi Valley, and *B.†crassicornis* of Alaska.

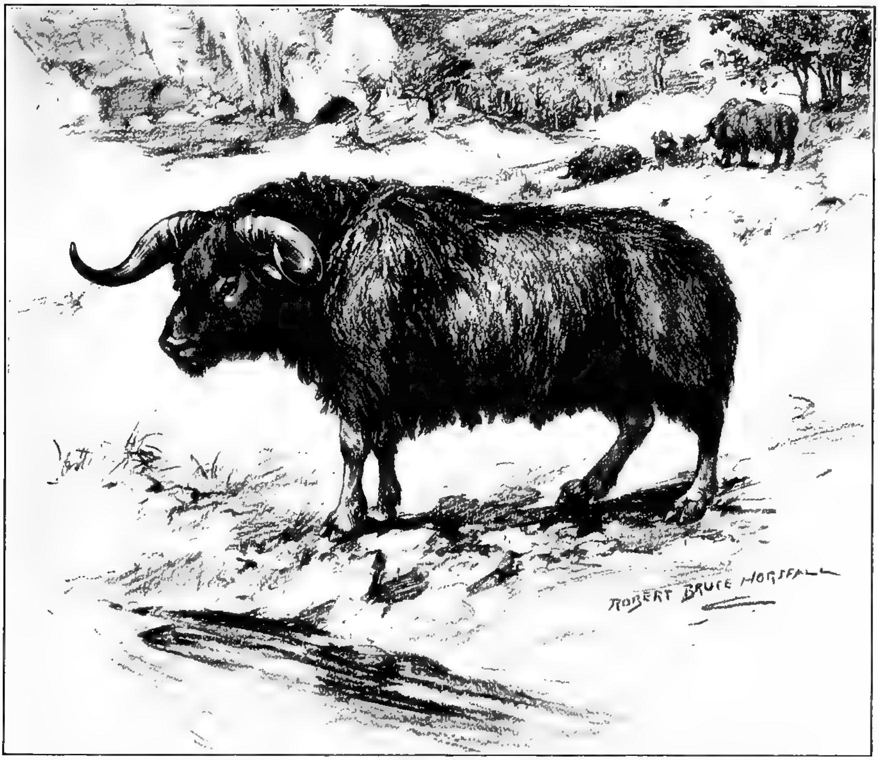

Fig. 116. — Restoration of †*Preptoceras*, a musk-ox like animal from the Californian Pleistocene. (From a skeleton in the museum of the University of California.)

Preying upon this great assemblage of hoofed animals was a corresponding array of Carnivora, most of which were indigenous and derived from American stocks, but there was a considerable migrant element also, such as the bears and badgers. Nearly all the modern kinds of flesh-eaters found in the North America of to-day were already here in the Pleistocene, minks, weasels, martens, skunks, otters, badgers, wolverenes, raccoons, foxes, wolves, coyotes, pumas, etc., etc., but there were several others which are either now extinct or no longer to be found in this continent. Of the extinct types much the most striking were the several species of †sabre-tooth tigers (†*Smilodon*, see Frontispiece) which have been found in the greater part of the United States and no doubt ranged over the whole. These were massive, short-tailed and rather short-legged, but very muscular and powerful, cat-like animals, in which the upper canine teeth were converted into great, recurved, scimitar-like tusks. These large beasts of prey, which about equalled the Leopard in height, but were far heavier, belonged to a group which, at one time or another, spread over nearly the whole world and persisted much later and attained a larger size and higher development in the western hemisphere than in the eastern. They had a very long American ancestry, from the lower Oligocene to the end of the Pleistocene, but the place of their origin is still unknown. In addition to the pumas and lynxes, there were some very large true felines (*Felis* †*atrox* and *F.*†*imperialis*), which closely resembled the Lion (*F. leo*) in size, appearance and structure, and have been found in California and the Mississippi Valley; probably these great cats were immigrants, but they may represent a native development of Miocene and Pliocene stock; the history of the family is too imperfect for a decision of this question.

Besides coyotes and wolves which are indistinguishable from existing species, there were some very large wolves, now extinct, of which the commonest and most widely distributed was *Canis* †*dirus* (also called *C.*†*indianensis*) so abundant in the asphalts of southern California. Bears were not so common in the middle Pleistocene and have not been found in the older part of that epoch, though they probably had already reached North America from the Old World, where they originated. Their absence from the older Pleistocene (Equus Beds) may be accounted for by the fact that those beds contain a fauna of the open plains, while bears are chiefly forest-living animals. An extinct type of the family is the group of species which constitute the †short-faced bears (†*Arctotherium*), very large and powerful creatures, with remarkably shortened jaws, which have been found from ocean to ocean. The smaller beasts of prey, badgers, weasels, etc., were, as intimated above, substantially the same as now.

The rodents of the Pleistocene were very nearly in their modern stage of development, most of the genera and many of the species surviving to present times. Just what members of the order were introduced from the Old World, the imperfect and fragmentary history will not permit us to say, but some interesting South American immigrants should be noted. One of these, the Capybara or so-called Water-Hog (*Hydrochœrus capybara*), the largest of existing rodents, failed to gain a permanent foothold, but another South American form, the Short-tailed or Canada Porcupine (*Erethizon dorsatus*), common all over the United States in the Pleistocene, has maintained itself to the present day. One especially peculiar form, not derived from South America or the Old World, is the †Giant Beaver (†*Castoroides*), one species of which, †*C. ohioensis*, was as large as a Black Bear and occurred in the later Pleistocene, while a smaller species (†*C.species indet.*) is found in the more ancient deposits of the epoch. In almost all respects †*Castoroides* was simply a gigantic beaver, but the grinding teeth were remarkably like those of the South American Capybara (*Hydrochœrus*), so much so that it has been mistakenly referred to the same family by some authorities.

By far the strangest elements of the Pleistocene faunas were the two suborders of gigantic edentates, the †Gravigrada, or †ground-sloths, and the †Glyptodontia, which might well be called giant armadillos, if that name were not already in use for a living Brazilian animal. Both suborders are completely extinct, but they long played a very conspicuous rôle in South America, where they originated and whence the North American representatives migrated. The †ground-sloths were great, unwieldy, herbivorous animals covered with long hair, and in one family (†Mylodontidæ) there was a close-set armour of pebble-like ossicles in the skin, not visible externally; they walked upon the outer edges of the feet, somewhat as the Ant-Bear (*Myrmecophaga*) uses his fore paws, and must have been very slow-moving creatures. Their enormous claws may have served partly as weapons of defence and were doubtless used also to drag down branches of trees and to dig roots and tubers. Apparently, the latest of these curious animals to survive was the very large †*Megalonyx,* which, it is interesting to note, was first discovered and named by Thomas Jefferson. The animals of this genus were very abundant in the forests east of the Mississippi River and on the Pacific coast, much less common in the plains region, where they would seem to have been confined to the wooded river valleys. The still more gigantic †*Megatherium,* which had a body as large as that of an elephant and much shorter, though more massive legs, was a southern animal and has not been found above South Carolina. †*Mylodon,* smaller and lighter than the preceding genera, would seem to have entered the continent earlier and to have become extinct sooner; it ranged across the continent, but was much commoner in the plains region and less so in the forested areas than †*Megalonyx,* being no doubt better adapted to subsisting upon the vegetation of the plains and less dependent upon trees for food.

The †Glyptodonts were undoubtedly present in the North American Pleistocene, but the remains which have been collected so far are very fragmentary and quite insufficient to give us a definite conception of the number and variety of them. It will be better therefore to defer the description of these most curious creatures until the South American Pleistocene is dealt with, as they were incomparably more varied and characteristic in that continent. In North America they have been found only in Mexico and the southern United States.

The many and great climatic changes which took place in the Pleistocene led to very extensive migrations of mammals from one part of the continent to another, as the conditions of temperature and moisture changed. In Interglacial stages, when the climate was much ameliorated, southern species spread far to the north, as when the †Mastodon ranged into Alaska, and the Manatee, or Sea-Cow, of Florida waters, came up the coast to New Jersey, while the increasing cold of oncoming glaciation caused a reverse movement and drove northern and even Arctic forms far to the south. Thus, the Musk-Ox, the Caribou and the northern †Mammoth came south beyond the Ohio and the Potomac, and the Walrus was found on the South Atlantic coast. It is these migrations which give such a mixed character to the Pleistocene faunas from the climatic point of view, as it is often very difficult to correlate or synchronize the fossiliferous deposits with the Glacial and Interglacial stages, though this has been definitely accomplished in several very important instances.

The latest of the Pleistocene faunas is less completely known than those of the earlier and middle portions of the epoch, for but few localities have yet been discovered with any extensive series of fossils. As worked out by Osborn, this fauna coincided with the last Glacial stage and was a greatly reduced and impoverished assemblage as compared with those of the middle and lower Pleistocene, though it is not safe to argue that all the animals not found in this fauna were already extinct, for the known list is still far too short to be entirely representative. The American †Mastodon (†*Mastodon americanus*, see p.196) was still abundant in the forested regions and was apparently able to withstand severe winter temperatures, as certainly was the †Mammoth (*Elephas* †*primigenius*, see p. 196), which was so abundant in the coldest part of Siberia and which extended south to the Potomac, presumably at this time. Horses were still present in North America, though apparently in greatly diminished numbers and variety. Tapirs have not been found, though they may have lingered on in the southern regions. The typically North American genus of deer (*Odocoileus*) was, of course, well represented, and Old World types had a much more southerly distribution than at present. The Caribou (*Rangifer caribou*) came down into Pennsylvania and Ohio, the Moose (*Alce americanus*) into Kentucky and Kansas, and the Wapiti (*Cervus canadensis*) is reported as far south as Florida. A very remarkable animal is the Stag-Moose (†*Cervalces scotti*), the best preserved skeleton of which is that in the museum of Princeton University. This was found in a shell-marl beneath a peat-bog at Mt. Hermon, N. J., *north of the great terminal moraine*, and therefore most probably this particular individual dates from a time not earlier than the beginning of the final retreat of the ice.

†*Cervalces*, as its name implies, was in some respects intermediate between the Stag (*Cervus*) and the Moose (*Alce*); in general proportions it most nearly resembled the latter, having a short neck, long body and very long legs; but the skull differed in many respects from that of the Moose, especially in parts which show that the great, inflated snout and prehensile upper lip had no such development in the extinct as in the living form. The antlers were unique among the known members of the deer family, resembling those of the Moose, though much less palmated and with the addition of great trumpet-shaped plates. The feet were large, almost as large as in the Caribou, and the whole structure indicates an animal well fitted to travel through deep snows and flourish in severe winters.

Even more typically northern than the Caribou were the Musk-Oxen, of which two genera occurred in the late Pleistocene. One of these, †*Symbos*, is extinct and was characterized by its short horns; the other, *Ovibos*, is the genus to which the existing species, *O. moschatus* and *O. wardi*, belong and is now con-

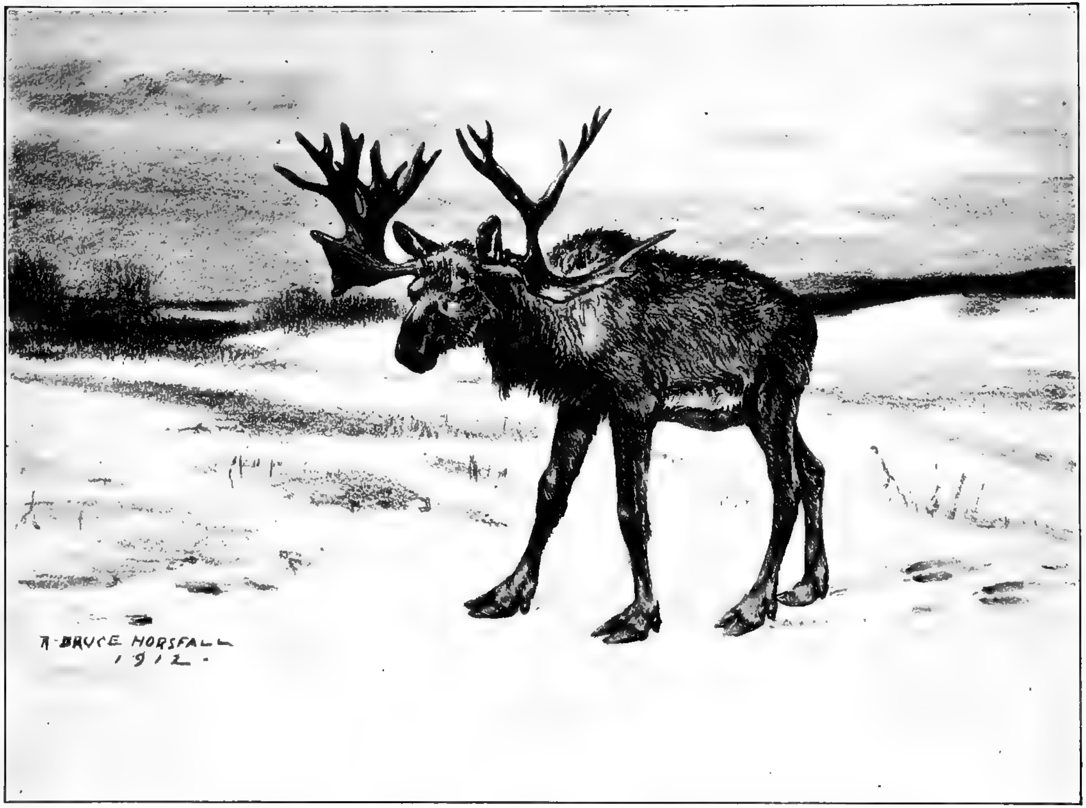

FIG. 117. — †*Cervalces scotti*; restored from a skeleton in the museum of Princeton University.

fined to the extreme north of the continent, the Arctic islands and Greenland. The remains of Musk-Oxen have been found mostly along the great terminal moraine which marks the front of the last ice-invasion, but they occurred also as far south as Oklahoma, and in Utah they ranged far to the south of the ice-front. Nothing could be more conclusive evidence of a climate much colder than the modern one than the presence of Caribou and Musk-Oxen in the United States and of the Walrus on the coast of Georgia.

The smaller animals were much as they are now, differing only in range. The †sabre-tooth tigers, the last of a most interesting line, persisted in the south, and an extinct genus of skunks has been discovered in Arkansas, but otherwise the Carnivora were entirely modern in character. Unfortunately, these smaller animals are very incompletely known, much the richest aggregation which has yet been found being that collected by Mr. Brown in the Conard Fissure, Arkansas. From this collection Mr. Brown has described thirty-seven genera and fifty-one species of mammals, of which four genera and twenty-four species are extinct. That is to say, less than one-ninth of the genera and one-half of the species represent extinct forms. Contrast this with the middle Pleistocene assemblage found in the Port Kennedy cavern in eastern Pennsylvania, of sixty-four species with at least forty extinct ones.

The foregoing sketch, brief and imperfect as it necessarily is, makes it sufficiently plain that North America during the Pleistocene was far richer in mammalian life than it was when the continent was first settled by Europeans. When we make the proper allowance for the many forms which undoubtedly remain to be discovered and for those which may have vanished without leaving a trace behind them, the contrast becomes all the more striking. Not only did Pleistocene North America have substantially all the mammals that it now possesses, but it had many more. The lions and †sabre-tooth tigers, the gigantic †short-faced bears, the tapirs and many varieties of horses, large and small, the camels and llamas, many species of bisons, some of enormous proportions, several forms allied to the Musk-Ox, the elephants and †mastodons, the †giant beavers and South American water-hogs, the huge †ground-sloths and †glyptodonts, have all disappeared, leaving a continent, that, by contrast, is "zoölogically impoverished." The Pleistocene fauna was strangely mixed in character, the free roads of migration bringing together Old World and South American types, and mingling them with indigenous forms in a cosmopolitan assemblage.

Turning to *South America,* we find in the pampas of Argentina a wonderful museum of Pleistocene mammals, such as occurs nowhere else in the known world, and this is supplemented by the very rich collections gathered from the caverns of Brazil and from deposits of Ecuador and Bolivia, and thus all the important regions of the continent, save the far south, are well represented. These faunas are far stranger than the corresponding ones of North America and differ more radically from those of modern times, since they include a much larger proportion of extinct types, and the extinctions have swept away not only species and genera, but families and orders as well.

The South American Pleistocene assemblage of mammals is very clearly divisible into two elements: (1) the immigrants from the north, which reached the southern continent in successive waves of migration, that have left records of themselves as early as the older Pliocene, perhaps even the upper Miocene, and (2) the indigenous element, which had a very long history of development in South America. To the immigrant class belonged all of the Carnivora, which therefore resembled their North American relatives, but were less varied in character. Of the bears, only the huge, †short-faced kind (†*Arctotherium*, Fig. 275, p. 549) are known, and it is not likely that true bears existed except in the Andes, as is also the case to-day. Of the cat family, the †sabre-tooth tigers (†*Smilodon*) were as common in

South America as in North, and, while there were no lions, there were large cats nearly allied to the Jaguar and Puma, and smaller ones, like the Ocelot. The dogs were quite numerously represented by species resembling closely the existing South American fox-like wolves and the Bush-Dog (*Icticyon*) and, strange to say, by one which seems referable to the same

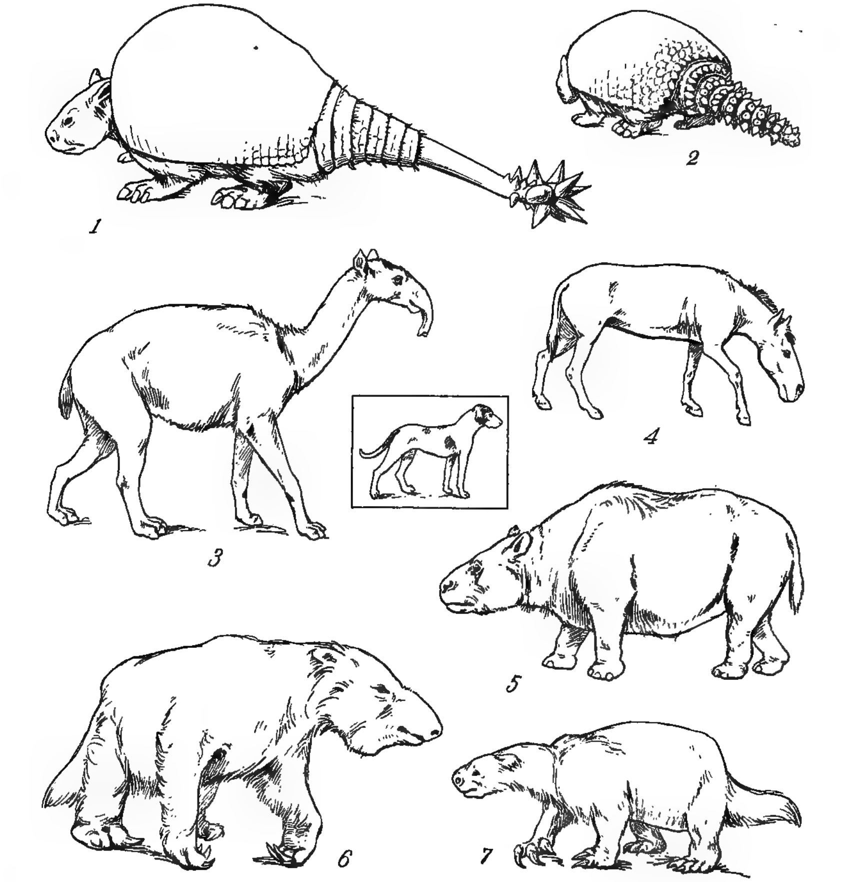

FIG. 118.—Some of the commoner Pampean mammals, reduced to a uniform scale, with a pointer dog (in the frame) to show the relative sizes. 1. † *Dœdicurus clavicaudatus*. 2. † *Glyptodon clavipes*, † glyptodonts. 3. † *Macrauchenia patachonica*, one of the † Litopterna. 4. † Pampas Horse († *Hippidion neogœum*). 5. † *Toxodon burmeisteri*, a † toxodont. 6. † *Megatherium americanum*. 7. † *Mylodon robustus*, † ground-sloths.

genus (*Cyon*) as the Dhole of India. The weasel family (Mustelidæ) were less numerous and varied than in the northern continent, as they still are; coatis (*Nasua*) and raccoons (*Procyon*) were abundant and one species of the latter was much larger than any existing one; extinct species of skunk (*Conepatus*), tayra (*Tayra*) and otter (*Lutra*) were also present, but the badgers, minks, martens and wolverenes were not.

The hoofed animals were represented by a great variety of forms, both immigrant and indigenous, of which the latter belonged to orders now entirely extinct. Horses were common in all parts of the continent, where fossils of this epoch have been obtained, and are referable to two very distinct groups: (1) to the typical genus *Equus*, of which three species have been described, all somewhat more primitive than the True Horse (*E. caballus*) and, like most of the Pleistocene species of North America, with a certain resemblance to the zebras and asses; (2) to an extinct group of four genera, the best known of which is †*Hippidion.* The species of this genus (which has also been reported from North America, though upon hardly sufficient evidence) had most exceptional characters in the skull, and the head was relatively large and clumsy, with narrow and very high facial region. The neck was comparatively short, the limbs heavy and the feet short. These animals can hardly have been very swift runners. A very interesting member of this group is †*Hyperhippidium*, a small horse found in the Andes, with remarkably short feet, well adapted for a mountain life. The only other perissodactyls were tapirs, which ranged down to the Argentine pampas, much farther south than now.

The Artiodactyla were much more varied; there were peccaries, many species of llamas, which then extended into Brazil, and were not confined, as at present, to the colder portions of the continent. There were also numerous deer, all of the South American type, and two different antelopes have been reported, though that family has no representatives

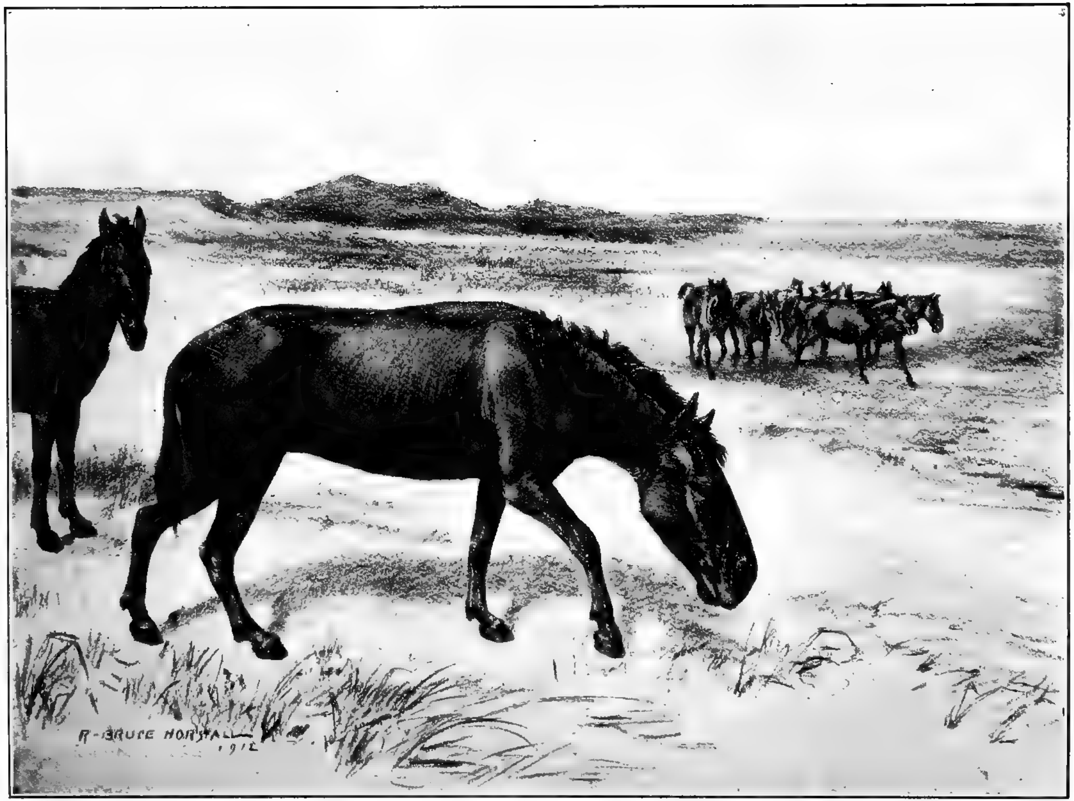

FIG. 119. — A Pampas Horse (†*Hippidion neogæum*). Restored from a skeleton in the National Museum, Buenos Aires.

in the southern continent now. Several species of †mastodons have been found in Brazil, Argentina, Bolivia and elsewhere, but none of the true elephants. Why the †mastodons were able to make their way into South America, while the elephants were not, is one of the puzzling questions of mammalian distribution to which no answer can be given.

All the preceding types of hoofed animals, the horses, tapirs, peccaries, llamas, deer, antelopes and †mastodons were migrants from the north, and four of these, tapirs, peccaries, llamas and deer, were able to gain a permanent footing in South America and are more or less abundant there to-day, while the horses, antelopes and †mastodons failed to do so and died out. In addition to these, there were the indigenous types, which are now extinct and have never been found outside of the Neotropical region. An extremely peculiar creature, †*Macrauchenia,* was the last surviving member of an order, the †Litopterna, which for ages played a very important rôle in South America. †*Macrauchenia* was a large animal, somewhat larger and of much heavier build than a camel, to which it had a considerable, though entirely superficial, resemblance. The head was relatively small and must have had quite a long proboscis; the neck was very long, suggesting that the animal browsed upon trees, which is also indicated by the character of the teeth; the legs were long and stout, the feet short and each provided with three toes. Another curious creature was †*Typotherium,* from which is named the group of the †Typotheria, which some authorities regard as a suborder, while others assign to it a full ordinal rank.

The †Typotheres throughout the Tertiary period were among the most abundant and characteristic of the South American hoofed animals, and the genus †*Typotherium* was the last of a very long series and was an animal of moderate size, with chisel-shaped incisor teeth so like those of the rodents that the genus was long referred to that order. Finally, we have †*Toxodon,* type of the order †Toxodontia, a ponderous

FIG. 120.—A Pampean †Litoptern (†*Macrauchenia patachonica*). Restored from a skeleton in the Museum of La Plata.

beast, as large as a rhinoceros, which, there is some reason to think, was largely aquatic in its habits. The first species of this extraordinary creature was found by Charles Darwin, who says of it: "Perhaps one of the strangest animals ever discovered; in size it equalled an elephant or megatherium, but the structure of its teeth, as Mr. Owen states, proves indisputably that it was intimately related to the Gnawers [*i.e.* Rodentia] . . . in many details it is allied to the Pachydermata: judging from the position of its eyes, ears, and nostrils, it was probably aquatic, like the Dugong and Manatee, to which it is also allied."[1] Modern views concerning the relationships of †*Toxodon* are very different from those advanced by Darwin, but he gives a vivid picture of its diverse likenesses. Neither †*Macrauchenia*, †*Typotherium* nor †*Toxodon* has been

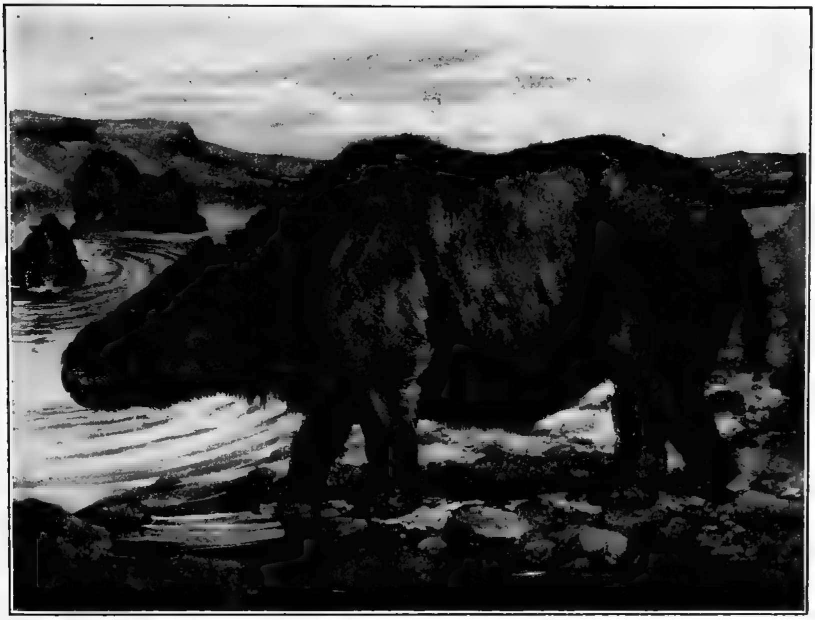

FIG. 121. — A Pampean †Toxodont (†*Toxodon burmeisteri*). Restored from a skeleton in the La Plata Museum.

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[1] Voyage of a Naturalist, Am. ed., 1891, p. 82.

found in the Brazilian caverns, but this is no doubt due to the accidents of preservation, for the latter animal ranged north to Nicaragua.

The rodents likewise were partially of immigrant and partially of native stock. To the former belonged the few mice and rats and a meadow-mouse (*Microtus*), a group not represented in present-day South America, and a rabbit. Very much more abundant and varied were the indigenous forms, all of which belonged to existing families and most of them to existing genera; the tree-porcupines, cavies, agoutis, spiny-rats, vizcachas, capybaras, coypus, etc., were abundantly represented, for the most part by extinct species.

The monkeys were of purely Neotropical type and several modern genera, such as *Cebus* and *Callithrix*, and one very large extinct genus, †*Protopithecus*, of the same family, have been found in the caverns of Brazil, but not in the pampas of Argentina, which would seem to have been a country of open plains.

In the South America of to-day one of the most striking and peculiar elements of the fauna is that formed by the Edentata, the sloths, anteaters and armadillos, and this was even more true of the same region in Pleistocene times. Anteaters and sloths are very scantily represented, but this is merely an accident of preservation; armadillos, on the other hand, were very numerous both in Brazil and in Argentina, and, in addition to many modern genera, there were several which are no longer in existence, such as †*Chlamydotherium*, which was a huge creature almost as large as a rhinoceros. Then there were the two extinct suborders of the †glyptodonts (†Glyptodontia) and the †ground-sloths (†Gravigrada) which were astonishingly abundant in Argentina and which, as was shown in a previous page (p. 205), were also well represented in North America.

Few more fantastic-looking mammals than the †glyptodonts have ever been found; the short, deep head, with its shield of thick, bony plates, the huge carapace made up of innumerable plates of bone firmly united at their edges and without the movable bands of the armadillo carapace, the enormous tail-sheath, the short legs and massive feet with broad hoofs, must have given these animals rather the appearance of gigantic tortoises than of mammals. The †glyptodonts were especially numerous and varied in the Argentine pampas, and a stately array of them is mounted in the museums of La Plata and Buenos Aires; in length, they ranged from six to twelve feet, including the tail. The skeleton and carapace did not differ very greatly in appearance among the various genera, but there were great differences in the form and size of the bony sheath enclosing the tail. In the genus †*Glyptodon* the sheath was composed throughout of movable overlapping rings, with prominent spines on them; in †*Sclerocalyptus* the hinder half of the sheath coalesced into a single piece, marked only by the elaborate ornamentation of the horny scales, while in †*Dœdicurus* the end had a tremendous, club-like expansion, which must have been set with great horn-like spines. The †glyptodonts were ponderous, slow-moving and inoffensive plant-feeders, almost invulnerable to attack, and probably used their massive tails, which could be freely swung from side to side, as redoubtable weapons of defence, much as the alligator uses his tail. In comparison with the bewildering variety in South America, the few that made their way into North America were quite insignificant.

Much the same statement applies to the †ground-sloths, and though these ranged far more widely through the northern continent than did the †glyptodonts, they were but few in comparison with the multitude which inhabited alike the forests of Brazil and the plains of the south. Two of the three genera of †ground-sloths which occur in the North American Pleistocene, †*Megatherium* and †*Mylodon*, are also found in South America; and though †*Megalonyx* has not yet been obtained there, the family of which it is a member was represented.

Fig. 122. — A gigantic Pampean †Ground-Sloth (†*Megatherium americanum*). Restored from a skeleton in the Museum of La Plata.

In size, these creatures varied from a tapir to an elephant, though all were much shorter-legged than any elephant; the extremely massive tail, which the larger forms had, served to support the huge body, when erected to tear down the branches and leaves upon which these strange creatures fed.

Opossums were extremely numerous, especially in the Brazilian caves, where in half a cubic foot of earth 400 jaws were collected.

The Pleistocene mammalian fauna of South America was a mixture of modern forms with ancient, vanished types similar to that which we found in North America. The †ground-sloths and †glyptodonts, the †litopterns, †toxodonts and †typotheres, the antelopes, horses and †mastodons have all disappeared from the continent, or vanished altogether from the face of the earth.

II. TERTIARY FAUNAS

1. *Pliocene*

North America. — No part of the Cenozoic history of North America is so imperfectly recorded and so unsatisfactorily known as that of the Pliocene, and the later portion of that epoch is especially obscure. If the Peace Creek formation of Florida is properly referred to the upper Pliocene, it would show that the mammals of that time were substantially the same as those of the early Pleistocene.

The only fauna, as yet discovered, which can be referred to the middle Pliocene, is that of the Blanco beds of north-western Texas, which have yielded but a scanty list of mostly ill-preserved fossils. Obviously, these give us a very incomplete picture of the life of that time. The great †ground-sloths had already reached North America, and the genus †*Megalonyx*, so common in the forested areas of Pleistocene North America, was perhaps already in existence. The †glyptodonts were likewise represented by one genus (†*Glyp-*

totherium) which was distinguished by the simple rings of the tail-sheath. No rodents have yet been found and only a few of the Carnivora, though a large cat, a musteline and a large †"bear-dog" are known. There were no true elephants, but several species of †mastodons, all of which were different from those of the Pleistocene; and in some, grinding teeth, though still low-crowned, had become much larger and more complex, marking a stage of advance toward the elephantine dentition. Horses of primitive type, the feet having three functional toes instead of one, were relatively abundant. Very large llama-like animals were present, but nothing has been ascertained with regard to the deer and antelopes of the time, and the only other representative of the Artiodactyla yet recovered is a peccary, interesting as being a species of the genus (†*Platygonus*) which became so abundant and widespread in the Pleistocene. Scanty and incomplete as this fauna is, it suffices to show that the middle Pliocene mammals were much more primitive than those of the Pleistocene.

The fauna of the Snake Creek formation in western Nebraska and that of the presumably somewhat later beds of northwestern Nevada, which are referable to the lower Pliocene, may be considered together. The rodents, which are not very fully represented, were quite modern in character and belonged mostly to extinct species of modern genera, such as hares, pocket-gophers, beavers, forerunners of the †Giant Beaver, marmots, sewellels, etc. A remnant of a more ancient world, especially characteristic of the Miocene, is found in the remarkable burrowers, the horned †mylagaulids which have been extinct since the lower Pliocene. Carnivora were abundant, and members of all the families which inhabit North America to-day have been obtained; wolves, †"bear-dogs," †"hyena-dogs" and forms like the Dhole of India were common. The terms †"bear-dogs" and †"hyena-dogs" are not to be understood as implying any relationships of these animals to bears or hyenas, but merely a certain superficial resemblance; these were very large members of the dog family (Canidæ), now extinct. Mustelines, large and small, are found, and possibly some bears had already made their way from the Old World, but this is still uncertain. †Sabre-tooth tigers and true cats, some as large as lions and one species fairly gigantic, were likewise characteristic of the time. There was a great wealth of horses, though the modern genus *Equus* was not among them; all the genera are now extinct and all were three-toed. Several distinct phyla were represented, some progressive and advancing toward the modern forms, others conservative and stationary. Browsing horses with low-crowned teeth, grazing horses with prismatic, cement-covered teeth, heavier and lighter, larger and smaller, must have covered the plains and thronged the woods. Ancestral tapirs were present, though far less common. A family which

FIG. 123. — †Horned Gopher (†*Epigaulus hatcheri*), lower Pliocene, Nebraska. Restored from a skeleton in the U.S. National Museum.

seems to be utterly exotic to North America, that of the rhinoceroses, was present, and of these there were three or four series, mostly without horns, or with a very small horn on the tip of the snout. The extremely aberrant perissodactyls (†Ancylopoda), in which the hoofs were converted into great claws, perhaps persisted, but the evidence is not conclusive.

The Artiodactyla were, for the most part, totally different from those of modern times, though several forms were ancestral to some now living. Peccaries more primitive than the living genus were the only representatives of the swine-like suborder; ancestral camels and llamas were among the commonest of the hoofed animals and an extinct phylum, that of the †"giraffe-camels" (†*Alticamelus*) continued over from the Miocene. The giraffe-camels are so called, not because of any actual relationships with the giraffes, but on account of certain likenesses in the proportions of the animals compared. †*Alticamelus* was a very large, camel-like creature, with remarkably elongate neck and limbs and comparatively small head, which no doubt resembled the giraffes in browsing upon trees which were above the reach of the ordinary camels and llamas of the time. It was the terminal member of a series, or phylum, which branched off from the main stock in Oligocene times and pursued a course of development which was independent of the principal series, but curiously parallel with it.

The deer of the lower Pliocene were little, graceful creatures (†*Blastomeryx*) which had no antlers, but the males were armed with sabre-like upper canine tusks, so that they must have resembled the Musk-Deer of Tibet, but were smaller and more slender. The remarkable group of †"deer-antelopes," now extinct, was represented by †*Merycodus*, a dainty little creature, less than two feet high at the shoulder, which had the antlers and general appearance of a small deer, but the high-crowned grinding teeth which most antelopes have. True antelopes of two different lines were also present, though they are as yet known from little more than the bony horn-cores; of these, one is the flat-horned and the other the twisted-horned or strepsicerine type, such as is illustrated by the Eland and Kudu of modern Africa. The latter may, however, be related to the peculiarly North American Prong-Buck (*Antilocapra*) and not to the strepsicerine antelopes of the Old World. The last survivors of an exclusively North American family, the †oreodonts, which were wonderfully numerous and varied from the upper Eocene onward, are found here.

The †mastodons (†*Gomphotherium*) of this formation had well-developed tusks in the lower as well as in the upper jaw, and in one species the chin-region or symphysis of the lower jaw was greatly prolonged, an ancient feature.

That the South American edentates had already reached the northern continent is sufficiently proved by remains of †ground-sloths, which are, however, too incomplete to permit identification of the genus. †Glyptodonts have not yet been found, but this fact does not demonstrate that they had not accompanied the †ground-sloths in their migration, for at no time did they range so far north as Nebraska or northwestern Nevada, and the only mammal-bearing formation of lower Pliocene date known in the south, the Alachua Clay of Florida, has yielded too scanty a list of fossils to make its negative evidence at all conclusive on this point.

The mammals of the middle and especially of the lower Pliocene were much stranger and more primitive than might be inferred from the foregoing brief account. Except several of the Rodentia and perhaps one or two of the Carnivora, the *genera* are all extinct and such familiar terms as horses, rhinoceroses, camels, etc., can be employed only in a very comprehensive sense, as equivalent to families.

The Pliocene of *South America* is involved in some obscurity; not that there is any question as to the formations, or their order of succession, but there is much doubt as to the limits of the epoch both above and below. The latest Pliocene fauna, that of the Tarija Valley in Bolivia, was essentially the same as that of the Pleistocene and contained a similarly large proportion of migrant elements from the north, but it was evidently older and many of the species were different. The two divisions of the Araucanian fauna, contained in the beds of Catamarca and Monte Hermoso respectively, are very much alike and need not be given separate consideration. In one respect these presumably upper Pliocene faunas formed a very strong contrast to the mammalian assemblage of the Pleistocene, and that is in the quite insignificant part taken by the migrants from North America. Of the Carnivora there were but two representatives, one referable to the raccoon family and one to the dogs, while a hare and a small member of the Artiodactyla, of indeterminate family, complete the list of northern forms, though this list will doubtless be extended by future discovery. The peccaries, deer, antelopes, tapirs, horses, †mastodons, cats, weasels, otters, squirrels, mice, etc. had not reached the southern continent, or were still so rare that remains of them have not been found. This rarity and relative insignificance of the northern forms gave a very different aspect to the fauna.

On the other hand, the indigenous South American groups were very fully represented. Many kinds of opossums and a few large carnivorous types, much like the so-called Tasmanian Wolf (*Thylacynus*), were the remnants of a much larger assemblage of marsupials which inhabited South America in the Miocene. Of the Edentata, there were great abundance and variety, many large †glyptodonts and some gigantic armadillos, as well as numerous examples of normal size; the †ground-sloths, though somewhat smaller than those of the Pleistocene, were mostly of gigantic size, and true or arboreal sloths (Tardigrada) have been reported. The very numerous rodents, with the exception of the intrusive hare, all belonged to typically South American families. Some of the rodents were gigantic and one (†*Megamys*), a member of the Chinchilla family, was equal to a rhinoceros in size and the largest known representative of the order. Especially characteristic was the abundance of the cavy family (Caviidæ).

The hoofed animals, with the single known exception of the immigrant artiodactyl, all belonged to the autochthonous orders, all of which are extinct at the present time. Forerunners of the extraordinary genus †*Macrauchenia*, which was one of the most conspicuous elements of Pleistocene life, were quite common in the Pliocene and differed from the Pampean genus chiefly in their smaller size and less advanced specialization. We find here also the last survivors of another family of the †Litopterna, the †proterotheres (†Proterotheriidæ), which imitated the horses in such a surprising manner that some authorities believe them to have been actually related to those perissodactyls. The Monte Hermoso genus (†*Epitherium*) had feet which were wonderfully, though but superficially, like those of the three-toed horses. The †Toxodonta were numerous and most of them were large, ponderous animals; one genus (†*Trigodon*) had the interesting peculiarity of a single median horn on the forehead, much like that of a rhinoceros. Horned species were always rare among the indigenous groups of South American ungulates, and all that have been discovered so far belonged to the †toxodonts. The remaining group, that of the †Typotheria, was also well represented, both by larger and by very small forms, some no larger than a rabbit (†*Pachyrukhos*).

The presumably lower Pliocene (perhaps upper Miocene) fauna of the Paraná formation is as yet known only from very fragmentary material. Representatives of the dogs, raccoons and bears have been reported, but the identifications are doubtful; at all events, these would seem to have been the most ancient of the northern immigrants. A considerable number of marsupials, both opossums and large predaceous types, have been found. The rodents were very numerous, all belonging to South American families and some of them very large. The edentates were gigantic †ground-sloths and †glyptodonts, with numerous armadillos of ordinary size. The hoofed animals all belonged to the indigenous South American orders, the predominant place being taken by the †toxodonts, some of which were large. There were many †typotheres, both of the larger and smaller kinds. The †Litopterna were represented both by the horse-like †proterotheres and the long-necked †macrauchenids, the latter smaller and less specialized than those of the Pampean.

FIG. 124. — Head of Horned †Toxodont (†*Trigodon gaudryi*). Pliocene of Monte Hermoso. Restored from a skull in the Ameghino collection.

2. *Miocene*

North America. — Upper Miocene beds cover extensive areas of the Great Plains region and are scattered from Montana far into Mexico. The rich fauna is an outgrowth and development of that of the middle Miocene, with but few immigrant additions and, on the other hand, passes so gradually into that of the lower Pliocene, that any line of separation between them is very difficult to draw. The rodents, numerous as they are among the fossils, are almost certainly very incompletely represented in the collections; the families are almost all still in existence, but nearly every genus is extinct, and thus the vernacular names used to designate them must be understood in a broad sense. Hares, mice, pocket-gophers, squirrels, marmots, beavers and the extraordinary †mylagaulids were all abundant.

In even more strongly marked sense must the broad meaning for the vernacular names of the other mammals be emphasized, for we have to deal almost exclusively with extinct genera, which differed much from their modern descendants. Many of the Carnivora have been obtained; there were numerous dogs, some rivalling the largest of existing bears in size, true felines and †sabre-tooth tigers, which were smaller and lighter animals than the great beasts of the Pleistocene; weasels, martens, otters and raccoons, but no bears. The bears, a family of Old World origin, are not certainly known in America before the Pleistocene, but had probably reached this continent in the Pliocene.

As is so very generally true, the commonest and best-preserved of the fossils are those of the hoofed animals. The †mastodons were of the four-tusked kind (†*Gomphotherium* or †*Trilophodon*), the skull and teeth of which differed so markedly from those of the true elephants. The relatively small, low-crowned and simple grinding teeth were common to all the †mastodons, but the tusks were different from those of the larger members of the group. The upper tusks were comparatively short and nearly straight and retained a band of enamel, while the lower tusks were still shorter, chisel-shaped and so worn as to prove that they were regularly used, no doubt in cropping leaves; the shortness of these lower tusks was compensated for by the great elongation of the lower jaw. The head was proportionately broad and low and, for Proboscidea, these were small animals, not more than five or six feet high at the shoulder. The body, limbs and feet had already attained substantially their modern grade of structure, advance among the Proboscidea being chiefly restricted to the teeth and skull.

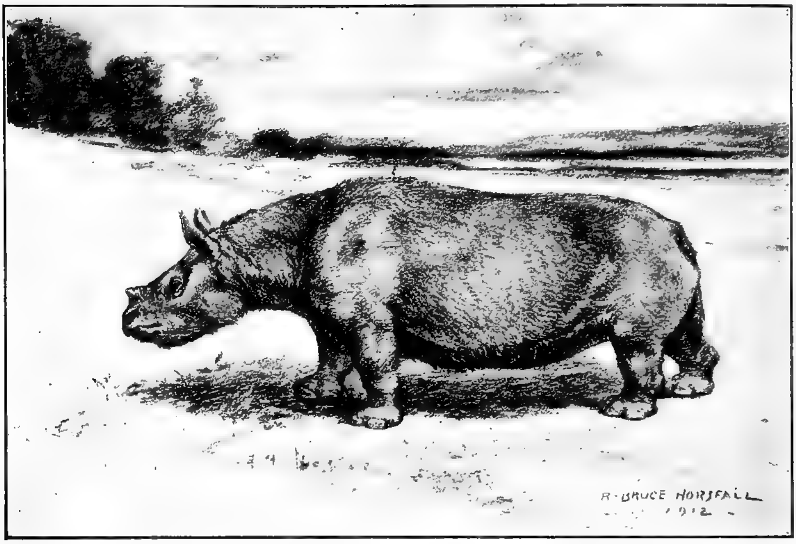

Fig. 125.—†*Teleoceras fossiger*, a short-legged rhinoceros, with small nasal horn; lower Pliocene and upper Miocene of Nebraska. Restored from a skeleton in the American Museum of Natural History.

Four families of Perissodactyla were represented in the upper Miocene. The rhinoceroses, which were very abundant, were present in considerable variety; some were hornless, others had a single small horn on the end of the nose. Among these rhinoceroses there was much difference in bodily proportions, some being extremely heavy, with very short legs and feet, and these were the commonest, while others had longer legs and less massive bodies. Tapirs, on the contrary, would seem to have been scantily represented; at least, they are rare among the fossils. The extraordinary, aberrant †chalicotheres, perissodactyls with claws instead of hoofs, still persisted, but are far better known from the lower Miocene, in connection with which they will be described. The dominant perissodactyl family was that of the horses, of which no less than five genera are already known. There were some with very low-crowned teeth, which must have fed principally by browsing upon leaves and such soft diet; but the grazing kinds, which had high-crowned, cement-covered and very complex grinding teeth, had come to the fore. Still retaining three toes in each foot, with the middle toe so enlarged as to bear nearly the entire weight, save in snow or soft ground, these eminently cursorial animals, which had the slender limbs of a deer, must have roamed the plains in great herds.

Still commoner were the Artiodactyla. Many species of grazing camels, which were the predominant artiodactyl family in North America during upper Miocene times, were the ancestors both of the true camels of the Old World and the South American llamas. †Giraffe-camels have not yet been found and no doubt they were much less abundant than in the middle Miocene, but that they had not completely disappeared is shown by their recurrence in the Pliocene. As compared with earlier ages, the †oreodonts had begun a rapid decline and had lost notably both in numbers and variety, but one most curious beast (†*Pronomotherium,* Fig. 197, p. 375) marked the final step in the development of the short-faced, proboscis-bearing series, which may be traced back to its beginnings in the Oligocene. In this wonderful creature the skull was so short and deep as to suggest that of a gorilla or some other great ape. No other artiodactyls even approximate these later proboscis-bearing

†oreodonts in the altogether exceptional form of the skull. Grazing †oreodonts (†*Merychyus*), of moderate and small size with high-crowned teeth, were evidently quite common on the upper Miocene plains. The †hornless deer and †"deer-antelopes" differed but little from those of the lower Pliocene. Peccaries were fairly abundant.

FIG. 126. — †*Procamelus elrodi*, a large camel from the upper Miocene. Restored from specimens in the Carnegie Museum.

The upper Miocene fauna was especially characterized by the large number of mammals, belonging to several different orders, which had acquired the high-crowned, persistently growing pattern of grinding teeth. Many of the horses, camels, ruminants and rodents displayed this structure, and, as was first pointed out by Kowalevsky, the explanation is probably to be found in the spread of grassy plains at the expense of the forests. On account of the silica which they contain, the grasses are very abrasive and rapidly wear the teeth down. In adaptation to this new source of abundant and nutritious food, many kinds of mammals developed a form of tooth which was fitted to compensate by growth for the loss through abrasion.

The middle Miocene, small areas of which occur in Montana, eastern Oregon and northeastern Colorado, has received various local names, the typical one being the Deep River of Montana. Very probably, these scattered areas are not strictly contemporaneous, but form a closely connected series. That a land-connection with the eastern hemisphere existed, is made clear by the appearance of several unmistakably Old World types of animals and the beginnings of migration from South America are perhaps also to be noted, though this cannot be positively stated. The evidence for the South American connection is the finding in the middle Miocene of Oregon of what are believed to be the earliest remains of †ground-sloths yet discovered in North America, but the material is too scanty for altogether certain determination.

The smaller animals are not very well represented in the middle Miocene faunas, as conditions appear to have been unfavourable to their preservation; something is known of them, nevertheless. The very curious extinct family of rodents known as the †Mylagaulidæ, the presence of which was noted in the upper Miocene and lower Pliocene, first appeared here. These †mylagaulids, which were distantly related to the modern Sewellel (*Aplodontia rufa*), were characterized by the great enlargement and complication of one of the grinding teeth in each jaw and the consequent reduction of the others. One genus of this family, as in the Pliocene, had the peculiarity, unique among rodents, of developing a large horn upon the nose, like a miniature rhinoceros. Among the Carnivora, we find a great variety of dogs, large and small, all belonging to extinct genera, as indeed is true of the other carnivores also. True felines have been found, but as yet, none of the †sabre-tooth series; the abundance of the latter, however, in both preceding and succeeding formations, is sufficient proof that the discovery of them in the middle Miocene is merely a question of time. Mustelines were present, and especially noteworthy is the appearance of the first American otters, immigrants from the Old World.

Of the hoofed animals, the most interesting are the Proboscidea, the most ancient of which that are definitely determinable in America occur in this horizon. The place of origin and ancestry of these animals were long exasperating puzzles. Appearing suddenly in the Miocene of Europe and North America, in which regions nothing was known that could, with any plausibility, be regarded as ancestral to them, they might as well have dropped from the moon, for all that could be told concerning their history. The exploration of the Eocene and Oligocene beds of Egypt has dispelled the mystery and shown that Africa was the original home of the group, whence they gradually spread to every continent except Australia. Little is known of these earliest American proboscideans, but they were doubtless small †mastodons of the four-tusked type.

Among the Perissodactyla, the rhinoceroses were perhaps the most conspicuous; the native American stocks of this family appear to have mostly died out and to have been replaced by two or more phyla of immigrants from the Old World, some of which were hornless, others had a small horn on the tip of the nose and others again had a second and smaller horn on the forehead. Tapirs, though unquestionably present, are rare as fossils and not well known. Several distinct phyla of horses may be distinguished, which were like small ponies in size, but of more slender form; they were all three-toed, but there were marked differences among them with regard to the degree to which the middle toe (the third of the original five) had been enlarged to carry the whole weight and the lateral toes (second and fourth) reduced to mere "dew-claws." While browsing horses, with low-crowned teeth, still persisted in large numbers, we find also the extremely interesting beginnings of the highly complex, cement-covered and high-crowned teeth of the grazing kinds. The clawed †chalicotheres were present, though very little is known about them because of the fragmentary character of the remains.

The Artiodactyla were much more varied and abundant, though they did not rival the great assemblage of these animals found in the European Miocene. Of the peccaries little more can be said than that they were present in these faunas. The †oreodonts were very numerous, both individually and generically; two stages of the proboscis-bearing kind are found here together, the older, long-faced genus (†*Promerycochœrus*) surviving from the Oligocene, while the newer Miocene type was short-faced and had a moderate proboscis (see Fig. 196, p. 373). Others had more the proportions of peccaries and still others were very small and presumably aquatic in habits. Camels abounded, both the grazing kinds which were ancestral to the modern forms of South America and Asia, and the great, browsing †giraffe-camels. The †hornless deer and the antlered †deer-antelopes were much like those of the Upper Miocene, slender and graceful little creatures, and there were also considerably larger ruminants (†*Dromomeryx*) with straight, simple and non-deciduous horns, which may be called antelopes.

The line of division between the lower Miocene and the uppermost Oligocene is a very obscure and difficult one to draw. Personally, I prefer to begin the Miocene with the widespread formation of the Great Plains, which has been variously named Arikaree, Harrison, Rosebud, etc., but this is a moot point. Concerning the lower part of these beds Osborn says: "They may be either: (1) Upper Oligocene or (2) transitional from Oligocene to Miocene, or (3) of pure

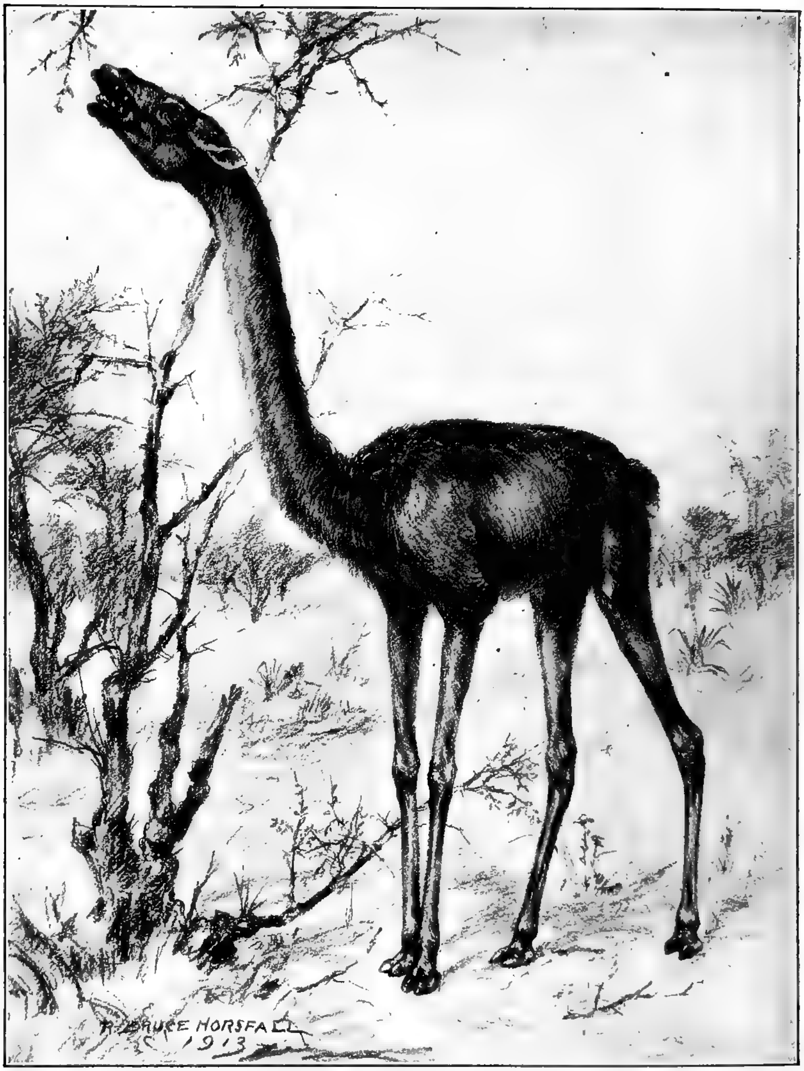

Fig. 127. — Gigantic †giraffe-camel (†*Alticamelus altus*) from the middle Miocene of Colorado. Restored from specimens in the American Museum of Natural History.

Lower Miocene age." The upper division is referred to the Miocene without question by any one, but for the purposes of this rapid sketch it will be best to treat the two faunas together. This many-named formation, for which the term *Arikaree* is here employed, as having priority, is found over extensive areas of South Dakota, northern Nebraska and central Wyoming. The fauna was almost entirely a development from that of the North American Oligocene, with very little admixture of foreign elements, so that the land communication with the eastern hemisphere must have been difficult. In this, as in most of the Miocene formations, the smaller mammals are not fairly represented, and it is evident that much remains to be learned with regard to them; this is especially true of the upper division of this stage.

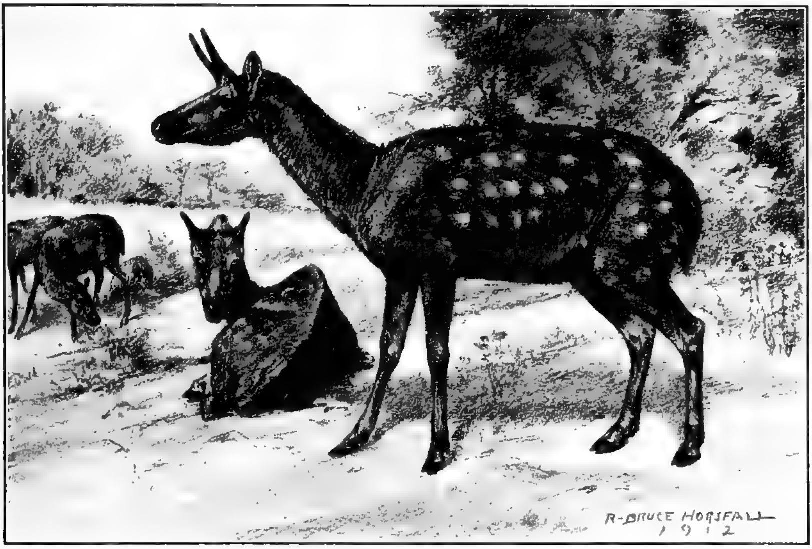

FIG. 128. — Most ancient American Antelope (†*Dromomeryx antilopina*), middle Miocene. Restored from specimens in the Carnegie Museum and Princeton University.

The rodents, which were fairly numerous, were directly continuous with those of the upper Oligocene and included forms which were more or less distantly connected with the modern hares, squirrels, beavers, sewellels, pocket-gophers and kangaroo-rats. A few Insectivora of doubtful reference have been found. Among the Carnivora there was also considerable variety: dogs, large and small, were abundant, but all of them were decidedly primitive from the modern standpoint; the cats were represented both by the true felines, which were probably immigrants, and by the †sabre-tooth series. There were several large and powerful mustelines, or members of the weasel family, which were likewise immigrants, one of which resembles in many ways the modern Wolverene (*Gulo*). Very interesting is the beginning of the raccoon family (Procyonidæ) or, at least, what is believed to be such, which arose from a branch of the dogs; this most ancient of the raccoons was †*Phlaocyon*, a small and slender animal.

The earliest traces of the Proboscidea in America have been reported from this formation, but the fragmentary specimens are inconclusive. The Perissodactyla are among the commonest fossils. The rhinoceroses belonged to native stocks, including both the horned and hornless forms. The horned genus (†*Diceratherium*) differed from all other rhinoceroses in having a transverse *pair* of horns on the nose, and the species of the lower Miocene were quite small and light; the hornless genus (†*Cœnopus*) was a larger and heavier animal. Tapirs are rare as fossils and consequently not well known. While there were several kinds of horses, they all agreed in having short-crowned and relatively simple grinding teeth and three-toed feet; they were smaller and of lighter, more slender build than those of the middle Miocene. The wonderful aberrant perissodactyls with clawed feet, the †chalicotheres (suborder †Ancylopoda), appear to have been more abundant in the Arikaree than at any other time in North America, though their history in this continent extends from the middle Eocene to the lower Pliocene. †*Moropus*, the lower Miocene genus, was as grotesque a creature as could well be imagined and, in advance of experience, no one ever did imagine such a beast.

With rather small and somewhat horse-like head, long neck, long fore limbs and shorter hind limbs, these extraordinary animals united short, three-toed feet, which were armed with enormous claws. The long persistence (to the Pleistocene of Asia) and wide geographical range of the †chalicotheres are sufficient evidence that their very unusual structure must have been advantageous to them, but the problem of their habits and mode of life is still unsolved. From the character of the teeth, the long neck and fore limbs, it may, however, be inferred that they fed chiefly upon the leaves of trees.

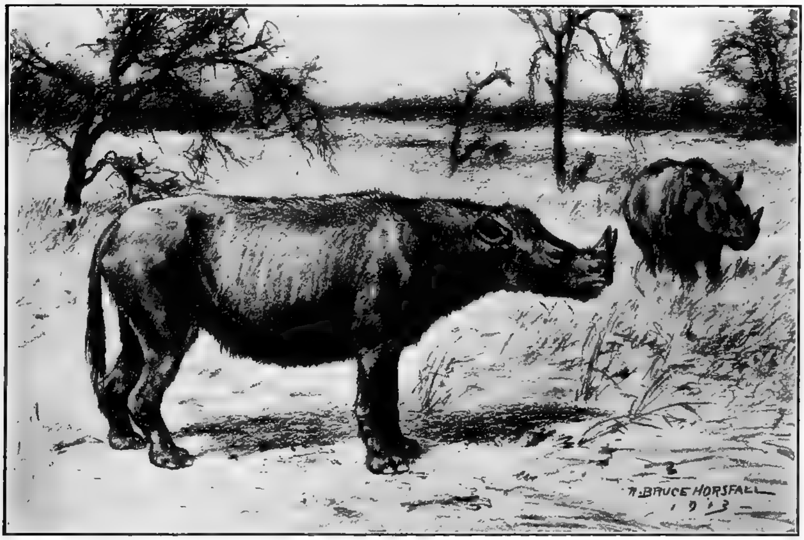

Fig. 129. — The small, †paired-horned rhinoceros (†*Diceratherium cooki*) of the lower Miocene. Restored from a skeleton in the Carnegie Museum, Pittsburgh.

Even more numerous and varied were the Artiodactyla. Peccaries of a primitive sort were common, and we find the last of the series of †"giant pigs," which had been a very conspicuous group throughout the Oligocene. The lower Miocene genus, †*Dinohyus*, was a monstrous beast, six feet or more in height, with formidable canine tusks and a very long head made grotesque by bony excrescences upon the skull and jaws. For a pig, the legs were very long and the feet slender, having

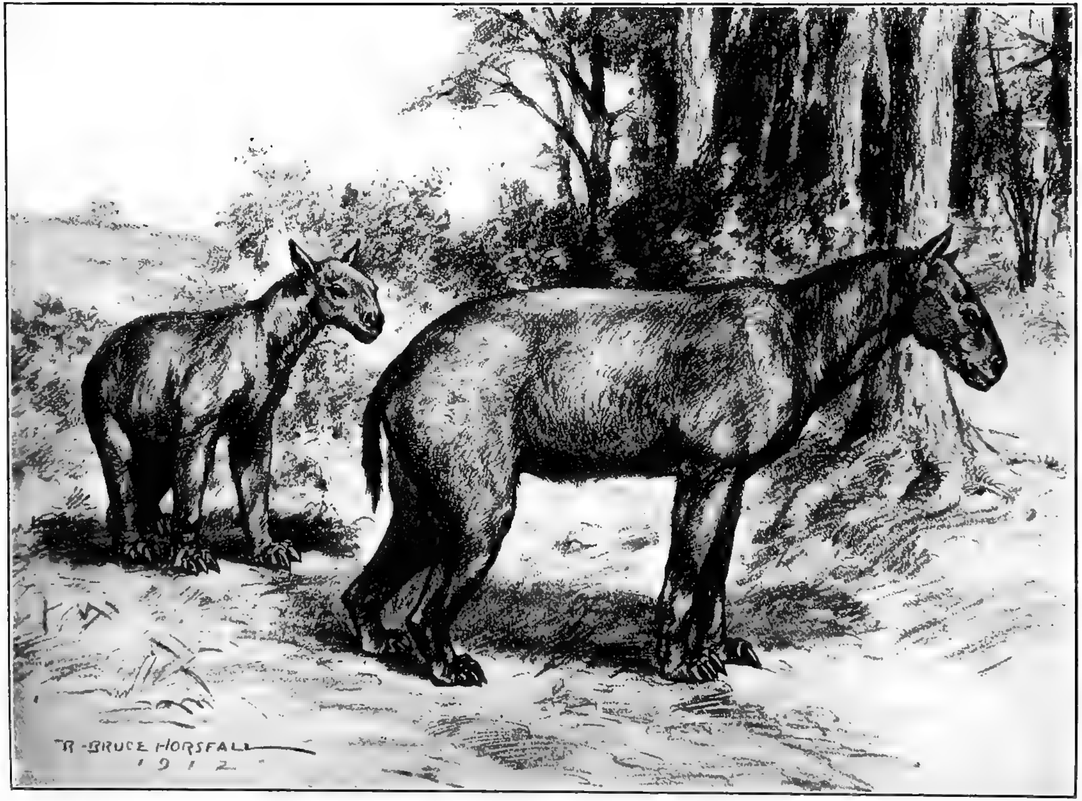

FIG. 130.—A †chalicothere (†*Moropus elatus*) of the lower Miocene. Restored from a skeleton in the Carnegie Museum, Pittsburgh.

but two toes. The †oreodonts were present in great numbers, both small and large forms; except for bodily stature and modifications of the head, they all looked very much alike; †*Merycochœrus*, with its incipient proboscis, here made its first appearance. The last representatives of a family (†Hypertragulidæ) of small and graceful artiodactyls are found in this formation. One of these (†*Syndyoceras, see* Fig. 215, p. 403), an animal considerably larger than the existing Musk-Deer, was in its way even more bizarre-looking than the †chalicotheres; with an antelope-like head, it had four horns, one pair over the eyes, curving inward, and a shorter pair, with outward curvature, on the muzzle. Another genus (†*Hypertragulus*) was very much smaller and very slender.

The camels were beginning to diversify and give rise to several phyla. One of the genera (†*Protomeryx*), which did not much exceed a sheep in size, probably represented the main stock, which led to the camels and llamas of to-day. A second (†*Stenomylus*) was a still smaller animal, with remarkably long and slender legs, and might be called a "gazelle-camel," while a third (†*Oxydactylus, see* Fig. 209, p. 392), which was larger and apparently the beginning of the †giraffe-camels, was noteworthy for its long neck. All of these lower Miocene camels had deer-like hoofs, the characteristic pad or cushion which gives such an exceptional appearance to the feet of modern llamas and camels not being fully developed till a later period. A very important new element in the North American fauna was the appearance of the first deer (†*Blastomeryx*), which came in the latter part of the Arikaree stage and were the forerunners of a renewed immigration from the Old World, which had been broken off during the upper Oligocene. This, however, is a disputed point; Professor Osborn and Dr. Matthew believe that these animals were truly indigenous and derived from a long line of American ancestry. The same genus continued through the middle Miocene, as we have already seen, and therefore no further description of it is called for.

The limits of the *South American* Miocene are very doubtful. The Paraná formation, here regarded as lower Pliocene, may prove to be more properly referable to the upper Miocene. No other upper Miocene is known.

To the earlier, probably middle, Miocene may be referred the wonderful Santa Cruz fauna of Patagonia. It is extremely difficult to convey to the reader any adequate conception of this great assemblage of mammals, because most of them belonged to orders which have altogether vanished from the earth and are only remotely like the forms with which we are familiar in the northern hemisphere. To one who knows only these northern animals, it seems like entering another world when he begins the study of the Santa Cruz fossils. If any North American mammals had then entered South America, which is not probable, they had not extended their range as far as Patagonia. Marvellously rich and varied as the Santa

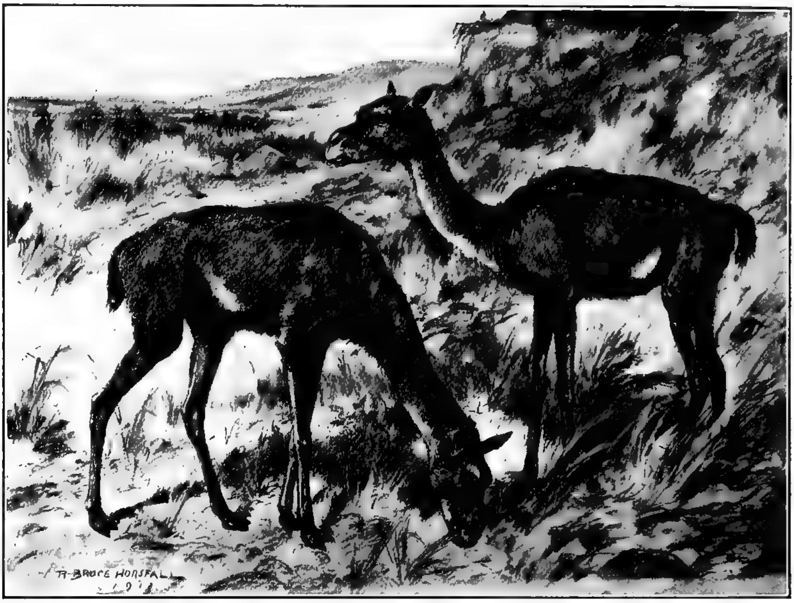

FIG. 131. — The †gazelle-camel (†*Stenomylus hitchcocki*) of the lower Miocene. Restored from skeletons in the Carnegie Museum, Pittsburgh.

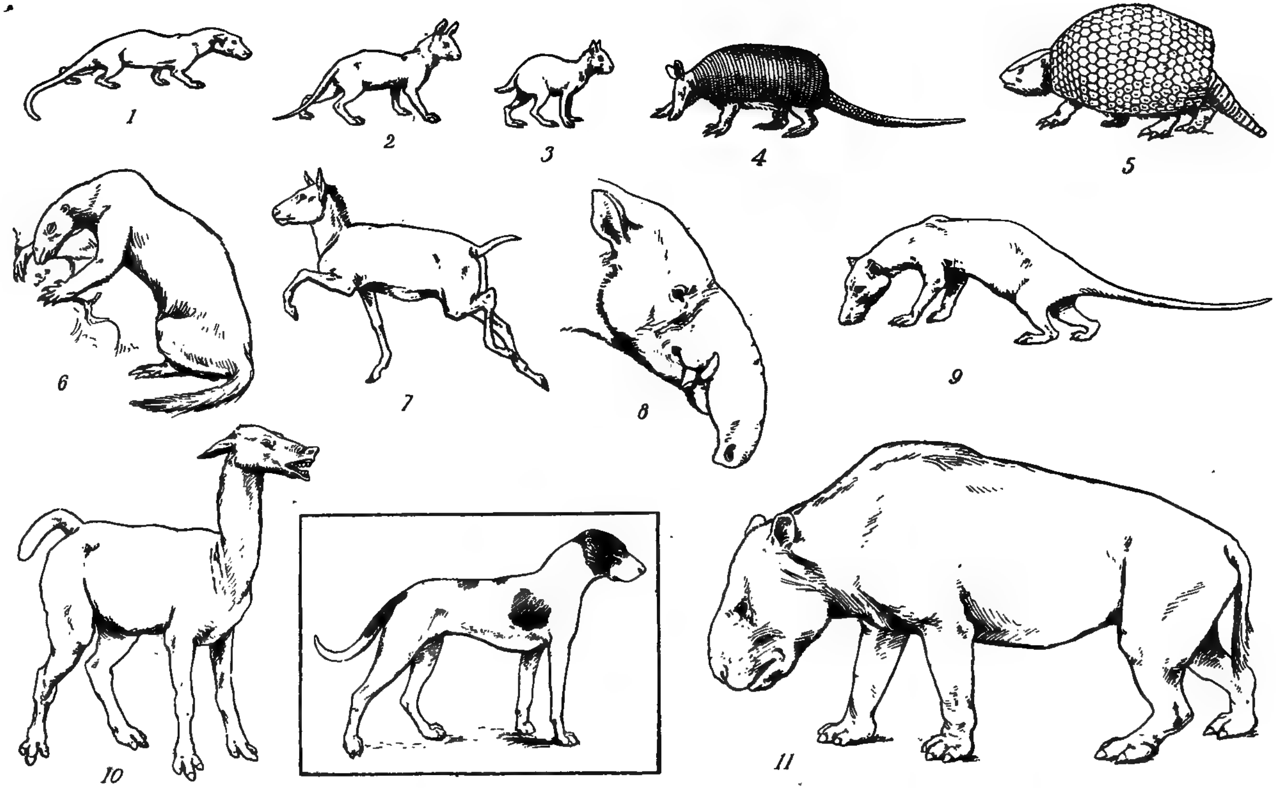

FIG. 132. — Diagram to illustrate the comparative sizes of the Santa Cruz mammals, a modern pointer dog, within the rectangle, to give the scale. 1. †*Cladosictis lustratus*, predaceous marsupial. 2. †*Protypotherium australe*, †typothere. 3. †*Eocardia excavata*, rodent. 4. †*Stegotherium tesselatum*, armadillo. 5. †*Propalæohoplophorus australis*, †glyptodont. 6. †*Hapalops longiceps*, †ground-sloth. 7. †*Thoatherium minusculum*, †litoptern. 8. †*Astrapotherium magnum*, †astrapothere. 9. †*Prothylacynus patagonicus*, predaceous marsupial. 10. †*Theosodon garrettorum*, †litoptern. 11. †*Nesodon imbricatus*, †toxodont.

Cruz fauna was, it did not contain everything that we should expect to find in it; several recent families of undoubtedly indigenous South American origin have left no ancestors in the early Miocene formations. For this, there are several obvious reasons. In part, these gaps in the history are merely due to the accidents of collecting and some of them will almost certainly be filled by future exploration. Other absentees will probably never be found, because the Santa Cruz beds are known only in the very far south, and the Miocene climate of the region, though much milder and more genial than the present one, must have been unsuitable for many tropical animals. Again, the Patagonia of that time appears to have been a country of open plains, with few trees, and hence arboreal forms were rare.

While great numbers of large, flightless birds, some of them of enormous size, were entombed in the volcanic ash and dust which were spread over such wide areas and to such great depths, the extreme scarcity of reptiles is surprising; a few remains of lizards have been found, but no snakes, crocodiles, or tortoises, and we have no information as to the plant-life of the region at that time. The mammals were almost all of small or moderate size; only one or two species were really large.

One very striking and characteristic feature of the Santa Cruz fauna is the great abundance of marsupials which it contained and which resembled more or less those of modern Australia. There were no true Carnivora and their places were taken by a variety of carnivorous marsupials, some of which (*e.g.* †*Prothylacynus*) were as large as wolves and were closely similar to the so-called Tasmanian Wolf (*Thylacynus*). Another genus (†*Borhyæna*) had a short, bullet head, not unlike a small Puma in appearance and, besides, there were many smaller beasts of prey, in size like badgers and minks. Opossums were common and there were many very small herbivorous marsupials, which resembled, though perhaps but superficially, the Australian phalangers. At the present day South America contains no Insectivora, but in the Santa Cruz there was one family (†Necrolestidæ) of this order which bore considerable resemblance to the "golden moles" of South Africa. An extraordinary variety of rodents inhabited Patagonia in Santa Cruz times, all of them belonging to the Hystricomorpha, or porcupine suborder, and all referable to existing South American families. There were none of the northern forms of rodents, neither rats, mice, squirrels, marmots, hares, nor rabbits, but a very numerous assembly of tree-porcupines, cavies, chinchillas, coypus and the like. The genera, though closely allied to existing ones, are all extinct, and the animals were very generally smaller than their modern descendants. A few small monkeys of unmistakably Neotropical type have been found, but like other arboreal and forest-living animals, they are very rare among the fossils.

The Edentata were more abundant and diversified than at any other time in South American history of which the record is preserved. Two of the modern subdivisions of this order have not been certainly identified in the Santa Cruz collections, the arboreal sloths and the anteaters, and though they may be found there at any time, it will only be as stragglers from the warmer forested regions to the north, where these forms had doubtless long been present. Unfortunately, however, nothing is directly known concerning the life of those regions in Miocene times. On the other hand, three groups of edentates, two of them now extinct, were very copiously represented in the Santa Cruz formation, the armadillos, †glyptodonts and †ground sloths. Of the many armadillos, some quite large, others very small, only a few can be regarded as directly ancestral to those now in existence; the truly ancestral forms were probably then living in the forests of Brazil and northern Argentina, in the same areas as the ancestral tree-sloths and anteaters. In comparison with the giants of the Pliocene and Pleistocene, the Santa Cruz †glyptodonts were all small, the carapace rarely exceeding two feet in length, and, what it is particularly interesting to note, they departed much less widely from the armadillo type than did their gigantic successors. The †ground-sloths were present in actually bewildering variety and they also were very small as compared with the huge animals of the Pleistocene, none of them exceeding the Black Bear in height or length, though proportionally much more massive, and many were no bigger than foxes. They had small heads, long bodies, heavy tails and short, thick legs; their teeth show that they were plant-feeders, but their feet were armed with long, sharp and formidable claws. Among this great host of Santa Cruz †ground-sloths may readily be noted the probable ancestors of the gigantic creatures which were such characteristic elements of the Pliocene and Pleistocene faunas.

There was an extraordinarily rich and varied assemblage of hoofed animals, all utterly different from those of the northern hemisphere and belonging to groups which have never been found outside of South and Central America. Of these groups there were five, which by different writers are variously regarded as orders or suborders, a matter of very secondary importance. Individually, the commonest of the hoofed mammals were the †Toxodonta, which ranged in size from a sheep to a tapir, heavily built and clumsy creatures, with absurdly small, three-toed feet; in some of the species there was a small median horn on the forehead. As with the †glyptodonts and †ground-sloths, the contrast in size between the Santa Cruz ancestors and the Pleistocene descendants was very striking. A very numerous and varied group was that of the †Typotheria, all small animals, some no larger than rabbits, others the size of small foxes. It requires a decided effort to think of these †typotheres as being really hoofed animals at all, as their whole appearance must have been much more like that of rodents, yet their structure clearly demonstrates their near relationship to the †toxodonts. Still a third group of the same series, the †Entelonychia, is of great interest, for, as in the †chalicotheres of the northern hemisphere, the hoofs had been transformed into claws and their five-toed feet had a truly grotesque appearance, not diminished by the long and powerful limbs and relatively small head.

This is the third example of that paradoxical creature, a "hoofed animal" with claws instead of hoofs, and in each of the three instances, there is every reason to believe, the transformation proceeded independently. Among the perissodactyls the †chalicotheres (p. 238) underwent this change; in North America the †Agriochœridæ, a family of artiodactyls, had a very similar history, while in South America the †Entelonychia arose from the same stock as the †toxodonts, with which they were nearly allied. They were among the largest animals of Santa Cruz times and ranged in size from an ox to a rhinoceros.

There was a fourth group, the †Astrapotheria, concerning which our knowledge is tantalizingly incomplete, some species of which were the largest of known Santa Cruz mammals, while others were much smaller. They had short, domed heads, with a considerable proboscis, and were armed with formidable tusks, which were the enlarged canine teeth, the only known instance of large canine tusks among the indigenous South American hoofed animals. The limbs were long and not very massive, the feet short, five-toed and somewhat elephantine in appearance. These bizarre animals would seem to have held a rather isolated position among the South American ungulates, and though they may be traced back to the most ancient mammal-bearing beds of that continent, their relationships are still obscure; much more complete material must be obtained before this problem can be definitely solved. Both the †Astrapotheria and the †Entelonychia died out shortly after the end of the Santa Cruz.

From many points of view the most interesting members of the Santa Cruz fauna were the †Litopterna, an order which also went back to the earliest South American Tertiary. In the Miocene and Pliocene the order was represented by two very distinct families, the †Macraucheniidæ and †Proterotheriidæ, which were superficially very unlike. In the Santa Cruz beds is found a genus (†*Theosodon*) which was apparently the direct ancestor of the Pampean †*Macrauchenia.* The Miocene genus was a much smaller animal and had hardly more than an incipient proboscis, but otherwise was very like its Pampean successor; it was somewhat larger and heavier than a Llama and probably bore some resemblance to that animal in appearance. The long, narrow head, with its prehensile upper lip, must have had an almost reptilian likeness from the numerous uniform and sharp-pointed teeth with which the front of the jaws was supplied; the neck was elongate, the body short and rather slender and the legs long, ending in three nearly equal toes.

The †proterotheres, on the other hand, were almost the only Santa Cruz ungulates which had nothing *outré* or grotesque about them to the eye of one habituated to the faunas of the northern hemisphere. They were small, graceful animals, very like the Miocene horses of the north in their proportions, though having much shorter necks and shorter, heavier heads. In some genera of this family (*e.g.* †*Diadiaphorus*, †*Proterotherium*) the feet were three-toed and most surprisingly horse-like in shape, but one genus (†*Thoatherium*) was absolutely single-toed, more completely monodactyl than any horse. The horse-likenesses ran all through the skeleton and are so numerous and so striking that several writers have not hesitated to incorporate the †Litopterna with the Perissodactyla, but this I believe to be an error. If the †proterotheres were not perissodactyls, as I am convinced they were not, they afford one of the most remarkable examples of convergent evolution among mammals yet made known.

3. *Oligocene*

North America.—The John Day formation of eastern Oregon represents the upper Oligocene and has yielded a very extensive series of mammals, though with some obvious gaps that remain to be filled by future work. The land-connection with the Old World which had existed in the lower Oligocene and was restored in the lower, or at latest in the middle, Miocene, was interrupted in John Day times, and so the mammals assumed a purely indigenous character.

No opossums or other marsupials have been found, and nothing is known of the Insectivora. Of the Carnivora, there were but three families, and one of these, the mustelines, was represented but scantily by a few small species. Cats of the †sabre-tooth subfamily were common and one species was quite large, almost equalling the Jaguar in length; but most of the species were small, much smaller than the Pleistocene members of the group. True cats are not definitely known to have been present, but there were two genera (†*Nimravus* and †*Archælurus*) which have been called the "false †sabre-tooths," which may prove to be referable to that series. The dogs, on the other hand, were remarkably numerous and diversified, more so than ever before or since; none of them was very large, the largest but little exceeding the Timber Wolf in size, and some were extremely small; but the number of distinct genera and species and the differences among them are quite remarkable. Both long and short-faced forms and early stages of the †"bear-dogs," and †"hyena-dogs," and ancestral forms of the wolves and dholes may be distinguished, a truly wonderful assemblage. The rodents also were numerous and varied, including ancient and extinct genera of the beavers, squirrels, mice, pocket-gophers and hares and the earliest distinguishable ancestors of the sewellels (Aplodontiidæ).

The remainder of the known John Day fauna was composed of artiodactyls and perissodactyls. The latter had suffered serious losses as compared with the preceding or White River stage. Up to and through White River times the perissodactyls had held their own in actual diversity, though the rise of the artiodactyls had put an end to the dominant position which they had maintained in the Eocene. With the John Day the actual decline may be said to have begun. The rhinoceroses were represented chiefly by the †diceratheres, with a transverse pair of horns, some species of which were much larger than those of the lower Miocene. Hornless rhinoceroses have not yet been certainly found, though there is every reason to believe that they then existed, as they unquestionably did both before and after. Tapirs occurred but rarely and the horses were individually abundant, though in no great diversity; they were smaller and lighter than the horses of the lower Miocene. Enough has been found to demonstrate the presence of the clawed †chalicotheres, but not to show how they differed from their immediate successors.

In the number of individuals, species, genera and families, the artiodactyls of the John Day much exceeded the perissodactyls. The peccaries were numerous, but smaller and more primitive than those of the succeeding age, as were also the †giant pigs, or †entelodonts, but the latter were very large. The peculiarly North American family of the †oreodonts was very numerously represented, and one genus (†*Promerycochœrus*), comprising animals not unlike the Wild Boar in size and shape, was the probable beginning of the series of proboscis-bearing †oreodonts, which led to such grotesque forms in the middle and upper Miocene. A family closely allied to the †oreodonts, and by many writers included in the latter, is the very remarkable group of the †Agriochœridæ, which was distinguished by the long, stout and cat-like tail and by the possession of claws instead of hoofs. The family is not known to have existed later than the John Day and no trace of it has been found in the succeeding formations. The camels seem to be all comprised in a single genus (†*Protomeryx*) which was the same as that found in the lower Miocene. A very small and dainty little creature (†*Hypertragulus*) belonged to another family, the relationships of which are not clear.

To the middle and lower Oligocene is referred the great White River formation of South Dakota, Nebraska, Wyoming, etc., which is divisible into three clearly marked substages. The White River contains the best-known fauna of all of the North American Tertiaries, for collecting in these beds has been carried on for more than sixty years, and a greater number of complete and nearly complete skeletons has been secured than from any of the other formations. It is plainly evident that a land-connection existed with the Old World, which was interrupted in the John Day, as is shown by the intermigration of characteristic forms; but some barrier, presumably climatic, prevented any complete interchange of mammals, and very many genera and even families remained confined to one continent or the other.

The aspect of the White River fauna changes in accordance with the direction from which it is approached. If one comes to the study of it from the Eocene, it displays a very modern aspect, given by the almost complete disappearance of the archaic groups of mammals and by the great multiplication of genera and species belonging to the progressive orders. These genera, it is true, are all extinct, but many of them stood in an ancestral relationship to modern forms. On the other hand, if approached from the Miocene side, the White River mammals seem to be very ancient and primitive and very different from anything that now lives. We speak of horses and rhinoceroses, dogs and cats, in this fauna, but those terms can be employed only in a very wide and elastic sense to designate animals more or less distantly allied to those of the present day.

Several species of opossums, some of them very small, were the only marsupials in North America then, as they are now.

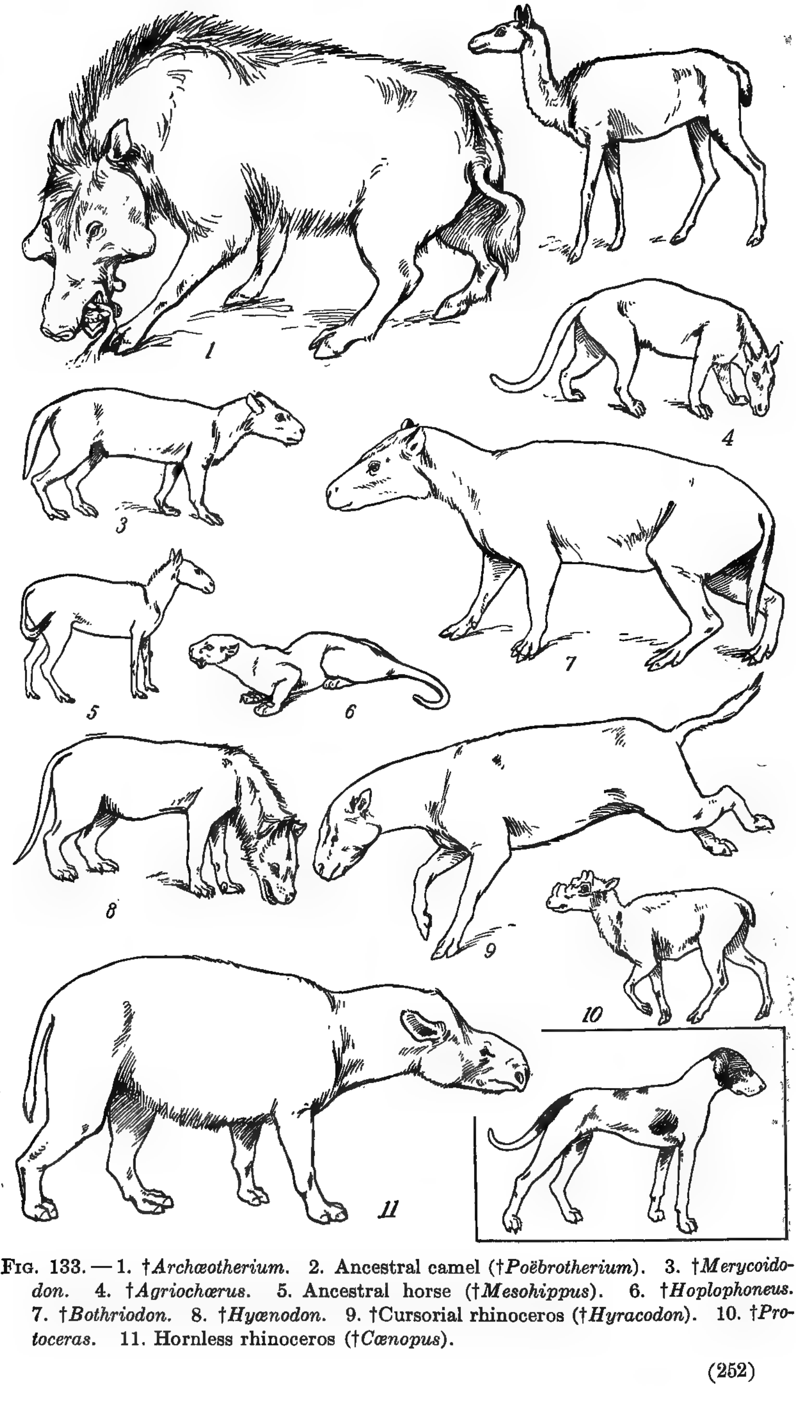

Fig. 133. — 1. †*Archæotherium.* 2. Ancestral camel (†*Poëbrotherium*). 3. †*Merycoidodon.* 4. †*Agriochœrus.* 5. Ancestral horse (†*Mesohippus*). 6. †*Hoplophoneus.* 7. †*Bothriodon.* 8. †*Hyænodon.* 9. †Cursorial rhinoceros (†*Hyracodon*). 10. †*Protoceras.* 11. Hornless rhinoceros (†*Cœnopus*).

There was quite a variety of Insectivora; some were survivals of a family that was abundant in the Eocene, others, like the hedgehogs, moles and shrews, were probably immigrants. Here we find the last of a group (order or suborder) of ancient and primitive flesh-eaters, the †Creodonta, that had played a great rôle in the Eocene and Paleocene of North America and Europe. In White River times but a single family (†Hyænodontidæ), with two genera, remained of the Eocene host. One of these genera (†*Hemipsalodon*), a very large beast of prey, which was almost identical with the Old World genus †*Pterodon*, was confined to the lower substage of the White River beds in the Northwest Territory of Canada; the other, †*Hyænodon*, which was also an Old World form, was represented abundantly in the United States by many species. In size, these species ranged from a small fox to a large wolf, but they all had disproportionately large heads, and small, weak feet, with blunt claws, so that they must have been very curious-looking creatures and were probably carrion-feeders rather than active catchers of prey. The White River members of the family

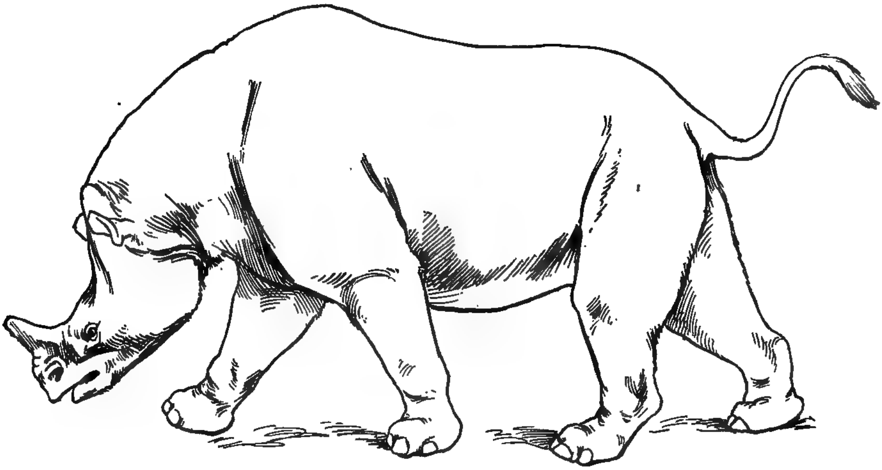

FIG. 134. — White River †titanothere (†*Titanotherium robustum*) reduced to the same scale as Fig. 133.

were migrants from the eastern hemisphere, for, though small and primitive representatives of it occurred in the North American Eocene, as well as in the corresponding formations of Europe, the family appears to have died out in America and to have been renewed by the Oligocene migration.

Coincident with this decline of the †creodonts and, no doubt, causally connected with it, was the rise of the true Carnivora, which for the first time were numerous and were divisible into three distinct families. Small and primitive representatives of the wolves (†*Daphœnus*) and possibly also of the foxes (†*Cynodictis*) were quite common, and there were a few species of the musteline family, evidently immigrants and the most ancient yet found in America. There were several species of the †sabre-tooth cats (†*Dinictis* and †*Hoplophoneus*) all of which, except in the uppermost substage, were quite small, few of them exceeding the Canada Lynx in size. A much larger animal (†*Eusmilus*, also European) appeared in the latter part of the stage. None of the true cats, or feline subfamily, has been obtained. Nothing is yet known of the time and place of origin of the †sabre-tooth series, for they appeared at approximately the same date in Europe and America, and in neither continent have any possible ancestors been found in preceding formations. The problem is like that of the Proboscidea (*see* p. 234), but Egypt has given no help in the case of the †sabre-tooths, and, by a process of elimination, we reach the conclusion that these strange creatures probably arose somewhere in Asia and sent out migrants eastward and westward.

The Rodentia were fairly abundant and present a strange mixture of ancient and comparatively modern types. One very common genus (†*Ischyromys*), which was the last remnant of a family almost limited to the North American Eocene, was associated with the earliest American mice, arboreal and ground squirrels, beavers and rabbits; some, if not all, of these were immigrants.

The hoofed mammals were present in fairly bewildering variety, but were restricted to the two orders of the Perissodactyla and Artiodactyla. The Perissodactyla, while they no longer had the relatively dominant position which they held in the middle Eocene (*see* p. 270), had suffered no actual loss; and no less than seven families of them, or six by another scheme of classification, had members in the North America of White River times, a very notable difference from the present order of things, when there are but three families in the entire world, none of which enters North America. The Eocene family of the †titanotheres became extinct at the end of the lower substage of the White River, but in that substage there was a marvellous abundance of these huge beasts, some of which were of almost elephantine stature and bulk. The pair of great bony, horn-like protuberances on the nose varied much in size and form in the different species, short to very long, triangular, cylindrical, flattened and shovel-shaped, and gave these ungainly creatures somewhat the appearance of strange and very large rhinoceroses. The †titanotheres were a typically North American family, but sent migrants to the Old World, at least two species reaching southeastern Europe. Rhinoceroses too were extremely numerous and diversified throughout the stage and are very plainly divisible into three strongly contrasted series, which are sometimes regarded as three subdivisions of the same family and sometimes put into two separate families. One of these series, the †hyracodonts (†*Hyracodon*), was composed of small, long-necked and long-legged, slender and lightly built, cursorial animals, but with short, heavy heads, which gave them a somewhat clumsy look; having neither horns nor tusks, they were entirely defenceless and depended for their safety upon speed alone. The second series, or †amynodonts (†*Metamynodon*), formed the very antithesis of the first, — large, heavy, short-necked, and short-legged and probably amphibious in manner of life, they were armed with formidable tusks; and their skulls were so curiously modified as to bear a distinct resemblance to the skull of a huge carnivore. The †amynodonts migrated to the Old World and occur in the Oligocene of France, but the †hyracodonts would seem never to have left North America. The third series, that of the true rhinoceroses, comprised several genera at different levels in the White River beds (†*Trigonias*, †*Cœnopus*, etc.); they were of uncertain origin and it has not yet been determined whether they were immigrants or of native stock. Many species have been found, varying much in size, up to that of a modern tapir, and not unlike one in proportions, for they were of lighter build and had relatively longer legs than any existing rhinoceros. The species of the lower and middle substages were all hornless, but in the uppermost substage we find skulls with a pair of nasal horns in an incipient stage of development. This was the beginning of the †paired-horned rhinoceroses (†*Diceratherium*) which so flourished in the John Day and the lower Miocene.

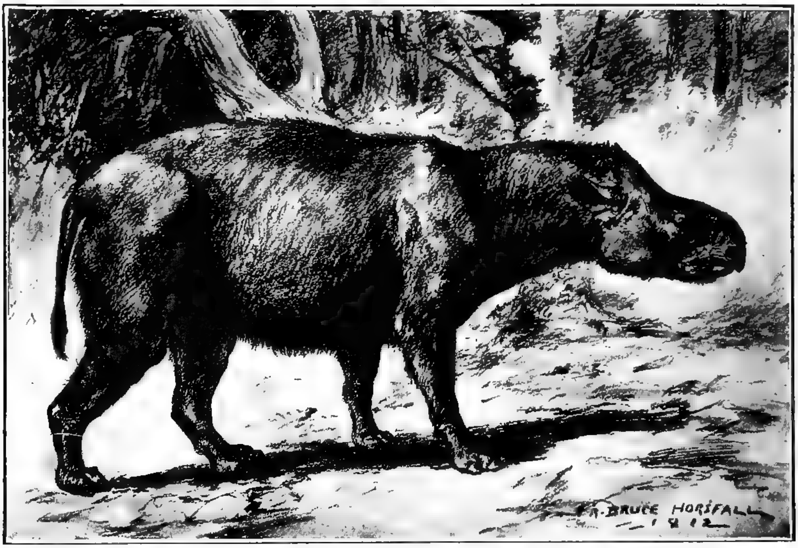

FIG. 135. — †Hornless rhinoceros (†*Cœnopus tridactylus*) of the White River stage. Restored from a skeleton in the American Museum.

Of the horses there was no great variety and all the species so far discovered are included in a single genus (†*Mesohippus*), though there was a decided increment in the size of the successive species from the earlier to the later portion of the stage. Looked at superficially, it seems absurd to call these little creatures "horses" at all and the term can be justified only as implying that they were ancestral members of the family. The largest of the White River species hardly exceeded a sheep in size and all of them had comparatively short necks, long and slender legs and three-toed feet. The low-crowned grinding teeth show that they were browsers, not grazers. The abundant Eocene family of the †Lophiodontidæ made its last appearance in the White River, where it was scantily represented by slender, long-legged animals (†*Colodon*), with feet singularly like those of the contemporary horses, except that there were four toes in the front foot. Tapirs (†*Protapirus*) were very much less common than rhinoceroses or horses and were hardly half as large as the existing species of the family and of relatively far more slender form; the development of the proboscis had already begun. Lastly, the presence of the clawed †chalicotheres has been reported from the lower Oligocene of Canada, but the material is too fragmentary for generic reference.

Though the number of artiodactyl families yet identified among the White River fossils is no larger than that of the perissodactyl families, the artiodactyls greatly preponderated in individual abundance. The peccaries, which were fairly common, resembled those of the John Day, but were considerably smaller. Of the camels, there were two series, one of which (†*Eotylopus*), lately described by Dr. Matthew, is of yet unknown significance, while the other (†*Poëbrotherium*) was apparently the ancestor common to all the subsequent phyla of camels and llamas. This extremely interesting genus had species which ranged in size from a gazelle to a sheep, had two toes in each foot, a moderately elongate neck and teeth which were beginning to assume the high-crowned character. From this it may be inferred that those animals were, partly at least, of grazing habit, which was rare among White River ungulates, most of which fed upon leaves and soft and succulent plants. An extinct family, the †Hypertragulidæ, were a greatly diversified group of dainty little creatures, one of which (†*Hypisodus*) was no larger than a rabbit and had high-crowned teeth. The other genera (†*Leptomeryx*, †*Hypertragulus*) must have resembled in form and proportions the tiny little chevrotains or "mouse-deer" of the East Indian islands. Late in the age arose a larger form of this family, nearly equalling the Musk-Deer in size, the extraordinary genus †*Protoceras*, which was, especially the males, a grotesque object. The males had a pair of upper canine tusks and two pairs of prominent long protuberances on the skull. This, or some similar form, must have been the ancestor of the still more bizarre †*Syndyoceras* of the lower Miocene.

The †oreodonts were by far the commonest of White River mammals, and evidently they roamed the woods and plains in great herds. There were several species, larger and smaller, of the abundant genus (†*Merycoidodon*) but the largest did not surpass a modern peccary in size and was somewhat like that animal in appearance, but had a shorter head and much longer tail. In the upper substage appeared a very peculiar genus of this family (†*Leptauchenia*), animals with short, deep, almost monkey-like heads, and presumably aquatic in habits. The †*agriochœrids* were very much less common; they may be described roughly as †oreodonts with very long, cat-like tails and clawed feet.

All of the foregoing artiodactyl families were exclusively North American in Oligocene distribution; even the camels did not reach Asia till the Pliocene, and the other families never invaded the Old World at all. There were, however, two additional families, which also occurred in the eastern hemisphere, whence one of them, and possibly the other, was derived. The unquestionably Old World family, that of the †anthracotheres, was represented in the White River by two genera (†*Bothriodon* and †*Anthracotherium*), which were short-legged, long-snouted, swine-like animals, which have no near relations in the modern world. The other family, the †giant pigs, which we have already met with in the lower Miocene and upper Oligocene, is of doubtful origin, and nothing has yet been found in the preceding formations of either North America or Europe which can be regarded as ancestral to them. The White River genus (†*Archæotherium*) was very like the John Day and Arikaree genera, but most of the species were much smaller and some were not so large as a domestic pig. In the uppermost beds, however, are found huge species, which rivalled those of the subsequent formations. That these strange animals were rooters and diggers and therefore pig-like in habits is indicated by the manner in which the teeth are worn.

FIG. 136. — †*Merycoidodon culbertsoni*, the most abundant of White River †oreodonts. Restored from a skeleton in the American Museum of Natural History.

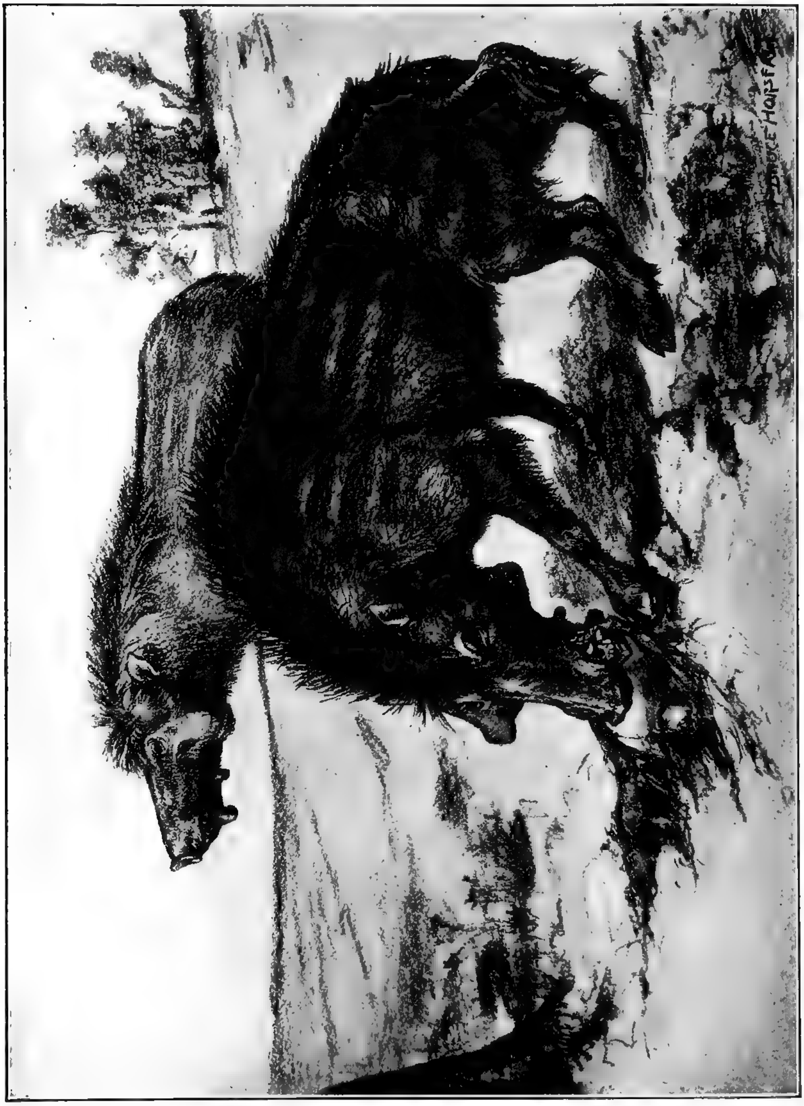

FIG. 137. — †Giant pig (†*Archæotherium ingens*) from the lower White River stage. Restored from a skeleton in the museum of Princeton University.

South America. — The older continental Tertiary formations of South America cannot be correlated with those of North America or Europe, because they have nothing in common. Difficult as it is to give a correct and adequate conception of the Tertiary mammalian life of the northern hemisphere to one who has not made a study of it, it is far more difficult in the case of South America. The stock of adjectives, such as "peculiar," "bizarre," "grotesque" and the like, already overworked in dealing with northern forms, is quite hopelessly inadequate where everything is strange. In addition to this, we are seriously handicapped in treating of the Oligocene and Eocene of South America by very incomplete knowledge. Many fossils have been collected and named, but the great majority of these are known only from teeth; a few skulls and limb-bones have been described, but no skeletons, and therefore much is very uncertain regarding these faunas.

The Deseado formation (Pyrotherium Beds) has been variously referred by different writers from the upper Cretaceous to the lower Miocene, but its most probable correlation is with the Oligocene. Though most of the mammalian groups are the same as those of the Santa Cruz, the proportions of the various orders in the two faunas are very different, but, to some extent, the difference is probably illusory and due to the conditions of fossilization, for, as a rule, the small mammals are much less frequent and well preserved in the older beds. As in the Santa Cruz, the marsupials were the only predaceous mammals, and some of them attained gigantic size; but no such variety of these beasts of prey has been found in these beds as occurred in the middle Miocene. In addition, there were numerous small herbivorous marsupials. One of the most striking differences from the Santa Cruz fauna was in the very much smaller number of Edentata, which, instead of being extremely common, are quite rare among the fossils. No doubt there was a real and substantial difference in this respect, but it was probably not so great as it seems, and the same three suborders are found in both formations. One of the few †ground-sloths that have been obtained was very large (†*Octodontherium crassidens*), a much larger animal than any species of the suborder that is known from the Santa Cruz. The †glyptodonts were also rare, and only two genera and species have been described from very scanty remains. Armadillos, on the other hand, were much more common, and no less than eleven genera have been named, three of which occurred also in the Santa Cruz. Among these was the remarkable genus †*Peltephilus*, in which the anterior two pairs of plates of the head shield were modified into horn-like spines.

Equally striking was the remarkable diminution of the Rodentia, as compared with those of the Santa Cruz, though, of course, this is an inaccurate mode of stating the truth, occasioned by the fact that we are following the history in reverse order. It would be preferable to say that the rodents underwent a remarkable expansion in the Santa Cruz. These rodents of the Deseado stage are the most ancient yet discovered in South America and represent only two families, both belonging to the Hystricomorpha, or porcupine group. If, as Dr. Schlosser and other European palæontologists maintain, the Hystricomorpha were all derived from a family of the European Eocene, this would necessitate a land-connection between South America and the Old World independent of North America, for the latter continent had no hystricomorph rodents until the connection between the two Americas was established.

The great bulk of the Deseado fauna is made up, so far as individual abundance is concerned, of hoofed animals belonging to the typically South American groups. The †Toxodonta were represented partly by genera which were the direct ancestors of the common Santa Cruz genera (†*Pronesodon*, †*Proadinotherium*), and, more numerously, by a very peculiar family, the †Notohippidæ, which had highly complex, cement-covered grinding teeth. Still a third family of this suborder, the †Leontiniidæ, was highly characteristic of the Deseado fauna and is not known from the Santa Cruz. These were large animals, with a small horn on the tip of the nose and low-crowned, comparatively simple grinding teeth. Even more abundant were the †Typotheria, small forms which were ancestral to the Santa Cruz genera, larger ones which died out without leaving successors and one quite large animal (†*Eutrachytherus*) which seems to have been the ancestor of the Pliocene and Pleistocene †*Typotherium.* This series is not known to have been represented in the Santa Cruz and may have withdrawn from Patagonia at the end of the Deseado stage.

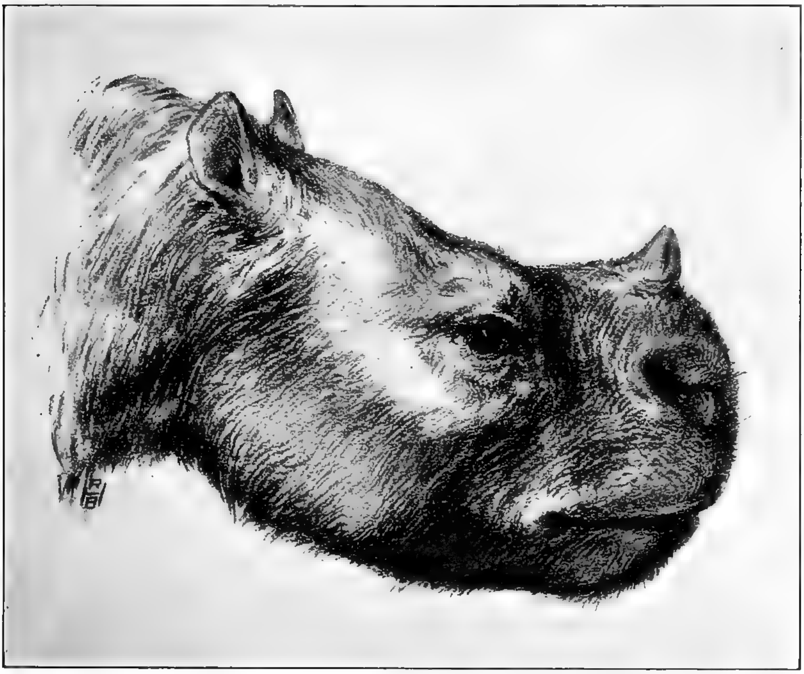

FIG. 138. — Horned †toxodont (†*Leontinia gaudryi*), Deseado stage. Restored from a skull in the Ameghino collection.

The †Entelonychia, those strange toxodont-like animals with claws instead of hoofs, were much more numerous and varied than they were afterward in the Santa Cruz, when they were on the verge of extinction, and included both very small and very large species. The †Pyrotheria, a suborder which is not met with in the Santa Cruz or later formations, likewise included some very large forms. The typical genus, †*Pyrotherium,* included large, relatively short-legged and very massive animals; the upper incisors formed two pairs of short, downwardly directed tusks, and in the lower jaw was a single pair of horizontally directed tusks; the grinding teeth were low-crowned and had each two simple, transverse crests. These grinding teeth and the lower tusks so resemble those of the ancestral Proboscidea in the Oligocene of Egypt, that the †pyrotheres have actually been regarded as the beginnings of the †mastodons and elephants, but this is undoubtedly an error. The †Astrapotheria, another group which became extinct at or soon after the end of the Santa Cruz, were relatively abundant in the Deseado and counted some very large species. Finally, the †Litopterna were represented by the same two families as continued through the Pliocene and one of them far into the Pleistocene. The horse-like †proterotheres were present, but not enough of them has been obtained to show whether or not they were in a notably less advanced stage of development than those of the Santa Cruz. The †macrauchenids were quite similar to those of the latter formation, though considerably smaller. In addition, there were a few genera, survivals from earlier times, which were not referable to either of these families.

The large number of genera, especially among the †toxodonts and †typotheres, which had high-crowned, cement-covered teeth, may be taken as an indication that grazing habits had already begun to be prevalent.

Of this wonderful assemblage of hoofed animals, divisible into six separate groups, whether of ordinal or subordinal rank, not a trace remains to-day. Not only are all the species, genera and families extinct, but the suborders and orders also. Further, this was a very strictly autochthonous fauna, so far as the hoofed animals were concerned, and no member of any of the six groups has ever been found outside of the Neotropical region.

4. *Eocene*

North America. — In the western interior of North America the Oligocene followed so gradually upon the Eocene, that there is great difficulty in demarcating them and much difference of opinion and practice obtains as to where the boundary line should be drawn. Not to depart too widely from the scheme used by Professor Osborn, the Uinta stage is here treated as uppermost Eocene, though this is a debatable procedure. For several reasons, the extraordinarily interesting and significant Uinta fauna is far less completely known than that of the preceding Bridger and succeeding White River stages. For one thing, it has been much less thoroughly explored, and it may be confidently expected that future exploration will greatly enlarge our knowledge.

The smaller mammals of the Uinta are particularly ill-known. No Insectivora have yet been found, though this gap will assuredly be filled; rodents are scanty in the collections and include only two families, one the †ischyromyids, which were still common in the White River, the other of doubtful position, but not improbably to be considered as the beginning of the pocket-gophers (Geomyidæ). The archaic flesh-eaters, or †Creodonta, were represented by two families, one comprising smaller animals with somewhat cat-like, shearing teeth (†Oxyænidæ), the other, very large beasts with crushing teeth (†Mesonychidæ), neither of which continued into the White River. As compared with the middle and lower Eocene, the †creodonts had greatly diminished and, to replace them, the true Carnivora were beginning to come in. As yet, however, only small and very primitive dog-like forms are known and no trace of †sabre-tooths or mustelines has been found. Indeed, it is very doubtful whether members of these families ever will be found in the Uinta, for their presence in the succeeding White River was probably due to immigration.

The Perissodactyla were the preponderant type of hoofed animals, and ancestral forms of most of the White River genera have already been identified. The †titanotheres (†*Diplacodon*, †*Protitanotherium*) were much smaller and lighter than those of the lower White River and had much shorter horns. The †hyracodonts, the lightly built, cursorial rhinoceroses, were represented by a genus (†*Triplopus*) which was smaller and more slender than the White River form (†*Hyracodon*) and its teeth were of distinctly more primitive character. The heavy, massive and presumably aquatic †amynodonts (†*Amynodon*) were likewise smaller and less specialized than their descendants of the Oligocene. No member of the true rhinoceros series has yet been identified in the Uinta, but there is some reason to think that they were nevertheless present. Tapirs are distinctly indicated by certain fossils, but they are still too incompletely known to make possible any statement as to their degree of development. The horses (†*Epihippus*), like the other families mentioned, were much smaller and distinctly more primitive than their successors in the Oligocene.

The Artiodactyla were, for the first time in the history of North America, as numerous and as varied as the perissodactyls and, with the exception of the peccaries and †anthracotheres, representatives of all the White River families are known. The finding of the peccaries is merely a question of further exploration, but the †anthracotheres were migrants from the Old World, and there is no likelihood that they will be discovered in the Uinta at any future time. Fairly large, pig-like animals, probably referable to the †giant-pigs or †entelodonts, occurred, but nothing has yet been found which can be considered as the direct ancestor of the White River genus. As was true of the perissodactyls, the Uinta artiodactyls were nearly all much smaller and more primitive than their Oligocene descendants and the differences are most interesting from the evolutionary point of view. The ancestral camel (†*Protylopus*) was a little creature no bigger than a fox-terrier, though the †hypertragulids (†*Leptotragulus*) were as large as †*Leptomeryx* and †*Hypertragulus* of the White River. The most ancient known members of the †oreodonts (†*Protoreodon*) and the †agriochœrids (†*Protagriochœrus*) are found in the Uinta.

The middle Eocene fauna, Bridger stage, though it passed upward very gradually into that of the Uinta, was yet, on the whole, very different from the latter. It was exclusively indigenous and so radically distinct from the mammals of corresponding date in Europe as to preclude the possibility of a land-bridge with that continent. In the lower Eocene, as will be shown in a subsequent page, the communication between the two continents was broadly open and the faunas of the two continents were much more closely similar than they have ever been since. It is really remarkable to see with what comparative rapidity the two regions, when severed, developed different mammals under the operation of divergent evolution. Had the separation continued throughout the Tertiary and Quaternary periods, North America would now have been as peculiar zoölogically as South America is, a result which has been prevented by the repeated renewal of the connection.

The characteristic features of the Bridger mammalian fauna were chiefly due to the great expansion and diversification of certain families, which began their career at an earlier stage, and to the disappearance of many archaic groups which had marked the more ancient faunas. Other archaic groups, however, survived and even flourished in the Bridger, and of these it is particularly difficult to convey a correct notion to the reader, because they were so utterly unlike anything that now lives. One of these orders, the †Tæniodontia, which had so many points of resemblance to the †ground-sloths that several writers have not hesitated to include them in the Edentata, survived only into the older Bridger, but the equally problematical †Tillodontia then reached their culmination, though they were not very numerous. Though not at all related to that group, the †tillodonts looked like huge rodents, with their chisel-like incisor teeth. There was a remarkable assemblage of Insectivora, more numerous and varied than in any subsequent formation, no less than six families being known. One of these somewhat doubtfully represented the moles and two others modern Asiatic groups. The very unexpected discovery of an armadillo in the Bridger has been reported, but the propriety of referring this animal to the armadillos, or even to the edentates, has not yet been proved, and it would therefore be premature to discuss its significance. The only marsupials were opossums.

So far as our information extends, there were no true Carnivora in the Bridger, all the beasts of prey of the time belonging to the archaic †Creodonta, which then reached their maximum development in numbers and diversity. One family (†Oxyænidæ) included large and powerful flesh-eaters, with cat-like dentition and short, rounded, lion-like heads, long bodies and tails and short, heavy limbs, giving them the proportions of otters. Another (the †Hyænodontidæ) comprised small, long-headed, fox-like and weasel-like animals, which doubtless preyed upon small mammals and birds. A third family (†Mesonychidæ) was made up of moderate-sized, long-jawed creatures, which must have resembled, rather remotely, short-legged and long-tailed wolves and hyenas. Their habits and mode of life are somewhat problematical, for their grinding teeth were blunt, not adapted to the shearing of flesh, and their claws were broad, almost hoof-like. Such creatures could hardly have subsisted by the pursuit of living prey and were probably carrion-feeders and more or less omnivorous. The †Miacidæ, a family which connected the †creodonts and true carnivores and might almost equally well be placed in either group, were externally much like the small †hyænodonts, but were more efficiently equipped for the capture and devouring of prey.

Of the archaic and extinct orders of hoofed animals, the only one which persisted from earlier times into the Bridger and greatly flourished there was the †Amblypoda, one family of which (†Uintatheriidæ) was preëminently characteristic of middle Eocene life, becoming very rare and then dying out in the upper Eocene. The †uintatheres of the Bridger underwent considerable modification in size and appearance within the limits of the stage, the larger and stranger species appearing toward the end of the time. Most of these great creatures may fairly be called gigantic, for they equalled the largest modern rhinoceroses and smaller elephants in size. The body, limbs and feet were so elephantine in character that they were once believed to be ancestral Proboscidea, but the teeth and the fantastic skull were so radically different that this belief was long ago abandoned. The upper canine teeth were converted, in the males, into formidable spear-like or scimitar-like tusks, protected by great flange-shaped expansions of the

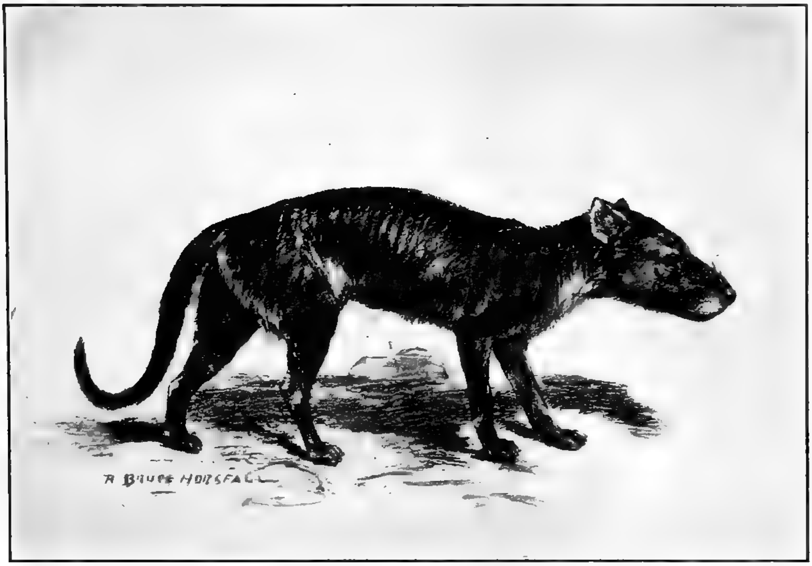

FIG. 139.—A mesonychid †creodont (†*Dromocyon velox*) of the Bridger stage. Restored from a skeleton in the Museum of Yale University.

lower jaw; bony knobs on the end of the nose probably supported a pair of dermal horns like those of a rhinoceros and, in addition, a pair of high, cylindrical, horn-like, bony protuberances arose above the eyes and another, more massive pair, near the back of the head. It would be difficult to imagine more extraordinary creatures than the †uintatheres, which were the largest land-mammals of their time. The family was entirely confined to North America, no trace of them having been found in any other continent.

While the backward and archaic orders, most of which have left no descendants in the modern world, had thus a stately representation in Bridger times, they were outnumbered in genera, species and individuals by the progressive orders, which are still in more or less flourishing existence. The Primates, whether lemurs or monkeys, were numerous, and this, so far as is definitely known, was their last appearance in extra-tropical North America. They may at any time be found in the Uinta, but there is small probability that they will ever turn up in the White River or later formations. The many rodents all belonged to the †ischyromyids, an extinct family which, there is much reason to believe, was ancestral to many families of the squirrel-like suborder of Sciuromorpha. Most of them were species of a single genus (†*Paramys*) and varied in size from a mouse to a beaver, or even larger.

The Perissodactyla may be said, in one sense, to have reached their culmination in the Bridger; not that many of them, such as the horses and rhinoceroses, did not advance far beyond their state of development in the Eocene, but at no subsequent time did the order as a whole possess such dominating importance. There were five or six families of perissodactyls in the Bridger, and their remains are much the most abundant fossils found there. Individually, the commonest perissodactyls of the time were the †titanotheres, of which there were several genera and many species, differing chiefly in size and proportions, though the largest hardly exceeded

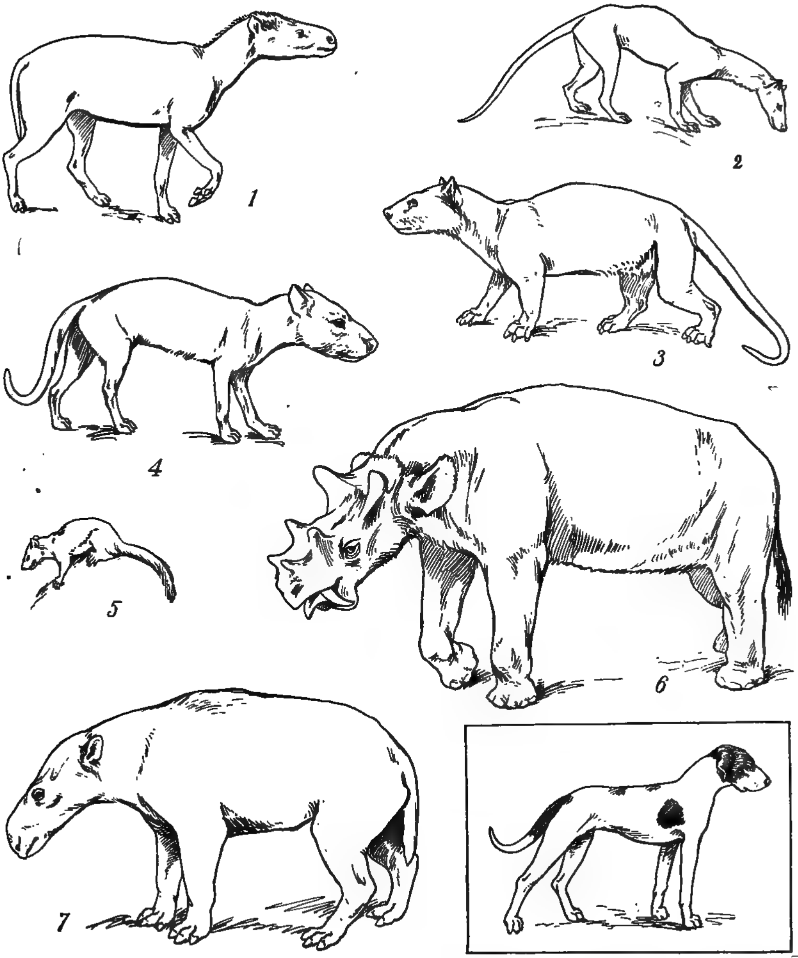

FIG. 140. — Some characteristic mammals of the Bridger Eocene reduced to a uniform scale, with a pointer dog, in frame, for comparison. 1. Primitive rhinoceros (†*Hyrachyus eximius*). 2. †*Tritemnodon agilis*. 3. †*Patriofelis ferox*, and 4, †*Dromocyon velox*, †creodonts. 5. Primitive rodent (†*Paramys delicatior*). 6. †*Uintatherium alticeps*. 7. †Titanothere (†*Mesatirhinus superior*).

a modern tapir in stature and was not dissimilar in appearance. These Bridger †titanotheres were considerably smaller than those of the Uinta and therefore very much more so than the White River forms; it was not till the latter stage that the family lived up to its name of "titanic beasts." By far the commonest of the genera in the middle and lower Bridger was †*Palæosyops,* which was hornless, while in the upper part of the beds are found genera (*e.g.* †*Manteoceras* and †*Dolichorhinus*) in which the horns were just beginning to appear. Another extinct family, the †Lophiodontidæ, which was very abundant in the European Eocene, formed a very subordinate element in this fauna and included a number of small tapiroid genera (*e.g.* †*Helaletes*).

The horses (†*Orohippus*) were very small and primitive creatures, no bigger than a fox, with four toes in the front foot and three in the hind. So completely different in appearance and proportions were these little animals from any of the modern horses, that it requires an effort of the imagination to think of them as belonging to the same family, and it is only by employing the family to designate a *genetic series* that such a classification can be justified. The †hyracodonts, or cursorial rhinoceroses, were very abundantly represented by a number of small and medium-sized animals (†*Hyrachyus*) which had less specialized teeth, shorter neck and limbs than their upper Eocene and Oligocene successors, and four toes in the front foot; one genus (†*Colonoceras*) had a pair of nasal horns, but would seem to have died out without leaving descendants. In the upper part of the beds is found the Uinta genus †*Triplopus,* with three-toed fore foot; and in the same division occurs another Uinta genus, †*Amynodon,* the most ancient known species of the supposedly aquatic rhinoceroses. True rhinoceroses, that is animals which were directly ancestral to the modern members of the family, have not been identified and may not have been present in North America; that is still an open question. Tapirs, all of them quite small, were relatively common, but are still very incompletely known. The earliest known members of the clawed †chalicotheres were of Bridger date.

It is worth remarking that, except a single genus in the upper and later portion of the stage (†*Triplopus*), all of the

Bridger perissodactyls had four toes in the front foot and three in the hind, while in the White River beds above the lowest substage the number three in both fore and hind feet was almost equally universal.

One of the most radical and striking differences between the Uinta and Bridger faunas was the rarity of Artiodactyla in the latter, which is in almost equally strong contrast with their abundance in the middle Eocene of Europe. Most significant of these rare Bridger artiodactyls were the little creatures (†*Homacodon*), hardly so large as a domestic cat, which may fairly be regarded as a very early stage, if not the actual beginning, of the great camel family, which was destined to play so conspicuous a part in the life of America, North and South. Small pig-like animals (†*Helohyus*) which were no doubt ancestral to the peccaries, were fairly common and there were, in addition, relatively large animals (†*Achænodon*) allied, but not ancestral, to the †giant-pigs of the Oligocene; some of these were considerably larger than a full-grown Wild Boar (*Sus scrofa*).

Among all the many hoofed mammals of the Uinta and Bridger there was not a single one that had the high-crowned, persistently growing teeth of the grazers; all of them must have had browsing habits and have fed upon such soft vegetable tissue as did not rapidly abrade the teeth. The same statement applies, *á fortiori*, to the stages antecedent to the Bridger and therefore to the entire Eocene and Paleocene. From these facts it may be inferred that the grasses had not yet taken possession of wide areas. Concerning the Bridger fauna, Professor Osborn, who has done so much to elucidate it, says: "On the whole, it is a very imposing, diversified and well-balanced fauna, with an equal distribution of arboreal, cursorial, aquatic, fossorial, carnivorous and herbivorous types."

The lower Eocene is divisible into two stages, in descending order, the Wind River and Wasatch, both extensively exposed in central Wyoming. As would be expected from its stratigraphical position, the Wind River fauna was largely transitional between that of the Bridger above and that of the Wasatch below. Unfortunately, the fossils are far less numerous than those of the Bridger and not so well preserved, and therefore give us a less adequate conception of the life of that time. The archaic, non-progressive orders were strongly represented, but already the progressive groups were in a numerical majority of species; most of these archaic orders may be most advantageously described in connection with the Wasatch. Opossums were almost certainly present, though the available specimens are too fragmentary for assured determination. The †tillodonts, †tæniodonts and insectivores differed little from the Wasatch representatives of these orders, except that the Bridger †tæniodont, †*Stylinodon,* which had rootless, persistently growing teeth, was associated with the Wasatch genus †*Calamodon.* On the other hand, the primitive flesh-eaters, or †creodonts, which were referable to Wasatch families, were less numerous and varied and formed a mixture of Bridger and Wasatch genera. The †Oxyænidæ, the family with cat-like teeth and head, had both the smaller Wasatch genus †*Oxyæna* and the very large Bridger †*Patriofelis.* Of the blunt-toothed †Mesonychidæ, one very large animal (†*Pachyæna*) survived from the Wasatch. The small forms of the family †Hyænodontidæ were common, and there were numerous species of the progressive family †Miacidæ.

Among the hoofed animals there were two of the antique orders which became extinct before the end of the Eocene, indeed, one of these groups, the †Condylarthra, made its last appearance in the Wind River. This extremely primitive group, which, in a sense, connected the hoofed with the clawed mammals, will be described under the more ancient faunas. The other order, the †Amblypoda, was represented by two very different families, one of which, the †uintatheres, was so flourishing in the Bridger, where it formed the most characteristic and by far the most striking element of the fauna.

The Wind River genus (†*Bathyopsis*) was a very much smaller animal than any of the Bridger forms and its horn-like protuberances were in an incipient state, while in various other respects it was decidedly more primitive than its successors. The second family was represented by the genus †*Coryphodon*, which did not survive into the Bridger, but was especially characteristic of the Wasatch fauna, with which it will be described.

Turning now to the progressive orders, we note that the rodents, lemurs and monkeys were very similar to those of the Bridger and belonged to the same families, but were decidedly less numerous. This difference, however, may be rather apparent than real and due to the much more favourable conditions for the preservation of small mammals in the middle Eocene. Among the Perissodactyla, the horses were intermediate in size and structure between those of the Bridger and those of the Wasatch, but were decidedly nearer to the latter. The †lophiodonts, so far as known, were represented by a single genus (†*Heptodon*) which also occurred in the Wasatch. The modest beginnings of the †titanotheres, the family which became so very conspicuous in the middle and upper Eocene and lowest Oligocene, may be noted in the Wind River fauna, in which there were two genera. One of these (†*Eotitanops*), the very probable ancestor of all the subsequent genera, was quite small, about two-thirds the size of a modern tapir, while the other (†*Lambdotherium*) was a much smaller, lighter and more slender animal and apparently belonged to an abortive, short-lived phylum. Then, too, the first of the †hyracodonts, or cursorial rhinoceroses, made their appearance here in the genus †*Hyrachyus*, which was afterward so common in the Bridger.

No Artiodactyla have yet been found in the Wind River, though there can be little doubt that they then inhabited North America, as they did both before and afterward.

The Wind River fauna was of so much less peculiar and isolated character than that of the Bridger as to suggest a connection with the eastern hemisphere, a suggestion which is strengthened by the unheralded appearance of the †titanotheres and †hyracodonts, of which no forerunners have been found in the Wasatch.

The lowest and most ancient of the Eocene faunas is that of the Wasatch formation, which is extensively developed in central and southern Wyoming, Utah and New Mexico. The fauna of this stage is plainly divisible into two groups: (1) those types which were the descendants of American Paleocene mammals and were therefore indigenous, and (2) the immigrants from other continents. The indigenous mammals, which almost all belonged to orders now extinct, few of which survived later than the Eocene, must have given a very bizarre appearance to the assemblage, especially as they were more numerous, varied and, for the most part, larger and more conspicuous than the newcomers. Marsupials have not yet been found, but the occurrence of opossums in the Bridger and probably in the Wind River gives some reason to believe that they were in North America during Wasatch times also. The †Tæniodontia, which bore a certain resemblance to South American edentates, had one pair of incisor teeth above and below enlarged and chisel-shaped, somewhat like those of rodents. The †Tillodontia were much smaller than those of the Bridger, and their incisors were only beginning to take on the chisel-like form. Insectivora were quite abundant, and three, or perhaps four, families were represented in the Wasatch; some of these resembled the modern aquatic insectivores of the west African rivers and others were more like European hedgehogs.

The flesh-eaters all belonged to the †Creodonta, and, though rather less diversified than those of the Bridger, were yet relatively abundant. In size, they ranged from little creatures not larger than a weasel up to truly enormous beasts, and differed, no doubt, largely in habits and manner of life.

For the most part, the families were the same as those of the Bridger †creodonts, but the genera all were different. The †oxyænids (†*Oxyæna*) were much smaller and lighter than the large and massive representatives found in the middle Eocene, and their teeth were not so cat-like. Another group of predaceous animals (†*Palæonictis*) which also inhabited Europe, but did not survive the lower Eocene in either continent, had short, broad and very cat-like heads. The †mesonychids were far larger than those of the Bridger, a departure from the ordinary rule, and the several species of the common Wasatch genus (†*Pachyæna*) had grotesquely large heads. A family (†Arctocyonidæ), of very extensive geographical range and great antiquity, had its last representatives here in a very curious animal (†*Anacodon*) which had the flat-crowned, tuberculated grinding teeth of the bears and the enlarged, scimitar-like upper canines of the †sabre-tooth cats. Such a combination seems utterly incongruous and no one would have ventured to predict it. The progressive family of †creodonts (†Miacidæ) was already quite numerously represented, but only by small forms, which must have preyed upon small mammals, birds and lizards.

Two archaic orders of hoofed mammals were fairly numerous. One, the †Condylarthra, comprised quite small, five-toed animals, with long tails and short feet and extremely primitive in structure. A genus (†*Phenacodus*) of this order was long regarded as being ancestral to most of the higher orders of ungulates, but this belief has proved to be untenable. More numerous were the †Amblypoda, one genus of which (†*Coryphodon*), though persisting into the Wind River, was especially characteristic of the Wasatch. The †coryphodonts were the largest of lower Eocene mammals, and some of the species equalled a tapir or small rhinoceros in length and height, but had heavier limbs; as the skeleton conclusively shows, these must have been heavy, clumsy and exceptionally ugly brutes, with formidable tusks, large head, but relatively more

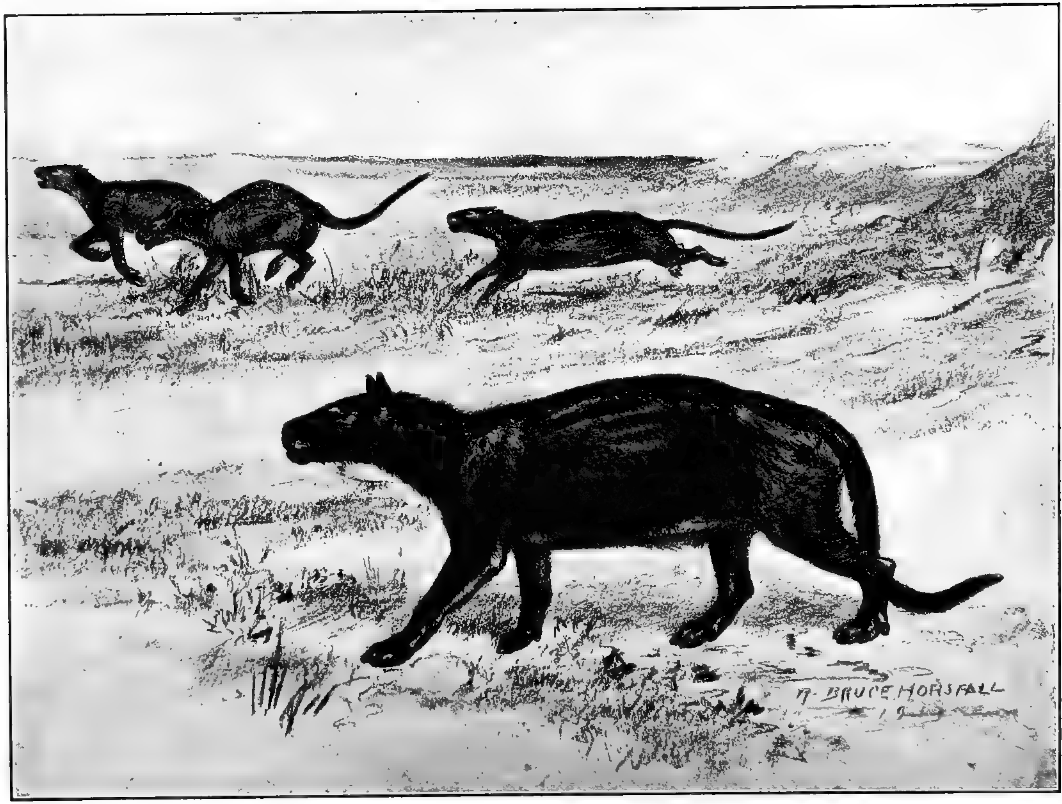

FIG. 141.—†*Phenacodus primævus*, the best known Wasatch representative of the †Condylarthra. Restored from a skeleton in the American Museum of Natural History.

slender body, short and massive limbs and elephantine feet. In appearance, these strange beasts were not altogether unlike the Hippopotamus and were perhaps more or less amphibious in habits. The other family of †Amblypoda, the †uintatheres,

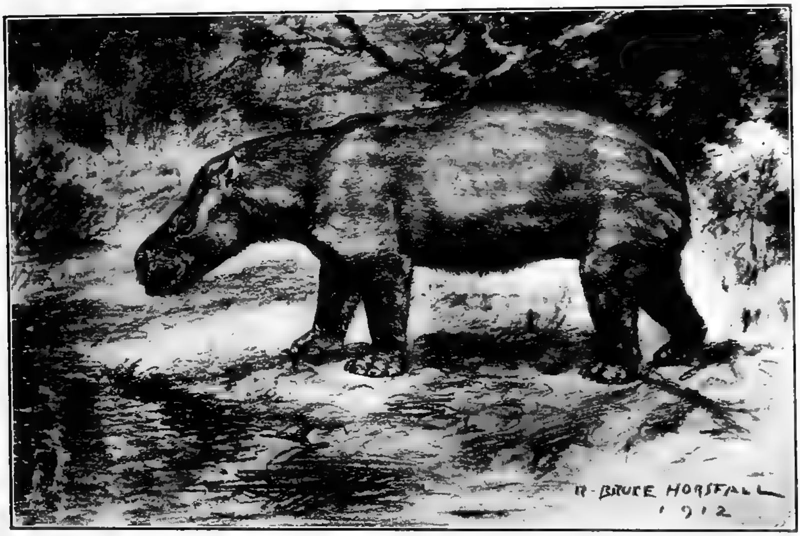

FIG. 142. — The commonest of Wasatch ungulates, the †amblypod, †*Coryphodon testis*. Restored from a skeleton in the American Museum of Natural History.

have not yet been registered from the Wasatch, but they will undoubtedly be found there, as they were unquestionably present at that time.

All of the preceding groups were of the archaic, non-progressive type and have long been extinct. With the sole exception of one †creodont family (†Miacidæ) and perhaps some of the insectivores, they have no descendants or representatives in the modern world. All of them appear to have been indigenous and derived from North American ancestors, though it is possible that a few were immigrants. We now turn to the orders which were more significant of the future, because they had within them the potency of a far higher development. These progressive groups were all immigrants, coming to North America from some region which cannot yet be positively identified, but most probably was Asia. From the same region and at a corresponding period of time Europe received many of the same forms, and so many genera were at that time common to the latter continent and North America that a broad and easy way of intermigration must have been open.

One of these immigrant orders, the Rodentia, the most ancient known members of which were these species from the North American Wasatch, was represented by the same family (†Ischyromyidæ) and some of the same genera (†*Paramys*, †*Sciuravus*) as throve also in the Bridger stage.

There were two orders of hoofed mammals, which were newcomers to the western world, Perissodactyla and Artiodactyla. Of the former was a genus (†*Eohippus*) of the most ancient American horses. These most interesting little animals, no larger than small foxes and domestic cats, would hardly be called horses, were it not for the long series of gradual and successive modifications which led from †*Eohippus* up to the modern horses. The graceful little creatures had a short neck, curved back, and relatively short, slender limbs, with four functional toes in the front foot and three in the hind; and, though they differed from existing horses in almost every detail of teeth and skeleton, there was something unmistakably equine about them. From the abundance of their remains it may be inferred that herds of them swarmed in the forests and glades of Wasatch times. The second perissodactyl family, the †Lophiodontidæ, which comprised considerably larger animals, never attained to importance in America, but flourished and became greatly diversified in Europe. What are believed to be the most ancient tapirs yet discovered (†*Systemodon*) were individually very common in the Wasatch. This tapir was no larger than a Coyote, had no proboscis and was so little like a tapir in outward appearance that an observer might well be pardoned for overlooking the relationship; even the skeleton is of so indifferent a character that the reference of this genus to the tapirs cannot be positively made.

Of equal significance for the future was the arrival of the Artiodactyla, of which there were members of three families in the Wasatch, though individually they were much less common than the horses. These were geologically the oldest known artiodactyls, Europe having yielded none of this date, and are still too imperfectly known to justify any very positive statements about them. One genus, however (†*Trigonolestes*), tiny little creatures, like rabbits in size, would seem to represent the beginnings of the great ruminant tribe, now so very important a factor in the life of the world. A second genus (†*Eohyus*), considerably larger, is very doubtfully referable to the pigs; while a third (†*Parahyus*), still larger, was the first in the short-faced series of the †entelodonts, which persisted in ever increasing size through the whole Eocene, but could hardly have been ancestral to the true †entelodonts, or †giant-pigs, of the Oligocene, the place and time of whose origin are unknown.

Another immigrant order of great interest, since we ourselves belong to it, the Primates, made its first appearance in North America in the Wasatch, but was not destined to long life or great importance in this continent, where it did not survive the Eocene. Several different kinds of small, lemur-like and monkey-like creatures dwelt in the tree-tops of the Wasatch forests. One genus (†*Anaptomorphus*) had a remarkable likeness to the modern Tarsier (*Tarsius spectrum*) of the Malay peninsula and islands.

South America. — The Eocene of South America, referred by some writers to the upper Cretaceous, is very incompletely and unsatisfactorily known. The Casa Mayor formation (or Notostylops Beds), which has yielded a great variety of mammals, for the most part very fragmentary, probably contains not one but several successive faunas which have not yet been fully discriminated, and that of the next succeeding Astraponotus Beds is still but a scanty list. This list, however, includes the most ancient †glyptodonts yet discovered and the most ancient †astrapotheres in the narrow sense of the term. The Astraponotus Beds may be either Eocene or Oligocene in date.

Taking the Casa Mayor faunas as a whole, they were a very numerous and diversified assemblage of small mammals, without a single large one among them. There were no monkeys or rodents; otherwise, the orders were in almost all cases the same as those which made up the Santa Cruz fauna. The marsupials were represented by the opossums and by several of the carnivorous kinds, the only beasts of prey that South America had until the migrations from the north brought in the true Carnivora, late in the Miocene or very early in the Pliocene. There were also numerous small marsupials of peculiar type, of which the last living survivor is *Cœnolestes,* of Ecuador. Throughout the stage, armadillos were present in considerable variety, but are known only from the bony plates of the carapace, and therefore little can be determined as to their relationships to the modern families. Only a single and very problematical genus of the †ground-sloths, which afterwards throve so mightily in the Miocene and Pliocene, has been obtained and that in the later portion of the stage.

The orders of hoofed mammals were represented by many small animals, most of which are known only from the teeth, which show these Casa Mayor genera to have been far more primitive and less specialized than their descendants in the Deseado and Santa Cruz stages. All of them had the low-crowned grinding teeth of the browsers, and no grazers were then in existence, so far as is known. No †toxodonts, in the more restricted sense of that term, have been found, but the two allied suborders of the †Typotheria and †Entelonychia were numerously represented. Of the former there were two families and of the latter three, which is more than in the Deseado or Santa Cruz formations. One of the families of the †Entelonychia (†Notostylopidæ) consisted of very small, rodent-like animals, with a pair of chisel-shaped incisors in upper and lower jaw, and a second family (†Homalodontotheriidæ) contained genera which would seem to have been directly ancestral to those of the Santa Cruz, but were very much smaller than their successors. The very large and massive †Pyrotheria of the Deseado stage were represented by small animals, in which the grinding teeth had two pairs of conical tubercles, not yet united into transverse crests. Two families of the †astrapotheres, in the broad sense, were far smaller than their Oligocène and Miocene descendants. To the †Litopterna are referred a number of genera, in which the grinding teeth were tuberculated and had very imperfectly developed crests, so as strongly to suggest the teeth of the †Condylarthra. However, until something is ascertained regarding the skeleton, especially the feet, of these animals, their relationships will remain more or less doubtful.

It will be observed that these Casa Mayor faunas not only were made up exclusively of small animals, but also that they already were typically and characteristically South American and bore the stamp which remained essentially the same until the successive waves of migration from the north so greatly modified the composition of the Neotropical fauna. The absence of rodents and monkeys and the comparative unimportance of the Edentata gave a somewhat different character to these ancient faunas from those of the Santa Cruz and later formations.

5. *Paleocene*

North America. — A very important discovery is one lately made by American Museum parties of a formation intermediate between the Wasatch and Torrejon. The interesting fauna of these beds has not yet been described, but it may be remarked that it contained none of the immigrant orders.

The vegetation of the Paleocene was already very modern in character, and nearly all of the common forest-trees were represented by species which differed but slightly from those of the present. The grasses were already in existence, but, there is good reason to believe, they had not attained to much importance and did not cover the plains and open spaces as they did in the Miocene and still continue to do. As the grasses afford the principal food-supply of so many grazing animals, the matter of their abundance and extension is a very significant one in the history of mammalian development, and, as we have already learned, eventually led to widespread and profound modifications of structure, especially of the teeth. While there is thus nothing very strange about the plant-world of Paleocene times, the higher animal life was almost totally different from that of modern times and made up a most curious and bizarre assemblage, from which nearly all the familiar Recent types were absent. The reptiles had been greatly impoverished by the world-wide and, as yet, unexplained destruction which overtook them at the end of the Mesozoic era, but it is possible that in both North and South America a few of the huge Dinosaurs survived the decimation of the class. Very characteristic of the Paleocene in North America and Europe were large, lizard-like reptiles, allied to the New Zealand Tuatara, while crocodiles and tortoises abounded; snakes were present, but do not appear to have been very common.

It is the mammals which were the strangest element of Paleocene life, and our imaginary observer would find no creature that he had ever seen before. The difference from modern mammalian life was not merely one of species, genera or even families, but of orders, for only one, or at most two, of the orders now living were then to be found in North America, and both of these (marsupials and insectivores) were primitive and archaic groups, which seem like belated survivals in the modern world. There were no rodents, or true carnivores, no lemurs, monkeys, artiodactyls, perissodactyls or proboscideans.

In the *Torrejon*, or upper Paleocene, there were many herbivorous marsupials, with very complex grinding teeth and chisel-like incisors, but no carnivorous or insectivorous members of the order have been found. Insectivora were present. Of the †creodonts, or primitive flesh-eaters, there were no less than five families; the bear-like †Arctocyonidæ, which died out in the Wasatch, were quite numerous, and the problematical †Mesonychidæ were much smaller and more primitive mammals than those of the Eocene. Passing over two families which did not survive the Torrejon, we may note the first of the †Miacidæ, the progressive family which led eventually to the true Carnivora. The hoofed animals all belonged to the archaic †Condylarthra and †Amblypoda; of the former there were many genera and species referable to three families, one of which contained the forerunners of the Wasatch †*Phenacodus*. The genus †*Pantolambda* of the Amblypoda may well have been ancestral to both the †coryphodonts and the †uintatheres of the Eocene.

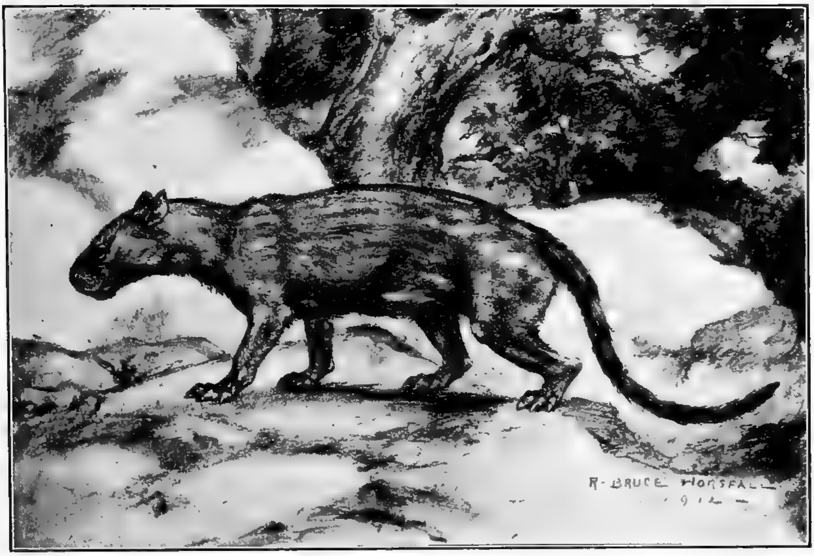

FIG. 143. — The Torrejon forerunner (†*Pantolambda bathmodon*) of †*Coryphodon*. Restored from a skeleton in the American Museum of Natural History.

The *Puerco* fauna was much like that of the Torrejon, but even less advanced and diversified. The herbivorous marsupials were more abundant, and some of them (†*Polymastodon*) larger than those of the Torrejon; Insectivora may have been present, but this is doubtful. The †creodonts, so far as they have been discovered, were less numerous, varied and specialized than those of the Torrejon and included but one of the families which passed over into the Eocene. The †Condylarthra were much less common and the †Amblypoda but doubtfully represented, but the edentate-like †Tæniodontia were conspicuous.

FIG. 144. — Head of an †allotherian marsupial (†*Polymastodon taöensis*) from the Puerco stage. Restored from a skull in the American Museum of Natural History.

Not only were the Paleocene faunas radically different from the mammals of our time, but they could not have been ancestral to the latter, being hardly more than an advanced and diversified Mesozoic assemblage. It is true that some of its elements, such as the †Condylarthra, †Amblypoda and †Creodonta, developed greatly and played an important part in the life of the Eocene, but of these only a few †creodonts continued into the Oligocene and all became extinct without leaving any descendants behind them. Another curious fact concerning the Paleocene mammalian faunas is that they were made up entirely of small and very small animals; not a single mammal as large as a sheep has yet been found in these beds, and the same is true of Europe.

That a land-connection with the Old World existed during the Paleocene epoch, is indicated by the similarity of the faunas of North America and Europe.

CHAPTER VIII

HISTORY OF THE PERISSODACTYLA

In attempting to trace the evolutionary history of the various mammalian groups, it is necessary to bear in mind the inevitable limitations of work of this kind. Speaking of plants, Dr. D. H. Scott says: "Our ideas of the course of descent must of necessity be diagrammatic; the process, as it actually went on, during ages of inconceivable duration, was doubtless infinitely too complex for the mind to grasp, even were the whole evidence lying open before us. We see an illustration, on a small scale, of the complexity of the problem, in the case of domesticated forms, evolved under the influence of man. Though we know that our cultivated plants, for instance, have been developed from wild species within the human period, and often within quite recent years, yet nothing is more difficult than to trace, in any given instance, the true history of a field-crop or garden plant, or even, in many cases, to fix its origin with certainty." [1] With some mammalian groups the task, though difficult enough, is not so hopeless, because of more complete records, yet in dealing with mammals a very troublesome complication is introduced by the existence within the families, and even within the genera, of two or more parallel phyla, or genetic series. Without complete and perfect material it is impossible to make sure that we are not confusing the different phyla with one another and placing in one series species and genera that properly belong in a different one. Thus, Osborn distinguishes no less than seven such phyla

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[1] D. H. Scott, Studies in Fossil Botany, London, 1900, pp. 524–525.

among the true rhinoceroses of the Old and New Worlds, which long followed parallel, but quite independent, courses of development, and five phyla among the American horses. While these phyla add so much to the difficulty of working out the genealogical series, it is possible to simplify the problem and treat it in a broad and comprehensive manner that will sufficiently establish the essential steps of change.

In external appearance and general proportions the different families of existing perissodactyls have very little in common; that tapirs and rhinoceroses should be related is not surprising, but the horses would seem to be as far removed from both of the former as possible. Why, then, should they be included in the same order? A study of the skeleton, however, reveals the community of structure which obtains between the three families, a community which removes them widely from all other hoofed mammals. In all existing perissodactyls, though not in most of the Eocene genera, all the premolars, except the first, have the size and pattern of the molars. The foramina of the skull, or perforations by which blood-vessels and nerves enter and leave the cranium, are arranged in a way characteristic of the order and different from that seen in other hoofed mammals. The femur always has the third trochanter. The number of digits in each

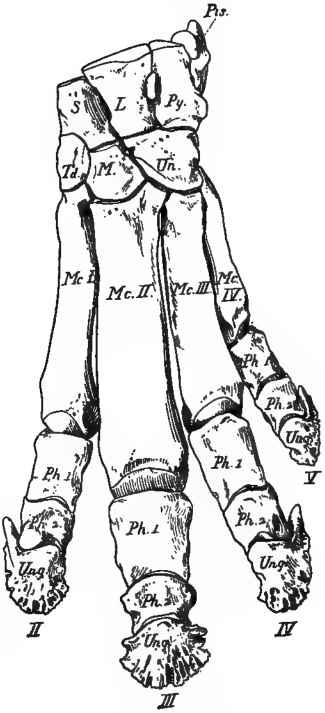

FIG. 145. — Left manus of Tapir (*Tapirus terrestris*). *S.*, scaphoid. *L.*, lunar. *Py.*, pyramidal. *Pis.*, pisiform. *Td.*, trapezoid. *M.*, magnum. *Un.*, unciform. The metacarpals are erroneously numbered. *Mc. I.*, second metacarpal. *Mc. II.*, third do. *Mc. III.*, fourth do. *Mc. IV.*, fifth do. *Ph. 1*, first phalanx. *Ph. 2*, second do. *Ung.*, ungual phalanx.

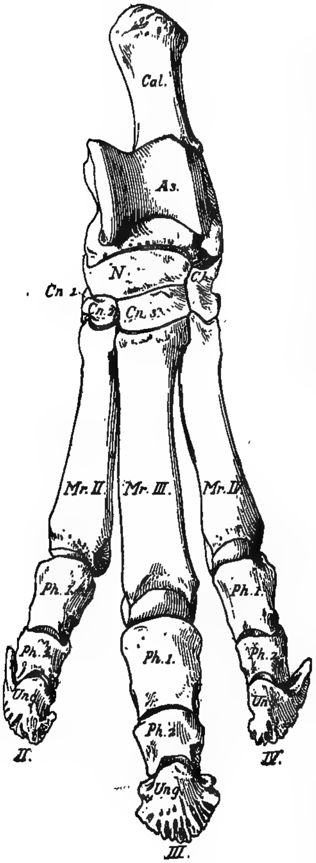

FIG. 146. — Left pes of Tapir. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn. 1*, *Cn. 2*, *Cn. 3*, first, second and third cuneiforms. *Mr. II*, *III*, *IV*, second, third and fourth metatarsals.

foot is usually odd, 1, 3 or 5, but four-toed forms occur, as the tapirs, which have four toes in the front foot, three in the hind; the important character is that the median plane of the foot bisects the third digit, which is symmetrical. The third and fourth, each asymmetrical, together form a symmetrical pair. Especially characteristic is the form of the astragalus and calcaneum (ankle and heel bones); the astragalus has but a single, deeply grooved and pulley-like surface, that for the tibia, the lower end is nearly flat and rests almost entirely upon the navicular, covering but little of the cuboid (see Figs. 146, 148). The calcaneum does not articulate with the fibula and its lower end is broad and covers most of the cuboid.

While the foregoing list includes the most important of the structural features which are common to all perissodactyls and differentiate them from other hoofed animals, there are many others which it is needless to enumerate.

The subjoined table gives the families and principal genera of the American Perissodactyla; extinct groups are marked †.

Suborder CHELODACTYLA. Normal Perissodactyls

I. EQUIDÆ. Horses.

†*Eohippus*, low. Eoc. †*Orohippus*, mid. Eoc. †*Epihippus*, up. Eoc. †*Mesohippus*, low. Oligo. †*Miohippus*, up. Oligo. †*Anchitherium*, up. Oligo. † *Parahippus*, low. Mioc. to low. Plioc. †*Des-*

matippus, mid. Mioc. †*Hypohippus*, mid. Mioc. to low. Plioc. †*Merychippus*, mid. Mioc. to low. Plioc. †*Protohippus*, up. Mioc. †*Pliohippus*, up. Mioc. and low. Plioc. †*Neohipparion*, up. Mioc. and low. Plioc. †*Hipparion*, Plioc. †*Hippidion*, Pleist., S. Amer. †*Hyperhippidium*, Pleist., S. Am. *Equus*, Pleist., N. and S. Amer.

II. †TITANOTHERIIDÆ. †Titanotheres.

†*Lambdotherium*, low. Eoc. †*Eotitanops*, low. Eoc. †*Palæosyops*, mid. Eoc. †*Telmatherium*, mid. Eoc. †*Dolichorhinus*, up. Eoc. †*Diplacodon*, up. Eoc. †*Titanotherium*, low. Oligo.

III. TAPIRIDÆ. Tapirs.

†*Systemodon*, low. Eoc. †*Isectolophus*, mid. and up. Eoc. †*Protapirus*, Oligo. †*Tapiravus*, mid. Mioc. *Tapirus*, Pleist., N. Amer., Pleist. and Recent, S. Amer.

IV. †LOPHIODONTIDÆ. †Lophidonts.

†*Heptodon*, low. Eoc. †*Helaletes*, mid. Eoc. †*Colodon*, low. Oligo.

V. RHINOCEROTIDÆ. True Rhinoceroses.

†*Trigonias*, low. Oligo. †*Cœnopus*, Oligo. and low. Mioc. †*Diceratherium*, up. Oligo. and low. Mioc. †*Aphelops*, mid. Mioc. to low. Plioc. †*Teleoceras*, mid. Mioc. to low. Plioc.

VI. †HYRACODONTIDÆ. †Hyracodonts and †Amynodonts, cursorial and aquatic Rhinoceroses.

†*Hyrachyus*, low. and mid. Eoc. †*Triplopus*, mid. and up. Eoc. †*Colonoceras*, mid. Eoc. †*Hyracodon*, low. Oligo. †*Amynodon* up. Eoc. †*Metamynodon*, low. Oligo.

Suborder †ANCYLOPODA. †Clawed Perissodactyls

VII. † CHALICOTHERIIDÆ. Chalicotheres.

†*Moropus*, up. Oligo. and low. Mioc. ? †*Schizotherium*, low. Oligo. †*Eomoropus*, mid. Eoc.

The earliest perissodactyls of which we have any knowledge are found in the older part of the lower Eocene (Wasatch stage) of Europe and North America, into which they must have migrated from some other region yet unknown, for no probable ancestors of the group are found in the Paleocene of either continent.

I. SUBORDER CHELODACTYLA. NORMAL PERISSODACTYLA.

1. *Equidæ*. *Horses*

In order to make intelligible the evolutionary changes which have led up to the modern horses, it will be necessary to say something concerning the dental and skeletal features which characterize these animals. Using the term *horses* in a broad sense to include all the existing members of the family Equidæ, true horses, asses, zebras and quaggas, we find a greater uniformity in the skeleton and teeth than would be expected from the external appearance. The differences in appearance are, however, largely due to colouring, growth of mane and tail and the size of the ears, which leave no record in the skeleton.

FIG. 147. — Asiatic Wild Horse (*Equus przewalskii*). — By permission of the N.Y. Zoölog. Soc.

The teeth (Figs. 45, p. 95; 154, p. 306) are extremely high-crowned, or hypsodont, and do not form roots till an advanced age; the incisors have a deep, enamel-lined pit, the "mark" in the centre of the grinding surface; the first premolar in each jaw is very small and of no functional importance; the other premolars have the same pattern as the molars, which is excessively complex in the arrangement of the enamel ridges and the areas of dentine and cement.

The skull (Fig. 154, p. 306) is long, especially the facial portion, the eye-socket (orbit) being shifted behind the teeth, which otherwise, on account of their great height, would press upon the eye itself; the orbit is completely encircled in bone. The lower jaw is deep vertically and the ascending ramus (see p. 66) very high, on account of the hypsodont character of the teeth, which thus necessitates a remodelling of the skull in several respects. The neck is long, each of its seven vertebræ being elongate; except in the atlas and axis, the anterior face of each centrum is strongly convex and the posterior of all except the atlas is deeply concave; the odontoid process of the axis (see p. 71) is spout-shaped, concave on the upper and convex on the lower side, lodging and protecting the spinal cord. The spines of the anterior dorsal vertebræ are very high, making a low hump at the withers between the shoulder-blades; the trunk-vertebræ are so arranged as to make the back almost straight and horizontal. The limbs and especially the feet are very long. The two bones of the fore-arm, the ulna and radius, are coössified into a single piece (Fig. 30, p. 81), but the limits of each are still plainly to be seen, especially in a young animal; and it is evident that the ulna is greatly reduced in size and has lost its middle portion, while all the weight is borne by the radius. Similarly, in the hind leg the enlarged tibia, or shinbone, alone supports the weight; and only the two ends of the fibula are preserved (Fig. 38, p. 87), and these are indistinguishably fused with the tibia in the adult animal, but may be made out in the colt. The thigh-bone has a very characteristic shape, which is difficult to describe without an undue use of technical terms, but the unusual prominence of the great trochanter (Fig. 35, p. 85) and of the rotular groove is an important factor in producing this appearance.

The very long and slender feet are so raised from the ground that the animal walks upon the very tips of the toes, the wrist being what horsemen call the "knee" and the heel is the "hock," and the gait is thoroughly unguligrade. Each foot has but a single functional toe, the third or middle one of the

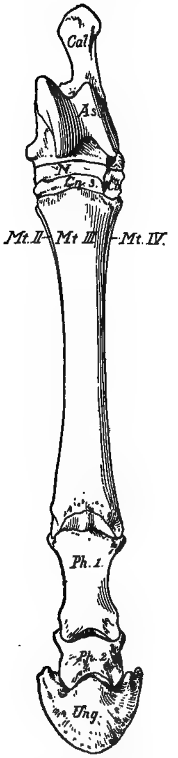

FIG. 148. — Left pes of Horse. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn.* 3, third cuneiform. *Mt. III*, functional (third) metatarsal. *Mt. II* and *Mt. IV*, splints.

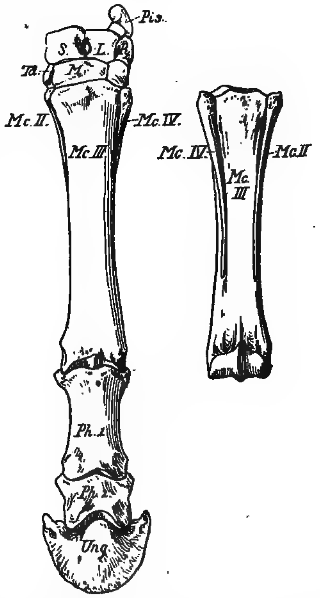

FIG. 149. — Left manus of Horse, front side; to the right, rear view of the metacarpus. *S.*, scaphoid. *L.*, lunar. *Py.*, pyramidal. *Pis.*, pisiform. *Td.*, trapezoid. *M*, magnum. *U.*, unciform. *Mc. II*, *Mc. IV*, rudimentary second and fourth metacarpals, or splints.

primitive five-toed foot; and, as this toe has to carry the whole weight supported by its leg, it is necessarily much larger than in animals which distribute the weight among several digits. The horses are therefore said to be *monodactyl*, or single-toed, but the term is not strictly accurate, for on each side of the functional digit is a rudimentary or vestigial one, the 2d and 4th of the original five. These rudimentary digits, which are not visible externally, have no phalanges and are merely "splint-bones," metapodials (see p. 90) which have very slender shafts and end below in blunt points. The single functional metapodial has encircling its lower articular end a prominent ridge or keel, which fits into a corresponding groove on the upper end of the first phalanx and serves to prevent lateral dislocation. In most mammals this keel is merely a projection from the lower articular surface and is confined to the posterior side, so as not to be visible from the front. The terminal or ungual phalanx is much enlarged to carry the great weight which it supports and is enclosed in the characteristic hoof, unlike that of any other mammal.

In brief, the whole structure of the horses is pre-eminently adapted to swift running; they are admirable "cursorial machines," as they have been called, and every part of the skeleton has been modified and specialized to that end; the narrow, rigid hoofs fit them for walking on firm ground and they speedily are made helpless in quicksand or bog. Did we know nothing of their mode of life, we might confidently infer from their teeth that the horses were grazers, feeding principally upon grass. A long-legged, grazing animal must needs have a neck of sufficient length to enable the mouth to reach the ground easily, unless a long proboscis is developed; and so we shall find in the history of the horses that the elongation of the head and neck kept pace with the lengthening of the legs and feet.

Though it can hardly be doubted that the horses passed through most of their development in North America, yet the immediate ancestry of all the existing species must be sought in the Old World, none of the many Pleistocene species of the western hemisphere having left any descendants. In North America all of the known Pleistocene forms belonged to the genus *Equus*, but the True Horse, *E. caballus*, was not among them. The more abundant and important of these species have been sufficiently described in Chapter VII (p. 199); it need only be recalled that there were ten or more distinct forms, ranging in size from the great *E.* †*giganteus* of Texas to the minute *E.* †*tau* of Mexico, while the plains and forests were the feeding grounds of moderate-sized species, about 14 hands high.

In the latest Pliocene, and no doubt earlier, species of the modern genus *Equus* had already come into existence; and in association with these, at least in Florida, were the last survivors of the three-toed horses which were so characteristic of the early Pliocene and the Miocene. However, little is known about those earliest recorded American species of *Equus*, for the material so far obtained is very fragmentary. In the absence of any richly fossiliferous beds of the upper Pliocene generally, there is a painfully felt hiatus in the genealogy of the horses; and it is impossible to say, from present knowledge, whether all of the many species of horses which inhabited North America in the Pleistocene were autochthonous, derived from a purely American ancestry, or how large a proportion of them were migrants from the Old World, coming in when so many of the Pleistocene immigrants of other groups arrived. It is even possible, though not in the least likely, that all of the native American stocks became extinct in the upper Pliocene and that the Pleistocene species were all immigrants from the eastern hemisphere, or the slightly modified descendants of such immigrants; but, on the other hand, it is altogether probable that some of these numerous species were intruders. Unfortunately we are in no position yet to distinguish the native from the foreign stocks.

In the middle Pliocene, which also has preserved but a meagre and scanty record of its mammalian life, we again meet with horses in relative abundance, but of a far more primitive type. They are still incompletely known, but it is clear that they belonged to three parallel series, or phyla, of three-toed grazing horses, with teeth which, though high-crowned, had not attained to the extreme degree of hypsodontism seen in the species of *Equus* and had a somewhat less complex pattern of the grinding surface, though distinctly foreshadowing the modern degree of complication. One of the genera (†*Pliohippus*) was not improbably the ancestor of a very peculiar horse (†*Hippidion*) of the South American Pleistocene. These middle Pliocene genera were much smaller animals than the Pleistocene horses, aside from the pygmy species of the latter, of light and more deer-like proportions, and with three functional toes or digits. The median digit (3d of the original five) was much the largest and carried most of the weight, on hard ground practically all of it; the lateral digits (2d and 4th) which in existing horses are represented by the rudimentary metapodials, or "splints," though much more slender than the median digit, yet had the complete number of parts and each carried a small hoof. Mere "dew-claws" as these lateral toes were, they may have been of service in helping to support the weight in mud or snow. In all parts of the skeleton there are little details which show that these species of the middle Pliocene were not so advanced and differentiated as are their modern successors, but it would be unprofitable to enumerate these details, which are of interest only to the anatomist.

In the lower Pliocene the horses were very much more numerous and varied than in the middle portion of the epoch. The same three genera of grazing animals, represented by less advanced and modernized species, are found; and, in addition, there was an interesting survival (†*Merychippus*) from the middle Miocene of an intermediate type, together with several species of browsing horses (†*Parahippus* and †*Hypohippus*). In these browsing forms the teeth were all low-crowned and early formed their roots, and the crowns were either without cement or with merely a thin film of it in the depressions of the grinding surface. The pattern of the grinding surface is so very much simpler than in the high-crowned, prismatic teeth of the grazers that it requires close analysis to detect the fundamental identity of plan. Such teeth imply that their possessors must have fed habitually upon a softer and less abrasive diet than grass, probably the leaves and soft shoots of trees and bushes and other succulent vegetable substances, very much in the fashion of existing deer, and must therefore have been chiefly inhabitants of the woods and groves and thickets along streams, as the grazing species were of the plains and open spaces. "This assemblage of the progressive and conservative types of horses was certainly one of the most distinctive features of Lower Pliocene time in North America" (Osborn).

In the upper Miocene very much the same conditions prevailed and, for the most part, the same genera of horses, with different and somewhat less advanced species, were found as in the lower Pliocene, so that no particular account of them is needed. In the middle Miocene, however, there was a change, the typically grazing horses being very rare or absent and those with intermediate forms of teeth taking their place. Evidently, it was about this time that the horses with more plastic organization and capable of readjustment to radically different conditions began to take to the grazing habit, while other phyla, less capable of advance, retained the ancient, low-crowned type of grinding teeth and, after persisting, as we have seen, into the lower Pliocene, became extinct before the middle of that epoch. It is of great interest to observe that in the genus (†*Merychippus*) intermediate between the browsing and grazing types, the milk-teeth retained the older and more primitive character of low crowns without covering of cement,

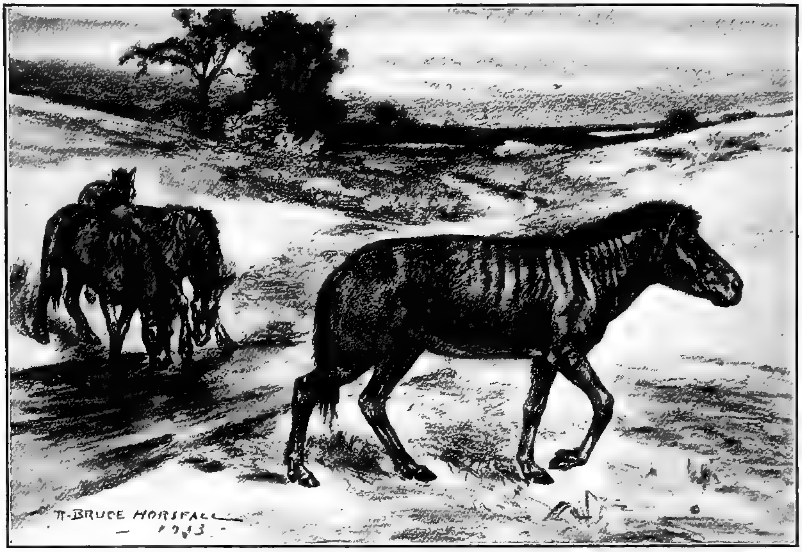

FIG. 150. — Three-toed, grazing horse (†*Neohipparion whitneyi*) of the upper Miocene. Restored from skeletons in the American Museum of Natural History.

while the permanent grinders had much higher, cement-covered and complex crowns. In the lower Miocene, the variety of horses was much diminished and all had the low-crowned, cement-free, browsing type of teeth. Reversing the statement, we see that in the middle and still more in the upper Miocene the primitive and more or less distinctly homogeneous phylum branched out into several series, like a tree, some of the branches continuing and further subdividing through the Pliocene and Pleistocene, while others, less progressive and less adaptable, underwent but little change and had died out before the middle Pliocene.

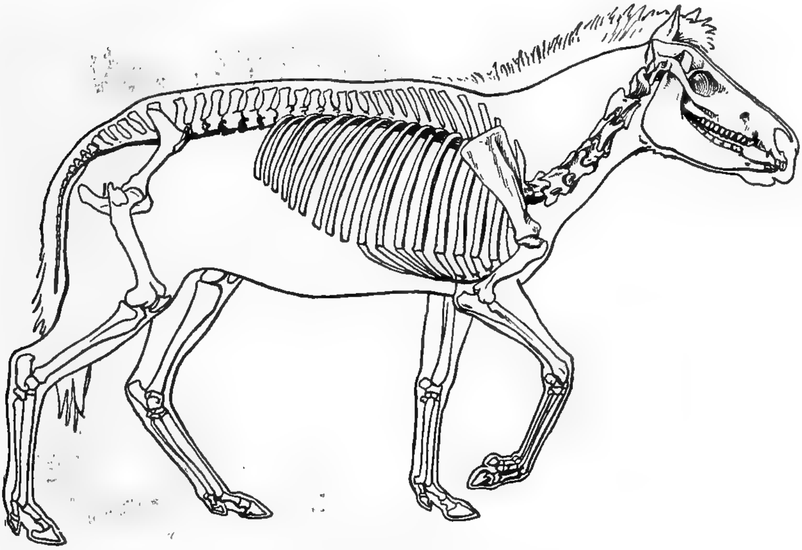

Fig. 151.—Skeleton of †*Neohipparion whitneyi*, American Museum.

The Oligocene horses deserve more particular attention, for they were almost the half-way stage of development in the long backward ascent to the earliest known members of the family in the lower Eocene. We may pass over the John Day horses (†*Miohippus*), which were somewhat larger than those of the White River, but otherwise very like them, merely noting the presence of a slightly different genus (†*Anchitherium*) which was the probable ancestor of †*Hypohippus* and the other non-progressive types of the Miocene and Pliocene. The genus (†*Mesohippus*) which characterizes the White River, or lower Oligocene, was a group of species of different sizes, becoming smaller as we go back in time, the commonest one being considerably smaller than a sheep and differing more or less in all its parts from the horses of the upper Miocene and all subsequent formations. The teeth were very low-crowned and fitted only for the mastication of soft vegetable tissue; but it is of particular interest to observe the beginnings of the "mark" in the upper incisors in the form of a low enamel-ridge arising behind the cutting edge of the tooth; the lower incisors still had the simple chisel-like crowns of the more ancient genera; all the premolars, except the first, had already acquired the molar-pattern.

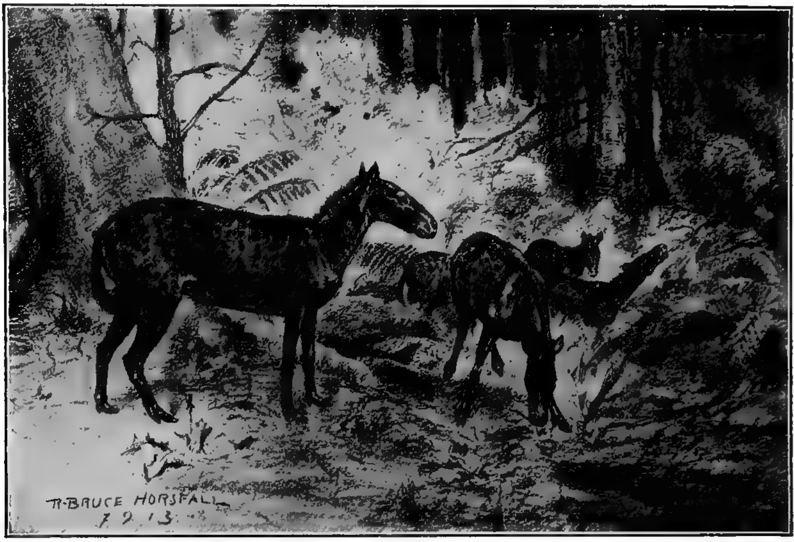

FIG. 152. — The small, browsing, three-toed, short-necked horse († *Mesohippus bairdi*) of the middle White River. Restored from a skeleton in the American Museum.

The skull resembled that of a very small modern horse, but with many differences of detail, the most obvious of which is the shallowness of the jaws, for depth was not needed to carry the very low-crowned teeth, and, for the same reason, the ascending ramus of the lower jaw was short. The face was relatively short and the eye-socket, which was incompletely surrounded by bone, was directly above the hindmost teeth; the cranium was proportionately large and capacious and the brain, as is shown by the cast, was richly convoluted. The neck was relatively far shorter than in the Miocene genera, the ball-and-socket joints between its successive vertebræ were less elaborated and the odontoid process of the axis was in the first stage of assuming the spout-like form, being semi-cylindrical, with convex lower and flat upper surface. The trunk was proportionately long and the back sloped forward, owing to the greater length of the hind legs. The limbs and feet were elongate and very slender, but the fore-arm bones are only partially coössified, and the ulna, though greatly attenuated, was still complete. The same is true of the bones of the lower leg; the shaft of the fibula was hardly more than a thread of bone, but its full length was preserved. In the fore foot there were three functional digits, the median one enlarged and supporting most of the weight, but its hoof was much thinner and flatter than in the corresponding digit in the Miocene and subsequent genera; the lateral digits touched the ground and were not entirely functionless and, in addition, there was a small splint, the rudiment of the fifth digit. The hind foot was three-toed, without splint.

The little Uinta horse (†*Epihippus*) is still very incompletely known, but gives us one point at least of greater primitiveness than the White River genus in that only the last two premolars had taken on the molar-pattern, the forward two being smaller and simpler. The known species of the Uinta genus was very much smaller than any of the White River forms and even smaller than some of those of the preceding Bridger formation; but it should be remembered that the Uinta has been but partially explored and much remains to be learned regarding its fauna.

The Bridger horses are fortunately much better known. There are several species of the genus †*Orohippus*, which form a connected and progressive series; and, though much smaller than the smallest and oldest of the White River forms, they were somewhat larger than the known representative of the Uinta, †*Epihippus*, but distinctly more primitive in all other respects. The incisors were simple cutting teeth, with no trace of even an incipient "mark," and only one premolar in each jaw, the hindmost one, had taken on the molar-pattern. The orbit was farther forward in the skull and less enclosed behind than in †*Mesohippus*, the cranium narrower and less capacious; the neck was even shorter and the odontoid process of the axis still retained the primitive peg-like form. The limbs and feet were conspicuously shorter in proportion than those of the White River genus; the ulna and fibula were stouter and less reduced and entirely separate from the radius and tibia respectively. The front foot had four functional toes; the fifth digit, which in †*Mesohippus* had been reduced to a splint, was completely developed in the Bridger horses, but the hind foot was three-toed.

Passing over, for lack of space, the transitional forms of the Wind River, we come finally to the most ancient known horses, the Wasatch species comprised in the genus †*Eohippus*, the "Dawn Horse," as its name signifies; these were little creatures ranging in size from a cat to a small fox. Despite an unmistakably equine look in the skeletons of these diminutive animals, it is only the long intermediate series of species and genera, together forming a closely linked chain, which we have traced back from the Pleistocene to the lower Eocene, that leads us to regard †*Eohippus* as the ancestral type of the horses. Were only the two ends of the chain known, he would be a daring speculator who should venture to connect them. In these little Wasatch horses we have the evidence of a still more ancient form with five fully developed toes in each foot, since the front foot had four functional digits and indication of a splint, and splints, as the whole history of the long series teaches, always are found to be functional digits in the ancestor; the hind foot had three toes and perhaps two splints. This preceding form is hardly to be looked for in America or Europe; it will be found, if ever, in the region whence the great migration came.

FIG. 153.—The "Dawn Horse" (†*Eohippus*) of the lower Eocene. Restored from a skeleton in the American Museum.

In all other respects, as well, †*Eohippus* was what we should expect the forerunner of the Wind River and Bridger horses to be. The premolars were all smaller and simpler than the molars and the latter in the upper jaw are particularly interesting, for they had no crests and ridges of enamel, but four principal conical cusps, arranged in two transverse pairs, and between the cusps of each pair was a tiny cuspule no bigger than the head of a pin. These cuspules were the first step in the formation of the transverse crests, which were destined to assume such importance in the subsequent members of the series. The neck was very short, the body long, with curved or arched back, the limbs and feet short, and the hind limb much longer than the fore, making the relative proportions of the various parts of the skeleton very different from what they afterwards became.

Reviewing this marvellous history of steady and long-continued change, beginning with the most ancient genus, †*Eohippus,* the following modifications may be noted:

(1) There was a nearly constant, if somewhat fluctuating, increase in size, leading by slow gradations from the diminutive horses of the lower Eocene to the great animals of the Pleistocene.

(2) The molar teeth, originally made up of conical cusps, changed to a highly complex pattern of crests and ridges, and the premolars, one by one, assumed the size and pattern of the molars; the low-crowned, rooted and cement-free teeth, fitted only for browsing, became very high-crowned, prismatic and cement-covered, admirably adapted to grazing. Beginning in the upper incisors of the White River †*Mesohippus,* the "mark" became established as an enamel-lined pit, growing in depth as the teeth increased their length.

(3) The face grew relatively longer, the eye-socket being shifted behind the teeth and becoming completely encircled in bone, and the jaws were greatly increased in depth to accommodate the very long teeth.

(4) The short neck was greatly elongated and the individual vertebræ modified so as to give flexibility with no loss of strength. The primitive peg-like odontoid process of the axis became first semicylindrical and then spout-shaped.

(5) The arched back was straightened and the neural spines, especially of the anterior dorsals, elongated.

(6) The limbs grew relatively much longer; the bones of the fore-arm and lower leg were fused together, the one on the inner side (radius and tibia) enlarging to carry the entire weight and the external one (ulna and fibula) becoming more or less atrophied.

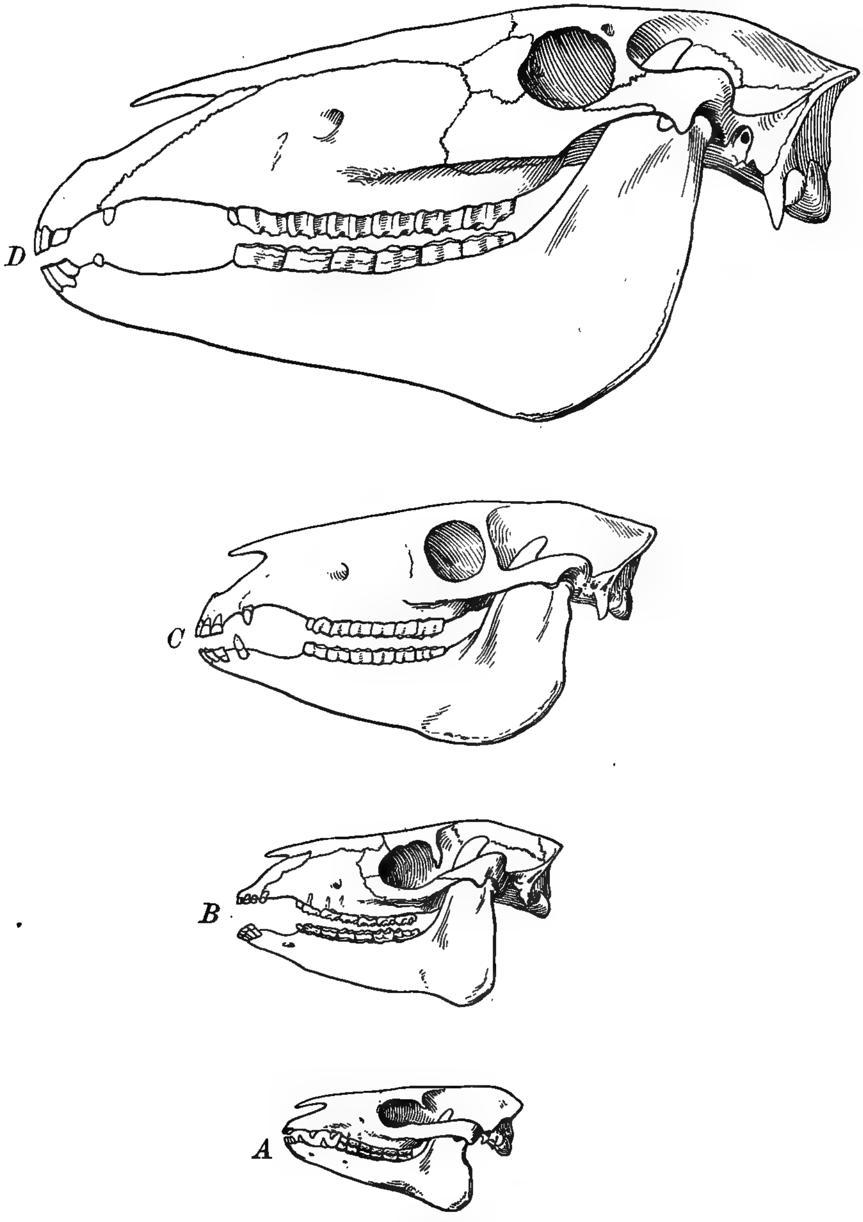

Fig. 154. — Series of horse skulls in ascending geological order. *A.*, †*Eohippus*, lower Eocene (after Cope). *B.*, †*Mesohippus*, lower and middle Oligocene. *C.*, †*Protohippus*, upper Miocene (after Cope). *D.*, *Equus*.

(7) The feet were much elongated and the median (3d) digit of each gradually enlarged until it carried the whole weight, at the same time modifying the shape of the hoof so as to fit it to be the sole support of the body. The other toes gradually dwindled and became functionless, though often retained as splints. The first digit (pollex and hallux) was first

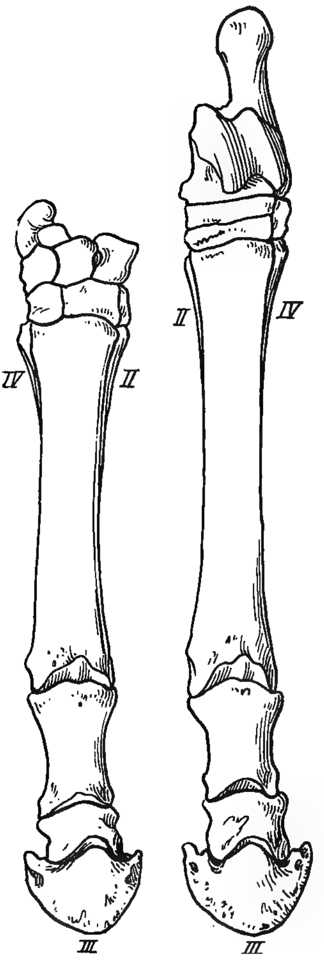

Fig. 155. — Right manus and left pes of *Equus*.

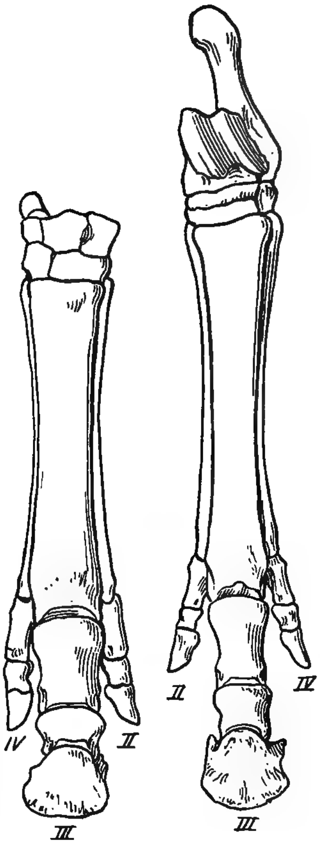

Fig. 156. — Right manus and left pes of † *Protohippus*.

lost, then the fifth, then the second and fourth were reduced to dew-claws and finally to splints. Thus the pentadactyl horses of the lower Eocene were transformed into the monodactyl species of the Pliocene and Pleistocene.

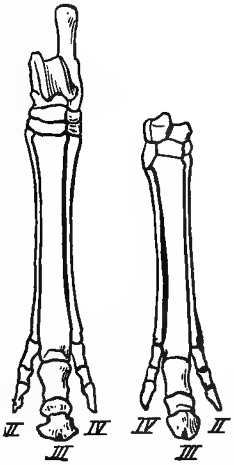

FIG. 157. — Right manus and left pes of †*Mesohippus*.

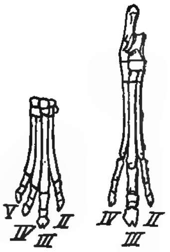

FIG. 158. — Right manus and pes of †*Eohippus*.

In South America the story of the horses was a brief one, for they were among the immigrants from the north and did not reach the southern continent till the Pliocene, probably late in that epoch, for none of the three-toed genera have been found in South America. So far as known, these southern equines were small and medium sized animals, with large heads, relatively short feet and somewhat ass-like proportions. There were two well-defined groups of these animals: (1) species of the genus *Equus*, which thus, at one time or another, inhabited every one of the continents, Australia excepted; (2) three genera peculiar to South America and developed there from northern ancestors, probably †*Pliohippus*. Two of these genera (†*Hippidion* and †*Onohippidium*) displayed curious modifications of the nasal bones, which were extremely slender and attached to the skull only at their hinder ends, instead of being, as is normally the case, supported for nearly their whole length by lateral articulation with other bones. What can have been the significance and function of these excessively slender, splint-like nasals, it is difficult to conjecture. The third genus (†*Hyperhippidium*) was a small mountain-horse, with extremely short feet, which were well adapted to climbing.

This is the merest outline sketch of a most wonderful series of gradual and progressive modifications, a sketch that might readily be expanded into a volume, were all the details filled in. While each set of organs, teeth, skull, neck, body, limbs and feet, might appear to advance independently of the others, in reality there was no such independence, for at every stage of the progression all the parts must have been so coördinated into a harmonious whole, that the animal could thrive and hold its own in the stress of competition. Could we but discover all the facts of environment, on the one hand, and organization, on the other, we should doubtless learn that the little †*Eohippus* was as exquisitely fitted to its place in the Wasatch world, as are the horses, asses and zebras of the present day to theirs. It was the response to changing needs, whether of food, climate, disease or competition, that was the main factor of development.

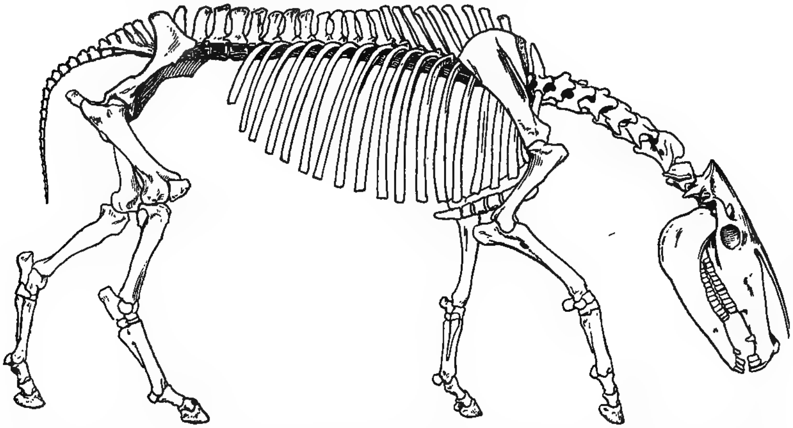

FIG. 159.—Skeleton of a Pampean horse (†*Hippidion neogæum*), National Museum, Buenos Aires. For restoration, see Fig. 119, p. 214. Note the splint-like nasal bones attached only at the hinder end.

2. †*Titanotheriidæ*. †*Titanotheres*

This family, all of whose members vanished from the earth ages ago, was a comparatively short-lived group and nearly the whole of its recorded history was enacted in North America;

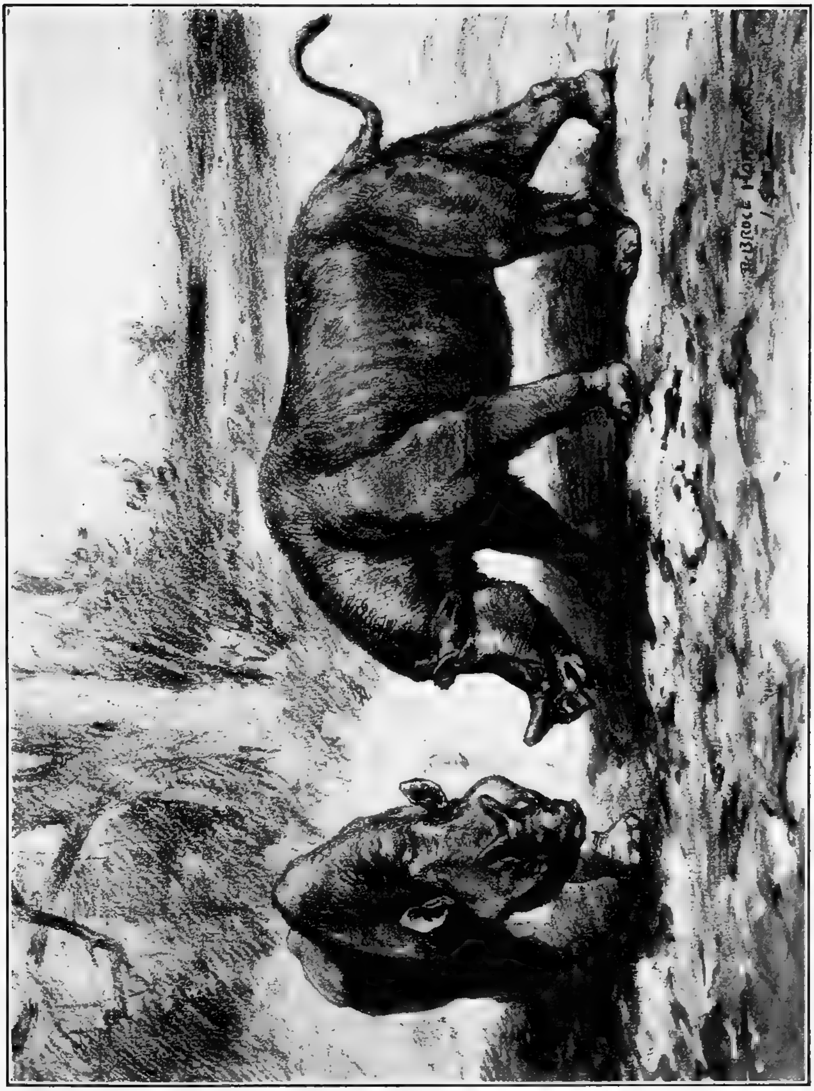

FIG. 160. — White River † titanothere († *Titanotherium robustum*) males fighting. Restored from a skeleton in the American Museum of Natural History.

only a few belated stragglers reached the eastern hemisphere, though the family may, nevertheless, have originated there.

In the lowest of the three substages of the White River Oligocene the most conspicuous and abundant fossils are the †titanotheres, the latest members of which were huge animals of almost elephantine proportions. They belonged to four parallel, or rather slightly divergent, phyla, differing in the development of the horns, in the shape of the head and in the relative length and massiveness of the limbs. The teeth were all low-crowned, or brachyodont, the canines much too small to have been of any service as weapons and the incisors had curious little, button-shaped crowns, which can have had little or no functional importance, since they show hardly any wear, even in old animals. With such front teeth, a prehensile lip and long tongue would seem to have been necessary for gathering and taking in food.

The †titanotheres were one of two perissodactyl families in which the premolars never became so large and complex as the molars. The upper molars had a longitudinal outer wall, composed of two deeply concave cusps, and two internal conical cusps, but no transverse ridges; the lower molars were composed of two crescents, one behind the other, a pattern which was very widely distributed among the early and primitive artiodactyls and perissodactyls.

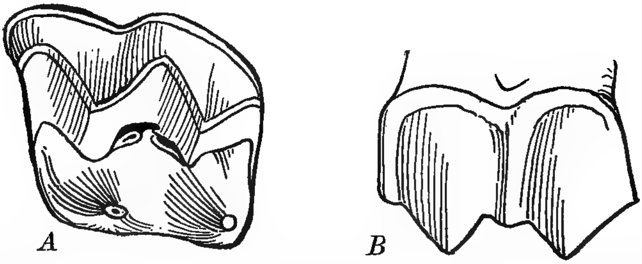

FIG. 161.—Second upper molar, left side, of †*Titanotherium*. *A*., masticating surface; *B*., outer side of crown.

The so-called "horns" were not strictly such, but a pair of bony protuberances from the front of the skull and, from their shape, could hardly have been sheathed in horn. The long, immensely broad and massive head resembled that of some fantastic rhinoceros, as did also the body and limbs. The brain was quite absurdly small, the cavity for it, lost in the huge skull, would hardly contain the fist of an ordinary man; these great beasts must have been incredibly dull and stupid, surpassing even the modern rhinoceroses in this respect. As is generally true in mammals which have horns, antlers, or similar weapons borne upon the skull, or very large tusks, the bones of the brain-case were made enormously thick and yet lightened by an intricate system of communicating cavities or "sinuses," separated by many bony braces and supports connecting the inner and outer denser layers, which form the surfaces of the bones. In this way the skull is made strong enough without any proportionate increase of weight to endure the severe shock of impact, when the horns or tusks are made use of. The principle is the same as the engineer employs in designing a steel truss-bridge. The upper profile of the head was deeply concave, just as it is in those rhinoceroses which are armed with nasal horns.

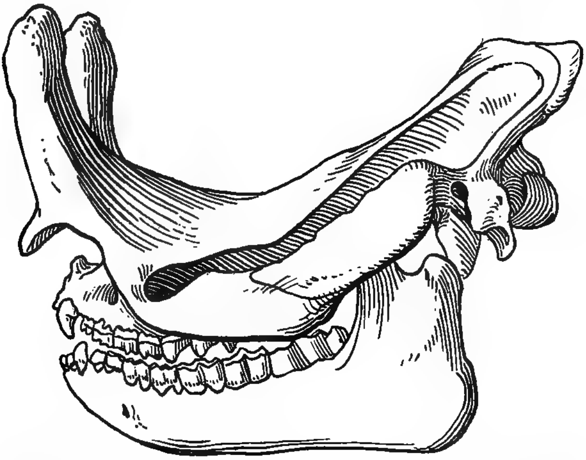

Fig. 162. — Skull of † *Titanotherium elatum.* American Museum.

The neck was of moderate length and the body, as indicated by the long, arched ribs and the greatly expanded hip-bones, was extremely bulky and massive. The spines of the anterior dorsal vertebræ were excessively long, forming a great hump at the withers. The limbs and feet were columnar, like those of an elephant; the feet were supported on a great pad, while the hoofs were mere excrescences on the periphery of the foot. The bones of the fore-arm were entirely separate and the ulna was very stout; in the lower leg also the bones were not coössified, but the fibula was but moderately heavy. This is a sharp contrast to the arrangement found in the horses and in those hoofed animals generally which are swift runners and have slender, elongate limbs and feet, such as deer, antelopes, camels, etc. Heavy, slow-moving animals, like elephants, tapirs, rhinoceroses, etc., almost always have separate fore-arm and leg-bones and generally a heavy ulna. The number of digits was four in the front foot and three in the hind. The genera differed in the proportions of limbs and feet, one having them longer and less ponderous than another, and, no doubt, the former was of swifter gait.

At a certain level in the White River beds the †titanotheres abruptly cease, disappearing with what seems like startling suddenness. In all probability, however, the extinction was more gradual and its apparent abruptness was due, partly at least, to the break in the deposition of the beds, which is very obvious. Such a break, or "unconformity," as geologists call it, almost always implies an unrecorded lapse of time, which may have been very long. However it came about, gradually or suddenly, the extinction of these great animals is difficult to explain; no Carnivora of the time could have been formidable enemies and they had no rivals in their own walk of life. Their stupidity may have been a factor, but it seems more likely that the onset of some new infectious disease, perhaps imported by incoming migrants from the eastern hemisphere, gave the *coup de grace*. In the lower substage, beneath the unconformity, where the remains of †titanotheres are so abundant, successive changes may be observed. The species with great "horns," rounded, flattened or triangular, are confined to the upper levels; in the middle section other species, somewhat smaller and with shorter "horns," are found, while in the bottom levels the animals are much smaller and have still smaller "horns."

The Uinta †titanotheres were much more numerous and varied than those of the White River; in the upper part of these beds are found two genera (†*Diplacodon* and †*Protitanotherium*) which already had quite prominent bony protuberances on the nose; their canines were large enough to be of value as weapons and the incisors were well developed and functional. Evidently, there was a change here in the manner of feeding, the front teeth were used for cropping and browsing, a function which in the White River members of the family must have been largely taken over by the lips and tongue, while the growth of the horn-like protuberances on the skull rendered the canines superfluous as weapons. This latter change is one which recurs frequently in different phyla of the hoofed animals, in which the earlier and more primitive members had canine tusks, and the later, more advanced representatives developed horns, the tusks diminishing as the horns increased. While this rule is a general one, it is not entirely without exceptions.

In the lower Uinta and in the Bridger the †titanotheres were extremely abundant and numerically they are the commonest of all fossils in those beds; no less than five series or phyla may be distinguished, three of them being added in the upper Bridger. The differences between the phyla, however, principally concern the forms of the teeth and the shape of the skull; in some the head was short and broad, in others long and narrow, and in others again of medium proportions; some had broad and extremely low-crowned grinding teeth, which in others were higher and more erect. But these are matters of minor detail, useful as they are in pointing the way to a proper arrangement of the various species; in essentials, the forms all agreed and constituted several series of closely allied genera. Comparing these Bridger animals with the great †titanotheres of the lower White River, the first and most obvious difference that strikes the observer is the very much smaller size of the more ancient types. With some variation in this respect, hardly any of the Bridger species exceeded a modern tapir in stature and very much resembled one in proportions. The canine teeth were tusks as large as those of a bear and must have been very effective weapons; the molar-pattern was identical with that found in the great Oligocene beasts, but the premolars were simpler and relatively smaller.

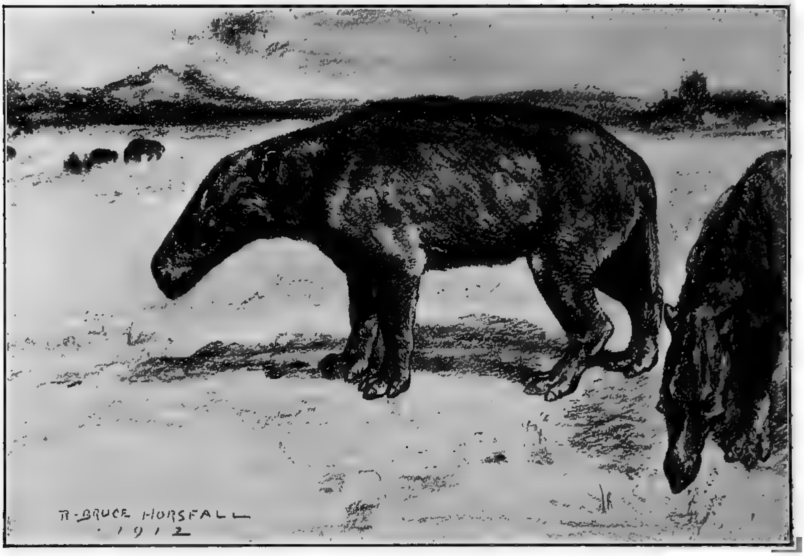

FIG. 163.—† Titanothere († *Mesatirhinus superior*) with long, narrow head; Bridger stage. Restored from a skeleton in the American Museum.

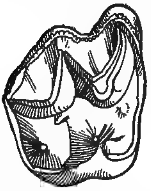

FIG. 164. — Second upper molar, right side of a Bridger †titanothere († *Palæosyops*).

The skull had a straight upper profile, though in several of the phyla small bony protuberances were developed over the eyes, and must clearly be regarded as incipient stages of the "horns" which were subsequently to become so long and prominent. Instead of being broad on top as it was in the White River genera, the cranium carried a high ridge of bone, the sagittal crest, which served for the attachment on each side of the great temporal muscle, one of the most important of the muscles of mastication. The trunk was less massive and the limbs were lighter than in the Oligocene genera, but the number of digits was the same, four in the front foot and three in the hind, and the hoofs were much better developed, serving actually to carry the weight and not being mere excrescences upon the periphery of a pad. Aside from the proboscis, which lends such a characteristic appearance to the existing tapirs, the †titanotheres of the Bridger must have looked much like tapirs, and in early days, when the mutual relationships had not been satisfactorily determined, they were frequently described as "tapiroid." The term is unobjectionable in so far as it is understood that a merely superficial likeness is implied, not any real relationship other than that which unites all the perissodactyl families.

As noted above, the phyla of the †titanotheres were much more numerous in the later than in the earlier part of the Bridger stage, when they were reduced to two. In the still older Wind River stage these two united into one. The Wind River animals (†*Eotitanops*) were similar, but much smaller, and occurred in incomparably less variety and abundance. Indeed, one of the most striking differences between the Wind River and the Bridger faunas consists in the great increase and diversification of the †titanotheres in the latter. There was, it is true, a second phylum of the family in the Wind River, represented by the genus †*Lambdotherium*, but this was a short-lived series, which left no descendants in the Bridger or subsequent formations. These were the smallest known members of the family and were light, slender-limbed animals, a very notable difference from the others.

With the Wind River the history of the †titanotheres breaks off short, and from present information, can be carried no farther back. Possibly, there was a Wasatch ancestor, which only awaits discovery, but it seems more likely that these earliest known genera were belated immigrants from the same as yet unknown region, whence came the modernized and progressive elements of the Wasatch fauna. Except for its obscure beginning, the family was pre-eminently characteristic of North America, and only two representatives of it have been found outside of that continent, one in Hungary and one in Bulgaria. No doubt others will yet be found in Asia.

Both in its resemblances and its differences, as compared with the far longer and more complex story of the horses, the history of the †titanotheres has instructive bearings upon evolutionary theory.

(1) Starting with two phyla, one of which speedily died out, the other ramified into four or five, which continued until the disastrous end, pursuing a nearly parallel course of development.

(2) There was a great increase in size and especially in bulk and massiveness from species no bigger than a sheep in the Wind River stage to those which rivalled small elephants in the lower White River.

(3) The teeth underwent comparatively little change; the incisors dwindled and lost functional importance and the canines were reduced, horn-like growths taking their place as weapons; the premolars grew larger and more complicated, but never attained the full size and complexity of the molars, as they did in other perissodactyl families.

(4) Horn-like, bony protuberances appeared first as small humps and knobs over the eyes and steadily enlarged, at the same time shifting their position forward, until they finally attained great size and were on the nose.

(5) The skull was modified so as to support these weapons and endure the shock of impact when they were put to use,

(*a*) by making the upper profile strongly concave from before backward; (*b*) by greatly widening the top of the cranium, where in the older and more primitive genera the high and thin sagittal crest was placed; (*c*) by immensely increasing the thickness of the cranial bones and at the same time hollowing them by means of an intricate system of cavities; in this way sufficient strength was secured without undue increase in weight.

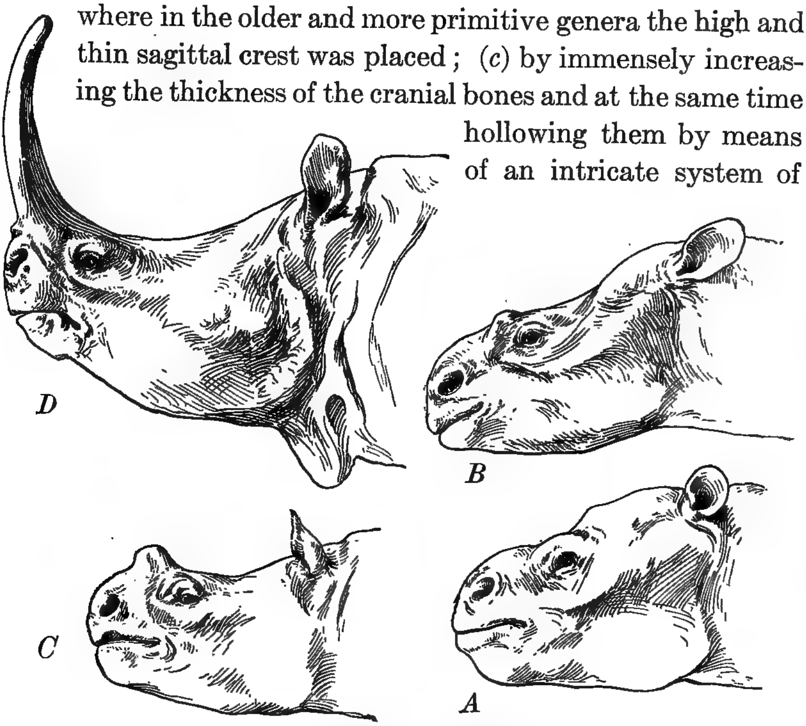

Fig. 165. — Series of heads of † titanotheres in ascending geological order. *A.*, † *Palæosyops*, lower Bridger. *B.*, † *Manteoceras*, upper Bridger. *C.*, † *Diplacodon*, Uinta. *D.*, † *Titanotherium*, extreme development of horns, White River. From models in the American Museum and Princeton University.

(6) The growth of the brain did not keep pace with the increase in the size and weight of the body and head, and this deficiency may have been a factor in determining the early extinction of the family.

(7) To support the huge head, stout ligaments and powerful muscles were needed in the neck and trunk and these in turn required large bony surfaces for their attachment. To meet this need, the spines of the anterior trunk-vertebræ were

very much lengthened, so as to form a hump at the shoulders, and this elongation of the spines went on in proportion to the growing weight of the head.

(8) The limb-bones increased in thickness until they became extremely massive, to carry the immense weight of the body, and they eventually lost the marrow-cavities, which were filled up with spongy bone, a great gain in strength. As is generally, though not universally, true of the large and heavy mammals, there was no coössification between the limb-bones and no great increase in their proportionate length. The thigh-bone, or femur, lost the cylindrical shape of the shaft, becoming flattened and very broad, and acquiring something of the appearance of the same bone in the elephants.

(9) There was no loss or coössification of elements in wrist (carpus) or ankle (tarsus) and *no reduction of digits* within the limits of the family. In the latest, largest and most specialized genera, as well as in the earliest, smallest and most primitive, there were four toes in the front foot and three in the hind. We have the most cogent reasons for assuming that all mammals were derived from ancestors which had five toes in each foot, neither more nor less. If this be true, then the most

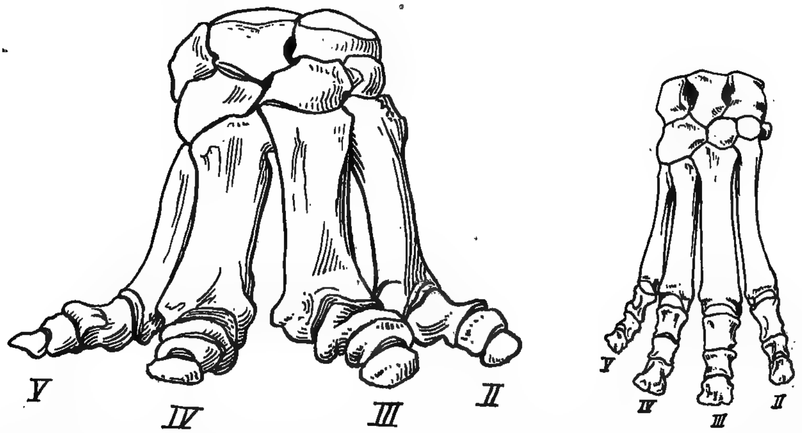

Fig. 166.—Right manus of † titanotheres. *A.*, † *Titanotherium*, White River (after Marsh). *B.*, † *Palæosyops*, Bridger, Princeton University Museum.

ancient known †titanotheres, which were small and light, had already suffered the loss of the first digit in the fore foot and of the first and fifth digits in the hind foot, but there reduction ceased. With the growing body-weight, long, narrow and slender feet would have been a detriment, whereas in swift-running animals, like horses and deer, long and very slender feet are a great advantage. The contrast is both striking and instructive, showing the importance of a short, broad, polydactyl and pillar-like foot to very large and heavy mammals, all of which have feet of this character.

(10) The hoofs, as shown by the terminal bones (ungual phalanges) which formed their bony cores, were reduced in size until they became mere nail-like excrescences around the border of the massive foot.

3, 4. *Tapiridæ and †Lophiodontidæ. Tapirs and †Lophiodonts*

The history of the tapir family is not at all satisfactorily known, partly because tapirs are comparatively rare as fossils in all of the Tertiary formations, and still more for the reason that the specimens so far collected are so fragmentary, not a single half-complete skeleton among them. Had these animals actually been as rare in North America as the fossils would seem to indicate, they could not possibly have maintained themselves for so long a time, throughout nearly the whole of the Tertiary and Quaternary periods. For some reason, probably because they have always been forest-haunting animals, their habits must have kept them in places remote from the areas where the accumulation of sediments was in progress, and thus only occasional stragglers were buried and preserved.

The rarity and incompleteness of the material render it impossible to give any such full account of the tapirs as is practicable for the horses and †titanotheres, but the circumstance is less unfortunate in the case of the tapirs than in that of many other families. This is because these creatures have been so conservative and unprogressive, that they have undergone comparatively little change since their earliest recorded appearance. They have been aptly termed "living fossils" and seem like belated survivors from some older world, out of place in the modern order of things. Attention has already been directed (p. 137) to the remarkable geographical distribution of the tapirs at the present time; Central and South America, southeastern Asia and the adjoining islands.

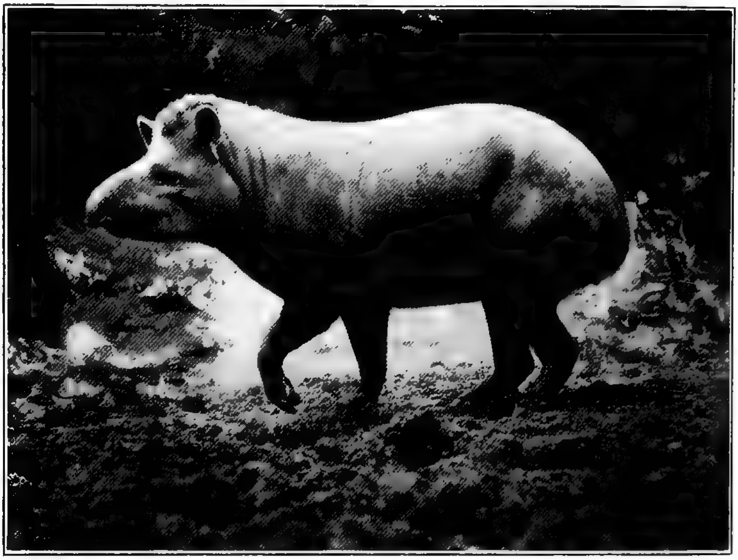

Fig. 167.—American Tapir (*Tapirus terrestris*). By permission of W. S. Berridge, London.

The tapirs are all of moderate size, going back to very small forms at the beginning of their history and never at any period developing into large animals. The only striking and unusual feature about any of the existing members of the family is the long proboscis, a flexible, dependent snout, and, were they all extinct and nothing known of them but the skull, this proboscis could have been confidently predicated of them from the great shortening of the nasal bones. Small tusks, not showing when the mouth is closed, are formed in an exceptional way by the enlarged external upper incisor and the lower canine, the upper canine being much reduced and without function. The grinding teeth have very low crowns, premolars (except the first) and molars are all alike and of a very simple pattern, which has been independently repeated in several different orders of herbivorous mammals; in both upper and lower teeth, there are two elevated, straight, transverse crests.

Except for the modification of the skull which is conditioned by the development of the proboscis, the skeleton might belong to any one of several Eocene or Oligocene families, and it is this generalized, indifferent character which has led to the dubbing of many early perissodactyls as "tapiroids." The limbs are short and moderately heavy, the bones of the fore-arm and lower leg all separate and the number of toes is four in the front foot and three in the hind. The toes end in well-formed separate hoofs, but behind them is a pad, which carries most of the weight. The body is covered with smooth, short hair, which in the American species is of a uniform dark brown, but in the Asiatic species the head, neck and limbs are black and the body is white. In both, however, the young have longitudinal, light-coloured stripes and spots on a dark ground (*see* Fig. 6, p. 47) indicating what the colour-pattern of the ancestral forms must have been. As might be inferred with certainty from the low-crowned teeth, the tapirs are browsing, not grazing, animals, feeding upon leaves and shoots and other soft vegetable tissues. They are shy and solitary in habit and live usually in thick forests and near water, which they frequently

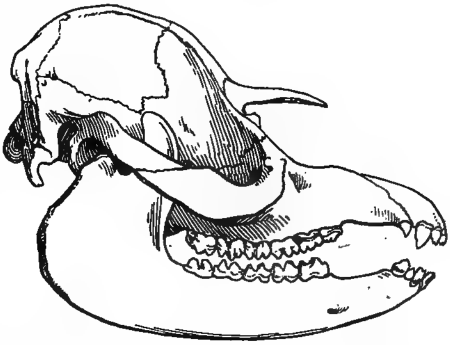
FIG. 168. — Skull of American Tapir, right side.

enter, both for bathing and as a place of refuge when pursued. Under modern conditions, the only perissodactyls of the western hemisphere are the tapirs of the Neotropical region, North America proper, which for ages was the principal home of the order, not having a single representative now.

In the Pleistocene, tapirs were apparently more abundant than in any of the Tertiary epochs, but this was probably due to the fact that the Pleistocene of the forested regions is far more fully recorded than is any Tertiary stage. One species, which was hardly distinguishable from the Recent Central American form, was common in the forested region east of the Mississippi and in California, and a second species (*Tapirus †haysii*) was larger and heavier than the other. Except in Texas, none have been found in the Great Plains area, nor are they likely to be, for that region, then as now, appears to have been devoid of forests. No doubt, these Pleistocene species had substantially the same habits as the existing ones, but they were adapted to a colder climate and a different vegetation, for, except the Pinchaque Tapir (*T. roulini*) of the high Andes, all the modern species are tropical in distribution.

Concerning the Pliocene and Miocene tapirs, but meagre information has been obtained. Enough material has been gathered by the collectors to demonstrate the continuous presence of the family in North America throughout those epochs, but the broken and fragmentary specimens are insufficient to show what the structural changes were. It should be remembered, however, that it is only in the region of the Great Plains and the Great Basin of Nevada that any considerable quantity of Miocene and Pliocene mammals have been found, and in those regions tapirs probably never were common. If the Peace Creek formation of Florida is properly classified as latest Pliocene, then at that time the American tapirs were essentially what they are to-day, for the Florida species is hardly separable from the modern *T. terrestris*.

Not till we reach the lower Oligocene, or White River beds, do we get material which permits the making of definite statements regarding the course of developmental changes. The White River genus, † *Protapirus*, which is also found in the middle Oligocene of Europe, was a much smaller animal than any of the known Pleistocene or Recent species, barely more than half the size, in fact. The teeth show that the small tusks were canines, both above and below, and that the curious substitution of the external upper incisor for the canine had not yet taken place. The grinding teeth were identical in pattern with those of the existing genus, but not all the premolars had yet acquired the form and size of the molars. In the skull the nasal bones had begun to shorten, but the change had not yet made much progress, and the proboscis must have been in merely an incipient stage of development. What little is known of the skeleton other than the skull was like that of the modern genus, but the bones were much smaller and proportionately lighter.

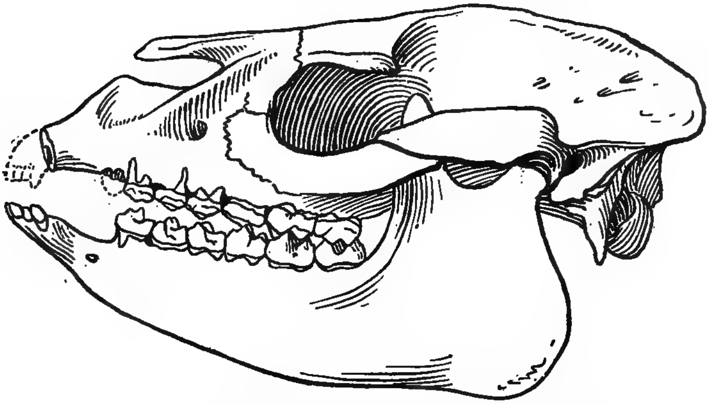

FIG. 169. — Skull of White River tapir (†*Protapirus validus*), left side. Princeton University Museum. N.B. This figure is much less reduced than Fig. 168.

The Eocene tapirs are still very imperfectly known; all that can be said of them is that they become successively smaller as they are traced backward in time, and that in them the premolar teeth were all smaller and simpler than the molars. The Wasatch genus (†*Systemodon*) is the most ancient member of the series yet discovered. Dating from the Eocene immigration, the tapirs are to be regarded as a North American family, for there is here a complete continuity from the lower Eocene to the Pleistocene, while in Europe they first appeared, probably by migration from North America, in the middle Oligocene.

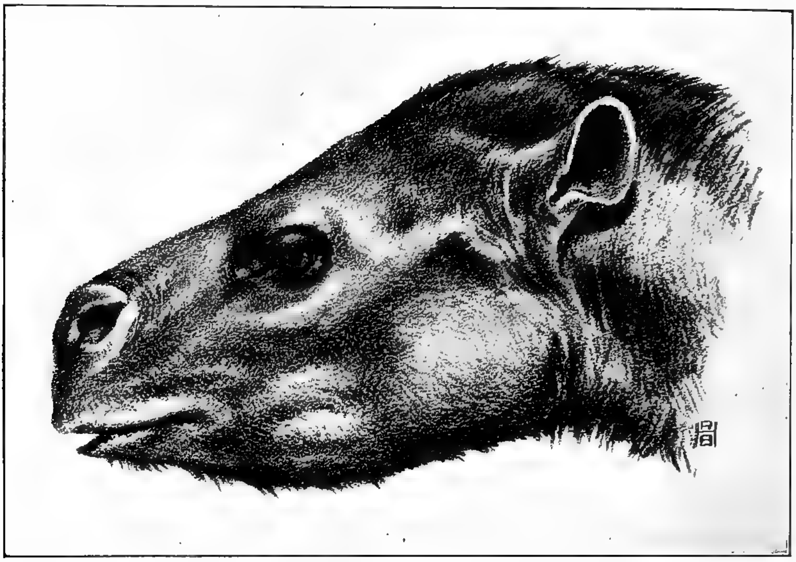

FIG. 170. — Head of the White River tapir († *Protapirus validus*). Restored from a skull in the museum of Princeton University.

In South America the history of the tapirs is even shorter and less eventful than that of the horses; the latter, as we have seen, reached the southern continent in the Pliocene and there gave rise to a number of peculiar and characteristic genera, but the tapirs have been found only in the Pleistocene of Argentina and Brazil and only the modern genus is represented.

Wofully broken and incomplete as the developmental history of the tapirs still is, the fragments are nevertheless sufficient to show a mode of evolution differing in certain important respects from that followed by the horses or †titanotheres. Certain features are common to all three groups, such as the increase in size and in proportionate stoutness from stage to stage and the gradual enlargement and complication of the premolar teeth. On the other hand, the tapirs have been very conservative, and they underwent far less radical changes than did either of the other families. Aside from the proboscis and the modifications of the skull which the development of that organ necessitated, these animals remain to-day very nearly what they were in Oligocene times. This, then, is an example of development practically restricted to a few organs, while all the other parts of the structure changed but little.

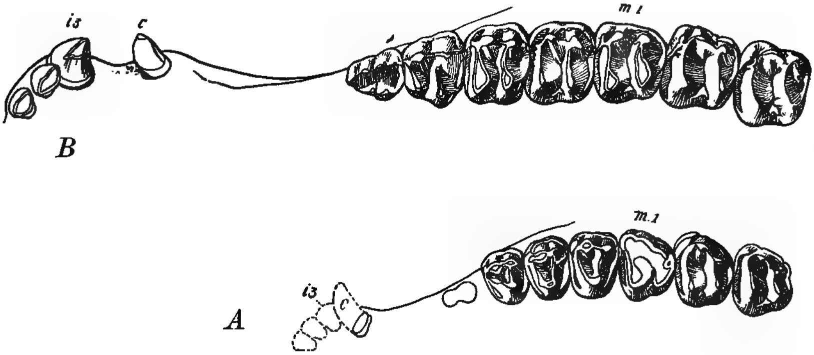

Fig. 171. — Upper teeth, left side, of tapirs, showing comparative sizes. *A*, †*Protapirus validus*, White River Oligocene. *B*, *Tapirus terrestris*, modern. *i 3*, external incisor. *c*, canine. *m 1*, first molar.

The extinct †lophiodonts, like the tapirs, of which they would seem to have been near relatives, are known only from incomplete material, and comparatively little has been learned regarding their history. While they were abundant and varied in Europe, during the Eocene epoch, they never were a striking or prominent element among the mammals of North America, where they persisted one stage later, and they did not reach South America. In North America they are found from the Wasatch to the White River.

The White River genus (†*Colodon*), which is fairly well known, might almost be described as combining the characters of horses and tapirs; but such an expression is not to be interpreted as meaning that this genus is in any sense a connecting link or transition between the two families, but merely that in certain important respects its course of development ran parallel with that followed by the horses. The teeth were very tapir-like, especially those of the lower jaw, which, indeed, are hardly distinguishable from those of a tapir, and the premolars had the molar-pattern. The limbs were very light and slender and the feet long and narrow; the fore foot retained a small fifth digit; the feet, especially the hinder one, had a resemblance to those of the contemporary horses (†*Mesohippus*), though the median digit was not so much enlarged, nor the lateral ones so far reduced. It is highly probable that, had this family persisted till the Pleistocene, instead of dying out in the lower Oligocene, it would have eventually terminated in monodactyl forms.

The †lophiodonts of the Eocene are represented by very fragmentary material; so far as that material goes, it does not show much change from the White River genus, except that the premolar teeth were smaller and simpler, the limbs and feet retaining the same characteristics of length and slenderness. The Wasatch genus (†*Heptodon*) had a similar lightness of limb and narrowness of feet, these characters thus appearing at the very beginning of the family history, so far as their North American career is concerned.

5. *Rhinocerotidæ. True Rhinoceroses*

The history of the great group of rhinoceroses and rhinoceros-like animals is a very long and complicated one, inferior in its completeness only to that of the horses. The complexity of the story arises from the large number of phyla into which the families are divisible, and, despite the great wealth of material and the admirable preservation of much of it, it is extremely difficult to find a clew through the mazes of this labyrinthine genealogy. From the standpoint of the existing geographical distribution of animals, few mammals could seem more foreign and exotic to North American life than do the rhinoceroses, and yet for a very long time that continent was one of the chief areas of their development, so far, at least, as that development can be followed. It is even probable, though not clearly demonstrable, that the family originated here and subsequently spread to the Old World, but not to South America, where no member of it has ever been found. The later history of the rhinoceroses ran its course in the Old World entirely, and the highest specializations within the family are to be found there; in North America these animals are not known to have persisted beyond the lower Pliocene, and if they did survive, it was only as a few stragglers in out of the way places.

The modern rhinoceroses are restricted to Africa, southern Asia and some of the larger Malay islands, Borneo, Sumatra and Java, and within these wide geographical limits are to be found the terminal representatives of at least three separate and quite distinct phyla, the African, Indian and Sumatran genera respectively (*Opsiceros*, *Rhinoceros*, *Dicerorhinus*). It will be advisable to begin the study of this peculiarly interesting family with a brief examination of its modern members, even though none of these are found in the western hemisphere.

All the existing rhinoceroses are large and massive animals, ranging from four feet to six feet six inches in height at the shoulder, and all have solid dermal horns, except in most females of the Javan species[1] (*R. sondaicus*). The Indian and Javan species have a single horn on the nose, while those of Africa and Sumatra have, in addition to the nasal horn, a second one on the forehead. The horns, thus, do not form a

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[1] The names, Javan and Sumatran rhinoceroses, are somewhat misleading, since both of these species are also found on the mainland of India.

transverse pair, but are placed in the median line of the head, one behind the other; it should also be noted that these horns are solid, dermal structures, made up of agglutinated fibres or hairs and not having a bony core formed by outgrowths of the skull, as do the horns of most ruminants, such as oxen, sheep and antelopes, which are therefore called "hollow-horned" (Cavicornia). The skull, however, betrays the presence of horns by the extremely rough areas which serve for their attachment and thus the presence or absence of these weapons may be readily determined in the case of an extinct species of which only the skeleton remains. The skin is very thick and coarse, typically "pachydermatous," and is quite naked in most of the species; but in the Sumatran form there is a sparse coat of hair, which is quite thick in the young animal. In the Indian *Rhinoceros unicornis* the enormously thick skin has conspicuous and regularly arranged folds, which make the creature look as though encased in armour; the ears and tail are tufted with hair. In the African and Sumatran genera the folds are obscurely marked and not definitely arranged, giving the body a smoother appearance. All the existing species, except one, are browsers and feed upon leaves

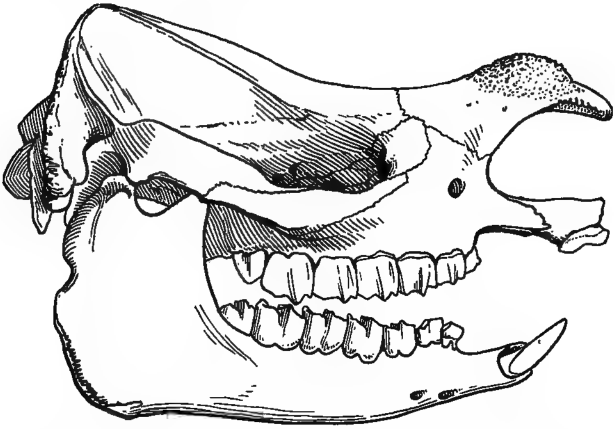

FIG. 172.—Skull of the Javan Rhinoceros (*R. sondaicus*). Note the single upper incisor, and the rough surface on the nasal bones for the attachment of the single horn.

and twigs, and they frequent forests and marshes where their food is abundant. Not that these and other browsing animals do not occasionally eat grass, but it is not their principal diet. The exception noted is the largest of all the living species, the Broad-Lipped Rhinoceros (erroneously called "White") of Africa, *Opsiceros simus*, which is strictly a grazing animal and therefore frequents more open country than the other African species, *O. bicornis*.

There are considerable differences in proportions and general appearance among the various species, but they all have short necks, very long and massive bodies, short and heavy limbs and short, columnar feet, which look much like those of elephants, but have only three toes each. In all but two of the living species the upper lip is prehensile and characteristically pointed and can be used to pick up very small objects, like the "finger" on an elephant's trunk; in the Sumatran species (*Dicerorhinus sumatrensis*) the lip, though pointed, is horny and inflexible, while in the African *O. simus* it is broad and straight-edged.

The teeth of the modern rhinoceroses are extremely characteristic and may always be recognized at a glance. In the African genus (*Opsiceros*) there are no front teeth, all the incisors and canines being lost; the other genera have on each side a single large and trenchant upper incisor, in shape like a broad, obliquely edged chisel, which shears against a still larger elongate and tusk-like lower incisor, that is procumbent and points directly forward. The Indian Rhinoceros (*R. unicornis*) is said to use its tusks as weapons in very much the same fashion as the Wild Boar. Between the large lower tusks there is a pair of very small incisors, which can have little or no functional value; the third lower incisor has been suppressed, as have also the canines of both jaws. The dental formula then is: $i\,\frac{1}{2}$ or $\frac{0}{0}$, $c\,\frac{0}{0}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 28$ or 34 (see p. 93). The premolars, except the first, though somewhat smaller than the molars, have essentially the same pattern. The upper molars have moderately high crowns, yet they are purely brachyodont, except in the grazing, broad-lipped African species (*O. simus*), in which they may fairly be called hypsodont. The external wall of the tooth is broad and nearly smooth, not divided into cusps, as it is in the horses and tapirs, and the two transverse crests, which in the tapirs are directly transverse, are very oblique. In all the existing species additional complications are given by the short spurs, which project inward from the outer wall or from the transverse crests. The lower molars are formed each of two crescents, one behind the other, but their arms or horns are angulate, not curved as they are in other perissodactyls which have crescentic lower teeth.

The upper surface of the skull is very concave in the antero-posterior direction and very broad over the cranium, where there is no sagittal crest. The nasal bones are immensely thick and strongly arched, with the convexity upward; both this arching of the nasals and the fore-and-aft concavity of the skull are devices for giving a strong and solid attachment to the great nasal horn, for the attachment of which these bones have an extremely rough surface, and in the two-horned species, a second roughened area on the forehead marks the place of attachment of the frontal horn. The bones of the cranium are very thick, but lightened by the many chambers which traverse them. The articulation of the lower jaw with the skull is in some respects unique among mammals; the post-glenoid process is a long spike, which fits inside of a bony lump (the *postcotyloid process*) behind the condyle of the lower jaw, and the posterior margin of the latter is greatly thickened. The neck is short and stout, the trunk very long, broad and deep, the long and strongly arched ribs and the widely expanded hip-bones providing space for the great mass of viscera. The bones of the limbs are short and very massive; the humerus has a very prominent deltoid ridge and the femur an unusually large third trochanter; the bones of the fore-arm and lower leg are separate, as in the massive ungulates generally. The foot-bones are likewise extremely short and heavy, and the number of digits is three in each foot. Each of the five or more existing species has its skeletal peculiarities, every portion of the bony structure showing characteristic features; but these are only minor modifications of the general plan and may be neglected in any comprehensive account of the living representatives of the family.

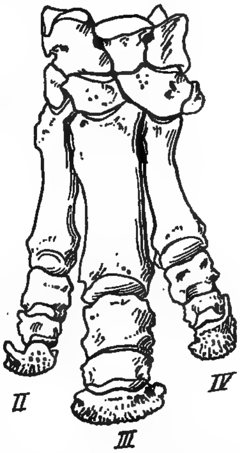

Fig. 173. — Left manus of Indian Rhinoceros (*R. unicornis*).

In order to find any American members of this family, it is necessary to go back to the lower Pliocene, where a great abundance of them is encountered, representing, according to Osborn's view, four or five phyla; and just as in the case of the horses of the same formation, they were an assemblage curiously made up of progressive and old-fashioned, conservative genera, — some were persistent native stocks, others the descendants of immigrants from the Old World, which reached America in the middle Miocene. There was great variety of form, size and proportions among these animals, North America at that time having a larger number of genera and species than Africa and Asia combined have now. Some were quite small, some large, though none equalled the larger modern species. Some of the genera had relatively long legs, but in one genus, †*Teleoceras* (Fig. 125, p. 230), an Old World type, they were most grotesquely short, the belly almost touching the ground, as in a hippopotamus. Most of these rhinoceroses were hornless, but †*Teleoceras* had a small horn on the very tip of the nose. In consequence of the lack of horns, the nasal bones were thin and weak, in marked contrast to the massive, convex nasals of the modern species, and, for the same reason, the upper profile of the skull was nearly straight. Except for minor details, the dentition was in very nearly the modern stage of development; there was a single trenchant upper incisor on each side, a procumbent lower tusk and between the tusks a pair of small incisors; the other incisors and the canines were already lost. One genus (†*Peraceras*) had lost all the upper front teeth. The grinding teeth had the same character as in the existing species, but were somewhat simpler, owing to less development of the accessory spurs. In the more progressive types the teeth were rather high-crowned, though in none were they actually hypsodont; while the persistent ancient genera had teeth with much lower crowns.

Aside from the differences in the skull, which are obviously to be correlated with the absence or very small size of the horn, the skeleton in these Pliocene genera differed but little from the type common to the existing rhinoceroses, and in all the species the feet were three-toed. In short, the dentition and skeleton, except the skull, had already attained to substantially the modern conditions. While the Old World at that time had both horned and hornless rhinoceroses in abundance, none of the genera with large and fully developed horns ever migrated to the western hemisphere. This is the more remarkable in that the great †Woolly Rhinoceros (*Opsiceros †antiquitatis*) of the Pleistocene, which had two very large horns, inhabited Siberia with the †Mammoth (*Elephas †primigenius*). The latter extended its range through Alaska and the northern United States, but the rhinoceros, for some unknown reason, did not accompany it in its eastward wanderings.

The rhinoceroses of the upper Miocene did not differ sufficiently from those of the lower Pliocene to call for particular attention. Needless to say, there were differences between the species of the two epochs, but in such a sketch as this only the broader and more obvious changes can be taken into account. Even in the middle Miocene the only feature which calls for notice was the first appearance in North America of the Old World genus †*Teleoceras*, which became so abundant in the upper Miocene and lower Pliocene. The middle Miocene species (†*T. medicornutus*) would seem to have been descended from †*T. aurelianensis* of the lower Miocene of France; the two species agreed not only in having a small horn on the tip of the nose, but also in the presence of a still smaller one on the forehead.

In the lower Miocene but two phyla of rhinoceroses have been found, both of which were the comparatively little changed descendants of Oligocene ancestors; and there was thus a notable difference from the rhinoceroses of the middle Miocene and subsequent stages, which were decidedly more modern in character. One of these phyla was constituted by those rhinoceroses (†*Diceratherium*, Fig. 129, p. 239) which had a transversely placed pair of horns on the nose, not one behind the other, as in all of the subsequent two-horned species, of which North America had but the one middle Miocene form (†*T. medicornutus*) mentioned above. The lower Miocene species of †*Diceratherium* was a very small animal, and smaller than any member of the family from later formations. The †diceratheres originated in North America, and the stages of their development may be clearly made out; they also migrated to the eastern hemisphere and have been found in France, though it is possible that the genus was not truly monophyletic and arose independently in both hemispheres.

The second phylum is that of the hornless forms (†*Cœnopus*) which were so abundantly represented in the Oligocene and persisted with little change into the Pliocene.

In the upper Oligocene, or John Day, the †diceratheres are the only rhinoceroses certainly yet obtained, and of these there were several species, large and small. The hornless forms may have been present in Oregon, but this has not been clearly demonstrated. That they continued to exist somewhere during that stage is hardly open to question, for they reappeared in the lower Miocene.

From the White River, or lower Oligocene, many well-preserved rhinoceroses, including complete skeletons, have been gathered in the various collections and display very interesting differences in the three substages of the White River beds. In the uppermost substage is found the apparent beginning of the †diceratherе phylum, though it may be traced back to the middle substage; the nasal bones had become much thickened so as to serve as a support for the horns, and these are indicated by a small, but very rough, area on the outer side of each nasal. Comparing this White River species with those of the upper Oligocene and lower Miocene, two differences may be observed: in the later species the horn-supports were well defined bony knobs or prominences, and these knobs were close to the anterior ends of the nasals; while in the White River animal the places for the attachment of the horns were mere roughened areas, and these were well behind the tips of the nasals. This is not an infrequent sort of change, that horns should shift their position forward or that the portion of the nasals in front of the horns should be shortened. Parallel changes occurred among the †titanotheres.

In the middle White River all the rhinoceroses were hornless, but the same two phyla may be distinguished; the actual starting point of the †diceratheres had no indication of the nasal horns, but may be identified as such by their close resemblance in other respects to the species of the upper substage in which the incipient horns appeared. Much commoner were the members of the typical hornless line (see Fig. 135, p. 256), which, though true and unmistakable rhinoceroses, were yet far removed in many details of structure from the progressive genera of the middle and upper Miocene. There are several species in this phylum, which constitute a series of diminishing size almost in proportion to their increasing antiquity. The dentition was already thoroughly and characteristically rhinoceros-like, but a more primitive feature was the presence of a second upper incisor, a small tooth placed behind the trenchant one, making the incisor formula $\frac{2}{2}$; the third incisor and the canines of both jaws were already lost. The assumption of the molar-pattern by the premolars varied much in degree of completeness in the different species; the upper molars, while having all the essentials of the rhinocerotic plan of structure, had a much less complex appearance than in the Recent genera, because of the absence of the accessory spurs; and all the grinding teeth were very low-crowned, in strong contrast to the high-crowned (yet not properly hypsodont) teeth of the middle Miocene and subsequent genera.

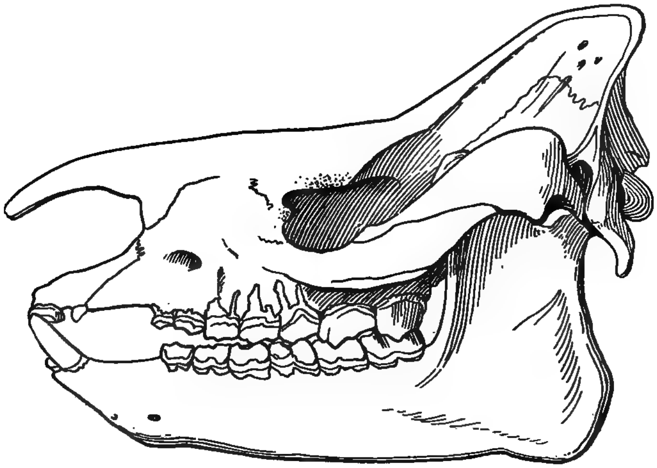

FIG. 174. — Skull of † hornless rhinoceros († *Cænopus tridactylus*); middle White River stage. (After Osborn.)

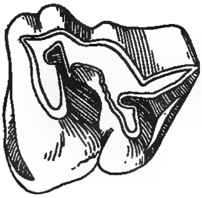

FIG. 175.— Second upper molar, left side, of † *Cænopus*, showing the masticating surface.

As already mentioned, there was much variation in size among the species, but none was as large as those of the Miocene and Pliocene genera, not to mention the enormous animals of the Pleistocene and Recent epochs in the Old World. The commoner species of the middle White River substage (†*Cænopus occidentalis*) was an animal nearly equalling in size the American Tapir (*T. terrestris*) and quite like that species in its proportions, the limbs being relatively longer and less heavy and the feet narrower than in the rhinoceroses of the subsequent geological epochs. The skull, being hornless, had thin, pointed and nearly flat nasal bones, an almost straight and horizontal upper profile, and a short and low, but distinct, sagittal crest; the cranial bones were quite thin, there being no extensive development of sinuses within them. The articulation of the lower jaw with the skull was only beginning to take on the characteristic peculiarities seen in the later genera, and the hinder margin of the lower jaw was not much thickened. Thus, many of the features which distinguish the skull in all Recent and Pleistocene and most Pliocene, and upper and middle Miocene rhinoceroses were entirely lacking in †*Cœnopus*, yet no anatomist could doubt that the White River animal was a genuine rhinoceros.

The neck was short, but not very heavy, the trunk elongate, but not massive, the ribs not being inordinately long nor strongly arched, and the hip-bones so little expanded that they were tapiroid rather than rhinocerotic in appearance. The limb-bones were relatively much more slender than in any existing species, and, although every one of them was characteristically that of a rhinoceros, yet the comparative lightness of body and slenderness of limb gave to these bones a certain resemblance to those of tapirs. The feet, which were moderately elongate and rather narrow, were three-toed, as in all subsequent North American species and in all existing members of the family.

The most ancient and primitive representative of the true rhinoceroses so far discovered occurs in the lowest division of the White River beds and is of particular interest as throwing light upon the origin of the family. The genus (†*Trigonias*) differed from that (†*Cœnopus*) which was so abundant in the middle White River substage in several highly significant particulars, though on a merely casual inspection one might easily be misled into thinking that the two animals were nearly identical, for †*Trigonias* was an undoubted rhinoceros. Such an identification, however, would be a great mistake, for the differences, though not striking, are very important. In the upper jaw the first or anterior incisor had already assumed the characteristic trenchant, chisel-like shape, but two other incisors were present also, thus bringing the number up to the original three, common to all early perissodactyls; even more interesting is the presence of a small upper canine. The lower jaw likewise had three incisors on each side, the first and third small, the second enlarged and tusk-like, but the canine had already been suppressed, and thus the dental formula was: i$\frac{3}{3}$, c$\frac{1}{0}$, p$\frac{4}{4}$, m$\frac{3}{3}$, $\times 2 =$ 42, or 14 more than the formula of the existing African species. The premolars were smaller and less complex than the molars.

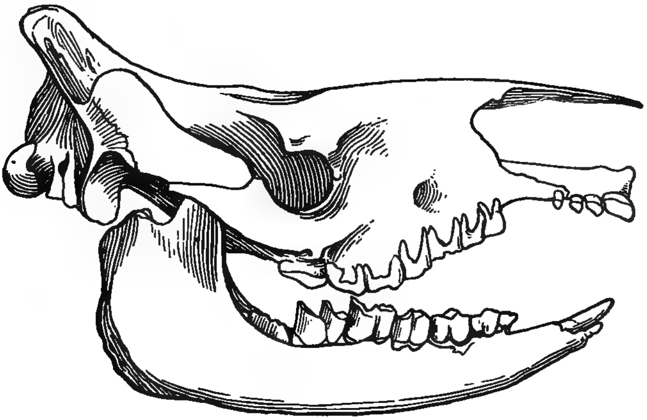

FIG. 176.—Skull of † *Trigonias osborni*, lower White River. (After Hatcher.)

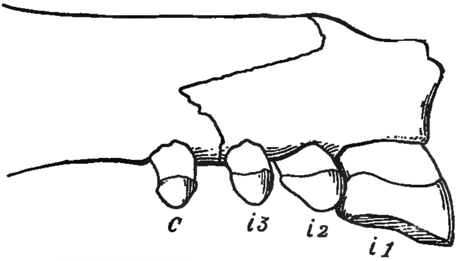

FIG. 177. — Anterior end of right upper jaw of † *Trigonias osborni* (after Lucas). *c.*, canine. *i 3*, external incisor. *i 2*, middle incisor. *i 1*, first incisor.

From this ancient genus may readily be inferred the steps by which the peculiar characters of the anterior teeth in the true rhinoceroses were attained. The first stage was undoubtedly an animal in which, as in all other Eocene perissodactyls, there were three well-developed incisors on each side of both jaws, 12 in all, and moderately prominent canine tusks; all these teeth were erect. The second stage was the enlargement of the first upper and second lower incisors, the latter becoming less erect and beginning to assume the recumbent position; at the same time the other incisors and the canines were reduced in size and were so little used that they lost their functional importance. The third stage, in which the first and second lower incisors were horizontal and pointed directly forward, and the first upper and second lower teeth were still further enlarged, the non-functional teeth reduced in size and the lower canine suppressed, was realized in the genus †*Trigonias*. There were thus but two hypothetical stages between this lower White Region genus and the tapir-like forms of the middle Eocene, so far, at least, as the anterior teeth are concerned.

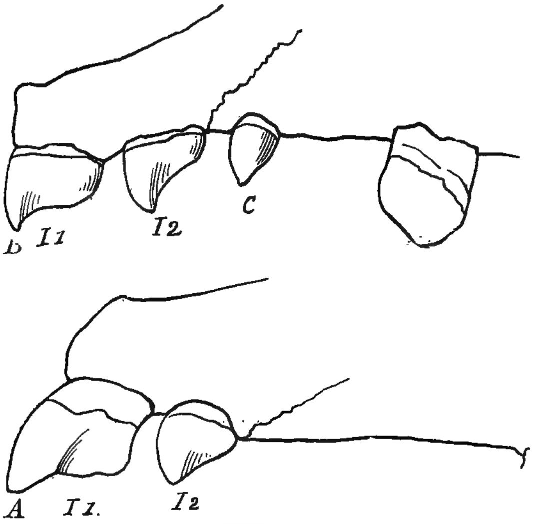

Fig. 178.—Anterior end of left upper jaw of † *Cœnopus*, *A*, adult; *B*, immature animal (after Osborn). *I 1*, first incisor; *I 2*, second incisor; *C*, canine.

The skeleton of †*Trigonias* was, on the whole, very much like that of the succeeding genus, †*Cœnopus*, of the middle substage of the White River, but with the important exception that the front foot had four digits instead of three. The pollex, or first of the original five, almost always the first to disappear, had been suppressed, the third or median digit was already the largest of the series, both in length and breadth; the second and fourth, somewhat shorter together made a symmetrical pair, while the fifth, though much the most slender of all, was still functional and had retained all of its parts. In the hind foot the digits had been reduced to three. This arrangement, four toes in the manus and three in the pes, is the same as is found in the existing tapirs and in the Eocene perissodactyls generally, with only two or three known exceptions. In the Oligocene, on the other hand, all the genera except the †titanotheres, tapirs, †lophiodonts and †amynodonts were tridactyl both before and behind.

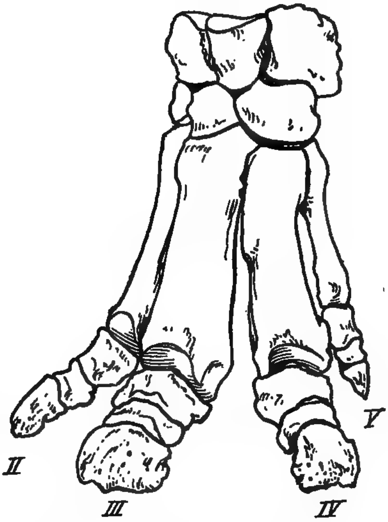

Fig. 179. — Left manus of † *Trigonias osborni*. (After Hatcher.)

With †*Trigonias* the definitely known history of the true rhinoceroses breaks off abruptly, and it is possible that that genus was an immigrant, though it is perhaps more likely that its ancestors existed in the upper and middle Eocene (Uinta and Bridger stages) of North America. Some fragmentary specimens from the Uinta beds, too imperfect for any definitive identification, are an encouragement to hope that the forerunner and direct ancestor of †*Trigonias* may yet be discovered in that formation. It is also quite possible that one of the larger species of the genus †*Hyrachyus*, so abundant in the Bridger and going back to the Wind River, may take its place in the same series.

6. †*Hyracodontidæ.* †*Cursorial and* †*Aquatic Rhinoceroses*

The luxuriant diversification of the rhinoceros-stem was not exhausted by the many phyla of what we have called the true rhinoceroses. Two other series, very distinctly marked and rather distantly connected with the first, are yet to be considered. These two series, the †hyracodonts (in the narrow sense) and the †amynodonts, ran courses which, in certain respects, were singularly alike; both were of North American origin and one, the †hyracodonts, was entirely confined to that continent, while the other sent out late migrants, which entered Europe, no doubt through Asia, and both ended their careers before the close of the White River time. Their history was thus a brief one when compared with that of the true rhinoceroses, three phyla of which persist to the present day, though their geographical range is greatly restricted in comparison with what it was in the Miocene and Pliocene, when they ranged over every continent except Australia and South America.

Just how to classify these three series of rhinoceroses and rhinoceros-like animals, so as most accurately to express their mutual relationships, is a question that has received several answers. One method suggested is to include them all in a single family and to make a subfamily for each of the three well-distinguished series; this is the arrangement which personally I should prefer. A second plan is to accord family rank to each of the three groups; while the most elaborate scheme, that of Professor Osborn, is as follows: for the rhinoceroses, in the broader sense, he makes two families, the Rhinocerotidæ and the †Hyracodontidæ, and divides the former into four subfamilies, which include all of the true rhinoceroses, living and extinct, of the Old and New Worlds, and the latter into two subfamilies, the †Hyracodontinæ and †Amynodontinæ. It is not a matter of very great moment as to which of these three schemes is followed, and I shall therefore adopt the one proposed by Professor Osborn, in order to avoid, so far as possible, the confusing effect of different methods of classification.

As before mentioned, the subfamily of the †hyracodonts (†Hyracodontinæ) became extinct in White River times, during most of which it was represented by the single genus †*Hyracodon*, whence are derived the names for the family and subfamily. The series was purely North American, and no member of it has ever been found in any other continent. The species of †*Hyracodon* were altogether different in appearance and proportions from the true rhinoceroses, being lightly built, slender, cursorial creatures, suggestive rather of horses than of rhinoceroses, to which they bore much the same relation as the slender-limbed, narrow-footed †lophiodonts did to the tapirs (*see* p. 326); in size, they were somewhat taller and considerably heavier than a sheep.

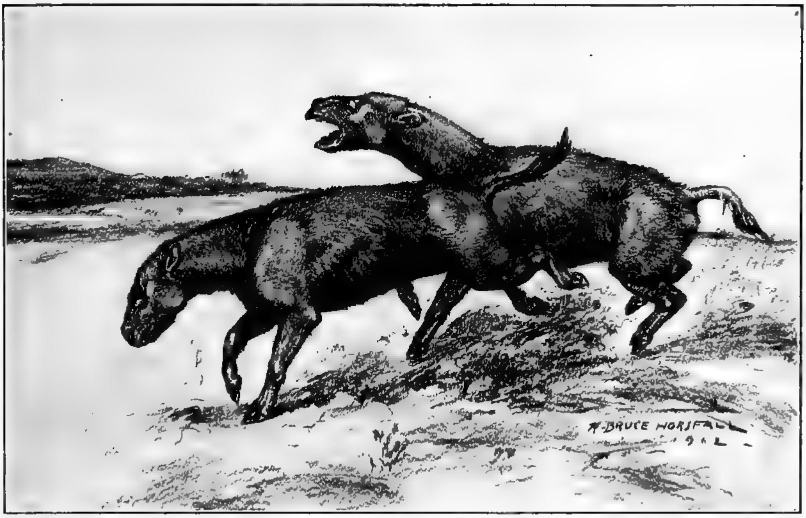

FIG. 180. — † Cursorial rhinoceros († *Hyracodon nebrascensis*), White River stage. Restored from a skeleton in the Museum of Princeton University.

The low-crowned grinding teeth had the unmistakable rhinoceros-pattern, and between them and the teeth of the contemporary †*Cœnopus* the difference was merely one of size, except for one small, but not insignificant feature. The last upper molar had not perfectly acquired the triangular form characteristic of all the true rhinoceroses, caused by the complete fusion of the outer wall with the posterior crest, but the wall projected a little behind the crest, as in perissodactyls generally. Premolars (except the first) and molars were alike in structure and of nearly the same size. While the grinding teeth were thus hardly to be distinguished from those of the true rhinoceroses, the anterior teeth, incisors and canines, were totally different; they were very small and had simple, pointed and slightly recurved crowns, and were all very much alike in size and form. Thus, there were in the front of the mouth eight small, hook-like teeth, above and below, which were obviously quite useless as weapons; and as the skull had no horn, the animal was defenceless, and must have depended entirely upon speed for its safety from the attacks of the larger and more powerful beasts of prey.

The skull was short, deep and thick, and the head must have been heavy and clumsy, quite out of keeping with the body and limbs. The neck was surprisingly long, longer indeed proportionately than in the contemporary genus of horses (†*Mesohippus*), but the neck-vertebræ were relatively stout and strong, as was required for the muscles to move and control the heavy head. The body was rather elongate, but not deep or massive, and the limbs were proportionately much longer than in any of the known rhinoceroses. The limb-bones, one and all, despite their length and slenderness, bore an unquestionable likeness to those of the true rhinoceroses. In this elongation of the limbs the fore-arm and thigh were the parts most affected, and the slenderness, though in notable contrast to the proportions both of the true rhinoceroses and the †amynodonts, was yet much less marked than in the middle Eocene representatives of the †hyracodonts themselves. The feet were long and narrow, approximating, though not actually attaining the proportions of the feet in the White River horses (†*Mesohippus*). There were three digits in each foot, and the median toe (third of the original five) was so much enlarged and the lateral toes (second and fourth) so reduced, though still functional, as strongly to suggest a monodactyl foot as the outcome of this course of development, had not the early extinction of the subfamily put an end to it. It is interesting to reflect that, had the †lophiodonts and †hyracodonts continued their existence to the present time and had persisted in advancing along their particular lines of specialization, we should, in all probability, have had monodactyl tapirs and rhinoceroses, as well as horses.

As in the case of so many other mammalian series, the †hyracodonts of the but partially explored Uinta formation are still very imperfectly known. Almost all that can be positively stated about them is that they were smaller than their White River successors and that the assumption of the molar-pattern by the premolars was incomplete. In the upper Bridger beds also not very much is known regarding the then representatives of the series, (†*Triplopus*). So much is clear, however, that they were still smaller and lighter animals, that the limbs were very light, and that the number of digits in

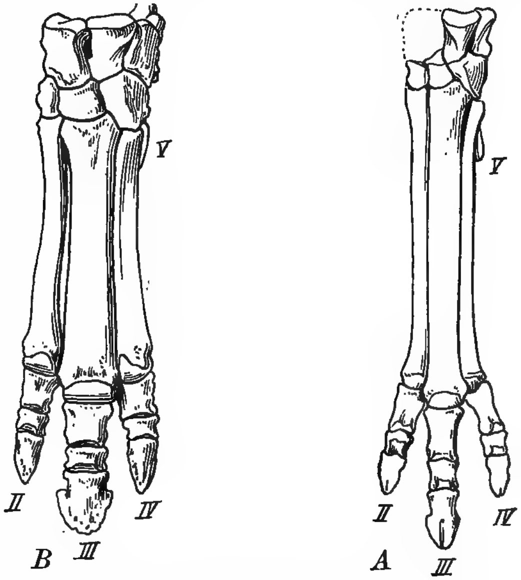

Fig. 181.—Left manus of †cursorial rhinoceroses. *A*, †*Triplopus cubitalis* (after Cope), upper Bridger. *B*, †*Hyracodon nebrascensis*, White River.

the fore foot had already been reduced to three, the only known Bridger perissodactyl of which this is true, all the others having four digits in the manus and three in the pes.

In the middle and lower Bridger, and even in the Wind River, occurs a genus (†*Hyrachyus*) which contained a large number of species, ranging in size from a full-grown modern tapir to creatures no larger than foxes. It is among these smaller species that the most ancient member of the †hyracodont line is to be sought, though it is not yet practicable to select any particular one. †*Hyrachyus*, indeed, may very possibly have contained among its many species the ancestors of all three lines of the rhinoceroses and rhinoceros-like animals, and thus formed the starting point from which they developed in diverging series. It is always a very significant fact when two or more groups approach one another the more closely, the farther back in time they are traced, because that can only be interpreted to mean that ultimately they converged into

FIG. 182. — Primitive † cursorial rhinoceros († *Hyrachyus eximius*), lower Bridger. Restored from a skeleton in the American Museum of Natural History.

a common term, even though that common ancestor should elude discovery.

†*Hyrachyus* may be described as a generalized, relatively undifferentiated perissodactyl, from which almost any other family of the order, except the horses and the †titanotheres, might have been derived. The incisors, present in undiminished number, were well developed and functional, but not large, and the canines were moderately enlarged, forming small tusks. The premolars were all smaller and less complex than the molars, which had a strong resemblance to those of the tapirs; in the lower jaw they were identical with the latter, but in the upper jaw there was more than a suggestion of likeness to the rhinoceroses. The skull was long, narrow and low, hornless, and with thin, slender nasals and straight, horizontal upper contour. The neck was short, the body very long and the limbs of medium length and weight; though relatively stouter than in †*Triplopus* of the upper Bridger and Uinta beds, they cannot be called heavy. The feet were not especially elongate and rather slender; the manus had four toes and the pes three.

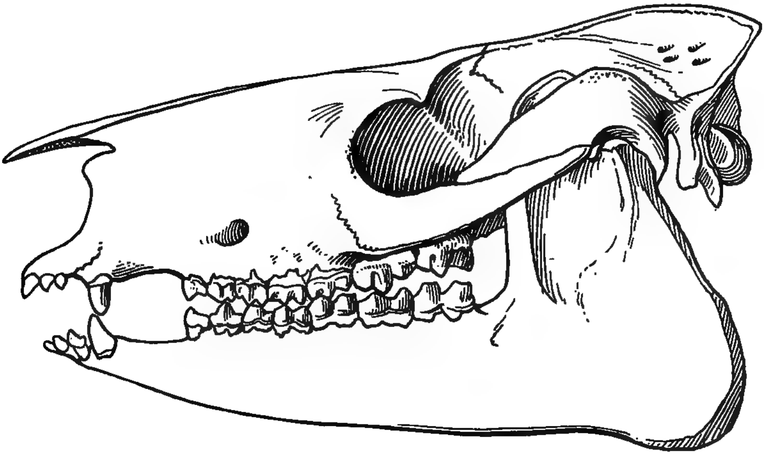
Fig. 183.—Skull of † *Hyrachyus*. (After Osborn.)

A brief and short-lived branch of this stock existed in the

Bridger stage, but was not, so far as is known, represented in any of the subsequent stages, and was made up of a single genus (†*Colonoceras*) which had a small pair of dermal horns upon the nasal bones. In other respects, it was like †*Hyrachyus*. It is surprising to find that the horned series should have so speedily died out, while the defenceless forms not only persisted, but actually became more defenceless through the reduction of the canine tusks. *À priori*, one would have expected the opposite result, but the key to the enigma is probably to be found in the more perfect adaptation of the surviving kinds to swift running.

The second subdivision (†Amynodontinæ) of this family contains a series of animals which developed in a very divergent fashion and went to quite the opposite extreme from the cursorial †hyracodonts, resembling the latter (aside from the fundamental characteristics common to all rhinoceroses, in the broadest sense of that term) only in the pattern of the molar teeth and in the absence of horns. The terminal member of the †amynodont series was a White River genus (†*Metamynodon*) of which the remains have been found almost exclusively in the consolidated and cemented sands filling the old river-channels of the middle substage of the White River beds. This fact, together with certain structural features of the skull and skeleton, leads at once to the suggestion that these animals were chiefly aquatic in their habits and somewhat like hippopotamuses in mode of life. †*Metamynodon* was quite a large animal, the heaviest and most massive creature of its time, after the disappearance of the giant †titanotheres, but was low and short-legged.

The true rhinoceroses, save those which, like the existing African species, have lost all the front teeth, all agree in the peculiar differentiation of the incisors, which was fully described in the preceding section of this chapter. The †hyracodonts had a second scheme, the incisors and canines being all similar in shape, small, pointed and recurved, while still

FIG. 184.—Supposedly †aquatic rhinoceros (†*Metamynodon planifrons*) of the White River. Restored from a skeleton in the American Museum.

a third mode of development was exemplified by the †amynodonts, in which the canines became large and formidable tusks, a very notable difference from all other rhinoceroses whatever.

In †*Metamynodon* the incisors were not enlarged, but were unreduced and functional; the upper canine was a short, heavy tusk, obliquely truncated by the abrasion of the lower tusk, which was very large. Another striking difference from all the other groups of rhinoceroses was the reduction of the premolar teeth, which, instead of equalling the molars in size, were much smaller and were diminished to three in the upper, two in the lower jaw. The molars were of the characteristic rhinoceros-pattern, but were very narrow, especially the inferior ones, in which the enamel did not surround the whole crown, as it normally does, but was lacking along vertical bands, where the dentine formed the surface. The skull was extremely peculiar and, with its very long and high sagittal crest and immensely expanded and heavy zygomatic arches, had a surprising likeness to the skull of some great beast of prey. The face was very much shortened and the skull depressed, so that the head was remarkably low, broad and flat, proportions which did not recur in any other group of rhinoceroses. The neck was short, the body very long and very massive, as is shown by the long and strongly arched ribs. The limbs were short and stout and the feet quite primitive in character, the front foot retaining four fully developed and functional digits. No other perissodactyls of the middle White River beds, except the †lophiodonts and tapirs, had more than three digits in the manus, and thus †*Metamyodon* was a belated exception to the general rule.

The Uinta member of this series was †*Amynodon*, a similar but smaller and lighter animal. The canine tusks were of more moderate size and none of the premolars had been lost, but were considerably smaller than the molars, and the last two had assumed the molar-pattern. The face was not conspicuously shortened and the zygomatic arches of the skull were not so heavy or so widely expanded as in the White River genus, and the skeleton was less massive.

The genus †*Amynodon* is also represented in the upper Bridger beds, but by a species different from that of the Uinta stage. This more ancient species was a smaller animal than its upper Eocene successor and had less enlarged canine tusks, but it already possessed the typical rhinoceros molar teeth, the only Bridger mammal of which this is true. Beyond this species the line, as at present understood, cannot be traced, though probably some species of †*Hyrachyus*, or an allied genus, will prove to be the ancestor sought; but the connecting link has not yet been brought to light.

The history of the rhinoceroses and rhinoceros-like animals, of which a very much simplified sketch has just been given, is a highly complex one, much more so than that of the horses, †titanotheres, or tapirs, and is less fully recorded, the earlier chapters of the story being still missing. However, in the progress of discovery these chapters will almost certainly be recovered, and it is already possible to draw close inferences as to what they will reveal. The complexity of the history is chiefly due to the fact that, as compared with the other perissodactyl groups, the rhinoceros stem ramified more widely and gave rise to more divergent and diversified forms. At one extreme, we find huge, massive, slow-moving types; and, at the other, light, slender, cursorial creatures, almost horse-like in appearance, with intermediate forms of moderate size. Some were long and others short legged, mostly adapted to terrestrial life, but some with aquatic habits. The three very different sorts of modification which the anterior teeth (incisors and canines) underwent in the three principal series may be taken as an illustration of this divergent development, and to these may be added a fourth, the complete suppression of all the incisors and canines above and below, as is exemplified by the modern African species.

Of the three rhinoceros groups, whatever rank be assigned them, family or subfamily, much the most prolific in divergent forms was that of the true rhinoceroses (Rhinocerotidæ) of which seven or more phyla have been distinguished, three of them surviving to the present time. Only in this series were horns frequently present, the brief experiment, as it might be called, of the Bridger genus †*Colonoceras,* being the only known instances of horns among the †hyracodonts, and the †amynodonts were all hornless. In making the comparison as to degree of ramification among the three series, it should be borne in mind that the true rhinoceroses were the only long-lived group, the other two dying out before or at the end of the White River stage. Within the series or family of the true rhinoceroses, there was no great divergence of type, and all the members were much alike, heavy and slow animals, but with very great variety in the details of structure. Take, for instance, the matter of horns; we find both hornless and horned genera, the former preceding the latter in time, but, so far as North America is concerned, continuing in association with them till the end. Among the horned genera, the horn may be single, double in a transverse pair (†*Diceratherium*) or arranged one behind the other in the median line of the head (*Dicerorhinus, Opsiceros,* etc.). The single horn may be on the nose or the forehead; if on the nose, it may be on the upper side of the nasal bones (*Rhinoceros*) or on the extreme tip and pointing obliquely forward (†*Teleoceras*). The single frontal horn was much less common, but in the extraordinary †*Elasmotherium,* of the European and Siberian Pleistocene, the horn was of gigantic size and the surface for its attachment an enormous, dome-like boss on the forehead.

All three of the series had their most ancient known representatives in North America, and it seems probable, though by no means certain, that they all originated here by divergence from a common stock, which was represented more or less closely by the genus †*Hyrachyus* of the Bridger and Wind River stages of the Eocene. However that may be, true rhinoceroses flourished exceedingly in the Old World from the upper Oligocene to the Pleistocene, the events of the latter epoch restricting them to their present range. The significance of the American genera for the ancestry of the modern types can be found only in the most ancient forms, †*Trigonias* and †*Cænopus;* the subsequent development which led up to the existing species of Asia and Africa went on entirely in the eastern hemisphere. The †hyracodont subfamily had no known representatives outside of North America, but the †amynodonts sent out emigrants, which appeared for a brief time in the Oligocene of Europe.

In the varied history of the rhinoceroses, the principles of evolutionary change which may be deduced from the recorded development of the horses, tapirs and †titanotheres are found to be applicable.

(1) There was the same gradual increase in size from the earlier to the later geological stages. Not that all the phyla kept equal pace in this respect, and even within the same phylum it was the rule rather than the exception to find larger and smaller contemporary species.

(2) In all of the early forms, up to the middle Miocene, the teeth were low-crowned; after that time there was a decided increase in the height of the teeth, though only in †*Elasmotherium* was the fully hypsodont, cement-covered crown attained. In the existing African Broad-Lipped Rhinoceros (*Opsiceros simus*), which is a grazing animal, the high, cement-covered teeth may also fairly be called hypsodont.

(3) In all of the lines, as in the other perissodactyl families, the premolars gradually took on the pattern of the molars; only in the †amynodonts were the premolars notably reduced in number and size.

(4) The three different modes of development of the anterior teeth, exemplified by the true rhinoceroses, the †hyracodonts and †amynodonts respectively, need not be recapitulated here. It is sufficient to call attention to the fact that the three

kinds of modification diverged from a common starting-point such as may be seen in the middle Eocene perissodactyls generally, and that in each series the transformation was gradual.

(5) The modification of the skull followed several different courses, as designated by the major and minor subdivisions of families, subfamilies and phyla. The development of horns, whether single or double, in transverse or longitudinal pairs, was the most important single influence in transforming the skull, as determined by the mechanical adjustment necessary to make these weapons effective, but even in the hornless forms changes went on, and in all the phyla the skull departed more and more widely from the primitive Eocene type in each succeeding geological stage. The most aberrant form of skull was that of the hornless and presumably aquatic †*Metamynodon*, in which the greatly shortened face, high sagittal crest and extremely wide zygomatic arches were altogether exceptional.

(6) When the history of any horned phylum is at all complete, the development of the horns may be followed step by step from the marks which they left upon the skull. As a rule, the story was one of gradual enlargement, but, in one case at least, an incipient horn apparently failed to enlarge and was eventually lost.

(7) In the light, slender and cursorial †hyracodonts the mode of development resembled that of the horses, as appears in the elongation of the neck, limbs and feet, in the enlargement of the median toe and concomitant reduction of the lateral digits. Also, as in the horses, the elongation of the limbs began to be noteworthy while the body-weight was small and was consequently accompanied by great slenderness; as the body-weight increased, the limbs became stouter, to yield the necessary support.

(8) In the phyla composed of massive animals the principle of change agreed with that exemplified by the †titanotheres,

increasing body-weight being the determining factor in both cases. When this increase began to be decided, the reduction of digits ceased at the point which had already been reached in any particular series, three in both manus and pes in the true rhinoceroses, four in the manus and three in the pes in the †amynodonts. Very heavy animals require broad, columnar feet to support them, and hence the similarity of appearance in such widely separated groups as elephants, rhinoceroses and hippopotamuses, not to mention several extinct orders and families. Among the larger and heavier rhinoceroses, as in those of the present time, there was great variety in the proportionate lengths of the limbs, body and feet.

In brief, the great complexity of the history of the rhinoceroses is due to the many divergent and parallel phyla into which these animals may be grouped. Broadly speaking, they may be subdivided into the slender, cursorial types and the heavy, slow-moving types, the former developing in a manner similar to that shown by the horses, while the latter were modified after the fashion of the †titanotheres. Obviously the load to be supported by the legs and feet was a very important factor in determining the character of evolutionary change.

II. †Ancylopoda. †Clawed Perissodactyls

The very extraordinary and aberrant animals which are referable to this suborder have been understood only since the year 1888, for, as was shown in an earlier chapter (p. 41) their scattered parts had been assigned to two different mammalian orders, the skull to the perissodactyls and the feet to the pangolins, or scaly anteaters (Pholidota) of the Old World, since it occurred to no one that the same animal could have such a skull and teeth in combination with such feet.

The history of the Ancylopoda is still very incomplete, only four genera, of the lower Pliocene, middle and lower

Miocene, and the middle Eocene respectively, being at all adequately known, but even in this imperfect form the story is worth telling. The suborder was probably of American origin and its most ancient known member existed in the middle Eocene. Both in Europe and North America the group persisted into the lower Pliocene and it is believed, though not clearly demonstrated, that in eastern Asia it continued even into the Pleistocene. All the genera of the suborder may be included in a single family.

7. †*Chalicotheriidæ.* †*Chalicotheres*

The specimens which so far have been found in the American middle and upper Miocene and lower Pliocene are very fragmentary, consisting of little more than teeth, and give no information other than to demonstrate the presence of the family in North America during that period of time. On the other hand, the European genera of the middle Miocene and lower Pliocene are well known and may or may not have been closely similar to their American contemporaries, though they were undoubtedly larger. In these most peculiar and grotesque animals (†*Macrotherium* and †*Chalicotherium*) the head was relatively small, the teeth were very low-crowned and adapted only to a diet of soft vegetable substances and the mode of feeding must have been that of browsing upon leaves and shoots of trees and bushes; the premolars had not acquired the molar-pattern, which was very exceptional for perissodactyls of so late a time, such a difference between the two classes of teeth being characteristic of the Eocene members of the order; the incisors and canines were reduced, but the formula is not definitely known.

The neck was of moderate length, the body very long, and the limbs were also elongate, especially the anterior pair, in consequence of which the back sloped downward from the shoulders to the rump; the two fore-arm bones were fused together, and these, with the thigh-bones, were the longest segments of the limbs. The special peculiarity of these animals was in the character of the feet, which had three toes, each armed with a huge claw, instead of terminating in a hoof, as it does in all normal perissodactyls. The external digit, which, in the absence of the fifth, was the fourth, was the largest of the series and apparently bore the most of the weight, a notable departure from the normal perissodactyl symmetry, in which the third or median toe is the largest. The hind feet were considerably smaller than the fore, but had similar claws.

Many suggestions have been offered as to the manner in which these great claws were employed. The teeth demonstrate that these animals could not have had predaceous habits, but must have been inoffensive plant-feeders. As no such herbivorous creatures are living now, it is impossible to reach a definitive solution of the problem, which is further complicated by the fact that in two other orders of hoofed mammals, Artiodactyla and †Toxodontia, a more or less similar transformation of hoofs into claws took place, and among the edentates the large, herbivorous †ground-sloths (†Gravigrada) had enormous claws. It is inadmissible to suppose that these great †chalicotheres could have been burrowers, or tree-climbers, or that they pursued and slaughtered prey of any kind, for, aside from the character of the teeth, such heavy and slow-moving beasts would have been utterly inefficient at work of that sort. No doubt, the claws were used, to some extent, as weapons of defence, as the existing South American Ant-Bear (*Myrmecophaga jubata*) uses his formidable claws; probably also some, if not all, of these clawed ungulates would employ the fore feet in digging for roots and tubers, as is done by the bears generally. Many years ago, the late Sir Richard Owen suggested with reference to the †ground-sloths that the principal use of the fore feet, other than that of locomotion, was to draw down within reach of the long tongue and prehensile upper lip the branches upon which they browsed. This explanation may perhaps be applicable to all of these aberrant and exceptional groups of hoofed animals.

In the lower Miocene (Arikaree stage) of North America well-nigh complete skeletons of a large †chalicothere (†*Moropus*, Fig. 130, p. 240) have been obtained, an animal which considerably exceeded a large horse in bulk and stature. In structure this genus had departed less widely from the normal perissodactyl type than the genera of the European Miocene and Pliocene above described and was in many respects more primitive. It could not, however, have been directly ancestral to the European forms, though indicating in a general sort of way what the ancestral type must have been. †*Moropus* had a relatively small, slender and pointed head, a long neck, much longer than in the European genera, and long fore legs; the shorter hind legs gave the back a steep inclination from the shoulders to the rump. The proportions of the head, neck and limbs suggest those of a giraffe, in less exaggerated form, but the likeness is more marked in the skeleton than in the restoration and is at best a distant one. The feet were armed with the great claws characteristic of the suborder, but the fore foot, in addition to the three functional toes, had a long splint, representing the rudimentary fifth digit; of the first, or pollex, no trace remained. The perissodactyl plan of symmetry had

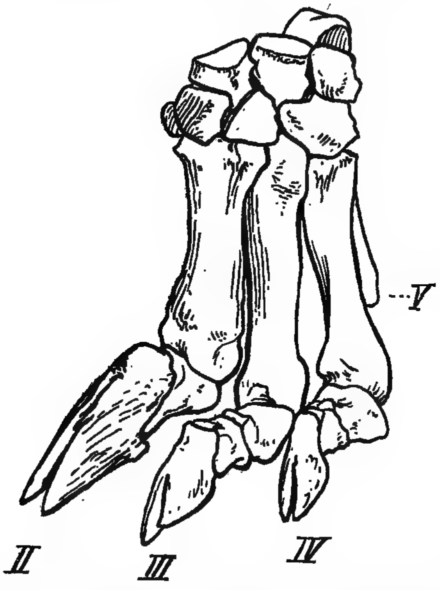

FIG. 185. — Left manus of lower Miocene †chalicothere (†*Moropus*). (After Peterson.)

not yet been lost, the third or median digit being the longest of the series. In the hind foot, which had only three toes, the departure from the perissodactyl arrangement had already begun, and the third and fourth digits (*i.e.* of the original five) were of nearly equal size, both in length and thickness, while the second was smaller.

The family is represented in the John Day, or upper Oligocene, by specimens which are sufficiently characteristic to prove that they are properly referable to this group. They have been assigned to the same genus as that of the lower Miocene, but whether the identification is justified remains to be determined.

In the lower White River beds of Canada is found a much smaller animal of this family, but the material is too fragmentary for generic identification. Something more is known of a genus (†*Schizotherium*) from the European Oligocene, likewise much smaller than the Miocene and Pliocene forms, which had four, or possibly even five, functional digits, in the manus, but it has not been ascertained whether the transformation of hoofs into claws had already taken place.

It is not yet practicable to determine the relationships of the European and American †chalicotheres to one another, because of the imperfect nature of most of the material.

The molar teeth of the †chalicotheres were suggestively like those of the †titanotheres, and, were the teeth alone to be taken into account, no one could hesitate to regard the two families as closely related.

The most ancient known member of the family is the genus †*Eomoropus*, from the Bridger Eocene, which will be described by Professor Osborn in a paper soon to appear. †*Eomoropus* was much nearer to the normal perissodactyls than were the genera from the Oligocene and Miocene above described.

CHAPTER IX

HISTORY OF THE ARTIODACTYLA

THE artiodactyls are and for a very long time have been a very much larger and more variegated group than the perissodactyls, and the Old World has been and still is their headquarters and area of special development, where they are represented in far greater number and variety than in the New; the perissodactyls, on the other hand, flourished especially in North America, as was shown in the preceding chapter. At the present time the artiodactyls are the dominant ungulate order, far outnumbering all the others combined, and include an assemblage of varied types, which, when superficially examined, appear to be an arbitrary and unnatural group. What could seem more unlike than a dainty little mouse-deer, no larger than a hare, a stag, a camel, a giraffe, a bison and a hippopotamus? Yet, in spite of this wonderful diversity of size, proportions, appearance and habits, there is a genuine unity of structure throughout the order, which makes their association in a single group altogether natural and proper, especially as these structural characters are not found united in any other group.

It would be superfluous to enumerate all of the diagnostic characters which, on the one hand, unite all the living and extinct artiodactyls and, on the other, distinguish them from all other hoofed animals, and it will suffice to mention a few of the more significant of these features.

As the name implies, the artiodactyls typically have an even number of toes in each foot, four or two; though this rule may be departed from and we find members of the order with five digits or three, just as the tapirs and nearly all the Eocene genera of perissodactyls had four toes in the manus. Much more important is the fact that the plane of symmetry, which in the perissodactyls bisects the third digit and is therefore said to be *mesaxonic*, passes between the third and fourth digit and is *paraxonic.* The third and fourth digits always form an equal and symmetrical pair and are the "irreducible minimum," beyond which the number of toes cannot be diminished. A single-toed artiodactyl would seem to be an anatomical impossibility; at all events, such a monstrosity was never known. Hence the term "cloven" or "divided" hoof, which seems to take the solid hoof of the horse as the norm; but "cloven or divided," while expressing the appearance of the foot with sufficient accuracy, is erroneous, if taken to mean the splitting of what was once continuous.

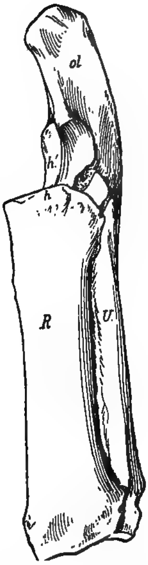

Fig. 186. — Left forearm bones of the Domestic Pig (*Sus scrofa*). *R.*, radius. *U.*, ulna. *ol.*, olecranon.

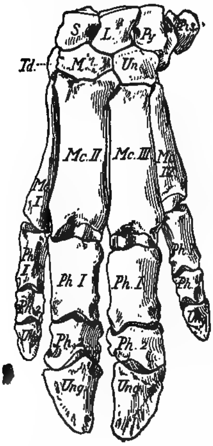

Fig. 187. — Left manus of Pig. *S.*, scaphoid. *L*, lunar. *Py.*, pyramidal. *Pis.*, pisiform. *Td.*, trapezoid. *M.*, magnum. *U.*, unciform. *Mc. I*, second, *Mc. II*, third, *Mc. III*, fourth, *Mc. IV*, fifth, metacarpals.

Especially characteristic of the order is the structure of the ankle, or "hock-joint" of the hind limb. The ankle-bone, or astragalus, has a double pulley, the upper and lower ends being of quite similar shape; its lower end is almost equally divided between the cuboid and navicular, which are made concave to receive it. This type of astragalus is altogether peculiar to the artiodactyls, all of which possess it; it is unlike that of any other mammal whatever and may be recognized at a glance. The calcaneum, or heel-bone, has a large convex facet, by means of which it articulates with the fibula, or external leg-bone; there is no such articulation in the perissodactyls. The lower end of the calcaneum is narrow and fits into a step cut in the cuboid, which is thus every whit as peculiar and characteristic as the calcaneum and astragalus. The femur never has the third trochanter, which is always present in the perissodactyls. Another respect in which the artiodactyls differ from all perissodactyls except the horses is in the much more complex mode of articulation between the vertebræ of the lumbar and posterior dorsal regions, which the former display, and even the horses have no such elaborate arrangement. Finally, another very marked difference from the perissodactyls is in the teeth, for the premolars and molars are never alike, and only in very rare instances does the last premolar assume the molar-pattern. Of this pattern, there are two principal kinds, one exemplified by the peccaries, in which the crown supports a series, fundamentally two pairs, of conical cusps, and called *bunodont*, and the other, to be seen in all the ruminating animals, in which the crown is composed of two pairs of crescents and is therefore said to be *selenodont.* The bunodont was the primitive type,

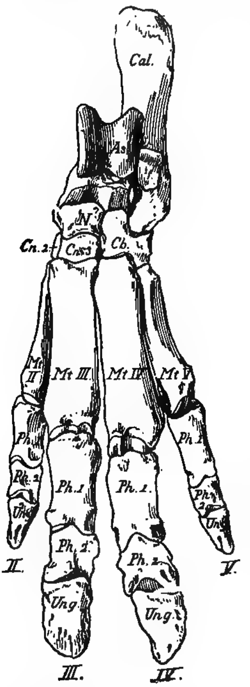

FIG. 188.—Left pes of Pig. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cb.*, cuboid. *Cn. 2*, *Cn. 3*, second and third cuneiforms. *Mt. II–V*, second to fifth metatarsals.

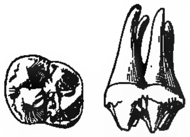

FIG. 189.—Bunodont upper molar of peccary (*Tagassu*).

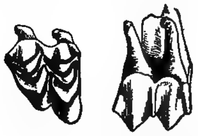

FIG. 190.—Selenodont upper molar of deer (*Odocoileus*).

whence the other was derived, and many transitional forms are known.

The classification of the immense horde of living and extinct genera and species which are referable to the artiodactyls is an extremely difficult problem, which has found no thoroughly satisfactory solution and will not until much more is learned concerning the history of the order and conflicting opinions can be reconciled. The most important American families and genera are given below, though the arrangement is but tentative.

Suborder A. ARTIODACTYLA †PRIMITIVA. (Extinct genera of doubtful affinities)

I. †TRIGONOLESTIDÆ.
  †*Trigonolestes*, low. Eoc.
II. †LEPTOCHŒRIDÆ.
  †*Leptochœrus*, low. Oligo. †*Stibarus*, low. Oligo.
III. †DICHOBUNIDÆ. †*Homacodon*, mid. Eoc. †*Bunomeryx*, up. Eoc.
IV. †ANTHRACOTHERIIDÆ.
  †*Anthracotherium*, low. Oligo. †*Bothriodon*, do. †*Arretotherium*, do.
V. ? †OREODONTIDÆ.
  †*Protoreodon*, up. Eoc. †*Merycoidodon*, low. Oligo. †*Eporeodon*, up. Oligo. †*Promerycochœrus*, up. Oligo. to up. Mioc. †*Merycochœrus*, Mioc. and low. Plioc. †*Pronomotherium*, up. Mioc. †*Mesoreodon*, low. Mioc. †*Merychyus*, low. Mioc. to low. Plioc. †*Leptauchenia*, low. Oligo. to low. Mioc. †*Cyclopidius*, mid. Mioc.
VI. †AGRIOCHŒRIDÆ.
  †*Protagriochœrus*, up. Eoc. †*Agriochœrus*, Oligo.

Suborder B. SUINA. Swine-like Animals

VII. TAGASSUIDÆ, Peccaries.
  †*Helohyus*, mid. Eoc. †*Perchœrus*, low. Oligo. †*Thinohyus*, up. Oligo. †*Desmathyus*, low. Mioc. †*Prosthennops*, up. Mioc. and low. Plioc. †*Platygonus*, mid. Plioc. to Pleist. *Tagassu*, Recent, Pleist. in S. A.
VIII. †ENTELODONTIDÆ. †Giant Pigs.
  †*Parahyus*, low. Eoc. †*Achœnodon*, mid. and up. Eoc. †*Archæotherium*, low. Oligo. †*Boöchœrus*, up. Oligo. †*Dinohyus*, low Mioc.

Suborder C. TYLOPODA. Camels and Llamas

IX. CAMELIDÆ.

†*Protylopus*, up. Eoc. †*Eotylopus*, low. Oligo. †*Poëbrotherium*, Oligo. †*Pseudolabis*, low. Oligo. †*Protomeryx*, up. Oligo. and low. Mioc. †*Oxydactylus*, low. Mioc. †*Miolabis*, mid. Mioc. †*Protolabis*, mid. and up. Mioc. †*Alticamelus*, mid. Mioc. to low. Plioc. †*Stenomylus*, low. Mioc. †*Procamelus*, up. Mioc. and low. Plioc. †*Pliauchenia*, up. Mioc. to mid. Plioc. *Camelus*, Pleist. *Lama*, Plioc. to Recent, S. A.

X. †HYPERTRAGULIDÆ.

†*Leptotragulus*, up. Eoc. †*Leptoreodon*, up. Eoc. †*Leptomeryx*, low. Oligo. †*Hypertragulus*, Oligo. †*Hypisodus*, low. Oligo. †*Protoceras*, low. Oligo. †*Syndyoceras*, low. Mioc.

Suborder D. PECORA. True Ruminants

XI. CERVIDÆ. Deer.

†*Blastomeryx*, low. Mioc. to low. Plioc. *Cervus*, Pleist. and Rec. *Rangifer*, Pleist. and Rec. *Alce*, Pleist. and Rec. †*Cervalces*, Pleist. *Odocoileus*, Pleist. and Rec., N. and S. A. *Mazama*, Pleist. to Rec., S. A.

XII. †MERYCODONTIDÆ. †Deer-Antelopes.

†*Merycodus*, mid. Mioc. to low. Plioc. †*Capromeryx*, Pleist.

XIII. ANTILOCAPRIDÆ. Prong-Bucks.

Antilocapra, Pleist. and Rec. ? †*Dromomeryx*, mid. and up. Mioc.

XIV. BOVIDÆ. Antelopes, Sheep, Goats, Oxen, etc.

†*Neotragocerus*, †*Ilingoceros*, †*Sphenophalus*, low. Plioc. †*Preptoceras*, †*Euceratherium*, †*Symbos*, Pleist. *Ovibos*, Pleist. and Rec. *Bison*, Pleist. and Rec.

This list of families and genera, portentous as it is, would be greatly increased by the addition of the Old World forms, which outnumber those of the western hemisphere.

SUBORDER SUINA. SWINE-LIKE ANIMALS

The history of the American types of pig-like forms is, in one sense, very full and complete in that the successive genera may be traced back to the Eocene, but, in another sense, the story is exasperatingly imperfect, because so much of the material is fragmentary. Of most of the genera, nothing is known but teeth and jaws, and these, though sufficient for identification, tell but little of the structural changes which it is desirable to know. It is merely a question of time, when more adequate material will be obtained.

1. *Tagassuidæ.* *Peccaries*

The peccaries, or American swine, are now chiefly of Neotropical distribution, extending into the Sonoran region only as far as Arkansas; but this has been true only since the Pleistocene, for nearly the entire history of the family has been enacted in North America. In many points of structure the peccaries of the present day are more advanced and specialized than the far more varied and diversified true swine of the Old World, for it is a singular fact that such a long-lived and persistent stock as the peccaries should have given rise to so few variants and side-branches. Existing peccaries all belong to a single genus (*Tagassu*) and are relatively small animals, of unmistakably pig-like character and appearance, but far smaller than the Wild Boar (*Sus scrofa*) of Europe, or the Wart Hog (*Phacochœrus æthiopicus*) of Africa, to mention only two of the Old World swine.

One characteristic and thoroughgoing difference between the peccaries and the swine is the shape of the canine tusks. In the former, the tusks, though very effective weapons, are not very large and are straight and have a vertical direction, while in all the true swine the upper tusk is curved upward and outward, projecting strongly from the side of the jaw, and the great, curved lower tusk wears against its anterior side. The peccaries further have smaller and simpler molars, each with four principal, conical cusps (quadritubercolate pattern) arranged in two transverse pairs, with numerous very small cuspules around and between them,

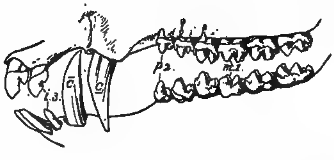

FIG. 191.—Dentition of the Collared Peccary (*Tagassu tajacu*) left side. *i 3*, external incisor. *C*, canine, *p 2*, second premolar (the first is lost), *m 1*, first molar.

obscuring the plan. In the true swine the teeth are much larger and covered with innumerable wart-like cusps, large and small, seldom arranged according to any definite plan.

In the following particulars the modern peccaries show advance over the Old World swine: (1) the last lower premolar has taken on the molar-pattern, a very exceptional feature among the artiodactyls; (2) the ulna and radius are coössified; (3) there are but two functional digits in each foot; the fore foot has, in addition, two complete, but very reduced and slender, lateral digits and the hind foot only one, whereas in all the pigs of the eastern hemisphere there are four functional toes in each foot; (4) in the hind foot the two functional metatarsals, the third and fourth, have coalesced to form a "cannon-bone," a structure which is not found in any other family of the sub-order; (5) the stomach is complex, approximating that of a ruminant.

In the North American Pleistocene the predominating kind of peccary was a genus (†*Platygonus*) which was more advanced than the existing form (*Tagassu*), and, to all seeming, better fitted to survive, though for some inexplicable reason it failed to do so. It was a considerably larger animal, with proportionately longer and heavier legs. Its molar teeth are of special interest because they reproduced a type which has been so often repeated and independently acquired in so many different groups of mammals. In this molar the two conical cusps of each pair were fused into a high, transverse ridge or crest. Precisely the same modification took place among the true swine in the genus †*Listriodon* of the French middle Miocene. †*Platygonus* first appeared in the middle Pliocene, and its predecessor in the lower Pliocene and upper Miocene showed the crests of the molars in process of formation. In the latter stage it was accompanied by a true peccary with tuberculated teeth, which differed from the modern species in the simplicity of the hindmost premolar, which had not taken on the molar-pattern. If the feet and limbs of this upper Miocene peccary were known, they would doubtless prove to be much more primitive than those of *Tagassu*, but they still await discovery.

Little can be said of the peccaries of the middle and lower Miocene other than to record the fact of their presence in those formations, but those of the upper Oligocene (John Day) are, however, represented by well-preserved skulls, which show that more than one phylum of the family had arisen, though there was no great difference between them; they were considerably smaller animals than those of the Pliocene and Pleistocene. Still smaller was the White River genus (†*Perchœrus*) of which some fragmentary skeletons have been obtained. Although an undoubted peccary, this animal was not far from what the common progenitor of the peccaries and the true swine might be expected to resemble. The molars were quadrituberculate without the numerous accessory cuspules of the modern genus; the bones of the fore-arm were separate and the feet had four functional digits each, while there was no cannon-bone in the pes, the metatarsals remaining free.

No peccaries have yet been found in the Uinta, but probably this is a mere accident of collecting. It is, however, possible that the White River genus was not of American derivation, but an immigrant from the Old World. In the middle Eocene, or Bridger stage, this series is known only from teeth and jaws and a very few scattered foot-bones, and these, though probably referable to the family, cannot be definitively assigned to it without more complete material. Several species, larger and smaller, of the genus †*Helohyus* occurred in the Bridger, where they were not uncommon, considering the general rarity of artiodactyls in that stage. Thus, the peccaries, though none of them were large, followed the usual law of mammalian development, and, beginning with very small forms, increased in size with each succeeding geological stage down to the Pleistocene.

2. †*Entelodontidæ.* †*Giant Pigs*

The †giant pigs, a most remarkable group of swine-like forms and of as yet unknown origin, appeared for the last time in North America in the lower Miocene, where the genus of that date (†*Dinohyus*) was the largest of known suilline animals, the hippopotamuses excepted. In nearly every part of the skeleton these great beasts displayed an unusual and aberrant kind of development. The incisors were long and pointed, and the canines formed stout and heavy, though not very long, tusks, which in shape were more like those of a bear than those of either peccaries or swine. The premolars were very simple, of compressed conical and trenchant shape, and occupied a very long space in the jaws, while the molars were relatively small and quadrituberculate, the crowns covered with very thick, coarsely wrinkled enamel. The skull was immensely elongate, especially the facial region in front of the eyes, while the brain-case was so absurdly small as to give the skull a reptilian aspect, when viewed from above. Evidently, these great pigs were profoundly stupid, in this respect rivalling the †titanotheres of the White River (p. 311). Beneath each eye-socket was a long, descending, bony flap, or process, and on the under side of the lower jaw were two pairs of prominent knobs, the function of which, as of the flaps beneath the eyes, is quite problematical. The eye-sockets themselves were completely encircled in bone, a rare character in the suborder.

The neck was short, as in the pigs generally, the body not very elongate and the tail of moderate length; at the shoulders, the spines of the dorsal vertebræ were very long, making a decided hump, and in the lumbar and posterior dorsal region the processes for articulation between the vertebræ were extremely elaborate. For one of the pigs, the limbs were very long and gave quite a stilted look to the animal. As in the modern peccaries, the fore-arm bones were indistinguishably fused together and the feet had only two toes each, the only members of the

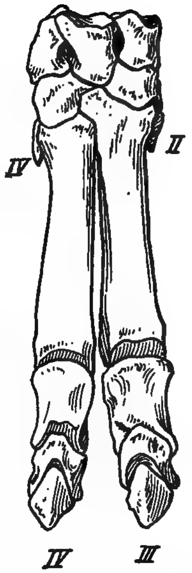

FIG. 192. — Right manus of †entelodont (†*Archæotherium ingens*) from lower White River beds. Princeton University Museum.

suborder in which digital reduction had proceeded so far, though the existing peccaries approximate this condition. There were, however, nodular vestiges of two other digits, which prove the derivation of this form from at least a four-toed type; no cannon-bone was formed. In view of the size of the animal, the hoofs were surprisingly small, which suggests that the weight was chiefly borne upon a pad. †*Dinohyus* was a very large animal, six feet or more in height at the shoulder.

In the upper Oligocene were very large species of another, but closely similar, genus (†*Boöchœrus*) though somewhat smaller than those of †*Dinohyus*, and the species of the upper White River beds († *Archæotherium*) were little, if at all, smaller than those of the John Day. A number of specimens in the museum of Princeton University throw a welcome light upon the habits of these strange creatures. In one, the external, or third, upper incisor tooth has a deep, triangular notch worn in its

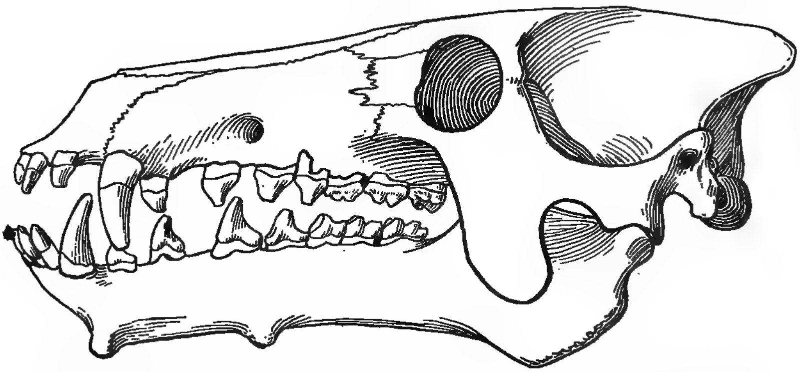

FIG. 193. — Skull of White River †entelodont (†*Archæotherium mortoni*). Princeton University Museum. For restoration, see Fig. 137, p. 260.

postero-external face, and the lower canine has a well-defined groove worn on the posterior side at the base of the crown; other individuals show less distinct marks of similar kind. (See Fig. 194.) It is out of the question to suppose that these grooves and notches could have been produced by abrasion with other teeth, for no other teeth could reach the worn areas, and it is altogether probable that they were made in digging up roots. The root, held firmly in the ground at both ends and looped over the teeth which pulled until it broke, and being covered with abrasive grit, would wear just such marks as the teeth actually display.[1] While the †entelodonts were thus rooters, they were doubtless omnivorous, like other pigs, and did not disdain a meal of carrion when they could get it. It is likely that the heavy canine tusks were also used as weapons, both in defence against the attacks of carnivores and in fighting between the males of the same species. It must have been in some such encounter that the animal represented by a complete skeleton in the Princeton Museum received its broken rib; that the fracture was made during life is demonstrated by the large callus growths on the broken ends, but the pieces did not knit.

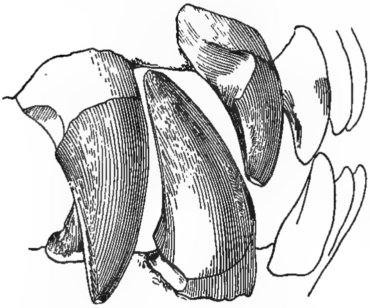

FIG. 194.—Specimen showing characteristic grooves of wear in the anterior teeth of †entelodont (†*Archæotherium*) from upper White River beds. Princeton University Museum.

In the middle and lower substages of the White River the genus (†*Archæotherium*) was the same as in the upper substage of these beds, but the species were all smaller and some of them very much so, not exceeding an ordinary pig in size. Throughout the series, as we now have it, from the lower Oligocene into

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[1] This plausible and no doubt correct explanation was suggested to me by my colleague, Professor C. F. Brackett.

the lower Miocene, there is very little change except in size, all the essential features of structure remaining the same; the genera are therefore distinguished by modifications of very secondary importance, and it is a question whether all the species should not be included in a single genus. The European genus †*Entelodon,* which gives its name to the family, is so like the American forms that by most writers the White River species are referred to it. It is of interest to note that the †giant pigs have also been found in the marine Miocene of New Jersey, one of the few records of the Tertiary land mammals of the Atlantic seaboard.

At present, the †entelodonts proper cannot be traced back of the lower White River beds, nor are they found in any more ancient formations in Europe. It is, therefore, probable that they were immigrants in both of these continents, presumably from Asia.

The whole Eocene of North America had a series of pig-like animals, called the †achænodonts or †short-faced pigs, which seem to have been related to the †entelodonts. They ended their career in the Uinta just before the appearance of the †entelodonts, and it would be natural to suppose that the latter were descended from them. If, however, the principle that an organ or structure once lost can never be regained, is valid, then there can be no relation of ancestor and descendant between the

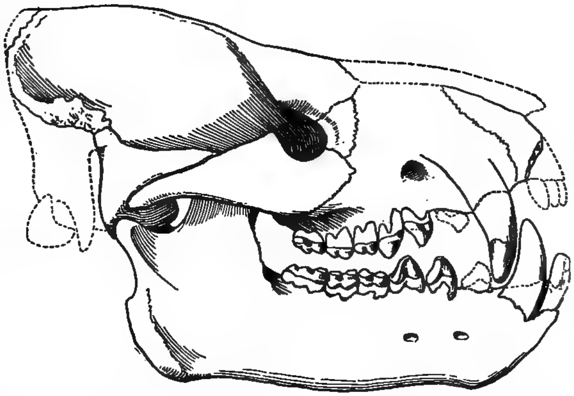

FIG. 195. — Skull of †short-faced pig (†*Achænodon robustus*) from the Bridger Eocene. Princeton University Museum.

two groups, for of the †achænodonts, even their most ancient representatives had lost the first premolar, giving the formula $p\frac{3}{3}$, while in the †entelodonts it is constantly $p\frac{4}{4}$. The †achænodonts, which are much less fully known than the †entelodonts, had teeth very similar in form to those of the latter; and their most conspicuous feature was the shortness of the face and jaws, as contrasted with the extreme elongation of these parts in the †entelodonts, nor did they have the bony flaps under the eyes or the knobs on the lower jaw which gave such a fantastic appearance to the †entelodont skull. Little is known of the skeleton except that there were four functional digits in the manus. The Uinta and Bridger genus (†*Achænodon*) was larger than the Wasatch form (†*Parahyus*), which was an immigrant, probably from the same region as afterwards sent out the †entelodonts to America and Europe; this would account for the similarity and probable relationship of the two subfamilies.

SUBORDER ARTIODACTYLA †PRIMITIVA. †PRIMITIVE ARTIODACTYLS

No doubt, this suborder is an artificial assemblage of unrelated families, a sort of waste-basket, into which are thrown the groups of which no other disposition can be made in the present state of knowledge. As information becomes more complete, the various families will be redistributed among the groups with which they had a genuine relationship.

3. †*Anthracotheriidæ.* †*Anthracotheres*

This family was abundantly represented in Europe from the middle Eocene through the Oligocene, in Asia persisting even into the Pliocene, and were abundant in the Oligocene of Egypt. Migrants from the Old World reached America in White River times, but speedily died out, as they did not survive into the upper Oligocene. The most fully known of these animals is an American species of a European genus †*Bothri-*

odon. Almost complete skeletons of this genus have been obtained in the channel sandstones of the upper White River substage. In size and proportions, †*Bothriodon* was not unlike a domestic pig, but had a very long head with slender, pointed snout; it had also a short neck, long body, short limbs and feet. The primitive character of this genus is made clear by many features of its structure; the molar teeth were extremely low-crowned and their cusps were so imperfectly crescentic in form as to be called *buno-selenodont,* as indicating their transitional nature, and the upper molars had five cusps instead of four, a very primitive feature. Another very significant character was the five-toed manus; the first digit, or pollex, was much smaller than the others.

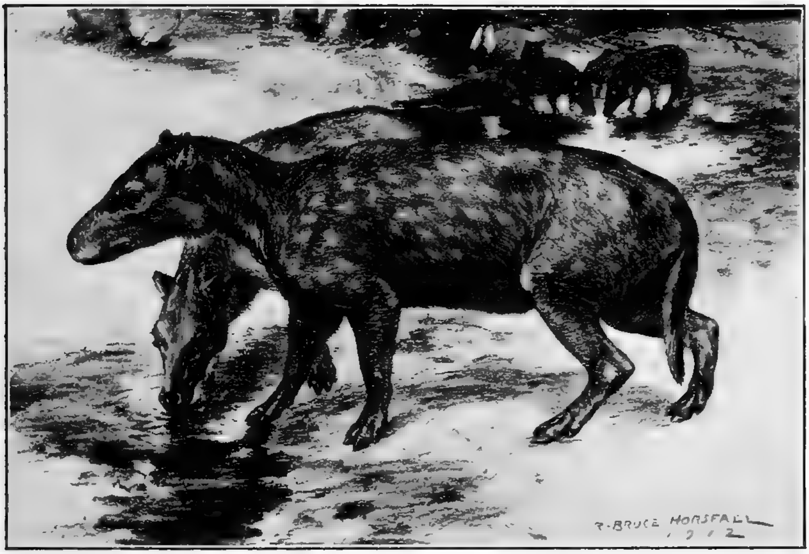

FIG. 196. — †*Bothriodon brachyrhynchus,* upper White River stage. Restored from a skeleton in the museum of Princeton University.

The second genus of the family which had American representatives was †*Anthracotherium,* which was much like †*Bothriodon,* but even more archaic in character; the molars could hardly be called selenodont at all.

4. †*Oreodontidæ.* † *Oreodonts*

This was one of the most characteristic of North American artiodactyl families, and its members were exceedingly abundant throughout the upper Eocene, the whole Oligocene and Miocene, ending their long career in the lower Pliocene. In distribution the family was exclusively North American, and no trace of it has been found in any other continent. In the course of their long history the †oreodonts underwent many transformations and branched out into several distinct phyla, yet through all these changes they remained singularly conservative, for the transformations, some of them sufficiently bizarre, affected chiefly the teeth and skull, the remainder of the skeleton changing but little. The †oreodonts were all small or of moderate size, none of them surpassing the Wild Boar in stature, nor was there any decided increase in size from stage to stage. One and all, they were strange beasts. Dr. Leidy, who first described and named most of the genera, spoke of them as combining the characters of camel, deer and pig, and called them "ruminating hogs," a conception expressed in the names which he gave to some of them, such as †*Merychyus* and †*Merycochœrus*, both of which mean ruminant swine.

The general proportions of most of the species were quite as in the peccaries, though, for the most part, with much longer tails; they had a short neck, elongate body, short limbs and feet. In one genus (†*Mesoreodon*) of the lower Miocene a rudimentary collar-bone has been found, and probably all of the more ancient genera possessed it, but only by an unusually lucky chance would so small and loosely attached a bone be preserved in place. As the collar-bone is superfluous in hoofed animals, in which the limbs are used only for locomotion and move in planes parallel with that of the backbone, it is almost universally absent in them, and in only one other group of ungulates, the extinct †Typotheria of South America, has its presence been demonstrated. In all of the †oreodonts the bones of the fore-arm and lower leg remained separate. The teeth were in continuous series, and there was a peculiar feature in the dentition common to nearly every one of the genera. On casual examination, one would say that the animals had four lower incisors on each side and that the lower canine closed behind the upper one, a most exceptional arrangement. More careful study shows that the apparent fourth incisor was the canine, a transformation which has also taken place in all of the ruminants except the camels, and the tooth which had assumed the form and function of the lower canine was really the first lower premolar; this latter change is not found among the ruminants, but was repeated in a few other extinct families.

FIG. 197. — Head of †*Merycochœrus proprius*, lower Miocene to lower Pliocene. Restored from a skull in the American Museum of Natural History.

Only two genera of †oreodonts (†*Merychyus* and †*Merycochœrus*) survived into the lower Pliocene. Both had the proportions common throughout the family, but †*Merychyus* was much more slender and lightly built, its lateral digits were reduced in size and very thin and it had hypsodont grinding teeth; while †*Merycochœrus* was of larger size (about that of a large domestic pig) and stouter build and had low-crowned teeth; its head, however, had a very different appearance, given by the possession of a short proboscis, the presence of which is indicated by the greatly reduced nasal bones; the jaws and face were also much shortened. The eye-sockets presented obliquely forward and upward, intead of laterally, as is usual among mammals, and were placed high in the head. This position of the eyes and of the entrance to the ear renders it probable that †*Merycochœrus* was largely aquatic in its habits. Both genera had short, four-toed feet, as was general throughout the family and in no genus did the reduction of digits proceed beyond the loss of the first of the original five, the pollex and hallux.

The two genera above described, representatives of two distinct phyla within the family, held over, as it were, from the upper Miocene without essential change. The phylum of the hypsodont and slender †*Merychyus* went back, with only minor modifications, into the upper substage of the lower Miocene, but cannot as yet be traced to an Oligocene ancestry; it is therefore still impossible to say just where and when it branched off from the main stem of the family. Future discoveries in the Oligocene will no doubt clear up this problem. The real terminal and most highly specialized member of the †*Merycochœrus* phylum and the most extraordinary member of the entire family was confined to the upper Miocene. The extreme peculiarity of this genus (†*Pronomotherium*) was displayed only in the head, which was an exaggeration of the †*Merycochœrus* type, the face being excessively shortened and the nasals so reduced as to show that the proboscis was much better developed than in the parent genus. The shortening of the face and the great vertical height of the skull and lower jaw gave a decided likeness to the skull of a great ape, though the proboscis would mask any such resemblance in the living head. †*Merycochœrus* itself went back to the upper division of the lower Miocene, but in the lower division it was replaced by an ancestral genus, †*Promerycochœrus*, which had an elongate face and jaws and no proboscis; but in other characteristic features, such as the extreme thickness and roughness of the zygomatic arches, it was like its descendant. †*Promerycochœrus* contained the largest known species of †oreodonts, some of them equalling a Wild Boar in stature, and its remains are found so abundantly in the middle and lower Miocene and upper Oligocene, that there must have been great herds of these animals over the plains. Probably it was itself derived from some of the larger species of †*Eporeodon* of the upper White River beds, but there is a gap in the history, due to the fact that the lower part of the John Day is almost barren of fossils and the connecting link has not been recovered.

FIG. 198. — Head of †*Pronomotherium laticeps*, upper Miocene. Restored from a skull in the Carnegie Museum, Pittsburgh.

It is an interesting and significant fact that ancestral and derivative genera may continue to live side by side in the same region. †*Promerycochœrus,* it is believed, gave rise to †*Merycochœrus,* but survived with it into the middle Miocene. †*Merycochœrus,* in its turn, produced †*Pronomotherium,* and, so far from being replaced by the latter, actually outlived it and persisted into the lower Pliocene.

A third phylum of the †oreodonts, which appeared for the last time in the middle Miocene (genus †*Cyclopidius*), was a series of small and very small species, of which the skull was almost as peculiar as that of †*Pronomotherium,* but in a different fashion. The face was very much shortened and on each side a great vacuity reduced the nasal bones to mere splints; the elevated position of the eye-sockets, which projected above the forehead, and of the tubular entrance to the ear is an evidence of an aquatic or amphibious mode of life, such as is illustrated by the hippopotamuses, which can float almost completely submerged, with only the ears, eyes and

FIG. 199. — †*Promerycochœrus carrikeri,* lower Miocene. Restored from a skeleton in the Carnegie Museum, Pittsburgh.

nostrils above the surface of the water. The tympanic bullæ (see p. 66) or bony chambers into which the ear-tubes opened, were of relatively enormous size and added much to the unusual appearance of the skull. The incisors were very small and the grinding teeth narrow and completely hypsodont, this and the †*Merychyus* series being the only two phyla of the family in which the hypsodont molar was fully acquired. The remainder of the skeleton differed but little from the type common to the whole family, except for a somewhat shorter tail.

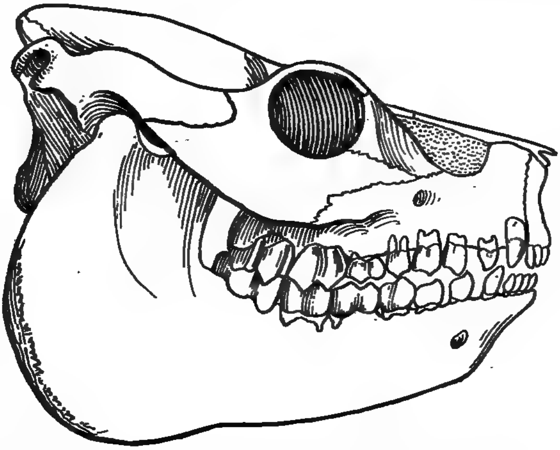

FIG. 200.—Skull of †*Leptauchenia nitida*, upper White River.

The animals of this series were common in the middle and lower Miocene and in the upper substage of the White River, but have not been found in the intermediate John Day. This may have been a matter of geographical distribution, these creatures not extending west of the main ranges of the Rocky Mountains. In the upper White River the genus †*Leptauchenia* is extremely common, but below that level they suddenly and completely vanish and, as in the case of the †*Merychyus* phylum, it is not yet practicable to determine the point in time or space of their branching off from the main stem of the family. Were the †oreodonts not entirely confined to North America, we should, as a matter of course, explain the seemingly sudden appearance of †*Leptauchenia* as due to immigration, and it is entirely possible that the series did actually originate in some part of North America which has left no record of its Eocene or Oligocene terrestrial life. On the other hand, no one can imagine that everything that can be known of the mammals of the middle and lower White River has already been learned, and at any time the sought-for ancestor of †*Leptauchenia* may be found in those beds.

The fourth phylum may be regarded as the main or central stem of the family and was the one which underwent the least change, though it probably gave rise to all the other phyla, which branched off from it at various stages in its history. This series terminated in the middle Miocene and comprised several genera, all very much alike, in the lower stages of that epoch. One of these genera (†*Mesoreodon*) displayed a very remarkable peculiarity of structure in the ossification of the great cartilage of the larynx, which seems to point to the possession of uncommon vocal powers. It is impossible to say whether this feature was confined to the single genus, or was general in the family, for only in rare instances would so ex-

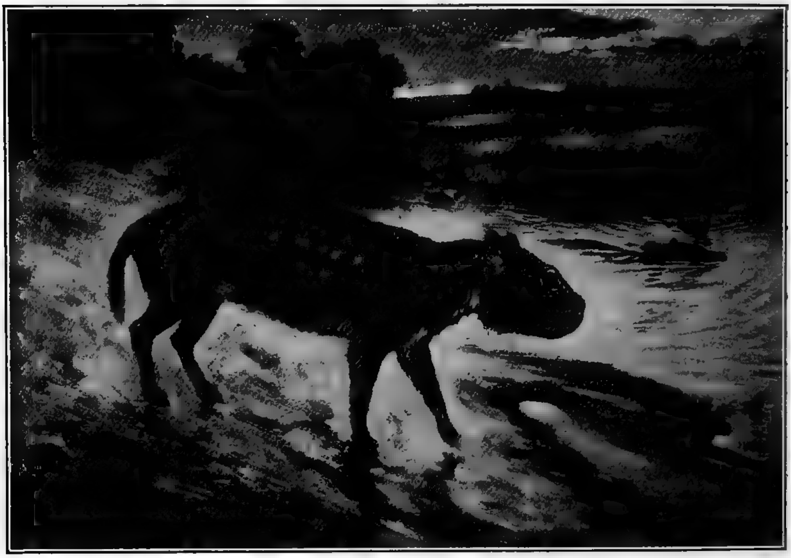

FIG. 201. — *Leptauchenia nitida*, upper White River. Restored from a skeleton in the Museum of Princeton University.

tremely delicate a structure be preserved. In the John Day the genus †*Eporeodon*, which was very abundant, was the representative of this phylum, and the same, or a closely similar, genus lived in the latter part of the White River stage.

In the middle and lower White River substages †oreodonts are the commonest of fossils, so that the collector soon wearies of them (see Fig. 136, p. 259); they must have lived in great herds in the forests and along the streams. There were several species, varying principally in size, the largest about as long as a wolf, but with shorter legs, and the smallest not so much as half of that size. All belonged to a single genus, for which the rigid law of priority compels us to use a most cumbrous name (†*Merycoïdodon*), the widely used term †*Oreodon* being a synonym. This genus was the central stock of the family, from which most, if not all, the others were directly or indirectly derived, though, as previously pointed out, we cannot in all cases trace the connection. In these White River animals the grinding teeth were very low-crowned and had considerable resemblance to those of a deer; the molars were typically selenodont and made up of two pairs of crescentic cusps. The skull differed little from that of the succeeding genera of this phylum; the neck was short, body and tail long. An especially interesting fact is that the fore foot had five digits, the first, or pollex, very small and of no functional value, but complete in all its parts; the hind foot was four-toed. In all of the subsequent genera of the family the number of digits was uniformly four in both manus and pes.

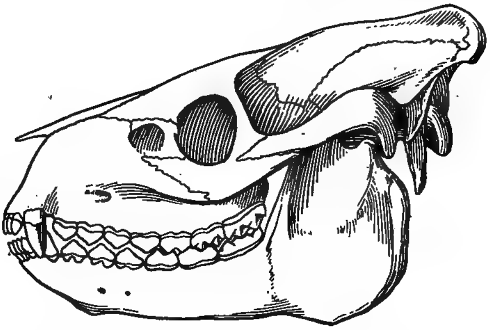

Fig. 202. — Skull of †*Merycoïdodon culbertsoni*, middle White River. (After Leidy.)

In the Uinta stage of the upper Eocene lived the most ancient and primitive member of the family yet discovered, the genus †*Protoreodon,* which is in every respect what the ancestor of the White River genus should be. The functional transformation of the lower canine into a fourth incisor and the replacement of the canine by the first lower premolar had already taken place, but the molars were much more primitive than those of the White River and succeeding genera; the crescents were thicker and less complete, plainly indicating their derivation from conical cusps, and a small fifth cusp was present between the anterior pair of the upper molars, as in the †anthracotheres and other European families of the Artiodactyla †Primitiva. Before the discovery of †*Protoreodon,* the character of its molars was predicted by Dr. Schlosser, of Munich. The skull resembled that of the White River genera, except that the eye-socket was open behind, and there was no glandular pit in front of the eye. The skeleton is but partially known, but it has been ascertained that there were five toes in the manus and probably also in the pes.

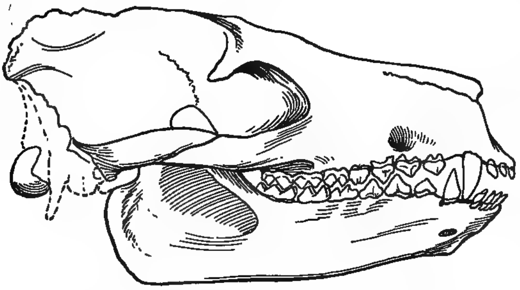

FIG. 203. — Skull of †*Protoreodon parvus,* Uinta Eocene. Princeton University Museum. N.B. This skull is actually much smaller than that shown in Fig. 202.

Nothing has yet been discovered in formations older than the upper Eocene which can be regarded as ancestral to the †oreodonts, and this is not surprising in view of the extremely meagre and unsatisfactory nature of our information regarding the artiodactyls of the Bridger. On the whole, however, it seems rather more probable that the Uinta genus was an immigrant (whence, we cannot say) than that the Bridger will ever yield the desired ancestral forms. So long as the early Tertiary mammals of northern and central Asia remain unknown, this and many similar problems can find no definitive solution. The question of relationship with other families is bound up with that of the origin of the †oreodonts; many characters point to a connection with the †anthracotheres and, from the standpoint of present knowledge, that appears to be the most probable affinity; but, on the other hand, there are structural features which suggest relationship with the primitive camels. Between these and other alternatives, only the recovery of the middle and lower Eocene forms can finally decide.

Reviewing the long history of the oreodont family from the evolutionary point of view, we find a course of development which differs in several respects from that exemplified by most of the families previously considered:

(1) There was a general increase in size, though it was far from steady, and almost every genus had larger and smaller species, and in some of the phyla the species were far larger than in others. The members of the †*Leptauchenia* phylum were very small and no member of the family ever attained to more than moderate size.

(2) The upper molars early lost the fifth cusp, and after that there was little change in the dentition, except that in the †*Merychyus* and †*Leptauchenia* phyla the grinding teeth became hypsodont.

(3) There was great variety in the modifications of the skull, each phylum having its own peculiarities. The orbit, which was open behind in the Uinta †*Protoreodon*, was closed in the White River and all succeeding genera. In the †*Merycochœrus* series, the skull first enlarged, with little change in proportions, then elongated the facial region, then shortened the face and so reduced the nasals as to indicate the presence of a proboscis, culminating in the grotesque, ape-like skull of †*Pronomotherium*. In the †*Leptauchenia* phylum the skull became depressed and flattened and the face was invaded by great openings, or vacuities; the tympanic bullæ were enor-

mously inflated and the orbits and ear-openings raised, presumably in adaptation to an amphibious mode of life. These were the extremes of change within the family; the other phyla need not be considered.

(4) At an early stage the digits were reduced from five to four, first in the pes and then in the manus, and there reduction ceased; though in †*Merychyus*, especially in the upper Miocene species, the lateral digits were very slender and, had this series survived, it would probably have led to didactyl forms.

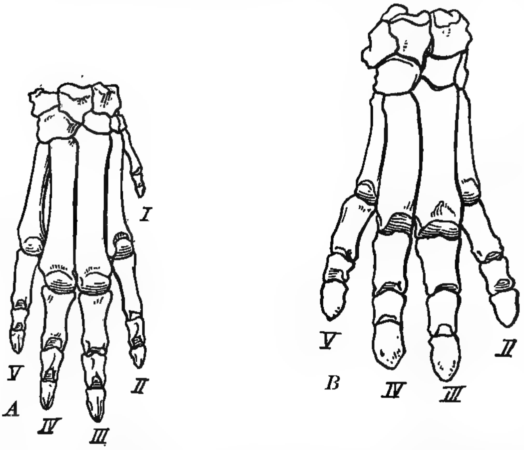

Fig. 204. — Left manus of †oreodonts. *A*, †*Merycoidodon culbertsoni*, White River. *B*, †*Merycochœrus proprius*, upper Miocene.

In other respects there was very little difference in the skeletons of the various phyla and herein lies the peculiarity in the history of the family, great variety in the form of the skull, and, relatively speaking, hardly any change in the body, limbs or feet. In the horses, rhinoceroses and †titanotheres the modifications of the successive genera affected all parts of the structure, but in the †oreodonts, except for the loss of one digit in manus and pes and variations in the length of the tail, the skeletons of the latest genera did not differ in any important respect from those of the earliest. Such a combination of mutability and plasticity in the skull with extreme conservatism in the remainder of the bony structure is an exception to the usual mode of development, though something of the same sort has already been pointed out in the case of the tapirs (p. 325) and will recur in that of the elephants (Chap. X).

5. †*Agriochœridæ.* †*Agriochœrids*

This family, one of the strangest and most aberrant of ungulate groups, was very closely allied to the †oreodonts and by many authorities is included in the same family. The history of the successive steps of discovery, by which the structure of these extraordinary animals was gradually made plain, is much the same as in the case of the even more peculiar perissodactyl family of the †chalicotheres (p. 356). The various parts, found scattered and at long intervals of time, had been referred to no less than three different mammalian *orders!* for, until the discovery of †chalicothere skeletons gave the clue, no one imagined that such discordant parts could belong to the same animal.

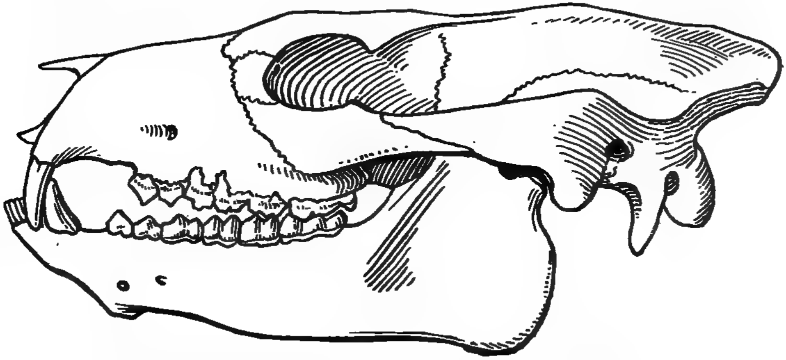

FIG. 205. — Skull of †*Agriochœrus latifrons*, White River. (After Wortman.)

The †agriochœrids had a very much shorter career than the allied family of the †oreodonts, extending only through the upper Eocene and the Oligocene (Uinta to John Day, inclusive); and only two genera of the family are yet known, †*Agriochœrus* of the John Day and White River, and †*Protagriochœrus* of the Uinta. In the former the teeth were not in a continuous, closely crowded series, but there were open spaces behind the upper canine and first lower premolar; the same exceptional character of the lower teeth which was found in the †oreodonts was repeated in the present family, the canine assuming the form and functions of an incisor and the first premolar those of the canine; the upper incisors were extremely small and were shed in the adult, just as in the true ruminants. The molars had the selenodont pattern, but the upper molars were very different in shape from those of the †oreodonts, resembling rather those of the †anthracothere †*Bothriodon* (see p. 370). Another difference from the †oreodont dentition was that the last lower premolar had acquired the molar form and the last upper one nearly so, a very unusual feature among the artiodactyls. The skull was almost exactly like that of the White River †oreodonts, save in a few details; the face was somewhat longer, the orbit was open behind and there was no glandular pit on the face in front of the eye. The neck was short and the body long, and the backbone in the region of the loins very stout, the vertebræ of this region having much resemblance to those of the great cats, as though †*Agriochœrus* were an agile

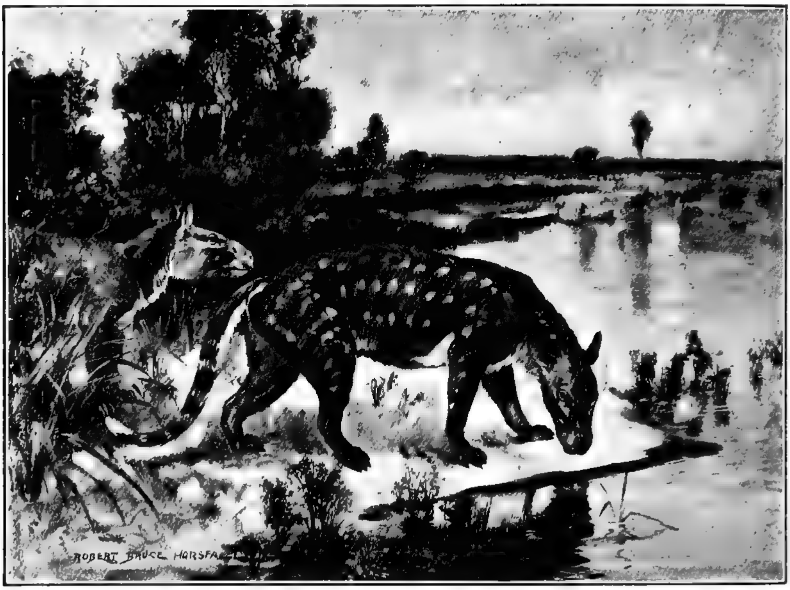

Fig. 206. — †*Agriochœrus antiquus*, White River. Restored from a skeleton in the American Museum of Natural History.

and powerful leaper. Another likeness to the cats was in the very long and heavy tail, which was much longer than in the †oreodonts, and its vertebræ were hardly distinguishable from those of a Leopard. The limbs were relatively longer than those of the †oreodonts and the separate bones had a suggestive likeness to those of carnivores, and, more specifically, of cats. The feet, save in one particular, were not only artiodactyl, but also characteristically †oreodont in structure and, as in the earlier members of that family, there were five toes in the manus and four in the pes. The exception was that, instead of narrow and slender hoofs, the feet were armed with sharp, though not very large claws, which were not comparable in relative size to the great claws of the †chalicotheres.

Altogether, a strange jumble of incongruous characters was united in this skeleton. Were only the skeleton known without the skull, one would be tempted to call it that of a carnivorous artiodactyl, but the teeth make such a suggestion absurd, since they could have been used only for masticating a diet of soft vegetable substances. No flesh-eater has, or ever had, teeth in the remotest degree like these, which were of characteristically herbivorous type. How such a creature lived and what were its habits, are questions to which no satisfactory answer has been found.

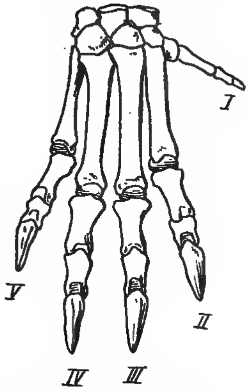

FIG. 207. — Right manus of †*Agriochœrus latifrons*, White River. (After Wortman.)

†*Protagriochœrus* of the upper Eocene is, unfortunately, known only from very imperfect and fragmentary specimens, which, however, are sufficient to determine some significant points. These remains show that, while the two families of the †agriochœrids and the †oreodonts were already distinct in the Uinta, they were decidedly nearer together than they became in the Oligocene. In other words, it is clear that the

two groups were converging back to a common ancestry. This may be discovered in the Bridger, but it seems more probable that these forms were immigrants. Another fact concerning the Uinta genus, which is important, is that the upper molars possessed the fifth or unpaired cusp which also occurred in the contemporary †oreodonts, as well as in the †anthracotheres and other Old World families.

Suborder Tylopoda. Camels and Camel-like Animals

Existing Tylopoda are all included in a single family, the Camelidæ, and by several authorities no other family, even of extinct forms, is admitted to the suborder. My own preference, however, is to refer the problematical little †hypertragulids to this group, as will be shown subsequently.

6. *Camelidæ. Camels and Llamas*

Under modern conditions, no mammals could seem more completely foreign to North America than those of the camel family, which, now restricted to two well-defined genera, inhabit central Asia and the colder parts of South America. Yet, as a matter of fact, this family passed through nearly the whole of its development in North America and did not emigrate to the other continents before the late Miocene or early Pliocene, and it is this North American origin of the family which explains its otherwise inexplicable distribution at the present time. To all appearances, the whole family had completely disappeared from this continent in the later Pleistocene, but in the middle and earlier portions of that epoch both true camels and large llama-like animals were very abundant on the Great Plains and in California, while they seem to have avoided the forested regions.

In order to appreciate the changes through which the camels and llamas have passed, it will be necessary to consider briefly the skeletal and dental structure which characterizes the modern genera. In the true camels (*Camelus*) the first and second upper incisors have been lost, but the third remains as a large, sharp-pointed tooth, as are also the upper canine and first premolar; thus there are three pointed, spike-like teeth in a row, with spaces between them, constituting with the lower canine a very effective lacerating apparatus. Behind the first premolar is a long gap, the second being suppressed; the third and fourth are grinding teeth, but unusually small. The molars are selenodont and high-crowned, though not extremely hypsodont. The lower incisors are large and shovel-shaped, the canine large and erect and there are but two lower premolars. The dental formula thus is: $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{2}$, $m\,\frac{3}{3}$.

The skull is long, with the facial region much and abruptly narrowed, which gives a triangular appearance to the head when seen from above; the orbit is completely encircled with bone and the sagittal and occipital crests are very prominent. The tympanic bullæ are large and filled with spongy bone. The condyle of the lower jaw is hemispherical and not, as it is in most ungulates, semicylindrical, and a curious, hook-like angulation is on the posterior border of the bone. The neck is very long, and the vertebræ have the exceptional peculiarity that the canal for the vertebral artery runs through the side of the neural arch, instead of perforating the transverse process, and thus is invisible externally; the odontoid process of the axis is spout-like. The legs and feet are very long; the humerus has a double bicipital groove and the fore-arm bones are coössified, and the ulna is so reduced that the radius carries the whole weight; in the lower hind leg the tibia supports the weight, and of the fibula only the lower end remains as the malleolar bone. There are but two digits in each foot, the third and fourth, the metapodials of which have coalesced to form a cannon-bone, which differs from that of the true ruminants, or Pecora, in the curious way in which the lower ends, separated by a Λ-shaped notch, diverge from each other, and by the fact that the keels of the lower articular surfaces are confined to the posterior side, not visible from the front. The ungual phalanges are small and nodular, and the hoofs, which carry no part of the weight, are hardly more than nails. Under the other phalanges is a broad pad of elastic tissue, upon which the weight rests, and the separation of the toes is very partial. The peculiar external appearance of the camels is largely due to structures which leave no trace in the skeleton, and especially to the great humps, one or two according to the species, which are accumulations of fat; the ears are short and rounded and the hair is not woolly, but almost straight.

The teeth and skeleton of the llamas (*Lama*) are closely similar to those of the camels, but the absence of humps, the long, pointed ears, the woolly hair and the much smaller size and lighter build give to the living animals a more marked difference of appearance from the camels than one would expect from a comparison of the skeletons alone. The dental formula is: $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $p\,\frac{2}{2}$, $m\,\frac{3}{3}$. The remaining upper incisor, the third, is recurved, as is also the canine, but the spike-shaped first premolar of the camels is absent and the other premolars are much smaller than in the latter. In the skull the brain-case is larger, and the sagittal and occipital crests are much less prominent. The skeleton differs hardly at all from that of the camels, except for its smaller size and more slender proportions. The toes are more distinctly separated, each having its own pad. Thus, among the existing representatives of the family are two very well-defined phyla, each characteristic of a different continent.

The Blanco stage of the middle Pliocene, which has preserved but a meagre representation of the life of its time, has yielded a number of very large, llama-like species, not, however, ancestral to the modern species, for they had but one premolar in each jaw. From the lower Pliocene we have fuller information. In the Snake Creek stage the separation of the two modern phyla was complete, and there was a third one, now extinct, that of the browsing or "†giraffe-camels" (†*Alticamelus*) (see Fig. 127, p. 236), a term which must not be taken as implying any relationship with the giraffes, but merely a resemblance to them in proportions. These browsing camels were very large animals, but with relatively small heads and low-crowned teeth not suited for grazing; the neck was extremely long, made so by the great elongation of five of the vertebræ (second to sixth, inclusive), and the legs were also very long, fitting their possessors to browse upon trees. Much of the description of the appearance and habits of the Giraffe given by Flower and Lydekker would no doubt be applicable to these extinct camels. "To produce the extremely elongated neck the seven cervical

FIG. 208. — Guanaco (*Lama huanacus*). — By permission of the New York Zoölogical Society.

vertebræ are proportionately long, which gives a somewhat stiff and awkward motion to the neck. . . . The Giraffe feeds almost exclusively on the foliage of trees . . . for browsing on which its prehensile tongue and large free lips are specially adapted."[1]

In teeth and skeleton the phyla of the true camels and of the llamas in the lower Pliocene did not differ very strongly from the living forms; the upper incisors were already reduced to one, but the premolars were not so small; the ulna and radius had coalesced and of the fibula only the lower end remained; the cannon-bones were completely formed, and that the pads of the feet had already been developed is shown by the phalanges, especially the irregular, nodular unguals.

The most ancient known camels of the Old World are found in the Pliocene of India, and the first llamas recorded in South America are also Pliocene. Since both camels and llamas existed together in North America, it may reasonably be asked why only one phylum migrated to Asia and only the other to South America. Why did not each continent receive migrants of both kinds? Without knowing more than we are ever likely to learn about the details of these migrations, it will not be possible to answer these questions, though plausible solutions of the problem suggest themselves. It is to be noted, in the first place, that a migration from the central portion of North America to Asia was by way of the far north and thus involved very different climatic conditions from those which must have been encountered in passing through the tropics to South America. It is perfectly possible that animals which lived together in temperate North America should have had very different powers of adaptation to heat and cold respectively, and the northern route may have been impassable to one and the southern route to the other. To this it might perhaps be objected that the llamas are cold-country animals, but this is true only of the existing species, for fossil forms are

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[1] Flower and Lydekker, Mammals Living and Extinct, p. 332.

found abundantly in the Pleistocene of Ecuador, Brazil and Argentina. Another possibility is that both phyla did actually migrate to both continents and that only the camels succeeded in permanently establishing themselves in Asia and only the llamas in South America, though for this solution the fossils afford no evidence.

The camels of the upper Miocene did not differ sufficiently from those of the lower Pliocene to call for special notice other than to remark that the two phyla of the true camels and the llamas were hardly distinguishable and one genus (†*Procamelus*) may have been ancestral to both. In the middle Miocene the browsing camels (†*Alticamelus*) reached the acme of their importance and made no great progress subsequently. The generalized stock, from which the upper Miocene and lower Pliocene †*Procamelus* descended, was represented by †*Protolabis* and †*Miolabis*, smaller animals, which had a full set of upper incisors and premolars and the grinding teeth were not so high-crowned. In most of the species the metapodials had not fused to form cannon-bones and probably there were no pads on the feet, though †*Alticamelus*, the †Giraffe-Camel, had already developed both cannon-bones and pads.

In the lower Miocene the †giraffe-camels were represented by the genus †*Oxydactylus*, which was a considerably smaller animal than its successor †*Alticamelus*, of the middle Miocene and later formations, and had shorter neck and legs. The teeth, though brachyodont, were not very low-crowned. There was no cannon-bone, the two metapodials of each foot remaining separate. An especially noteworthy feature in this genus is to be observed in the character of the hoofs, which, as the ungual phalanges demonstrate, were narrow and pointed, like those of antelope and deer, and carried most of the weight. The member of the grazing series (†*Protomeryx*) was smaller in every way than its contemporary (†*Oxydactylus*) of the browsing line and had shorter neck and legs, though these were

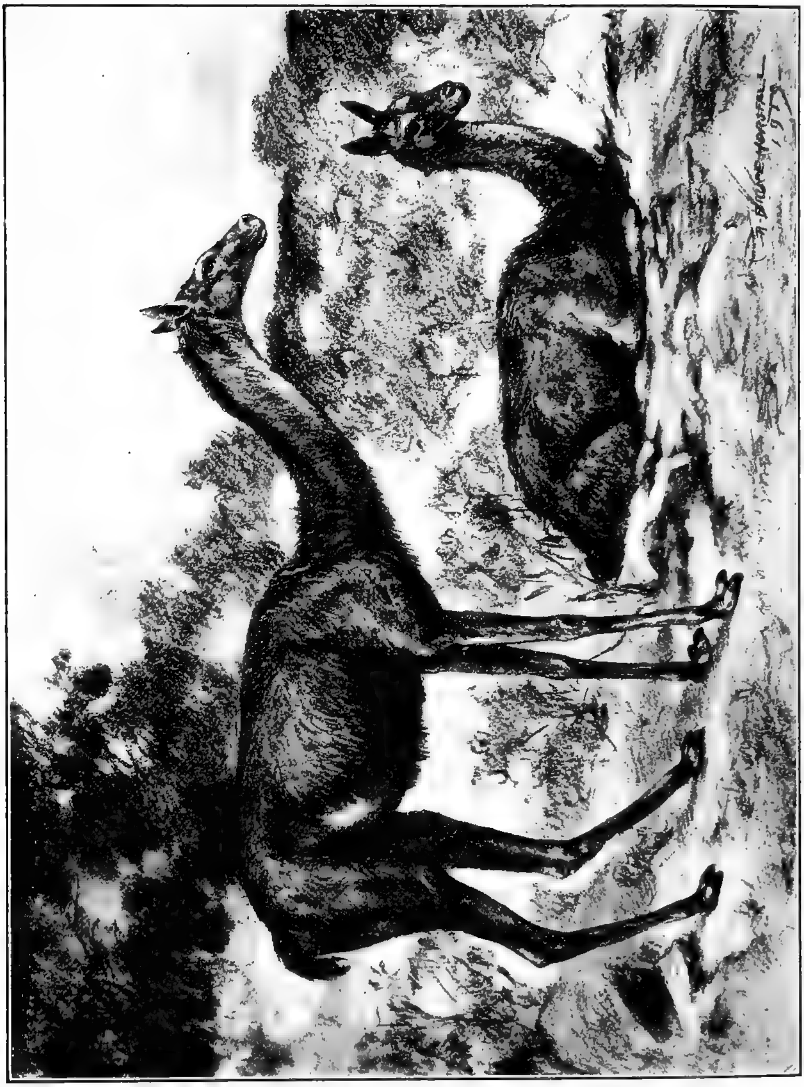

FIG. 209. — Lower Miocene †giraffe-camel (†*Oxydactylus longipes*). Restored from a skeleton in the Carnegie Museum, Pittsburgh.

already long. The teeth were present in undiminished number, and the grinders, while not properly to be called hypsodont, showed a decided tendency to assume that character. The feet were in the same stage of development as in †*Oxydactylus*, that is to say, with two free digits and pointed, deer-like hoofs. We have thus the remarkable and most significant fact that, while the grazing and browsing camels of the lower Miocene were already distinctly separated, neither had yet attained to the type of foot-structure which *both* of them afterwards independently acquired. This is a very instructive example of parallel evolution in closely related series.

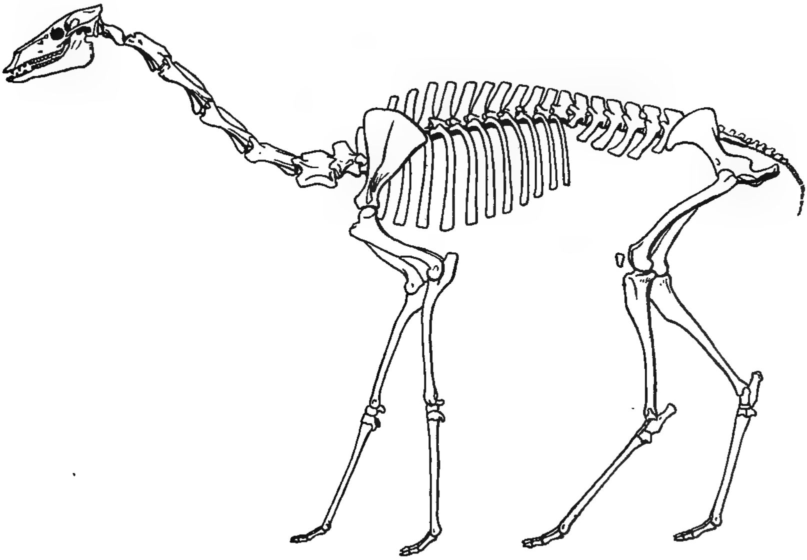

Fig. 210.—Skeleton of †*Oxydactylus longipes*. Lower Miocene. (After Peterson.) For restoration, see Fig. 209.

Of still another phylum of the camel family, the lower Miocene contains the only representatives yet discovered, the little "†gazelle-camels," as they may be called. The single known genus (†*Stenomylus*, Fig. 131, p. 242) of this series was quite a small animal, much smaller than its contemporaries of the grazing or browsing series. †*Stenomylus* was an extremely slender, cursorial creature and had a very exceptional feature in its dentition in the apparent presence of ten lower incisors, five on each side, the canine and first premolar having assumed the form and functions of the incisors; the molars were low-crowned. The head was rather small and rounded, the neck long and light, the limbs and feet elongate and excessively slender. The feet had two digits each, which were separate, not forming a cannon-bone, and the hoofs were narrow, pointed and deer-like. These delicate and graceful little animals had but a brief career, which seems to have reached its close in the lower Miocene. Perhaps their complete defencelessness made it impossible for them to maintain themselves against their enemies, despite their evident capacity for swift running.

The camels of the upper Oligocene (John Day) are still incompletely known, but appear all to have belonged to the series of grazers which led up to the modern genera. Future discovery may bring to light in the John Day earlier members of the †giraffe-camel series, of which a possible member is found in the uppermost substage of the White River, or perhaps both phyla united in the upper Oligocene, a question which remains to be determined. At all events, in the middle substage of the White River, or lower Oligocene, there is no evidence of more than a single phylum, from which the others were almost certainly derived, branching off from the main stem at different levels. First was given off the branch of the †giraffe-camels, then (or perhaps even earlier) that of the little †gazelle-camels, and, finally, the main stem bifurcated into the two phyla of the llamas and the true camels. The point of origin of the †gazelle-camels is still uncertain.

The typical White River genus (†*Poëbrotherium*) included a series of species which increased in size from the earlier to the later portions of the stage, but showed no such structural changes as to call for special notice. The larger of these species was somewhat taller than a sheep, but of much lighter proportions, with small, pointed head, long neck and body and long, very

FIG. 211. — The White River camel (†*Poëbrotherium labiatum*). Restored from a skeleton in the museum of Princeton University.

slender limbs and feet. The teeth were present in undiminished number, 44 in all; the lower incisors were small, simple, nearly erect and chisel-shaped, very different from the large, procumbent and shovel-like teeth of the modern genera, and the trenchant canines were much smaller than in the latter. The first premolar had an isolated position, the second and third were trenchant and much extended antero-posteriorly, quite as in many other groups of primitive artiodactyls. The molars, which were typically selenodont, were low-crowned in the upper jaw, but in the lower showed an incipient tendency to hypsodontism. The skull, by its shape and the characteristic narrowing of the face, immediately suggests the modern type, but differed in many details of structure, the most obvious of which were the incompletely closed orbits, the shallow and slender jaws, and the very large, hook-like process from the angle of the lower jaw, which, in greatly reduced form, is present in both of the Recent genera. The neck was relatively long, though by no means so long proportionately as it subsequently became, and the vertebræ had already acquired the peculiarity found in all the succeeding camels, of the exceptional position of the canal for the vertebral artery, save in the sixth vertebra, where it pierced the transverse process, as in mammals generally; the odontoid process of the axis was neither spout-like nor peg-like, but of intermediate form, convex below and flat above. The body was long and light, and the ribs were much more slender than in the Recent genera. The fore and hind limbs, which were of nearly equal length, were very slender; the humerus had a single bicipital groove; the fore-arm bones were fully coössified and in the lower leg only the two ends of the fibula remained. The feet were already in the stage of development which persisted through the lower Miocene in all of the phyla, with two separate digits and nodular remnants of two others, and deer-like hoofs.

It would be of interest to compare this little White River camel with its contemporary genus of horses, †*Mesohippus*, and to observe in how many respects they have followed a parallel course, and how nearly †*Poëbrotherium* occupied the same position with reference to the modern camels and llamas as †*Mesohippus* did to the Recent horses; but such a comparison would involve too many technicalities to be profitably undertaken here. Suffice it to say that in many details there was a genuine parallelism in the progress of these two widely separated families from a polydactyl ancestry towards an extreme of digital reduction, ending in the horses in the single-toed and in the camels in the two-toed foot. The members of the two series kept nearly equal pace in their slow progress, with the camels a little in advance, since they were the first to attain the modern state of development in the height of the teeth and the structure of the feet, though eventually the horses surpassed them in both respects.

In the upper Eocene (Uinta stage) there were at least two kinds of camels, the time-relations of which to each other are not known, that is, whether they were contemporary or successive. The best-known genus, †*Protylopus*, may perhaps not be in the direct line of camel descent, but it so nearly represents the proper ancestral stage that, for all practical purposes, it will serve nearly as well. It was a much smaller animal than the smallest of the White River species, and was hardly larger than a "jack-rabbit." The teeth of each jaw were in continuous series and the canines were but slightly longer than the incisors; the premolars had less antero-posterior extension than in †*Poëbrotherium*, and all the molars above and below were very low-crowned. The skull was almost a miniature copy of that of †*Poëbrotherium*, but more primitive in a number of details, the most important of which was that the tympanic bullæ were much smaller and hollow, not filled with spongy bone. The neck, concerning which it would be very desirable to have information, is almost the only part of the skeleton that is not known. The fore limb was considerably shorter than the hind, making the back slope downward from the rump to the shoulders; in the fore-arm the two bones were entirely separate and in the lower leg the fibula, though very slender, was still complete. In the manus there were four functional digits, the laterals not very much smaller than the median pair; but in the pes the lateral metatarsals were reduced to mere bony threads, to which small phalanges, in full complement, were attached, making tiny dew-claws.

With †*Protylopus* ends the genealogy of the camels so far as it can be definitively traced, but in the middle of the Bridger stage is found a genus, †*Homacodon* (family †Dichobunidæ), which is a probable member of the series. However, until the connecting link can be found in the upper Bridger, this conclusion cannot be demonstrated and †*Homacodon* itself is incompletely known. It was a very small animal, even less in size than †*Protylopus*, and had not yet acquired the selenodont molars. These teeth were quadritubercular, *i.e.* with four principal cusps arranged, in the upper molars, in a square, and with a minute cuspule between each transverse pair, while the lower molars were narrower and had only the four principal cusps. The cusps were not conical, as they are in the pigs, but angular and pyramidal, the first step toward the assumption of the selenodont form. The skull was not specifically cameline in appearance, but rather indifferent, as though almost any kind of an artiodactyl might have been derived from it. The feet were decidedly more primitive than those of the Uinta genus, having four functional digits each, perhaps five in the manus. While it cannot be positively stated that †*Homacodon* was the actual ancestor of †*Protylopus*, it nearly represents what we should expect that ancestor to be.

In the lower Eocene (Wasatch stage) lived a tiny creature, †*Trigonolestes* (family †Trigonolestidæ), smaller even than †*Homacodon* of the Bridger, and one of the most ancient and primitive of known artiodactyls, but, unfortunately, still represented only

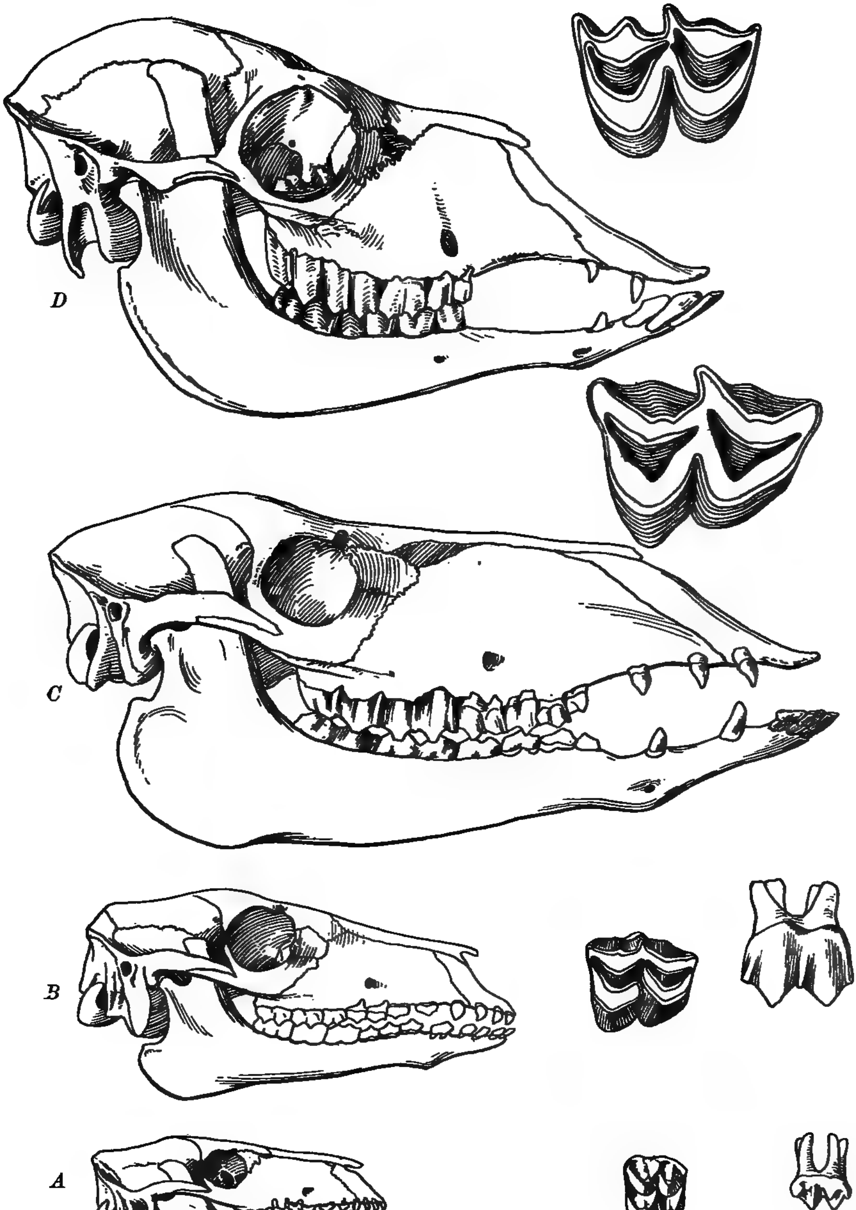

FIG. 212. — Diagram to illustrate the development of the skull and molar teeth in the camel tribe, in ascending geological order. *A*, †*Protylopus petersoni*, Uinta Eocene. *B*, †*Poëbrotherium wilsoni*, White River. (After Wortman.) *C*, †*Procamelus gracilis*, upper Miocene. (After Cope.) *D*, *Lama huanacus*, the modern Guanaco.

by very imperfect specimens, so that much which it would be highly desirable to learn must await the finding of better material. The upper molars were triangular and tritubercular, *i.e.* with three principal cusps arranged in a triangle, and are hardly to be distinguished from those of other early mammalian orders. From the teeth alone the artiodactyl nature of the animal would not have been suspected, and, in fact, they were, when first discovered, referred to primitive monkeys. The feet probably had five toes each, but this is not certain, and the femur had the third trochanter, the only known artiodactyl of which this is true. As this little Wasatch genus is so imperfectly known, it would be premature to claim it as the starting point of the camel family, and yet it may very well have been so. Better material of this genus and the links of the chain which belong in the upper Bridger and the Wind River respectively must be recovered before this earliest portion of the family history can be written in more than tentative fashion.

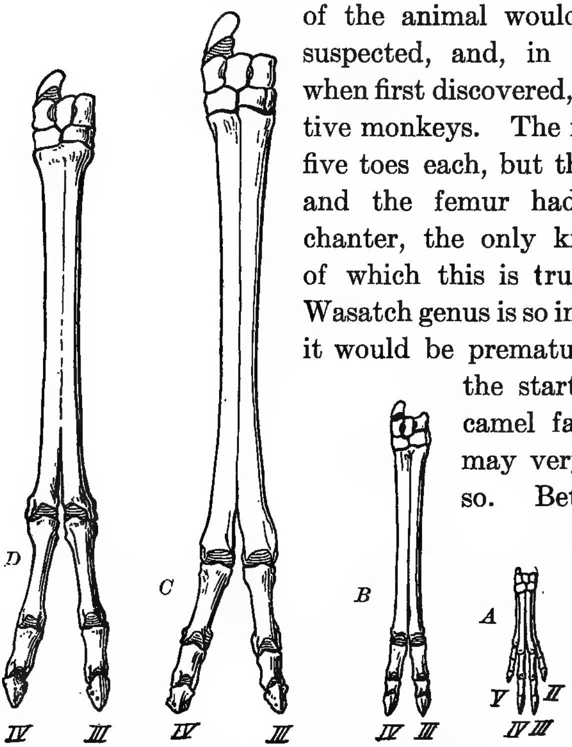

Fig. 213.—Right manus of camels. *A*, †*Protylopus*, Uinta. *B*, †*Proëbrotherium*, White River. *C*, †*Procamelus*, upper Miocene. (After Cope.) *D*, Recent Guanaco.

The mode of evolution displayed by the camels does not differ in any significant respect from that seen in the horses. There was the same increase in bodily stature and in the relative lengths of the limbs and feet, the same kind of diminution in the number of digits from the original five, the same reduction of the ulna and its coalescence with the radius and the loss of the fibula save for its two ends. There was also a

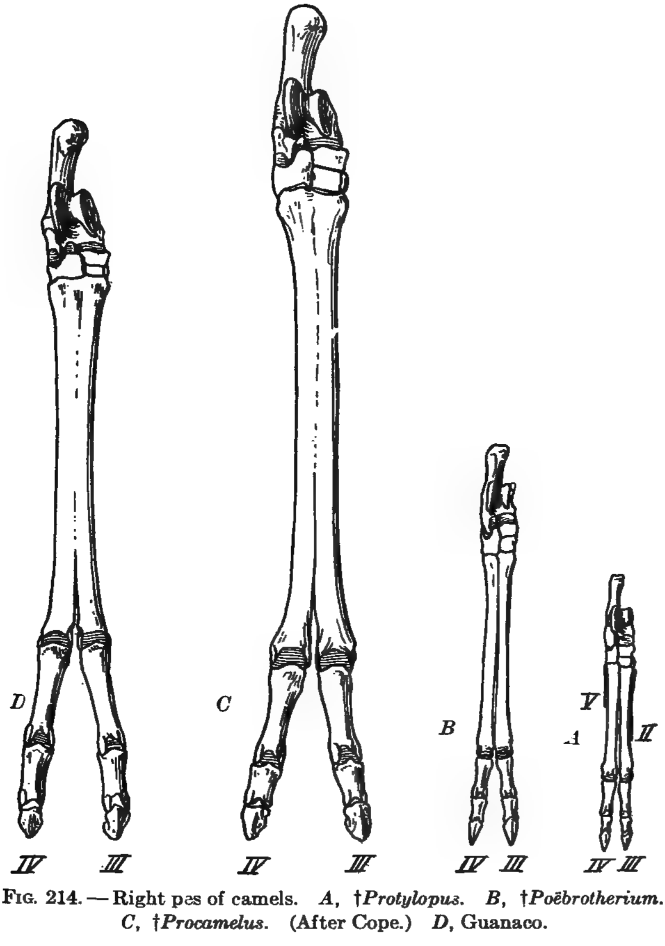

Fig. 214. — Right pes of camels. *A*, †*Protylopus*. *B*, †*Poëbrotherium*. *C*, †*Procamelus*. (After Cope.) *D*, Guanaco.

similar development of the high-crowned, or hypsodont, grinding teeth, from the low-crowned, or brachyodont, type. In still another respect there was a similarity in the mode of development of the two families, namely, in the way in which the several phyla of each originated. For the earlier portion of their history there was in each but a single distinguishable series, though it is very possible that fuller knowledge and more complete material would enable us to distinguish more than one. This monophyletic condition continued through the Eocene and most of the Oligocene, but in the upper portion of the latter and, more markedly in the lower Miocene, the two families branched out, each in its own fashion.

Of course, there were differences in the development of the camels and horses, some conditioned by the fundamental distinction between artiodactyl and perissodactyl, such as the didactyl foot as the possible minimum and the formation of cannon-bones in the camels. Other differences are characteristic of the latter family, such as the great elongation of the neck and the peculiar structure of its vertebræ, the formation of pads on the feet and concomitant reduction of the hoofs. In a general way, the two families kept quite an even pace in their advance from the more primitive to the more specialized condition and, though the camels were the first to acquire certain modifications, the horses ultimately surpassed them.

Even more close was the parallelism in evolution between the camels and the true ruminants (suborder Pecora), and this case is of particular importance as clearly demonstrating the development, in two independent but related lines, of similar structures not derived from a common ancestry. This comparison must naturally await the description of the Pecora.

7. †*Hypertragulidæ.* †*Hypertragulids*

This was a very peculiar family, of exclusively North American distribution and of doubtful systematic position, the known history of which extended from the upper Eocene into the lowest Miocene and then abruptly terminated. None of its members attained to considerable size, the largest hardly surpassing a sheep, and some were extremely small. In view of its comparatively brief career, this family was surprisingly ramified, and no less than four phyla may be distinguished within its limits.

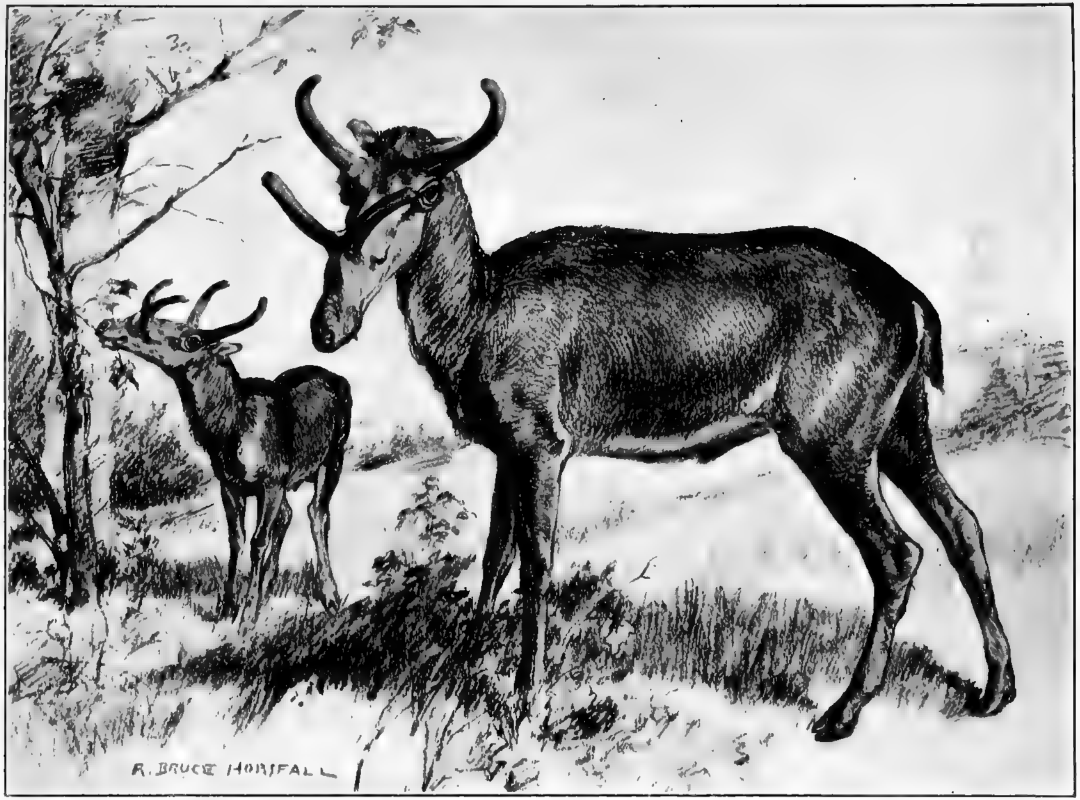

FIG. 215. — †*Syndyoceras cooki*, lower Miocene. Restored from a skeleton in the museum of the University of Nebraska.

One of the phyla which persisted into the lower Miocene was there represented by a most fantastic creature (†*Syndyoceras*) with four horn-like outgrowths from the skull, one pair arising from the anterior part of the face and curving outward away from each other, and the hinder pair, which were placed over the eyes, curved toward each other at the tips and were shaped much like a cow's horns in miniature. The shape of these bony protuberances makes it unlikely that they were sheathed in horn and probably they were merely covered with skin like the horns of the giraffes. This description applies only to the skull of the male; that of the female is not yet known, but there is good reason to believe that in that sex the horns were much smaller or wanting, as in nearly all existing deer. The skull was long, narrow and low; the orbits were small, completely enclosed in bone and unusually prominent; the nasal bones were exceedingly short, as though indicating the existence of a proboscis, but this can hardly have been the case, for the nasal opening was divided into anterior and posterior portions by the bony bridge which united the bases of the forward pair of horns. In no other known mammal does such a division of the nasal opening occur. The upper incisors had all disappeared, but there was a small upper canine tusk and another formed by the first lower premolar, while the real lower canine had gone over to the incisor series. This exceptional arrangement is a point of resemblance to the †oreodonts (see p. 372). The grinding teeth were brachyodont. The fore limb is not known, but the hind limb has been completely recovered; it was stout and not very long in proportion to the length of the head. The fibula was completely reduced, only the ends remaining, and the pes was didactyl, the two metatarsals uniting in a cannon-bone; the hoofs were like those of deer and antelopes.

No representative of this series has yet been found in the upper Oligocene; and it is not yet possible to say whether their absence from the John Day beds, as in several other cases

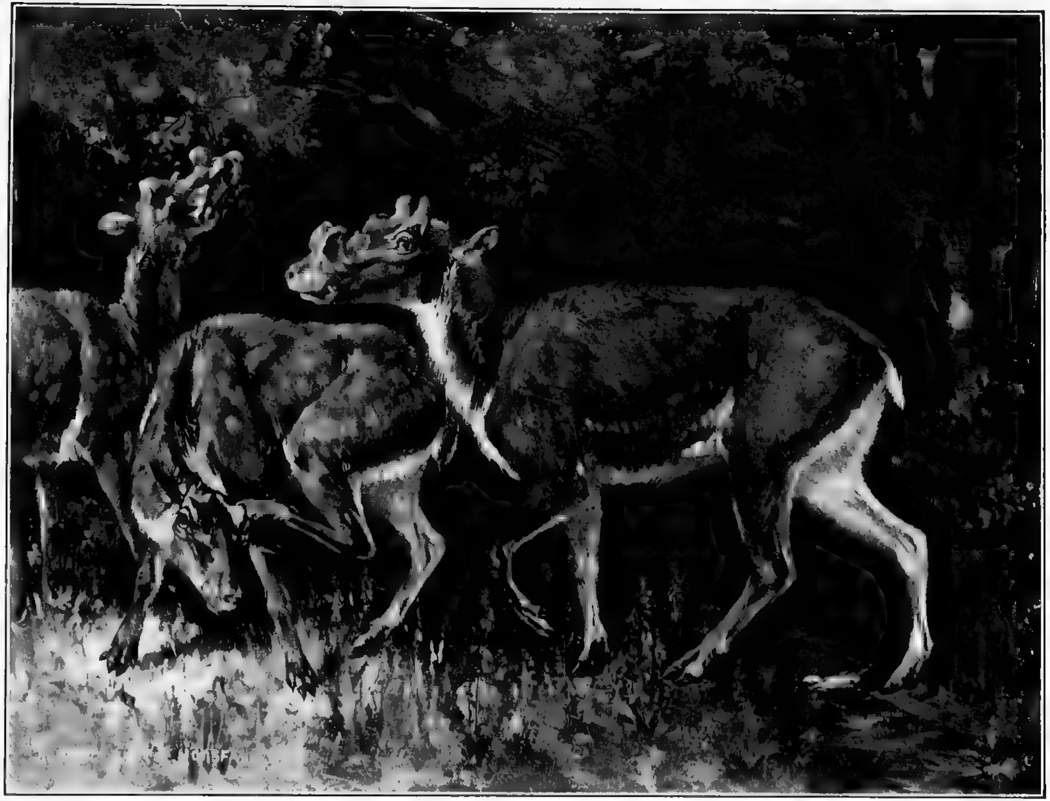

Fig. 216. — †*Protoceras celer*, upper White River; males on the right and left, female in the middle. Restored from skeletons in the American Museum and Princeton University.

already referred to, was due to an actual geographical difference in contemporary faunas, or whether it is merely one of the accidents of preservation and collecting. In the upper White River, however, was another most curious animal (†*Protoceras*), a forerunner, if not a direct ancestor, of †*Syndyoceras*. The exact relationship between the two forms can hardly be determined, until the genera, one or more, which once connected them shall have been recovered, though it is obvious that they belonged to the same series. †*Protoceras* was a smaller animal and, if anything, an even more bizarre-looking object, for the anterior protuberances were broad, prominent and everted plates of bone, not even suggesting horns in their form, and the posterior pair were short and club-shaped; in the female neither pair was more than indicated. The dentition was very similar to that of †*Syndyoceras*, except that the upper tusk was considerably larger and scimitar-shaped; the female had no tusks. In the fore-arm the two bones were just beginning to coalesce, but in the lower leg the fibula was completely reduced. The manus had four complete and functional digits, the laterals not very much shorter and thinner than the median pair; but the pes was already didactyl, though the metatarsals were separate, not fused into a cannon-bone; two long and

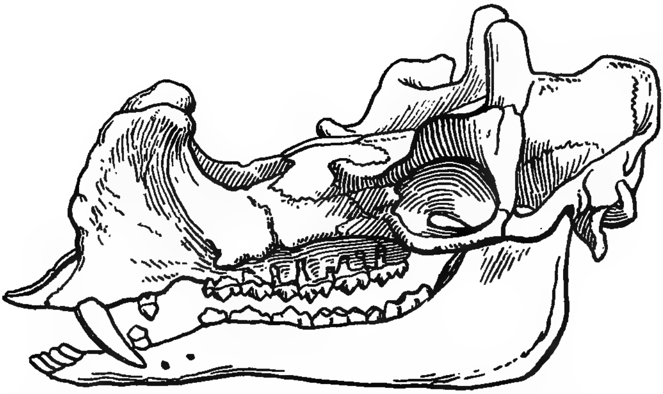

FIG. 217. — †*Protoceras celer*, skull of male. (After Osborn and Wortman.)

pointed splints were the vestigial remnants of the second and fifth digits.

It is not yet possible to trace this phylum below the level of the uppermost White River beds, yet that will very probably be accomplished by future exploration.

The second phylum of the family was represented in the lowest Miocene by †*Hypertragulus*, a genus of much smaller animals than those of the preceding series, which went back to White River times without essential change, and was abundant in the John Day stage. Despite this fact, the structure of the genus is still incompletely known and much remains to be learned, but enough has already been ascertained to justify the association of this phylum with the †*Protoceras*-†*Syndyoceras* series in one family as reasonable. The number of upper incisors in †*Hypertragulus* has not been ascertained, but the canines were enlarged and tusk-like, the lower one not having gone over to the incisors, as it had in the preceding group. The skull had much resemblance to that of the contemporary camels, the sudden narrowing of the facial region giving it a very llama-like appearance; the orbit was open and on the face in front of it was a conspicuous vacuity. The ulna and radius were coössified and there were four digits in the manus, two in the pes, but no cannon-bone was formed.

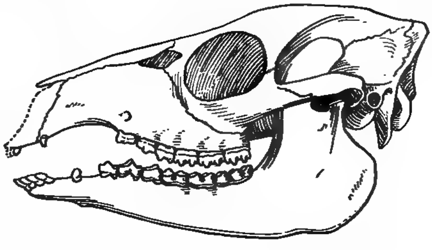

FIG. 218.—Skull of †*Leptomeryx evansi*, White River. (After Matthew.)

The third phylum, that of †*Leptomeryx*, had about the same range in time as the preceding one, though it has not yet been found in the John Day, and the genus is assuredly known only from the White River beds, in which it is not uncommon. †*Leptomeryx* comprised a number of species, all very small animals, and none larger than a jack-rabbit. (See Fig. 277, p. 563.) In size, proportions and appearance, these dainty little creatures must have been very like the existing chevrotains or "mouse-deer" of Asia and the Malay islands, and by many writers they have been classed in the same suborder, the Tragulina. The upper incisors had been suppressed and the upper canine reduced to very small size, while the lower canine had become functionally one of the incisors. The skull had a very long and slender facial region, but had a less llama-like appearance than in †*Hypertragulus*. The neck was short and the fore limbs much shorter than the hind, so that the back sloped downward from the rump to the shoulders, as in the chevrotains. There was a remarkable, indeed quite unparalleled, difference between the fore and hind limbs and feet, the hinder extremity being not only much longer, but also much more specialized, while the anterior one retained in very large degree its primitive characteristics. Thus, in the fore-arm the ulna was complete and separate from the radius, but in the lower leg the fibula was reduced to its minimum. In the manus there were four entire and functional digits, in the pes only two, which were joined in a cannon-bone.

Finally, there was a fourth phylum, that of †*Hypisodus*, which was confined to the White River stage and is still incompletely known. This was a tiny creature, much smaller than any of the preceding ones, and is the only known White River ungulate with fully hypsodont grinding teeth. Another very exceptional peculiarity of its dentition was that in the lower jaw it had ten incisor-like teeth; not only the canine, but the first premolar as well, had assumed the character of the incisors. This same peculiarity is found in the lower Miocene †gazelle-camel, †*Stenomylus* (see p. 394), but in no other mammal.

A considerable assemblage of genera belonging to this family occurs in the upper Eocene, but the material yet obtained is too fragmentary to permit the assignment of these forms to the different phyla, though it is very probable that among them are to be found ancestors of all the White River and subsequent genera.

While there is little difference of opinion as to the propriety of including in the family †Hypertragulidæ the four phyla described in the foregoing pages, the systematic position and the relationships of that family as a whole are matters of debate and likely long to remain so. Dr. Matthew refers the entire group to the suborder Tragulina and regards †*Leptomeryx* as being closely related to the direct ancestry of the American deer, a view which is accepted by Professor Osborn, but in which I am unable to concur. My own belief is that the family was an early offshoot from the cameline stock and therefore referable to the Tylopoda, in which suborder they are here included. It would be out of place to enter upon a discussion of this perplexing problem, which can hardly receive a definitive solution until the artiodactyls of the Uinta stage are thoroughly understood. As in so many other series, the key of the mystery lies hidden in the Uinta fauna, which is still so inadequately known.

Suborder Pecora. True Ruminants

This is the most advanced, specialized and diversified group of the artiodactyls, though the ruminating habit is shared by both Tylopoda and Tragulina. In this multitude of forms, giraffes, deer, antelopes, sheep, goats, oxen, buffaloes, bisons, etc., it is difficult to find a clue to a natural arrangement or classification. As a whole, the suborder is a well-defined group, and many structural characters, not all of which is it needful to enumerate here, are common to all of its members. The upper incisors are invariably absent, and, save in a few of the deer, the upper canine also, while the lower canine has become incisiform; the premolars are always three in number in each jaw and the molar-pattern is selenodont throughout. The odontoid process of the axis is spout-shaped. Except in a few deer, the Pecora all have bony outgrowths of the skull in the form of antlers or horns, at least in the males, many females being hornless. The ulna is coössified with the radius and the fibula is lost, except the lower end, which is a separate malleolar bone. There is always, in both fore and hind feet, a cannon-bone, the lower ends of which are parallel, not divergent, as they are in the Tylopoda, and each articular surface is encircled all around by a prominent median keel, as in the horses, which in the other suborders, as in mammals generally, is confined to the posterior side and not visible from the front. (*Cf.* Figs. 220 and 214, p. 401.) In no existing member of the Pecora are there complete lateral digits, and in several modern genera they have been completely suppressed; but in most there is, behind the functional pair of digits, a pair of "dew-claws," the bones of which are more or less completely reduced, often to mere nodules. The stomach, which in the Tylopoda and Tragulina is three-chambered, is in the Pecora divided into four distinct parts.

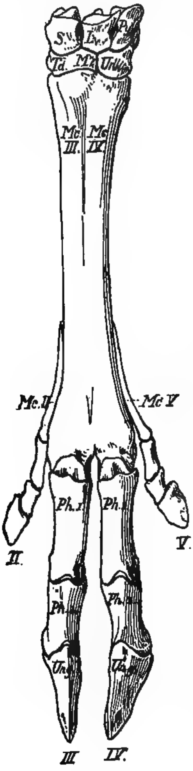

Fig. 219. — Left manus of Patagonian Deer (*Hippocamelus bisulcus*). *S.*, scaphoid. *L.*, lunar. *Py.*, pyramidal. *Td.*, *M.*, coossified trapezoid and magnum. *Un.*, unciform. *Mc. II* and *V*, rudimentary second and fifth metacarpals. *Mc. III* and *IV*, cannon-bone. *Ph. 1*, *2*, first and second phalanges. *Ung.*, ungual phalanx.

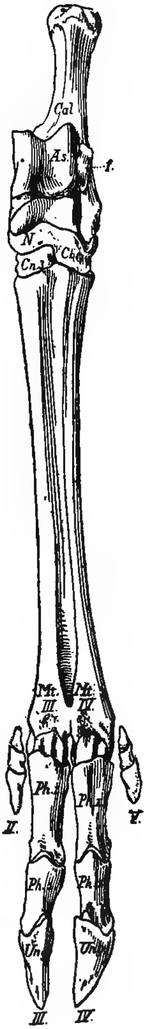

Fig. 220. — Left pes of Patagonian Deer. *Cal.*, calcaneum. *As.*, astragalus. *N.*, *Cb.*, coossified navicular and cuboid. *Mt. III*, *IV*, cannon-bone. Other letters as in Fig. 219.

As already intimated, the subdivision of the Pecora into smaller groups is far from easy. "The great difficulty which all zoologists have felt in subdividing them into natural minor groups arises from the fact that the changes in different organs (feet, skull, frontal appendages, teeth, cutaneous glands, etc.) have proceeded with such apparent irregularity and absence of correlation that the different modifications of these parts are most variously combined in different members of the group."[1] Two main sections of the suborder are, however, sufficiently well defined, (1) the Cervicornia and (2) the Cavicornia.

SECTION CERVICORNIA. DEER AND GIRAFFES

This section includes two families, the giraffes and the deer. Inasmuch as the former have not now and never did have any representatives in the western hemisphere, for the purposes of this book the section becomes identical with the deer family.

8. *Cervidæ.* *Deer*

In most of the deer now existing the male has antlers. The antler is a bony outgrowth from the frontal bone of the skull and is annually shed and replaced, increasing, as a rule, in size and in the number of branches with each renewal. During the period of growth the antler is richly supplied with blood-vessels and covered with skin and is then said to be "in the velvet," which dries and peels off when growth is complete; after the rutting season a layer of bone at the base of the antler is resorbed, loosening the antler, which is then shed. There is, however, a permanent, cylindrical process, of greater or less length, from each frontal, the "*pedicle,*" from which the antler is annually reproduced, and around the base of the antler and shed with it is a roughened ring, the "*burr.*" Among the different genera of deer there is great variety in the form and size of the antler, from a single spike to the immense and complicated appendages of the Wapiti (*Cervus canadensis*). As a rule, the "*beam*" or main stem of the antler and its

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[1] Flower and Lydekker, *op. cit.*, pp. 307–308.

branches or "*tines*" are cylindrical and tapering; but in some cases, as in the Moose (*Alce*) and the Fallow Deer (*Dama*), the antler is very broad and flat and is then said to be "*palmated.*" Except in the Reindeer and Caribou (*Rangifer*) the female is without antlers.

In the skeleton there is little difference between the deer and the Cavicornia, but there are some differences in the teeth. In the males of those deer which have no antlers, such as the Musk-Deer (*Moschus moschiferus*) and the Chinese Water-Deer (*Hydropotes inermis*), as well as in certain forms with very small antlers, like the muntjacs of Asia (*Cervulus* and *Elaphodus*), the upper canine is a long, thin, recurved and sabre-like tusk, a very effective weapon. Speaking of the Indian Muntjac or "Barking Deer" (*Cervulus muntjac*), Flower and Lydekker say, "When attacked by dogs the males use their sharp canine teeth with great vigour, inflicting upon their opponents deep and even dangerous wounds." In other forms of deer the upper canines are small or absent. The grinding teeth are brachyodont, but in the existing genera they have higher crowns than in the Tertiary progenitors of the family, and in the Axis and Hog Deer of India (*Axis axis* and *A. porcinus*) the molars are quite hypsodont.

As was shown in Chapter V, the existing deer of North America are of two kinds: (1) the northern, which are plainly of Old World origin and so closely similar to Old World species that many naturalists deny the necessity of making distinct species for the American forms. The best known of these are the Wapiti (*Cervus canadensis*), the Caribou (*Rangifer caribou*) and the Moose (*Alce americanus*). (2) The southern deer, of which the common Virginia Deer (*Odocoileus virginianus*) is a familiar example, though overlapping in their range that of the northern genera, are peculiar to the Americas, and, though not exactly autochthonous, they must have had a long American ancestry. In the Pleistocene we find the same genera and mostly the same species, their distribution over the continent shifting in accordance with the many climatic changes of that epoch. There was, however, at least one Pleistocene genus (†*Cervalces*) different from any now living and different from any known in the eastern hemisphere. The most complete specimen of this animal is a skeleton in the museum of Princeton University, found beneath a bog in northern New Jersey, though other bones, collected in Kentucky and elsewhere, are very probably referable to it. †*Cervalces* was very nearly related to the Moose, the neck, body, limbs and feet being almost identical in the two genera, but the skull and antlers were notably different; the nasal bones were not nearly so much shortened as in the Moose, indicating that the proboscis-like snout was not so large or inflated as in the latter. The antlers were quite unique; though in general like those of the Moose, they were much less palmated and they had, in addition, a great trumpet-like plate of bone on the lower side of each antler (see Fig. 117, p. 209), such as occurs in no other known member of the family. Although †*Cervalces* has not been found in the Old World, it was almost certainly an immigrant from eastern Asia.

The Moose, Caribou and Wapiti were unquestionably immigrants and came in not earlier than the Pleistocene. Nothing is known in the Pliocene or more ancient Tertiary epochs of North America which could be twisted into forms ancestral to these typically Old World genera. With the southern deer (*Odocoileus*, etc.) the matter stands differently, for these have a probable American ancestry extending back to the lower Miocene and possibly much farther. On the other hand, it is not altogether certain that these may not have been Pliocene immigrants, for their genealogy is still in an extremely fragmentary and unsatisfactory condition. The North American genus, *Odocoileus*, extended back to the Pliocene with very little change. The annoying, unrecorded gap of the upper Pliocene and the meagre representation of the middle Pliocene mammals given by the Blanco leave us without information regarding the deer of that time. In the lower Pliocene and through the whole Miocene we meet with frequent remains of a genus (†*Blastomeryx*) which was quite probably the ancestor of the American types of deer. It was considerably smaller than any of the existing North American species and had no antlers, but possessed the sabre-like, upper canine tusks, which characterize the muntjacs and hornless deer of Asia. The limb-bones had already attained nearly their present state of development, as regards the reduction of ulna and radius, formation of cannon-bones, etc. †*Blastomeryx* probably entered North America in the lower Miocene, but, as was mentioned previously (p. 409), Dr. Matthew and Professor Osborn regard the genus as autochthonous and descended from the †Hypertragulidæ.

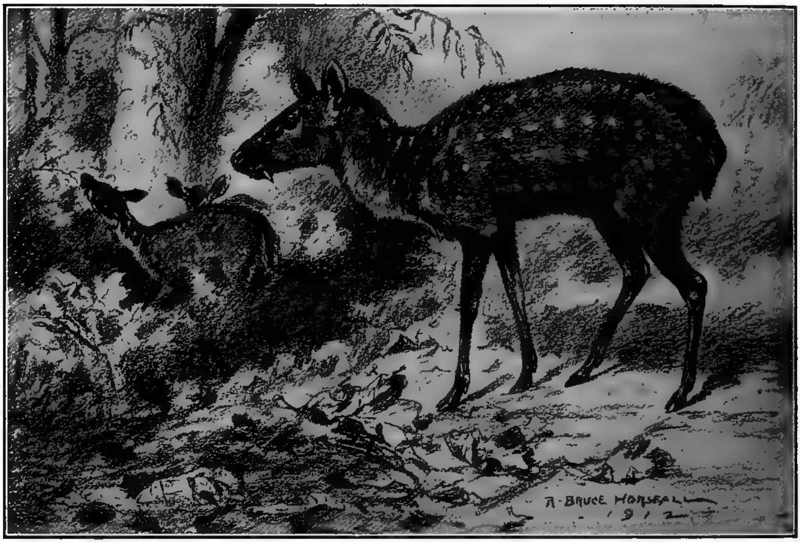

Fig. 221.—Lower Miocene †hornless deer (†*Blastomeryx advena*). Restored from a skeleton in the American Museum of Natural History.

In the middle Miocene †*Blastomeryx* gave rise to an aberrant genus (†*Merycodus*) which has been made the type of a distinct family (†Merycodontidæ, see table, p. 362), but this is perhaps unnecessary. †*Merycodus* had deer-like antlers, but completely hypsodont teeth such as no known member of the Cervidæ possesses. The middle Miocene species (†*M. osborni*) was a little creature, not more than eighteen or twenty inches high at the shoulder, and had a branched antler of three tines, which was considerably longer than the skull, while in the species of the upper Miocene (†*M. furcatus*) the antler was shorter and simply forked. From the number of specimens of these animals found in which the burr is incomplete or absent, it may be inferred that the antler was not always deciduous. The legs were long and very slender, and apparently there was no trace of the lateral digits, even in the fore foot. These peculiar hypsodont deer persisted even in the older Pleistocene.

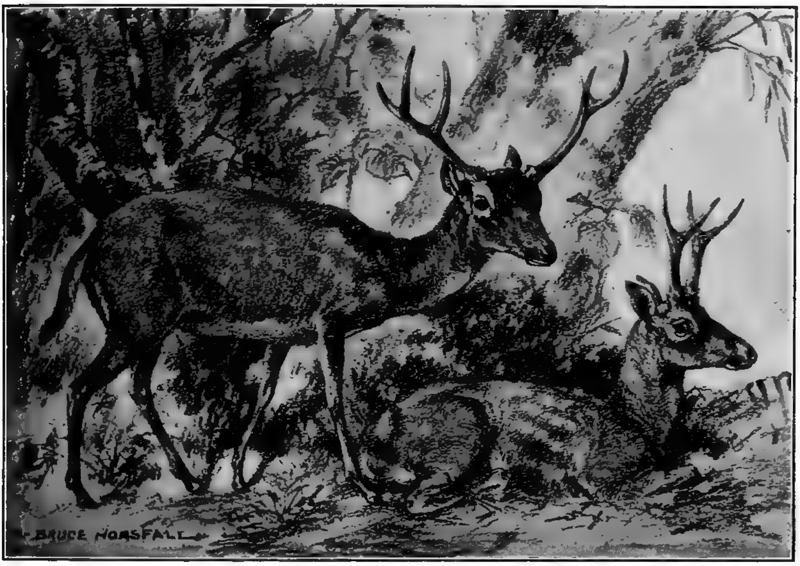

FIG. 222. — Miocene †deer-antelopes (†*Merycodus osborni*, middle Miocene, and †*M. furcatus*, upper Miocene). Restored from specimens in the American Museum.

Deer are the only members of the Pecora which inhabit South America, where there are several genera of them, all much more nearly allied to North American than to Old World forms. No record of the presence of the family in the southern continent has been found in beds older than the Pleistocene, but in view of the degree of specialization which they have there undergone, it is probable that the immigration took place in the Pliocene.

SECTION CAVICORNIA. HOLLOW-HORNED RUMINANTS

In the animals of this second and far larger section of the Pecora there are bony outgrowths of the skull, from the frontal bones, outgrowths which are permanent and non-deciduous; these are the *horn-cores*, which are tapering and unbranched. The horn-core is, in turn, covered with a sheath of horn, likewise unbranched and permanent, but growing from year to year until the maximum size is attained, a process which is familiarly illustrated in the growth of a calf. Among Recent Cavicornia there is but one exception to the rule that the horny sheath is non-deciduous and unbranched and that one is the Prong Buck (*Antilocapra americana*). In the Cavicornia it is the very general rule that both sexes are horned, though the females commonly have smaller horns and in several genera of antelopes the does are hornless. There is almost as great variety in the shape and size of the horn as of the antler; we find small, medium-sized and enormously large horns, which may be straight, simply curved, complexly curved, spiral, lyrate or twisted. The antelopes have many types of horns, as have the sheep and goats, the oxen, buffaloes and bisons; but only a few of them are exemplified in the western hemisphere, which now, as in the preceding geological periods, is singularly poor in representatives of the Pecora.

9, 10. *Antilopidæ and Antilocapridæ. Antelopes*

Two very different kinds of antelopes are found in North America at the present time; one of them, the erroneously named Rocky Mountain Goat (*Oreamnos montanus*), is evidently a late immigrant from the Old World, and fossil remains of it have been found in the Pleistocene cave-deposits of California. This animal is a member of the true antelope family (Antilopidæ) and belongs to the chamois group of mountain-antelopes; it has no near relatives among other American mammals, living or extinct.

The Prong Buck, or Prong-horned Antelope (*Antilocapra americana*), occupies a very isolated position, so much so that a distinct family, the Antilocapridæ, has been created for its reception. It differs from all other Cavicornia in having a branched horn, though the bony core is simple, and in annually shedding and renewing the horny sheath; the horn is directly over the eye; there are no dew-claws and all traces of the bones of the lateral digits have completely disappeared. The grinding teeth are thoroughly hypsodont. The genus occurred in the older Pleistocene, where it was associated with the last of the †deer-antelope, or †*Merycodus* series (†*Capromeryx*), and which, so far as it is known, would seem to connect the two families, though this is doubtful. A middle Miocene genus (†*Dromomeryx* Fig. 128, p. 237) would be a more probable ancestor of the Prong Buck, if it were not for the long, unfilled gap of the upper Miocene and the whole Pliocene. †*Dromomeryx* had erect horn-cores placed directly above the eyes as in the modern genus, but low-crowned grinding teeth; it was the most ancient American cavicorn yet known. It remains to be determined by future exploration, whether this middle Miocene genus was actually the ancestor of *Antilocapra*, or merely an anticipation of it.

In the lower Pliocene have been found the remains, very incomplete, of several antelopes, which appear to have been immigrants from the Old World, but are too imperfectly known for any definitive reference. One resembles the flat-horned, or goat-horned, antelopes of the European Miocene and Pliocene. Others had spirally twisted horns like those of the Recent strepsicerine, or twisted-horn antelopes of Africa and Asia, but may, nevertheless, be referable to the Antilocapridæ.

Antelopes even penetrated to South America, and three genera of them have been reported from the Pleistocene of the Brazilian caverns and the Argentine pampas, but they were less successful in establishing a foothold than were the deer, and form no part of the modern Neotropical fauna.

11. *Bovidæ. Sheep, Bisons, Oxen, etc.*

A series of genera, of disputed systematic position, is represented to-day by the so-called Musk-Ox (*Ovibos moschatus*), which is now exclusively North American, but in the Pleistocene ranged over northern Asia and Europe as far west as Great Britain. The Musk-Ox, which is at present found only in the extreme north, is a heavy, short-legged animal, three and a half to four feet high, and six feet or more in length; the body is covered with a dense coat of woolly hair overlaid by a thatch of long, straight hair, which gives the animal a very shaggy appearance. The horns are broad at the base, especially so in old males, in which they meet in the middle line and cover much of the head as with a horny casque; they curve downward and then upward and forward, with the tips directed toward the front; in the females and young males the horns are very much smaller.

This series cannot be traced back of the Pleistocene, in which epoch it was not only far more widely distributed, but also very much more diversified, no less than three extinct genera, in addition to the existing one, having been found in the North American Pleistocene. One of these (†*Symbos*), which extended from Alaska to Arkansas, had horns which were smaller and shorter than in the modern genus, and, even when fully developed, did not meet in the middle line of the head. The other two genera, from California (†*Euceratherium* and †*Preptoceras* Fig. 116, p. 203), are of great interest as showing affinities to the Musk-Ox and also to sheep and to certain antelopes, such as the Takin (*Budorcas*) of northern India and Tibet. They serve to connect the musk-oxen with other Cavicornia, but the origin of all these animals is to be sought in Asia.

In Recent North America there are four or five species of sheep (*Ovis*) which are confined to the mountainous and broken areas of the western part of the continent and extend from Alaska to Mexico. The "Bighorn" or Rocky Mountain Sheep (*Ovis canadensis*) is characterized by great, spirally coiled horns in the rams, in the ewes the horns are very much smaller and nearly straight; the other species differ but slightly from this type. The species *O. canadensis* has been found in the Pleistocene, but nothing further is known of its history. Evidently, the sheep were late immigrants.

"The geographical distribution of wild sheep is interesting. The immense mountain ranges of Central Asia, the Pamir and Thian Shan of Turkestan, may be looked on as the centre of their habitat." "Sheep are essentially inhabitants of the high mountainous parts of the world, for dwelling among which their wonderful powers of climbing and leaping give them special advantages. No species frequent by choice either level deserts, open plains, dense forests or swamps. By far the greater number of species are inhabitants of the continent of Asia, one extending into North America [should read, four or five] one into Southern Europe and one into North Africa. . . . No remains that can be with certainty referred to the genus [*Ovis*] have been met with in the hitherto explored true Tertiary beds, which have yielded such abundant modifications of Antelopes and Deer."[1]

The only other division of the family which is represented in North America is that of the bisons, of which the fast vanishing remnant of a single species[2] (*Bison bison*) is all that is left of what was once an extensive and varied assemblage. The bisons differ from the true oxen in the form and structure of the skull, in the shoulder-hump, which is produced by the very long spines of the dorsal vertebræ and in consequence of which the back slopes downward from the shoulders to the croup.

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[1] Flower and Lydekker, *op. cit.*, pp. 355 and 357.

[2] The Woodland Bison of Canada is now regarded as a distinct species.

They differ further in the character of the hair, which is short and woolly on the body and hind quarters, very long and shaggy on the head and neck. In the Pleistocene of North America there were at least seven recognizable species of bisons, which ranged over the continent from Alaska to Florida, though it is not probable that they were all contemporary. One of the earliest and by far the largest of these was the gigantic *B. †latifrons*, a specimen of which in the American Museum of Natural History measures six feet across the horns in a straight line; this was a Mississippi Valley species and extended from Ohio to the Gulf of Mexico and westward to Kansas and Texas. Another gigantic species (*B. †crassicornis*) lived in Alaska in association with a second and smaller species (*B. †occidentalis*) which ranged as far south as Kansas. *B. †occidentalis,* though smaller than the preceding species, was larger than the existing one and was remarkable for the great size of the hump. The bisons were migrants from the Old World and are the only members of the great ox-tribe that ever reached America. At present the Old World has but a single species of *Bison* (*B. bonasus*), which has been saved from extermination only by the most rigid protection.

Neither sheep nor bison extended their range to South America; both are and have been essentially northern groups and seem to have been unable to cross the tropics.

From the foregoing account, confused as it unavoidably is, one thing at least stands out clearly, that North America played a very insignificant rôle in the evolution of the Pecora, and has only two peculiar groups, the Prong Buck and the American types of deer, and of these, the probable American ancestry does not extend back of the lower Miocene and perhaps not so far. Even in the Old World the story, so far as it has been deciphered, is by no means clear and consistent, which is no doubt due to the fact that the regions from which Tertiary mammals have been obtained are so small in comparison with those that have yielded nothing. Certain broad outlines of the history may, nevertheless, be discerned.

The suborder Pecora at an early date became divided into the two great branches of the Cervicornia and Cavicornia, the former giving off the giraffe series, which in the Miocene and Pliocene ramified and extended through Asia and southern Europe, though now confined to Africa. In the lower Miocene of Europe the muntjac-like deer and the antelopes, the first of the Cavicornia, were already well distinguished. From the primitive antelopes arose not only the wonderful assemblage of modern antelopes, but also the goats and sheep and the great and varied ox-tribe. From the middle Oligocene forms it may obviously be inferred that both Cervicornia and Cavicornia united in a single trunk, or, traced in the other direction, diverged from a common stock, to which also the suborder of the Tragulina goes back.

On the other hand, it is equally obvious that the camels and llamas have been separated from the Pecora at least since the middle Eocene, and, consequently, the many points of agreement between the two suborders, other than those shared with all artiodactyls, are not due to inheritance from a common ancestry, but have been independently acquired in the two series. It will be instructive to note some of the more important of these independent similarities: (1) the selenodont and more or less hypsodont character of the grinding teeth; (2) the spout-shaped odontoid process of the axis; (3) the great reduction of the ulna and its coössification with the radius; (4) the loss of the fibula, except for its lower end, which persists as a separate malleolar bone; (5) the formation of cannon-bones by the fusion of the third and fourth metapodials; (6) the development of a complex, many-chambered stomach. Other points of likeness might be cited, but those already given will suffice to show how very important this parallel mode of evolution often proves itself to be.

CHAPTER X

HISTORY OF THE PROBOSCIDEA

UTTERLY foreign as the elephant-tribe appears to be to present-day North America, it was a very conspicuous element in the fauna of that continent from the middle Miocene to the end of the Pleistocene, and in the latter epoch it spread over South America also. Like so many others of the mammals which have, from time to time, flourished in the Americas, the elephants and their allies, the †mastodons, were immigrants from the Old World, and, until comparatively lately, the region of their origin was a complete mystery. They appeared suddenly and unheralded and at approximately the same time in Europe and North America and nothing is known from preceding geological formations of either continent which could with any plausibility be regarded as ancestral to them. The mystery was dispelled by the discoveries of Dr. C. W. Andrews in Egypt, which demonstrated that these strange and huge beasts had originated in Africa and had migrated thence through Asia to Europe, on the one side, and to North America on the other.

The proboscideans occupy a very isolated position among the hoofed mammals, and in structure they display a curious mingling of high specialization with an extreme conservatism of primitive characters, the specialization being exemplified in the teeth and head and the conservatism in the body and limbs, very much as in the †oreodont family of artiodactyls (p. 382). The most conspicuous of the external features in the order is the long trunk, or proboscis, which gives its name to the group, and is a great prolongation of the nose, with the nostrils at the end and a finger-like tip, which can be used to pick up minute objects.

In the true elephants the dental formula is: $i\,\frac{1}{0}$, $c\,\frac{0}{0}$, $p\,\frac{0}{0}$, $m\,\frac{3}{3}$, $\times 2 = 14$, though this formula is misleading, to the extent that the milk premolars, three in number in each jaw, take the place and perform the functions of the premolars, thus adding 12 to the effective number of teeth. The single upper incisor on each side grows into an immense tusk, which has enamel only on the tip, where it is speedily worn away; the lower jaw is without incisors and there are no canines above or below. The grinding teeth are very large and have a highly complex structure and a most exceptional method of eruption on coming into use. They are thoroughly hypsodont and each is composed of a large number of high, broad and thin plates of dentine covered with enamel and the spaces between the enamel ridges are filled with cement (see Fig. 47, p. 97); indeed, the whole tooth is so thickly covered with cement that, when unworn, it looks like a mere lump, with no ridges showing on the surface. The teeth increase in size and in the number of component ridges from before backward, and in the Indian species (*Elephas maximus*) the number of ridges in the six grinding teeth, including the milk premolars, is: 4, 8, 12, 12, 16, 24. In the African Elephant (*Loxodonta africanus*) the teeth are not so high and have fewer and thicker plates, the formula being: 3, 6, 7, 7, 8, 10. The teeth do not succeed one another vertically in the

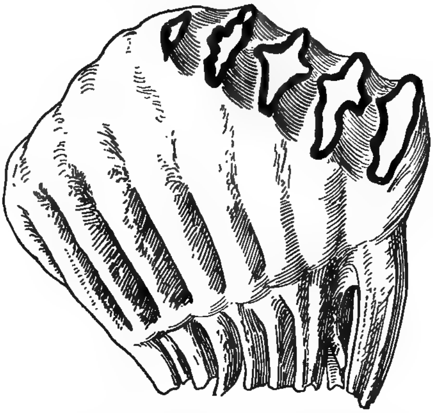

FIG. 223. — Molar of the African Elephant (*Loxodonta africanus*) showing the oblique mode of wear. Heavy black lines indicate enamel, enclosing areas of dentine, cement covering the whole tooth.

normal mammalian fashion, but come in successively from behind and the series moves forward, so that the foremost tooth is pushed out, when it is so worn down as to be of no further service. As these teeth are very large and the jaws are relatively short, only one tooth on each side, above and below, is in use at the same time, though part of a second may also be involved. The movement of the successive teeth is not directly forward, but oblique, an upper tooth coming forward and downward and a lower tooth forward and upward. In consequence of this arrangement the teeth are abraded obliquely, the anterior part first coming into use, and, by the time a tooth is fully in place, the front portion is worn down to less than half the height of the hinder part. All of these peculiarities in the dental system imply a very high degree of specialization and a notable difference from other mammals.

The skull is equally specialized, as is indeed required by the character of the teeth and the development of the long and heavy proboscis. The premaxillæ are converted into sheaths for the great tusks; the nasals are extremely abbreviated and the anterior nasal opening is shifted to the top, directly above the posterior opening, so that the nasal canal passes vertically downward through the skull. All of the bones forming the cranium are enormously thickened and at the same time lightened by the formation of an extensive system of communicating sinuses, and thus the brain-chamber is, as it were, hidden away in the middle of the huge mass of the skull. This explains the difficulty of killing an elephant by shooting it in the head; the shot must be so directed as to reach the brain, which requires knowledge and skill.

The neck is short, the body long and extremely massive, the tail of moderate length. The shoulder-blade is very large and has a prominent metacromion given off from the spine; the hip-bones are immensely expanded in correlation with the breadth of the thorax and abdomen. The limbs are long, massive and columnar, their upper segments, especially the thigh, are very long, so that the knee-joint is brought below the body and free from it to the position of the hock-joint in the Horse; hence, the hind leg appears to bend in the opposite direction from the bend in the legs of ordinary quadrupeds, in which the true knee-joint is concealed. The fore-arm bones are separate and, for most of its length, the ulna is far heavier than the radius, a wide departure from the proportions usual in hoofed animals. The femur has no pit in its head for the round ligament and no third trochanter; the shaft is broad and much flattened, having quite lost the normal cylindrical shape. The bones of the lower leg are also separate, but the fibula, though stout, is very much more slender than the ulna. The long bones have no marrow-cavities, but are filled with spongy bone. The feet are extremely short and broad and of columnar shape, the weight resting upon a pad of elastic tissue and the small, nail-like hoofs are mere excrescences upon the periphery. There are five digits in manus and pes, but not all of them have hoofs; in the Indian and West African species the number of hoofs is five in the fore foot and four in the hind, in the East African four and three respectively. In the adult the skin is quite hairless, though the young calf has a considerable quantity of hair.

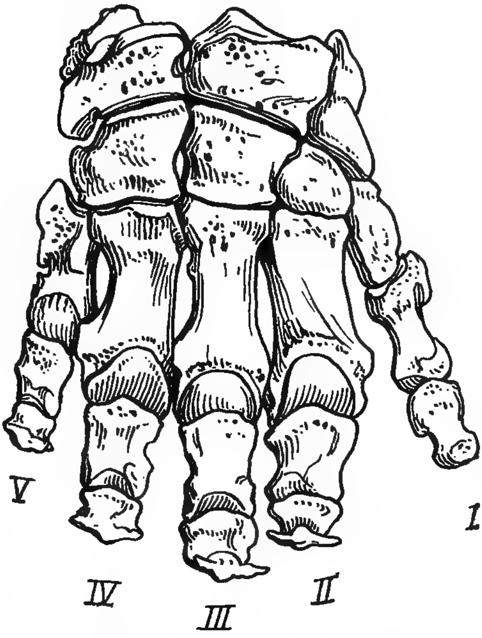

FIG. 224. — Right manus of the Indian Elephant (*E. maximus*).

At present, the Proboscidea are restricted to the warmer parts of Asia and Africa, where five species, four of them African, are recognized. This is a very great reduction in the number of species and in the area inhabited during the Pleistocene epoch, when they ranged through every continent, except Australia, and were adapted to every climate from the tropics to the shores of the Arctic Sea. Four distinct species of proboscideans existed in Pleistocene North America, three elephants and a †mastodon, though not all in the same areas, nor probably all at the same time, their ranges both in time and space overlapping to a greater or less degree, but not exactly coinciding in either respect.

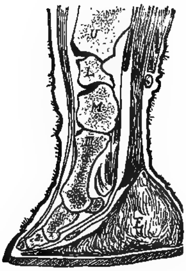

FIG. 225.—Vertical section through the manus of the Indian Elephant. *U*, lower end of ulna. *L*, lunar. *M*, magnum. *III*, third metacarpal. *1*, *2*, *3*, phalanges. *E*, pad of elastic tissue. (After M. Weber.)

The first species was an immigrant, the northern †Mammoth (*Elephas* †*primigenius*), which extended over the greater part of the northern hemisphere, both in the Old World and in the New. This is the species of which complete carcasses with hide and hair have been found in the frozen gravels of northern Siberia, its structure and appearance being thus almost as well known as those of any modern elephant. That the †Mammoth was perfectly adapted to life in a climate of severe cold is shown not only by the contents of the stomach, which are comminuted fragments of present-day Siberian vegetation, but also by the dense coat of woolly hair, covered by long, coarse outer hair, which afforded full protection against the cold. The tusks, with considerable variation of form, had a tendency to spiral curvature, curving first downward and outward, then upward and inward; the grinding teeth were characterized by their relative breadth and the numerous thin enamel-ridges which traversed them. The number of these ridges was very variable in different individuals, but may be expressed for the six successive teeth as follows: 3–4, 6–9, 9–12, 9–15, 14–16, 18–27. The skeleton was more like that of the Indian Elephant than of the other species, though with a number of small differences in the skull. In size, the †Mammoth was comparatively small, standing about nine feet six inches at the shoulders. In North America its range was from Alaska southeastward across the continent to New England.

The second species, the †Columbian Elephant (*E. †columbi* Fig. 114, p. 198), was eighteen inches or more taller than the †Mammoth and rivalled the largest existing elephants in stature; its huge tusks curved first downward and then upward and inward, their tips crossing when full-grown. The grinding teeth had fewer and thicker enamel plates than those of the †Mammoth. The range of the †Columbian Elephant overlapped the southern border of that of the †Mammoth, but was, on the whole, much more southern; it crossed the continent from ocean to ocean and covered nearly the whole of the United States, extending down to the southern end of the Mexican plateau. The two species were very closely related and in some cases are so intergraded that it is difficult to distinguish them; the †Mammoth was an undoubted immigrant and the †Columbian Elephant was probably a local North American variant of it, adapted to a somewhat warmer climate. Nothing is known of the skin or hair in the latter animal, but, from the fact that it was not a tropical species and was exposed to very cold winters, it may be inferred that it had a hairy covering of some sort.

The third species of elephant (*E. †imperator*) was older geologically than the others, as it was more characteristic of the lower Pleistocene and uppermost Pliocene; its range coincided with the western half of the region covered by *E. †columbi*, extending far into Mexico, but not occurring east of the Mississippi River. It was an enormous creature, the largest of known elephants, with an estimated height of thirteen and a half feet at the shoulder (Osborn). The grinding teeth

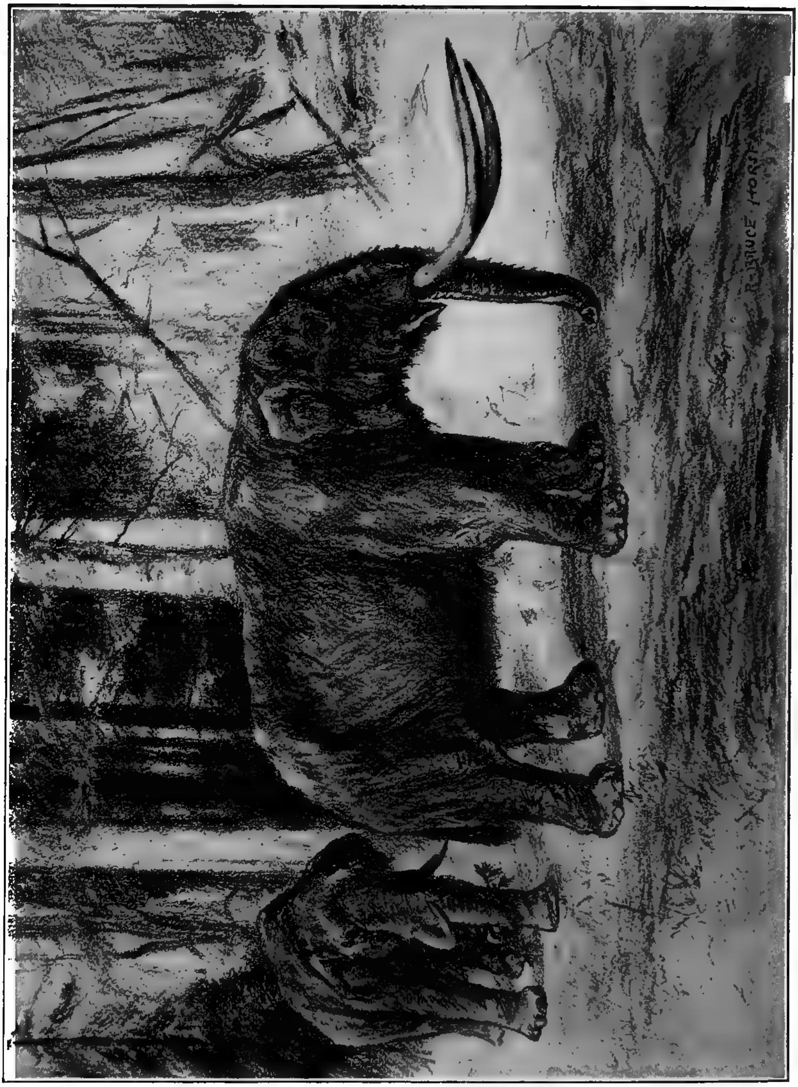

FIG. 226. — The American †Mastodon (†*Mastodon americanus*), Pleistocene. Restored from a skeleton in the museum of Princeton University.

had thicker and more crumpled enamel plates than in either of the other species.

The fourth of the Pleistocene proboscideans of North America was a member of a different and much more ancient genus, †*Mastodon,* which in the Old World became extinct before the end of the Pliocene. The American †Mastodon (†*M. americanus*) was thus a belated survival of an ancient type, seemingly out of place even in the strange Pleistocene world, which had so many bizarre creatures. The distinguishing characteristic of the genus was in the simple, low-crowned and comparatively small grinding teeth, which had three or four prominent transverse ridges, covered with heavy enamel, and, usually, with no cement on the crowns. As these teeth were so much smaller than those of the elephants, as many as three on each side of each jaw might be in simultaneous use. In this species there was no vertical succession of teeth, but in some of the Tertiary †mastodons such succession has been observed. The long tusks were directed nearly straight forward and were almost parallel, with but slight curvature, the convexity downward. In the males there was a short single tusk or, less commonly, a pair of such tusks, in the lower jaw, which were probably not visible externally; these were the vanishing remnants of an earlier stage of development, when the †mastodons had a fully developed pair of lower tusks, nearly as large as the superior pair.

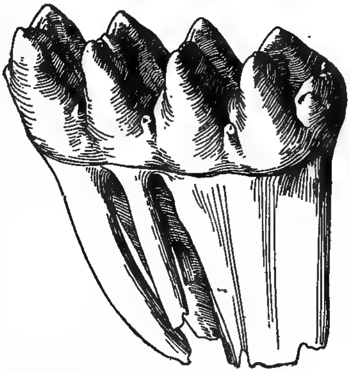

Fig. 227. — Last lower molar of the American †Mastodon.

The skull, while essentially proboscidean, was yet much lower and flatter and less dome-like than in the elephants; the thickening of the cranial bones was less extreme. The remainder of the skeleton differed so little from that of the elephants as to require no description. In size, this species about equalled the †Mammoth, the larger individuals measuring nine feet six inches at the shoulder. Remains have been found which prove that the American †Mastodon had a covering of long, coarse hair, and that it fed upon the leaves, shoots and small branches of trees, especially of conifers. There is much reason to believe that the species outlived the elephants in this continent and persisted until after the establishment here of the American Indian, and it may well have been human agency which finally extinguished the dwindling race. The range of the species nearly coincided with that of the †Columbian Elephant, but did not extend so far into Mexico, and in the central part of the continent reached much farther north, even into Alaska.

In the Pliocene of Texas, Nebraska and Idaho lived the American representatives of a genus (†*Stegodon*) which was a connecting link between the elephants and the †mastodons, and which was especially characteristic of the Pliocene of India. The tusks, which were confined to the upper jaw, had lost their enamel and the last molar, above and below, had five or six enamel ridges, but the crowns, which in the Asiatic species were buried in cement, had but a small amount of this material. Several species of †*Mastodon* occur in the same beds, but only isolated teeth have been found.

The †mastodons, in a broad sense of the term, have been divided into several genera and subgenera in accordance with different schemes; the simplest perhaps is to group into a second genus those species which had fully developed lower tusks. This four-tusked genus has received several names, of which †*Tetrabelodon* is most commonly used in this country, but the term †*Gomphotherium* is much older and, according to the law of priority, must therefore be employed. The lower Pliocene species of †*Gomphotherium* had a pair of large lower tusks, of cylindrical shape, and both upper and lower tusks had longitudinal bands of enamel, and in order to support the weight of these great tusks the symphyseal, or chin, region of the lower jaw was greatly elongated; the molars had four cross-crests.

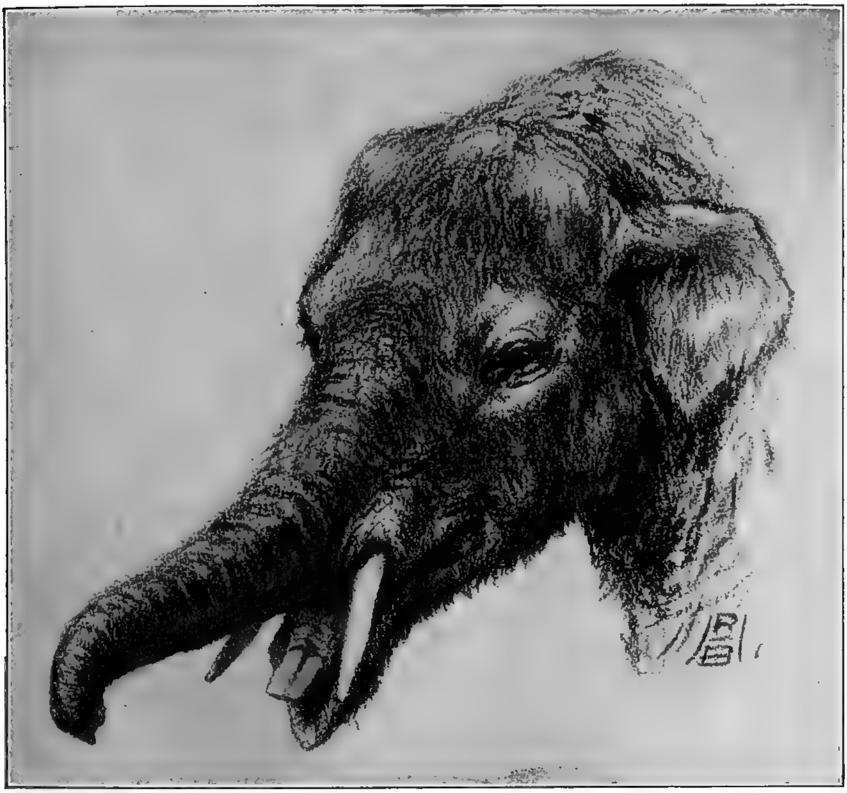

FIG. 228. — Head of upper Miocene †mastodon (†*Gomphotherium productum*) showing the chisel-like lower tusks. Restored from a skull in the American Museum of Natural History.

In the upper Miocene is found another and more primitive stage of proboscidean development. In these species the grinding teeth were three-ridged; the upper tusks were quite short and curved downward, diverging somewhat from each other, and they had enamel bands. The lower tusks were still shorter and of depressed, flattened and somewhat chisel-like form and so worn as to show that they were regularly employed in cropping and browsing. The skull was low and broad and the symphysis of the lower jaw was greatly prolonged to carry the tusks.

A very important fact concerning these early †mastodons is that they had the normal method of tooth-succession, permanent premolars forming beneath (in the lower jaw, above in the upper) the milk-teeth and pushing them out at maturity.

Of the middle Miocene proboscideans not much is known beyond the mere fact of their presence in North America at that time and indeed little of the skeleton, other than the skull, has yet been found in the American Miocene; but well-nigh complete skeletons have been obtained from the middle Miocene of Europe, and these bring out the surprising fact that the body and limbs of these species did not differ in any noteworthy manner from those of the existing elephants; the modern skeletal structure of these animals had been attained at a time when the dentition and skull were still in a far less advanced stage of development. In size, however, there was a decided difference, the species of the American Miocene rarely attaining a height of six feet.

Proboscidea have been reported from the lower Miocene of the Great Plains, but the material is insufficient for a definitive judgment. There is no doubt as to their presence in Europe at that time, but in neither continent can the history be traced any farther and we must turn to Africa for a backward continuation of the story. In the lower Oligocene of the Fayûm, southwest of Cairo in Egypt, occurs the highly interesting genus †*Palæomastodon*, which was much more primitive than any of the genera described above, though it was an unmistakable member of the order and even of the family Elephantidæ. The dentition was already much reduced, giving the formula: $i\,\frac{1}{1}$, $c\,\frac{0}{0}$, $p\,\frac{3}{2}$, $m\,\frac{3}{3}$. The upper tusks were short, compressed, directed downward, and slightly divergent, and had a broad band of enamel on the outer side; the lower tusks were still shorter and procumbent, pointing straight forward, and were covered with enamel, which was very thick on the lower side and thin or wanting on the upper. All of the grinding teeth were in place and function at the same time, which was not true of any of the genera previously considered, and each of the premolars had its predecessor in the milk-series, which it succeeded and displaced in the normal vertical manner. The premolars were smaller and simpler than the molars, which were made up of three pairs of conical tubercles arranged to form a three-crested crown. The skull, as compared with that of the elephants, was long and narrow, the premaxillaries extending into a long snout; the nasals were shortened, though not so much as in the succeeding genera, and there was probably rather a long and flexible snout than a true proboscis. The skull had a long and well-defined sagittal crest, which none of the later genera had, and the development of sinuses in the cranial bones, though considerable, was much less than in the elephants. The occiput was relatively high and the thickened parietals did not tower above it to any such degree as they do in the elephants. The symphysis of the lower jaw was greatly prolonged, extending out beyond the ends of the upper tusks, and this implies that the lower lip had a corresponding prolongation.

The skeleton is still incompletely known, though it may be said that the neck was probably longer than in the subsequent genera of the family. The limb-bones were already proboscidean in character, differing only in details from those of the more typical members of the order, but the animal was more lightly built and had less massive limbs. The presence of the third trochanter on the femur, which is lacking in all of the succeeding forms, is an interesting approximation to other and still more primitive groups of ungulates. The several species of †*Palæomastodon* represent a considerable range in size, from animals which were not much larger than a tapir to those which equalled a half-grown Indian Elephant.

It is possible to take another and very long step back from †*Palæomastodon*, so long, indeed, as to make it apparent that one or more links in the chain are still missing. The genus †*Mœritherium* is found together with †*Palæomastodon* in the lower Oligocene, but also occurs separately in the upper Eocene. It seems likely that it is a persistent middle Eocene type and that the known species of it were somewhat aside from the main line of descent, but that it very closely represents, nevertheless, a very early stage in the elephant genealogy. These known species were quite small animals, about the size of a tapir, and therefore not much less than the smaller members of †*Palæomastodon*. The dental formula of †*Mœritherium* was: $i\,\frac{3}{2}$, $c\,\frac{1}{0}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 36$. The first or median upper incisor was a relatively small and simple tooth, but the second was quite a large, downwardly directed tusk, which was much smaller and less curved than in † *Palæomastodon*, and was not capable of indefinite growth. The third incisor and the canine were small, spike-like teeth of no functional importance, but their presence is significant as approximating the primitive, unreduced dentition of the ungulates. The lower incisors were nearly procumbent, with a slight upward inclination; the first one was long and the second a thick, enamel-covered tusk, with a chisel-like edge, which was produced by wear. The premolars were smaller and simpler than the molars, which were quadritubercular, the four conical cusps arranged so as to form two transverse crests, giving a pattern like that of the early pigs and peccaries and of precisely the kind that might have been predicted from the teeth of †*Palæomastodon.*

The skull had an utterly different appearance from that of †*Palæomastodon*, the difference being much greater than between the latter and the Miocene †*Gomphotherium.* It was long and narrow, and, except for the very prominent zygomatic arches, of nearly uniform, tubular shape, the brain-case being of small capacity, though, as compared with other Eocene mammals, the brain was proportionately large. "It is possible that the early tendency toward a considerable cerebral development shown in these primitive Proboscidea is one of the causes why the group has survived and flourished through so long a period" (Andrews). The cranium was very long and the facial region extremely short, the premaxillaries not being prolonged into a snout, as they were in †*Palæomastodon;* the occipital bones formed nearly the entire posterior surface of the cranium and even encroached slightly upon the roof. There was a long, but not very prominent, sagittal crest, and some of the cranial bones were much thickened; in one species the hinder part of the cranial walls was distinctly inflated, a beginning of the enormous thickening which has culminated in the true elephants. The nasal bones were already much shortened, though they were twice as long as those of †*Palæomastodon*, and the animal would appear to have had an incipient proboscis.

The neck was of moderate length and the body very long, with at least twenty pairs of ribs, and there was probably a long tail. The hip-bone differed remarkably in its extreme narrowness from that of the later Proboscidea and the limb-bones were much more slender, though not dissimilar in shape.

At a very early period the order became divided into two main branches, one of which includes all the forms so far considered, and the other the very strange †*Dinotherium.* The †dinotheres entered Europe together with the †mastodons in the lower Miocene and continued into the Pliocene without much change and then died out, leaving no descendants. They never invaded North America, probably because they were of more or less aquatic habit, like the hippopotamuses, and therefore less likely to find suitable conditions in the narrow and unstable land-bridges which connected the Old World with the New, than were animals of purely terrestrial habitat. The †dinotheres were of huge size, equalling the larger elephants in this respect and closely resembling them in the skeleton of the body and limbs. As usual in this order, the generic peculiarities were to be found in the teeth and skull. There were no superior tusks, all the upper incisors and canines being lost, but there was a pair of large lower tusks, which were directed downward, with a strong backward curvature. The dental formula then was: $i\frac{0}{1}$, $c\frac{0}{0}$, $p\frac{2}{2}$, $m\frac{3}{3}$, $\times 2 = 22$. The grinding teeth were relatively quite small and had, except the first molar, two transverse crests, giving a pattern singularly like that seen in the tapirs. The skull was remarkably long, low and flat, and no doubt these animals had a proboscis of some sort. That the †dinotheres were derived from the same ancestral stock as the †mastodons and elephants is perfectly obvious and is not questioned by any one, but it is not yet possible to trace the connection.

The proboscideans were late immigrants into South America, being known there only in the Pleistocene and late Pliocene times, and only the †mastodons entered the southern continent, where they gave rise to several peculiar local species in Argentina, Bolivia, Chili and Brazil; one of these (†*Mastodon andium*) had a deposit of cement on the crowns of the grinding teeth. Why the elephants, which extended to the northern border of the Neotropical region, should have failed to reach South America and maintain themselves there, is but one of many similar questions to which no assured answer can be given.

The evolution of the Proboscidea was, in a certain sense, very similar to that of the †oreodont family (p. 381) among the Artiodactyla, in that the developmental changes affected chiefly the dentition and the skull, the skeleton of the body and limbs having very early acquired a character which was afterward but little modified. Were the skull and teeth of the lower Miocene †*Gomphotherium* not known, we should hardly hesitate to refer the skeleton to the genus *Elephas*, and even in the Oligocene †*Palæomastodon* all the bones of the skeleton, other than the skull, were characteristically and unmistakably proboscidean. On the other hand, the transformations of the

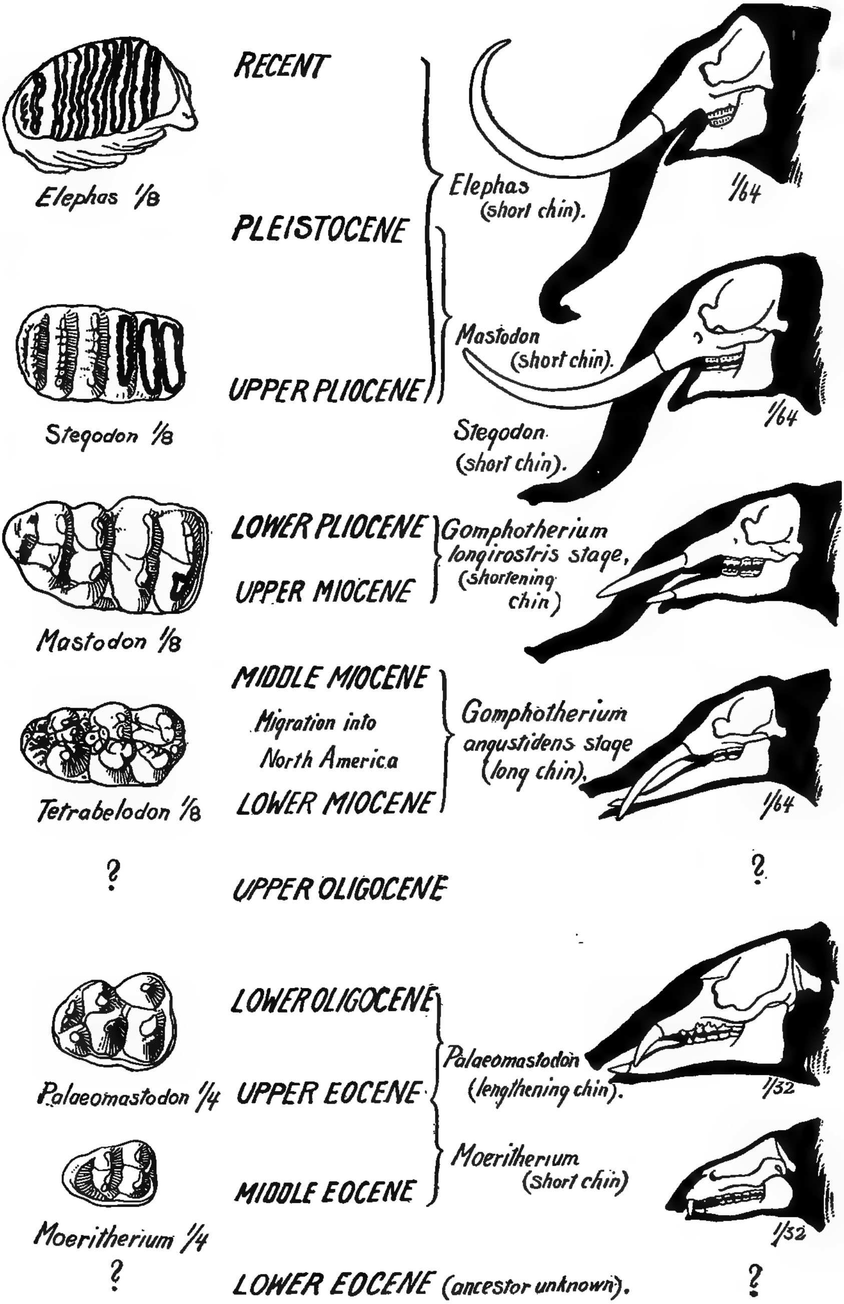

Fig. 229. — Evolution of the Proboscidea: on the right, a series of skulls; on the left, last lower molar. (After Lull, modified by Sinclair.) N.B. †*Tetrabelodon* should read †*Gomphotherium.*

teeth and skull were very profound and far-reaching, very much more so than those which took place in the †oreodonts.

In the dentition we may consider separately the development of the tusks and of the grinding teeth. The first step in the known series, as exemplified by †*Mœritherium,* was the enlargement of the second incisor in each jaw to form a tusk which, though actually quite long, was very small when judged by the proboscidean standard. The upper tusk was directed vertically downward and the lower one was procumbent, pointing almost directly forward; the third incisor and the canine were small and in the lower jaw already lost. In the next known stage, †*Palæomastodon,* all of the anterior teeth, except the tusks, had been suppressed; the upper tusks were longer and more curved and of an oval cross-section; they extended less directly downward and more forward, while the enamel was restricted to the outer side of the tusk; the lower tusks were more fully procumbent than in the preceding genus. The third stage, that of the lower Miocene †*Gomphotherium,* showed the upper tusks greatly elongated and directed more forward than downward, while the lower tusks were but little larger than before. From the middle Miocene two phyla may be distinguished by the tusks alone; in one, which was not destined to long life, the lower pair increased greatly both in length and in diameter, while in the other series they rapidly diminished and eventually disappeared. Even in the Pleistocene, however, the American †Mastodon had remnants of these tusks in the males. In the later †mastodons, the †stegodonts, and true elephants, the upper tusks, which alone remained, lost the enamel bands and attained enormous proportions, differing in the various genera and species in the extent and direction of curvature. An aberrant mode of tusk development was to be seen in the †dinotheres, in which the upper pair was suppressed and the lower pair enlarged and so curved that the points were directed backward.

The grinding teeth underwent much more radical and striking changes. At first (†*Mœritherium*) they were small, very low-crowned and of simple pig-like or quadritubercular pattern, making two interrupted cross-crests; all were in use simultaneously and the succession of milk-teeth and premolars was by vertical replacement, as in normal mammals generally. In †*Palæomastodon* there were three pairs of tubercles on the molars and in †*Gomphotherium* these coalesced into ridges, but in all the †mastodons there was more or less distinctness of the conical tubercles. In one or more phyla the three-ridged plan persisted for a long time, one such phylum terminating in the Pleistocene †*Mastodon americanus.* In the other series the number of ridges increased, first to four, then to five, six and more (†*Stegodon*); the crowns of the teeth became much larger and higher, and the ridges, as their number increased, became much thinner, and the valleys between them were filled with cement, and finally, in the true elephants, with their fully hypsodont, many-crested teeth, were thickly covered all over with cement. The vertical succession of milk-teeth and premolars was retained in †*Gomphotherium,* at least in some species, but the large molars, which could not find room to be exposed while the premolars were in place, came in successively from behind. This horizontal mode of succession is the only one to be seen in the true elephants, in which but one tooth, or parts of two, on each side of each jaw are in simultaneous use and the premolars have entirely disappeared, but the milk-teeth are retained.

The changes in the skull, which amounted to a reconstruction, were very largely conditioned by the great increase in the length and consequent weight of the tusks, in the size of the grinding teeth and the development of the proboscis. In the earliest known type (†*Mœritherium*) the skull had little about it that would, at first sight, suggest proboscidean affinities; it was long and narrow, with sagittal crest and occiput of normal type, very long cranial and very short facial region. The nasal opening was directed forward and the nasal canal was relatively long and horizontal in direction, but the nasal bones were already much shortened, indicating that the proboscis was probably in an incipient stage. The symphysis of the lower jaw was procumbent and somewhat elongated, but to only a comparatively slight degree.

While the skull of †*Mœritherium* was not obviously proboscidean, that of its successor, †*Palæomastodon*, was unmistakably so, yet retained several primitive features, which were lost in all of the subsequent genera, such as the sagittal crest, the relatively low cranium and moderate thickening of the cranial bones, the forward direction of the nasal opening, etc.; the symphysis of the lower jaw was very greatly prolonged.

As the tusks enlarged and the proboscis grew longer, the weight of the head and its appendages necessitated a largely increased area of attachment for the neck-muscles, and this was attained by a very great thickening of the cranial roof, the occiput not increasing proportionately; at the same time, the thickened bones were honeycombed with sinuses, so as to reduce their weight without sacrifice of strength. In those species of the Miocene †*Gomphotherium* which had large and heavy tusks, this thickening was not very much less than in the true elephants. The enlargement of the tusks had other consequences, as, for example, in lengthening and broadening the premaxillaries and, in the elephants, in their downward bending, so as to shorten still further the facial region of the skull. With the development of the proboscis, the nasal bones were reduced to a minimum and the anterior nasal opening was no longer directed forward, but obliquely upward, while the nasal passage lost its horizontal direction and became almost vertical. The lower jaw continued to elongate the symphysis, reaching a maximum in certain species of †*Gomphotherium;* but the reverse process of shortening this anterior region of the jaw began with the reduction of the lower tusks, and, when these had disappeared, nothing remained of the immensely elongated symphysis, except the short spout of the elephant's jaw. As the grinding teeth increased in height, there was a concomitant increase in the vertical depth of the jaws for their lodgment.

It was an obvious advantage in the mechanical problem of supporting the enormous weight of head, tusks and trunk to shorten the neck and thus bring the weight nearer to the point of support at the withers, the lengthening proboscis rendering it unnecessary for the mouth to reach the ground in feeding or drinking. The other parts of the skeleton underwent comparatively little change, the degree of modification being greatest between †*Mœritherium* and †*Palæomastodon.* Throughout the series the bones of the fore-arm and lower leg remained separate, and the feet very short and five-toed. In size also the great stature and massiveness were attained early. After the great migration of the Proboscidea to the northern continents, we find considerable differences of size between the various phyla, though all were very large, and even as early as the lower Miocene of France, there were species which rivalled the modern elephants in bulk. It was this rapid attainment of great size and weight which appears to have been the determining factor in the conservatism of the skeleton. After the skeleton had become fully adjusted to the mechanical necessities imposed by immense weight, and that adjustment, as we have seen, was effected at a comparatively early period in the history of the order, then no further modification of importance would seem to have been called for. No doubt the habits and mode of life of these massive, sedate and slow-moving animals underwent but little change from the lower Oligocene onward. There is reason to think that †*Mœritherium* was semi-aquatic and a haunter of marshes and streams, but, if so, the change to a life on dry ground was complete in the lower Oligocene, for the structure of †*Palæomastodon* gives no reason for supposing that it was anything but a dweller on solid land and a denizen of forests.

Although this book does not undertake to deal with the obscure problems connected with the marine mammals, it may be noted in passing that one of these problems has been brought near to solution, if not actually solved, by the discoveries in Egypt and that is the question concerning the origin of the Sirenia. The order includes the existing Manatee or Sea-Cow (*Manatus*) of the coast of Florida, northeastern South America and western Africa, and the Dugong (*Halicore*) of the Indian Ocean. These are mammals which are adapted to a strictly marine habitat and are incapable of existence on land, having lost the hind limbs and converted the fore limbs into swimming paddles. Unlike the whales, porpoises and other Cetacea, the Sirenia are herbivorous and feed upon seaweed and eel-grass and the aquatic plants of large rivers. The Egyptian discoveries tend very strongly to the conclusion that the Sirenia and Proboscidea were both derived from a common stock and that the genus †*Mœritherium* was not very far removed from the probable ancestor from which both of the orders descended.

CHAPTER XI

HISTORY OF THE †AMBLYPODA AND †CONDYLARTHRA

These are two orders of hoofed animals which long ago vanished from the earth and no member of either is known to have survived later than the Eocene epoch; both were of great antiquity, dating back to the Paleocene, perhaps even to the Cretaceous. The last of the †Amblypoda are found in the lowest Uinta or highest Bridger, but they were relatively abundant in all the more ancient beds. The following table gives the more important American forms:

Order †AMBLYPODA. †Short-Footed Ungulates

Suborder †Taligrada

I. †Periptychidæ.
    †*Periptychus*, Paleoc.
II. †Pantolambdidæ.
    †*Pantolambda*, Paleoc.

Suborder †Pantodonta

III. †Coryphodontidæ.
    †*Coryphodon*, Wasatch and Wind River.

Suborder †Dinocerata

IV. †Uintatheriidæ.
    †*Bathyopsis*, Wind River. †*Elachoceras*, Bridger. †*Uintatherium*, do. †*Eobasileus*, do.

As is shown in the table, the suborder †Taligrada is entirely Paleocene in distribution, the †Pantodonta are lower Eocene and the †Dinocerata chiefly middle Eocene, though persisting into the upper. The †Dinocerata were the most striking and characteristic of Bridger mammals, and two or three phyla of them may be distinguished, though for our purposes this is hardly necessary, for these strange and bizarre creatures were all very much alike. From the commonest and best-known genus (†*Uintatherium*) they are called †uintatheres. They were large and ponderous animals, the veritable giants of their time, far exceeding any of their contemporaries. In appearance they were among the most fantastic of the many curious beasts which the fossils have revealed.

The skull carried three pairs of bony protuberances, or horn-like outgrowths; one pair on the nasal bones suggest by their shape and character that they formed the support of dermal horns like those of the paired-horn rhinoceroses (†*Diceratherium*) of the Oligocene and lower Miocene. (See p. 239.) The second pair, which were moderately high and thick prominences, almost cylindrical in shape and tapering but slightly to their bluntly rounded ends, were chiefly outgrowths of the maxillaries, or upper jaw-bones. From their shape, it is likely that these were not sheathed in horn, but were merely covered with skin, as were also the third pair, which arose from the parietals. These were massive, club-shaped prominences, eight or ten inches high and broadening to the free ends, a shape which makes it impossible to suppose that these were true horn-cores covered with horny sheaths. A high crest of bone, representing the occipital crest, enclosed the top and back of the cranium, connecting the posterior pair of "horns" and dying away in front of them. The top of the cranium had thus a deep, basin-like character, such as is to be found in no mammal outside of this suborder and was one of the most peculiar features of this extraordinary skull. The brain-cavity was absurdly small, the growth of the brain not having kept pace with that of the body; the cavity is hidden away in the postero-inferior portion of the skull, the immense thickness of the cranial walls being somewhat lightened by the formation of sinuses, but these were much less extensive and pervasive than in other very large, horned or tusk-bearing mammals, such as elephants, rhinoceroses, etc. Probably, as in the case of the †titanotheres and †entelodonts, this deficiency of brain-development was at least one of the factors which led to the early extinction of the group. The premaxillaries were slender and rod-like bones, which did not meet in the middle line and carried no teeth. The long and massive nasal bones and the position of the nasal opening show that these animals cannot have had a proboscis of any kind. The lower jaw was remarkable for the great bony flange which, in the males, descended on each side from the lower border, near the anterior end, and served to protect the great canine tusks from fracture.

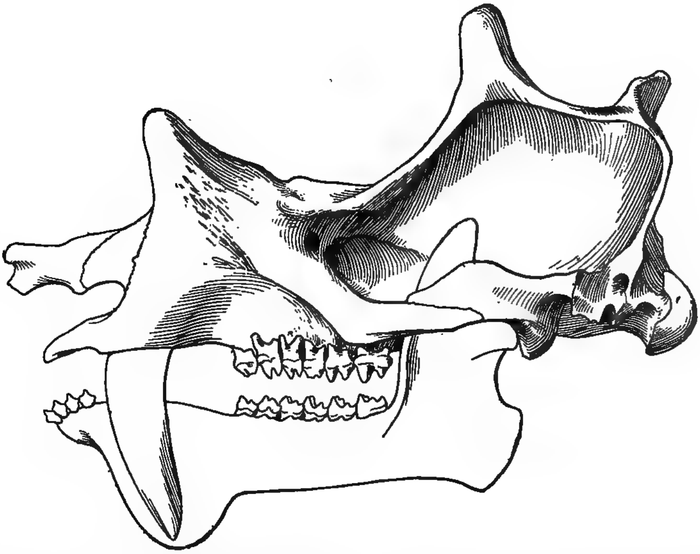

Fig. 230.—Skull of †uintathere (†*Uintatherium alticeps*), lower jaw supplied from another species. Princeton University Museum. For restoration, see Fig. 231, p. 447.

The female skull differed in two respects from that of the male: (1) the horn-like protuberances were much more slender and less prominent; (2) as the upper canine did not form a tusk, the lower jaw had no flanges. The skull of the artiodactyl †*Protoceras* (p. 406) was remarkably similar to that of the †uintatheres.

The dental formula was: $i\,\frac{0}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 34$. The upper incisors were completely lost and the lower ones had the very unusual peculiarity of being bilobate, or having the crown separated into two well-defined cusps. The upper canines in the males were very large, relatively thin, recurved and sabre-like tusks, with acute points and sharp edges, which must have been terrible weapons, though it is difficult to see how they were used; probably the mouth was widely opened, so as to clear the points of the tusks, and the animal then struck with them, as a snake does with its fangs. The lower canine was very small and was included in the incisor series, the shape and function of which it had assumed. Thus, the †uintatheres, with their toothless premaxillaries and, to all appearances, eight lower incisors, formed a curious parallel to the true ruminants (Pecora), and, as in the latter, they must have had a firm elastic pad on the premaxillaries, against which the lower incisors could effectively bite, when cropping the soft plants which formed the diet of these great beasts. The grinding teeth were low-crowned and surprisingly small in comparison with the size of the skull. The premolars and molars were nearly alike and had two or more transverse crests.

Aside from the altogether exceptional character of the skull, the skeleton was quite strikingly elephantine in appearance, so much so, in fact, that these animals have repeatedly been referred to the Proboscidea and some writers are still of the opinion that the two orders were related. There is, however, no sufficient ground for this view; the undeniable likenesses are much more probably to be ascribed to the operation of convergent development.

The neck was of moderate length, sufficiently long to enable the animal to reach the ground with the lips, a necessity in the absence of a proboscis. The body was very long and, as is shown by the length and curvature of the ribs and the great breadth of the hip-bones, extremely bulky. The limbs were very massive, and the long bones had lost the marrow-cavities, being filled with spongy bone, as in the elephants, †titanotheres

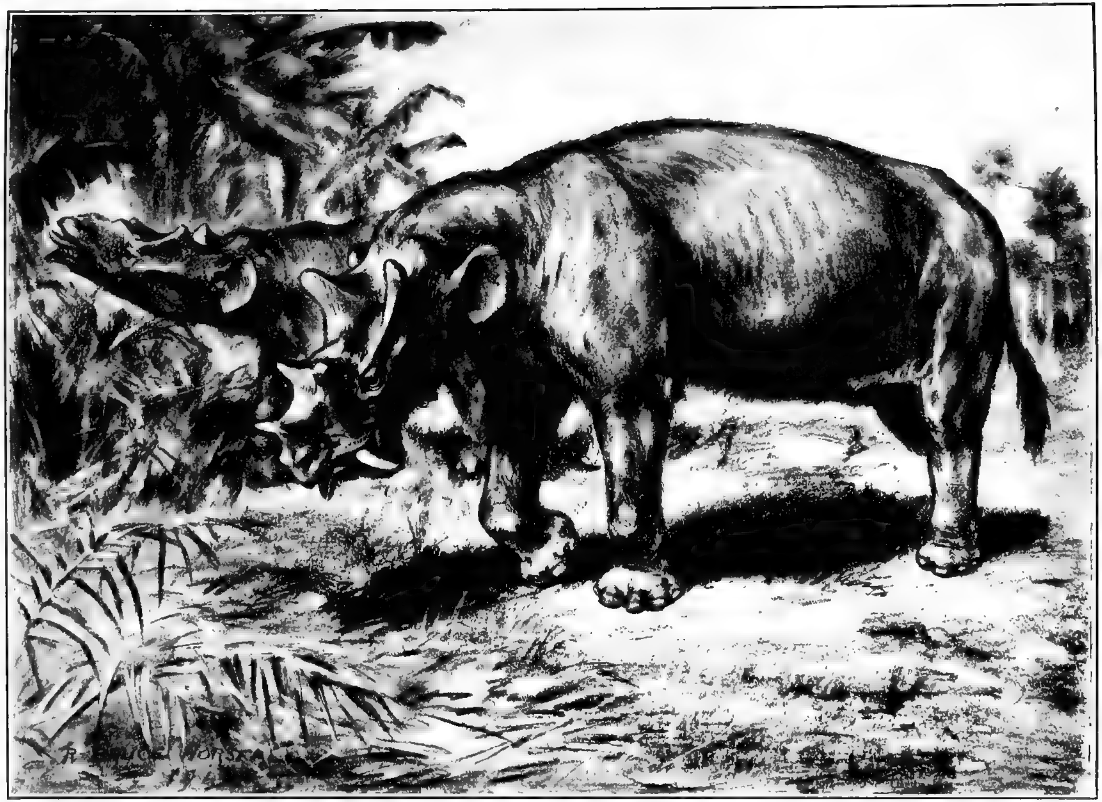

Fig. 231. — One of the elephantine †amblypods (†*Uintatherium alticeps*) of the Bridger stage. Male in foreground, female behind. Restored from specimens in the museums of Yale and Princeton universities.

and most other very heavy mammals. The bones of the forearm and lower leg were separate. The hip- and thigh-bones and shin-bones were remarkably elephantine in character and, if found isolated, might readily be referred to some unknown proboscidean, but the bones of the fore limb were quite different from those of the elephants. The feet likewise had a very proboscidean appearance, notwithstanding important and significant deviations in structure; they had the same shortness and massiveness and a similar reduction in the size of the hoofs, and the presence of all five digits added to the resemblance. Undoubtedly, the feet had the same columnar shape and arrangement of elastic pads. The living animal must have had an appearance quite similar to that of a rather small elephant, not exceeding six or seven feet in height at the shoulders and therefore not surpassing the largest modern rhinoceroses, the broad-lipped species of Africa (*Opsiceros simus*). Of course, the head must be excepted from the comparison, as that was totally unlike the head of any existing creature; with its long and narrow shape, its fantastic protuberances and its lack of a proboscis, it had no suggestion of likeness to any proboscidean. Whether the great body was naked, or clothed with hair, it is of course impossible to determine with confidence, but, all things considered, it seems unlikely that the hair should have been completely lost in any terrestrial mammal at so early a period. As we have seen in the preceding chapters, hairy elephants and rhinoceroses continued into and through the Pleistocene, not only in the cold regions of the north, as is shown by the hair of the American †Mastodon. In the tropics conditions were different, and in that uniformly warm climate the loss of hair by the very large mammals probably took place long before the Pleistocene. At all events, it is a significant fact that no hairless land mammals are now known in any region which has severe winters. It is true that the middle Eocene climate over most of North America was warm-temperate or subtropical, and the †uintatheres may, in consequence, have been hairless, but there is no evidence of this.

Within the limits of the †uintathere family, considerable modification and change may be traced, which, as in the case of the Proboscidea, principally affected the skull and the general stature. It is hardly worth while to deal separately with the two or more phyla which may be distinguished, for the differences between them are relatively unimportant. In the uppermost part of the Bridger stage almost the latest representatives of the family are found and the genus (†*Eobasileus*) was of the largest size. These animals had remarkably long and narrow heads and very large, shovel-shaped nasal protuberances; in the males the upper canine tusks were very long and curved back nearly in a semicircle. In the middle portion of the stage the species of †*Uintatherium* were somewhat smaller and had shorter, wider and higher heads, the tusks, though well developed, were not quite so long, nor so strongly recurved; in some species they were nearly straight, with "hastate" or spear-head point. In the same horizon is found a third genus (†*Elachoceras*) which was probably a survival persisting from the lower Bridger, in which none of these animals and little of anything else has yet been found. †*Elachoceras* was hardly half as large as the common species of †*Uinta-*

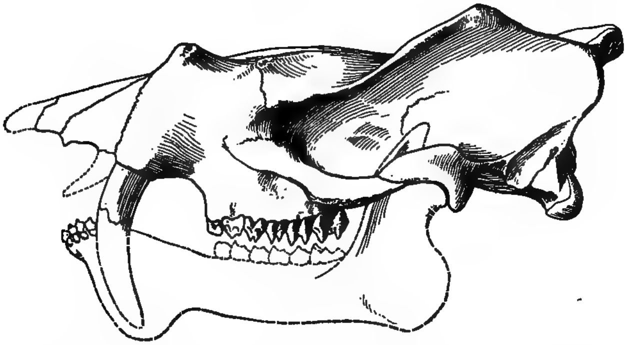

FIG. 232. — Skull of †*Elachoceras parvum* (lower jaw restored). Princeton University Museum.

therium and its skull might be described as a preliminary sketch for that of the latter; the nasal horns were extremely small, or, more probably, entirely absent; the median pair were mere low knobs, hardly an inch in height, and the posterior pair were simply thickenings of the crest which enclosed the top of the cranium on three sides, scarcely rising above it. This crest itself was much less prominent than in †*Uintatherium* and the basin-like top of the skull, in consequence, very much shallower. The upper incisors and the first premolar had already been lost and the upper canine enlarged into a sabre-like tusk, which, however, was relatively smaller than in the succeeding genera. The grinding teeth were quite the same as in the latter. Unfortunately, the skull of †*Elachoceras* is the only part of the animal which is known, but, so far as that is concerned, it is precisely what we should expect the forerunner of †*Uintatherium* to be; an ancestor made to order could hardly be more diagrammatic. It might, of course, be objected that no such relation as that of ancestor and descendant could obtain between these two genera, because they were contemporaries, but the case is like that of the ancestral elephants described in the preceding chapter. †*Mœritherium* and †*Palæomastodon* are found together in the Egyptian Oligocene, the former surviving for a considerable time after it had given rise to the latter, and in the upper Eocene only †*Mœritherium* occurs. Many similar instances might be given, just as grandfathers often live long with their grandchildren.

In the Wind River stage, or upper division of the lower Eocene, lived the still incompletely known †*Bathyopsis*, of which, however, sufficient material has been obtained to show that it was much less specialized than any of the Bridger genera. This genus comprised animals much smaller than its successor, †*Elachoceras* of the middle Eocene, being smaller than a tapir; it stood in much the same relation to †*Elachoceras* as the latter did to †*Uintatherium*. In the American Museum of Natural

History is a highly interesting skull of †*Bathyopsis,* which will shortly be described by Professor Osborn. The premaxillaries have not been preserved, and it is therefore impossible to say whether the upper incisors had already been suppressed or not, and though the upper canine has not been found, there can be no reasonable doubt that it was a tusk. The lower canine had not yet gone over to the incisor series, but was a thin though large tusk. There was one more lower premolar, four in all, than †*Uintatherium* possessed, and all the premolars were somewhat smaller and simpler than the molars. The small skull had a broad and somewhat concave cranial roof, with slightly raised enclosing crest, and the horn-like protuberances of the posterior and median pairs were present in an incipient stage. Whether those of the nasal pair were also indicated is not known, but probably they were not. The lower jaw was of very peculiar shape; the flange of the inferior border was not so well defined as in †*Uintatherium,* but had no hinder margin and rose very gradually backward.

The series of genera in descending order, †*Eobasileus,* †*Uintatherium,* †*Elachoceras* and †*Bathyopsis,* immediately impresses the observer as being a natural phylogenetic series of successive ancestors and descendants. Unfortunately, only the skull is known in the two last named, but there is no ground for supposing that the discovery of the skeletons would require any alteration in the series as we now have it. No member of this series has yet been found in the Wasatch, but there can be no doubt that it was represented in that stage, for a recent expedition from the American Museum has collected teeth of a †*Bathyopsis*-like form in still older beds.

SUBORDER †PANTODONTA

During the older part of the lower Eocene the †uintatheres must have been a rare and unimportant element of the fauna, at least in those parts of the continent whose history we know. Their place was taken by another suborder, the †Pantodonta, which was not ancestral to them, but collaterally related and descended from a common ancestry. The largest and most dominating of Wasatch mammals was the genus †*Coryphodon*, which also occurred in the lower Eocene of Europe, and the species of which ranged in stature from a tapir to an ox, though of much heavier form than the latter. The latest surviving species lived in the Wind River stage as a contemporary of †*Bathyopsis*, but then the suborder gave way to the †uintatheres.

In †*Coryphodon* (see Fig. 142, p. 279) the number of teeth was unreduced, a fact which is recorded in the name of the suborder, the dental formula typical of all the primitive ungulates being applicable to the genus. This formula was: $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 44$. The upper incisors were rather small, but functional, and the canines of both jaws were formidable tusks, though not rivalling in size the great sabres of the †uintatheres; the premolars had a simpler structure than the molars, which resembled those of the †uintatheres in a general way, but not closely. The skull differed greatly from that of the †uintatheres in having no horn-like protuberances, and was relatively large and heavy, the cranium having a broad, flat roof and no sagittal crest, and the lower jaw had no descending flange from the inferior border; in every way this skull was more normal and less bizarre-looking. The neck was proportionately longer than in the †uintatheres, the body long and the tail of medium length; the trunk-vertebræ had surprisingly small and weak spines, perhaps an indication of aquatic habits. The limbs were quite short and very heavy, and the bones, in comparison with those of the †uintatheres, were less proboscidean and more perissodactyl in character. For example, the femur retained the third trochanter and the long bones had marrow-cavities. The feet, on the contrary, were very like those of the †uintatheres, being extremely short and five-toed and with reduced, nodular hoof-bones; even in the details of the wrist and ankle joints there was no important difference between the two groups.

SUBORDER †TALIGRADA

None of the ungulate series considered in the foregoing chapters can be traced back to a time earlier than the Wasatch, and many of them not so far, but in the case of the †Amblypoda the line may be carried down through the Paleocene. In the upper stage of that epoch (Torrejon) the order was represented by †*Pantolambda* (Fig. 143, p. 285), a member of the third suborder, †Taligrada. The best-known species of the genus was an animal with head and body somewhat smaller than those of a sheep and much shorter legs. The teeth were present in unreduced number, 44 in all; the canines were tusk-like, but very much smaller proportionately than those of †*Coryphodon;* the premolars were smaller and simpler than the molars, which closely represent the common starting point, whence the curious tooth-patterns found in the subsequent genera of the various families were derived. The skull was long and narrow and had a prominent sagittal crest; the neck was of ordinary length, about equal to that of the head; the body was long and the tail very long, much as in the great cats. The hip-bones were narrow and slender and not bent outward, having no such breadth as in †*Coryphodon.* The limbs were short and relatively heavy, and the various bones were of such primitive character that, if found isolated and not in association with teeth or foot-bones, one would hardly venture to consider them as belonging to any hoofed animal; the humerus had a very prominent deltoid crest and an epicondylar foramen, and the femur had the third trochanter. The five-toed feet were very short, and the digits were arranged in a spreading manner and were relatively much more slender than in †*Coryphodon.* Each digit terminated in a flat, pointed, well-developed hoof; evidently there was no elastic pad to bear the weight, such as recurs in nearly all very heavy ungulates. The gait of the animal was probably semi-plantigrade, the hoofs being the principal points of support.

While †*Pantolambda* was an undoubted ungulate and a member of the †Amblypoda, there were many structural features in its skeleton which point to a relationship with the primitive flesh-eaters. In the lower stage of the Paleocene, the Puerco, the genus †*Periptychus* would seem to be the most ancient known member of the order, but it is still very imperfectly understood.

In the mode of evolution of the †Amblypoda, so far as that is recorded by the fossils, there is much to recall the development of the Proboscidea, though the story began and ended at far earlier dates and may be traced back to a much more primitive stage.

(1) There was a rapid increase of stature, especially of bulk, in the †coryphodonts, but decidedly more gradual in the †uintatheres, which eventually attained a far larger size.

(2) The upper incisors were suppressed and the canines grew into formidable tusks, at first straight, then the superior one, enlarging still farther, acquired a curved, scimitar-like shape, while the inferior one dwindled and became functionally one of the incisors.

(3) The grinding teeth remained low-crowned throughout, but acquired a more complex pattern, and the premolars became almost like the molars.

(4) The skull underwent a most remarkable transformation. Beginning with a form that might have belonged to almost any of the ancient mammals, hoofed or clawed, having very prominent sagittal and occipital crests, long cranium and short face, it became in †*Coryphodon* flat-roofed, with moderately elongated face, while in the †uintatheres the top of the cranium gradually took on a deeply concave basin-shape and, with equal gradualness, three pairs of horn-like protuberances; the lower jaw developed a great bony flange for the protection of the upper tusks. These peculiarities grew more and more

exaggerated and were most striking in the terminal genus of the series, †*Eobasileus.*

(4) Unfortunately, nothing is yet known of the skeleton of †*Bathyopsis* and †*Elachoceras,* so that it is not practicable to follow out all the stages of skeletal modification, though the general course of development is sufficiently plain. The neck did not change greatly, except to become very strong and heavy and to grow shorter proportionately as the skull was lengthened. The body remained long throughout the series, but gained greatly in bulk, as the stature of the animal increased.

(5) The limb-bones lost their primitive character, such as the epicondylar foramen of the humerus and the third trochanter of the femur, and then, with the great increase of the weight to be supported, the marrow-cavities were filled with spongy bone and the hip-bones increased enormously in width; the femur lost its cylindrical shape and was flattened antero-posteriorly, which gave it a very elephantine appearance. None of the limb-bones was suppressed or greatly reduced in size, nor was there any coössification between them.

(6) The feet early gained their definitive character; at no time was there any loss of digits, but the originally divided toes were, in the genera of the Wasatch and subsequent stages, united into the columnar foot, and the hoofs were reduced from their primitively pointed shape to nodular form.

As in the Proboscidea, therefore, there was comparatively little change in the skeleton after the massive and bulky proportions had been acquired, but great and continual modification of the skull. At the time when the †Amblypoda finally disappeared, no ungulate had acquired the hypsodont dentition. Had the group survived till the middle Miocene, a time when the spread of grassy plains so profoundly affected the feeding habits of many herbivorous mammals, the high-crowned teeth might have been developed in them also, and this, in turn, would have produced other changes in the skull, making closer the parallel with the Proboscidea.

In conclusion, a few words may be said concerning the geographical distribution of the †Amblypoda. In the Paleocene the only known representatives of the order were those of North America, but the †coryphodonts of the lower Eocene migrated to the Old World; indeed, the genus †*Coryphodon* was first described and named from English specimens, but there were no such abundance and variety of these animals in Europe as there were in the western United States. The †uintatheres were strictly North American in distribution and no member of the suborder has ever been found outside of this continent. Animals referred to the †Amblypoda by some authorities have been obtained in the Oligocene and Miocene of South America, but the assignment has been made upon insufficient evidence. (See p. 508.)

ORDER †CONDYLARTHRA

The †Condylarthra were a group of exceedingly primitive ungulates, which served to connect the hoofed and clawed mammals in quite an intimate manner. So few indeed were the distinctively ungulate characters which they had acquired, that it is still premature to make any positive statements regarding their geographical distribution, because unusually well-preserved specimens are required to make sure of their presence in any particular region. Concerning North America there is no room for question, and there is hardly any doubt that they existed in the Paleocene of Europe. The South American remains which have been referred to this order may very well prove eventually to belong to it properly, but until both feet and skulls have been obtained in unequivocal association, the reference can be only tentative. In North America they ranged through the Paleocene and lower Eocene, but are not known from any subsequent formation, and even in the Wind River only a few stragglers survived.

The principal American families and genera are as follows:

I. †MENISCOTHERIIDÆ.
  †*Meniscotherium*, Wasatch and Wind River.
II. †PHENACODONTIDÆ.
  †*Protogonodon*, Puerco. †*Euprotogonia*, Torrejon. †*Phenacodus*, Wasatch and Wind River.

1. †*Phenacodontidæ*

The typical Wasatch genus †*Phenacodus*, which is very fully known from nearly complete skeletons, included species which varied in size from a fox to a small sheep; the same genus occurred in the Wind River, but not later. †*Phenacodus* had the unreduced dental formula: $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 44$.

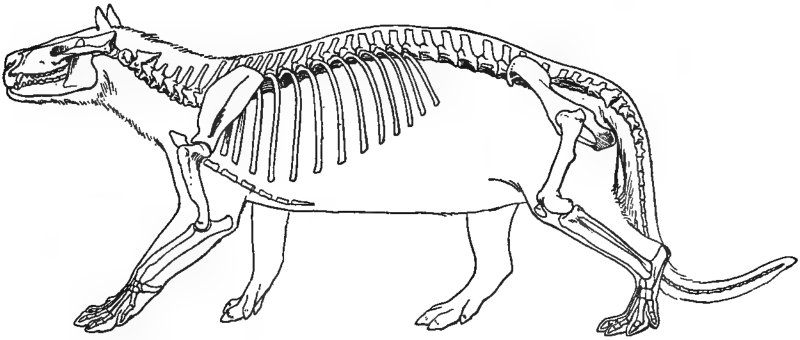

FIG. 233.—Skeleton of the Wasatch †condylarth, †*Phenacodus primævus*. American Museum. For restoration, see Fig. 141, p. 278.

The incisors were small and simple, the canines tusk-like, but of no very great size, the premolars smaller and simpler than the molars. The latter were of the quadrituberculate pattern, of four simple, conical cusps arranged in two pairs, a pattern which is common to the earlier and less specialized members of many ungulate groups. The skull was long, narrow and low, with long and well-defined sagittal crest. As in primitive skulls generally, the cranial region was long and the face short, the eyes being very far forward; this does not imply large brain-capacity, indeed, the brain was very small, but merely that the portion of the skull behind the eyes was relatively long. The jaws were short and shallow, in accordance with the small and low-crowned teeth which they carried. The neck was of medium length, but the body was elongate and the tail was very long and stout. The hip-bones were narrow and slender, as in primitive ungulates generally. The limbs were short and stout and retained many very primitive characteristics. The humerus had a prominent deltoid crest and an epicondylar foramen; the fore-arm bones were separate and the ulna quite unreduced, being almost as stout as the radius. The femur had the third trochanter and the leg-bones were distinct, though the fibula was slender. The feet, which were short, had five digits each, but the third toe was enlarged, while the first and fifth were shortened, as though preparing to disappear and thus give rise to a three-toed perissodactyl foot. The ankle-bone (astragalus) had a rounded, convex lower end, fitting into the navicular, so that it might readily be taken for that of a clawed mammal.

2. †*Meniscotheriidæ*

A second family of Condylarthra was represented in the lower Eocene by the genus †*Meniscotherium* and was in some respects considerably more advanced than the †phenacodonts. These were small animals, in which the molars had acquired a crescentic pattern, recalling that seen in the early horses and in the †titanotheres and †chalicotheres, and other perissodactyl families. In the upper molars the two external cusps had been so extended as to form a continuous outer wall, each of the cusps having a concave external face and the two uniting in a prominent median ridge. The lower molars had two crescents, one behind the other, as in several families of both perissodactyls and artiodactyls. The body and tail were long, the limbs relatively longer and lighter than those of †*Phenacodus* and the five-toed feet were so like those of the modern conies, or klipdasses, of Africa and Asia Minor, that by some investigators the family has been referred to the same order, the Hyracoidea, but the suggestion is not a probable one. It is much more likely that these problematical little †meniscotheres were merely a short-lived branch of the †Condylarthra.

The †condylarths were quite abundantly represented in the Paleocene, where the genus †*Euprotogonia* was the forerunner of the Wasatch †*Phenacodus*, but had an even more primitive type of dentition. The upper molars were not quadritubercular, but tritubercular, the three cusps arranged in a triangle, the two outer ones forming the base and the single inner one the apex. This type of upper molar was, or is still, common to the primitive and unspecialized members of a great many mammalian orders, marsupials, insectivores, rodents, carnivores, lemurs, artiodactyls, etc., and there is strong reason to believe that the tritubercular molar was the common starting point for almost all types of mammalian dentition. However that may be, †*Euprotogonia* is of great interest as materially helping to close the gap between the clawed and the hoofed mammals, belonging, as it did, to the latter and yet

FIG. 234. — Lower Eocene †condylarth, †*Meniscotherium terræ-rubræ*. Restored from a skeleton in the American Museum.

retaining in dentition, limbs and feet so many characteristics of the former.

†Condylarthra were probably present in the lowest Paleocene (Puerco stage), but the material so far obtained is so fragmentary that there can be no certainty on this point.

It is not at all probable that any of the North American †Condylarthra should be regarded as ancestral to any of the more advanced ungulate groups; on the contrary, they would appear to have come to an end in the Wind River, leaving no descendants behind them. It is further true, as was mentioned above, that the presence of †Condylarthra in other continents, while very probable, cannot be positively asserted, because the evidence is incomplete. Yet it would be a great mistake to assume, for this reason, that these most primitive of ungulates were devoid of evolutionary importance and interest. As is so often the case, where, in the absence of the direct ancestry, the collateral relations afford very valuable information as to the course of descent and modification, the †Condylarthra throw useful light upon the origin of the ungulate groups. It is extremely probable that the †condylarths, or some very similar series of primitive hoofed mammals, had a very wide and perhaps cosmopolitan range at the end of the Cretaceous and beginning of the Tertiary period, and that, in the still unidentified region, where the artiodactyls and perissodactyls arose, it was from a condylarthrous ancestry. Possibly, all the other ungulate orders may yet be traced back to the same stock, but it is rather more likely that the ungulates include several series of quite independent origin. At all events, it is quite certain that the clawed mammals long antedated the hoofed types and that the latter arose, either once or at several separate times, from the former. The †Condylarthra show how one, at least, of these transitions was effected, and thus, in principle, how all were accomplished.

CHAPTER XII

HISTORY OF THE †TOXODONTIA (OR †NOTOUNGULATA)

It is a regrettable circumstance that, while the successive Tertiary faunas are very fully represented in South America, approximately complete skeletons have, as yet, been obtained from only a few of the various stages; from the others the known material is very fragmentary and largely made up of teeth and jaws. No doubt, the history of fossil-collecting in North America will, in due course of time, be repeated in the southern continent and more and more complete and satisfactory specimens be obtained. At present, however, it is not possible to trace the modifications of structure in any given series with such detail as in those which were developed within the limits of Arctogæa. No such story as that of the horses, the rhinoceroses or the camels, can yet be told of the South American groups, whatever future exploration may teach us. Nevertheless, much has already been learned concerning the strange creatures that once inhabited the Neotropical region and long ago vanished completely, leaving no trace in the modern world.

As was mentioned in Chapter VI, on the present geographical distribution of mammals, South America is to-day the richest and, after Australia, the most peculiar zoölogically of all the regions. All of the modern hoofed animals found in that continent at present, the tapirs, peccaries, llamas and deer, are immigrants derived at a comparatively late date from the north, but throughout the Tertiary and the Pleistocene there were several indigenous types of ungulates, and of these the largest and most varied assemblage was that included in the order †Toxodontia. The most important and best known of the families and genera are listed in the table:

Suborder †TOXODONTA. †Toxodonts Proper

I. †TOXODONTIDÆ.
  †*Toxodon*, up. Plio. and Pamp. †*Xotodon*, do. †*Trigodon*, Monte Hermoso. †*Nesodon*, Santa Cruz. †*Adinotherium*, do. †*Pronesodon*, Deseado. †*Proadinotherium*, do.
II. †NOTOHIPPIDÆ.
  †*Notohippus*, Patagonian. †*Rhynchippus*, Deseado. †*Morphippus*, do.
III. †LEONTINIIDÆ.
  †*Leontinia*, Deseado. †*Colpodon*, Patagonian.

Suborder †TYPOTHERIA. †Typotheres

I. †TYPOTHERIIDÆ.
  †*Typotherium*, Plioc. and Pleist.. †*Eutrachytherus*, Deseado.
II. †INTERATHERIIDÆ.
  †*Interatherium*, Santa Cruz. †*Protypotherium*, do.
III. †HEGETOTHERIIDÆ.
  †*Hegetotherium*, Santa Cruz. †*Pachyrukhos*, Santa Cruz to Pampean.
IV. †NOTOPITHECIDÆ.
  †*Notopithecus*, Casa Mayor. †*Adpithecus*, do.
V. †ARCHÆOPITHECIDÆ.
  †*Henricosbornia*, Casa Mayor.
VI. †ARCHÆOHYRACIDÆ.
  †*Archæohyrax*, Deseado.

Suborder †ENTELONYCHIA. †Homalodotheres

I. †NOTOSTYLOPIDÆ.
  †*Notostylops*, Casa Mayor.
II. †ISOTEMNIDÆ.
  †*Isotemnus*, Casa Mayor. †*Pleurocœlodon*, Deseado.
III. †HOMALODONTOTHERIIDÆ.
  †*Homalodontotherium*, Santa Cruz. †*Asmodeus*, Deseado. †*Proasmodeus*, Astraponotus Beds. †*Thomashuxleya*, Casa Mayor.

Suborder †PYROTHERIA. †Pyrotheres

†PYROTHERIIDAE.
  †*Pyrotherium*, Deseado. †*Propyrotherium*, Astraponotus Beds. †*Carolozittellia*, Casa Mayor. †*Paulogervaisia*, do.

SUBORDER †TOXODONTA. †TOXODONTS PROPER

Among the remarkable animals which Charles Darwin found in the Pampean deposits of Argentina and took with him to England, was a skull of one which Sir Richard Owen named †*Toxodon*, or "Bow-Tooth," from the strongly curved grinding teeth, those of the opposite sides almost meeting in the median line above the hard palate. For many years †*Toxodon*, of which hardly anything was known, save the skull and teeth, was a zoölogical puzzle and no one was able to reach any satisfactory conclusion as to its systematic position and relationships, as all the attempts made to force it into one of the known ungulate groups were obvious failures. The discovery of complete skeletons, two of which are mounted in the La Plata Museum, showed the necessity of making a new group for its reception, as Owen had originally proposed. Through the exploration of Argentina and its Patagonian provinces, the history of the suborder was followed far back into the Tertiary period and its indigenous character demonstrated. This and all the other subdivisions of the †Toxodontia were exclusively Neotropical in distribution, and none have been found farther north than Nicaragua and there only in the Pleistocene.

The suborder was represented in the Pampean beds by several genera, which differed in size and in the complexity of the grinding teeth, but only of †*Toxodon* is the skeleton at all fully known. The Pampean species of this genus were massive, elephantine creatures, rivalling the largest rhinoceroses in bulk, but not equalling them in height. The teeth were all thoroughly hypsodont and apparently continued to grow throughout life without forming roots; the dental formula was: $i\,\frac{2}{3}$, $c\,\frac{0}{0}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 34$. The first upper incisor was broad and chisel-shaped, the second more tusk-like, but in some species these proportions were reversed; the lower incisors were procumbent, pointing straight forward, and of these the third was the largest. The canines were lost and there was a long, toothless gap behind the incisors. The premolars were smaller and simpler than the molars, and the anterior ones were very small and were frequently shed at an early stage, making the number of these teeth variable in different specimens. The upper molars also were of quite simple pattern; the broad and smooth external wall showed no distinct signs of a division into cusps, and from it arose two oblique transverse ridges; the deep cleft or valley which separated these ridges was divided and made Y-shaped on the grinding surface by a prominent spur from the outer wall between the two principal crests. The lower molars were composed of two crescents, one behind the other, of which the posterior one was very much longer, and both were very narrow transversely.

The skull had shortened nasal bones, an indication that some sort of a proboscis or prehensile upper lip was present. There was no trace of a horn, and the general aspect of the skull was not unlike that of one of the hornless rhinoceroses, except for its great vertical depth; the sagittal crest was very short and had almost disappeared. The auditory apparatus was very extraordinary, though it can hardly be described without an undue employment of anatomical terms; suffice it to say that in addition to the usual outer ear-chamber, formed by the inflated tympanic bone, there was a second chamber in the rear wall of the skull, communicating with the first by a canal. This arrangement would seem to imply an unusual keenness in the sense of hearing. The external entrance to the ear was placed very high up on the side of the head, as in the pigs and in many aquatic mammals, suggesting that †*Toxodon* was more or less amphibious. The anterior, or symphyseal, region of the lower jaw was very broad, flattened and shovel-like, hardly projecting at all below the plane of the lower incisors.

The neck was short and stout, the body long and extremely bulky, having an immense, almost hippopotamus-like girth; the spines of the anterior dorsal vertebræ were very long, making a high hump at the shoulders. The limbs were short and very heavy, the bones very massive and with large projections for muscular attachments. The fore leg was much shorter than the hind, depressing the neck and head in very curious fashion. The shoulder-blade was rather narrow, the spine without acromion or distinct metacromion; the hip-bones were greatly expanded and turned outward, quite in elephant-like fashion, a character which almost invariably accompanies great increase in bodily mass. The thigh-bone was also very elephantine in appearance, a likeness due to its shape and proportions, to the loss of the third trochanter and the flattening of the shaft, so that the width much exceeded the antero-posterior thickness. All of these characters are, as a rule, associated with greatly augmented weight and have been independently acquired in several series of large and massive animals, elephants, †uintatheres, †titanotheres, and to this list should be added the †toxodonts. In the fore-arm the bones were separate and the ulna was quite unreduced and very stout, but in the lower leg, which was very short in comparison with the thigh, the tibia and fibula were coössified at the upper end, but not at the lower, a most exceptional arrangement. The feet were surprisingly small and had but three digits, the reduction from the original five having proceeded to that extent before the process was arrested by augmenting weight. The heel-bone (calcaneum) was so articulated with the other bones of the tarsus as to project almost straight backward, nearly at a right angle to the position normal in a digitigrade foot, a feature which is not known to occur in any other mammal. The hoof-bones were so small and nodular that the foot must have been of the columnar type, the weight resting upon the usual elastic pad.

The restoration (Fig. 121, p. 217) shows †*Toxodon* as a very heavy, slow-moving, water-loving animal; the aquatic habits are, of course, conjectural, but the general proportions are accurately given by the skeleton.

From the Pleistocene, †*Toxodon* may be followed back without notable change to the Pliocene, but there it was in association with the last of a curious phylum, the genus †*Trigodon* (Fig. 138, p. 263), as yet known only from the skull. In these animals a very prominent bony knob or boss on the forehead clearly demonstrates the former presence of a large, rhinoceros-like, frontal horn. But very few of the indigenous South American ungulates possessed horns, or horn-like protuberances of the skull, and all of these so far discovered belonged to the suborder †Toxodonta. †*Trigodon* was, from present knowledge, the only horned creature of its time and region, for the deer and antelopes which had probably arrived in South America had not advanced so far south as Argentina. Another very peculiar feature of this genus was that the lower incisors were present in uneven number, two on each side and one in the middle. Nothing has been found of the skeleton, but it was doubtless that of a smaller and somewhat lighter †*Toxodon*.

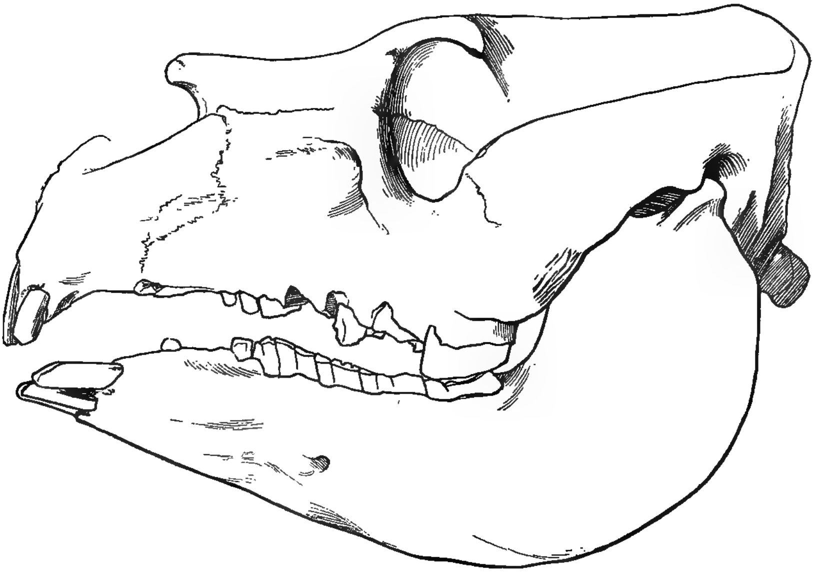

FIG. 235. — Skull of †*Toxodon*, Pampean formation, the upper molars much broken. La Plata Museum.

The material from the lower Pliocene adds nothing to our knowledge of the suborder, but in the Santa Cruz time of Patagonia, which was Miocene, it was very abundantly represented and preponderatingly by the genus †*Nesodon*, which was the first discovered member of the marvellous Santa Cruz fauna, named nearly 70 years ago by Sir Richard Owen. It so chanced that Owen's specimen was the imperfect lower jaw of a young animal with the milk-teeth, which were mistaken for the permanent dentition, and when the latter was found long afterwards, it was naturally supposed to belong to a different animal and received a different generic name. Nor was this all; the changes which took place in the appearance and relative size of the permanent teeth within the life-time of the individual were so remarkable, that the successive stages of development were by several investigators supposed to be distinct genera and species and named accordingly. In this way nearly 30 different names have, at one time or another, been assigned to the common species, †*N. imbricatus;* and it was not until the late Dr. Ameghino had brought together a complete series of skulls and jaws illustrating these changes, and showing the gradual transition from one to the other, that the confusion could be cleared up.

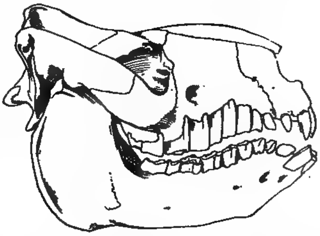

FIG. 236.—Skull of Santa Cruz †toxodont, †*Nesodon;* same scale of reduction as Fig. 235.

There was a long hiatus in time between †*Toxodon* and †*Nesodon* and so great was the structural difference between them, that there is much doubt whether the latter was directly ancestral to the former; in any event, †*Nesodon* so nearly represents what the desired ancestor must have been, as to serve for all practical purposes of the study.

All the species of this Santa Cruz genus were much smaller animals than the species of †*Toxodon*, †*N. imbricatus* being no longer than a tapir, with considerably shorter legs, and of much slighter and more slender build than †*Toxodon*, though every tooth and every bone proclaims its relationship to the latter.

In †*Nesodon* the dental formula was unreduced; $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times\ 2 = 44$, though several of the teeth were much reduced in size, so as to have lost their functional importance, and frequently individuals are found in which one or more of these insignificant teeth are lacking. The first upper incisor was a broad, chisel-shaped tooth, which continued to grow for a period, then formed its root, and growth ceased; the second incisor was a pointed, triangular tusk, which grew throughout life, becoming longer with advancing age; while the third, which was lost in †*Toxodon*, was small and unimportant. In the lower jaw the first and second incisors were chisel-like and had a limited growth; being rather narrow, they both bit against the broad first upper incisor; the third incisor was a persistently growing tusk, not so large as the upper one, against the posterior face of which it impinged and was obliquely truncated by wear, so that its length was limited, while the upper tusk continued to elongate and was made narrower and sharper by wear. All the lower incisors were far less procumbent than in †*Toxodon*, and were directed obliquely upward and forward. The remarkable changes of appearance which, as mentioned above, took place within the life-time of the individual, were largely due to the differential growth of the incisors. The milk-incisors were all nearly alike and formed no tusks; when the permanent incisors were first protruded, the first upper and the first and second lower were large and the tusks were not visible, and, when the latter did appear, they were for some time smaller than the other incisors. These, however, formed roots and ceased to grow, actually becoming smaller with advancing age, for the crowns narrowed to the roots and, the more they were worn down, the smaller they became. The tusks, on the other hand, grew throughout life and became larger as the other incisors were reduced by wear, and thus the whole appearance of the anterior part of the jaw was totally changed.

This mode of forming the tusks by the enlargement of the second upper and third lower incisor is an unusual one, though it was repeated in another South American ungulate order, the †Litopterna, and nearly so in the Proboscidea, in which both upper and lower tusks were the second of the three original incisors.

In both jaws, the canines of †*Nesodon* were insignificant and sometimes absent. The premolars, which were smaller and simpler than the molars, had quite high crowns, but early ceased to grow and formed long roots. The molars were truly hypsodont and formed no roots till late in life; they were constructed on the same plan as those of †*Toxodon*, but were decidedly more complex, the upper ones having several spurs and crests given off inward from the external wall, in addition to the two principal transverse crests, and they had a certain superficial likeness to the teeth of a rhinoceros. As in †*Toxodon*, these upper molars were curved inward, so as almost to meet those of the opposite side above the palate. The lower molars had the same bicrescentic plan as in †*Toxodon*, but were more complicated, and in the concavity of the hinder crescent was a vertical pillar, which was well-nigh universal among the indigenous South American ungulates.

If †*Nesodon* was really the ancestor of †*Toxodon*, then the development of the grinding teeth must have been a process of completing the hypsodontism, until the teeth grew persistently, never forming roots, and, at the same time, of simplifying the pattern. This is contrary to the usual course of evolution, in which the pattern grew more complex in the successive stages; but such steadily increasing complexity was not invariable, and several instances of undoubted simplification are known among mammals, though not yet in other ungulates. Only the recovery of the intermediate genera will enable us to determine whether †*Nesodon* was the actual ancestor of

FIG. 237. — †*Nesodon imbricatus*, Santa Cruz stage. Restored by C. Knight from a skeleton in the museum of Princeton University.

†*Toxodon,* or whether it was merely one of a short-lived branch from the main stem, in which the teeth had acquired an unusual degree of complexity.

A few years ago Dr. Ameghino announced the very surprising discovery that, instead of having merely the normal arrangement of two dentitions, the milk and the permanent, †*Nesodon* developed three successive dentitions, one preceding the milk-series, and therefore called *pre-lacteal.* In certain other mammals traces of a pre-lacteal series had already been found, in the shape of tooth-germs, which never attain full development or even cut the gum; and quite recently Dr. Ameghino has shown that in the tapir at least one functional pre-lacteal premolar is formed. The significance of this fully developed pre-lacteal dentition in †*Nesodon* is not yet clear, though it seems reasonable to suppose that it was the almost uniquely late retention of a primitive character.

The skull was closely similar to that of †*Toxodon,* on a smaller scale, but there were several minor differences, which were, in part, conditioned by the larger and much more completely hypsodont teeth of the Pampean genus, as well as by its generally increased size and bulk. In †*Nesodon* the sagittal and occipital crests were much more prominent and the former was much longer, while the thickening of the cranial bones was in only an incipient stage. The nasal bones were considerably longer. The jaws were lower and shallower, in correlation with the less perfectly hypsodont teeth, and in the lower jaw the chin was much more erect and rounded. The entire head of this curious Santa Cruz animal had something remarkably rodent-like in its appearance, though it is quite inadmissible to suppose that the likeness was due to relationship.

The skeleton was far smaller and lighter and otherwise differently proportioned from that of †*Toxodon,* but there was, nevertheless, a close agreement between the two genera. The neck was of moderate length and thickness, the body long and heavy, but with no such relative bulk as in the Pampean genus. The hump at the shoulders, as indicated by the spines of the anterior dorsal vertebræ, though already well defined, was less prominent. The shoulder-blade (scapula) was relatively broader than in †*Toxodon,* its spine had a distinct acromion and two very long and conspicuous processes given off backward from the spine, only one of which, and that a mere vestige, is indicated in †*Toxodon.* The hip-bones were almost parallel with the backbone and were not nearly so broad or so everted as in the latter, a difference which is amply accounted for by the great discrepancy in girth.

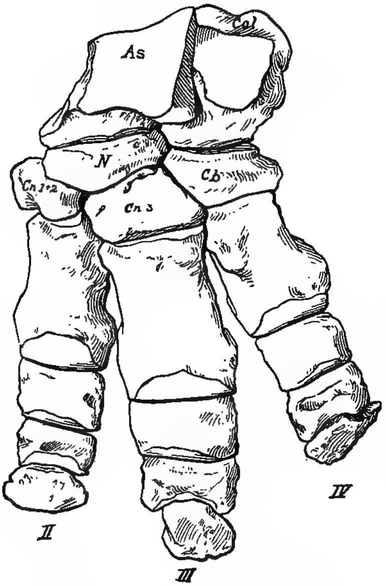

Fig. 238. — Left pes of †*Toxodon.* La Plata Museum. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn. 1* and *2*, coössified internal and middle cuneiforms. *Cn. 3*, external cuneiform. *Cb.*, cuboid.

The limbs were of nearly equal length and there was no such shortening of the fore-arm or elongation of the thigh as in †*Toxodon,* and so the descent of the backbone forward, which gave such grotesqueness to the skeleton of the latter, was far less pronounced. The limb-bones were rather slender, in size and proportions not unlike those of a tapir, but in structure very like the very much larger and more massive ones of †*Toxodon.* The bones of the fore-arm were separate, but those of the lower leg were coössified in the same exceptional manner as in the Pampean genus, that is, the upper ends, but not the lower, were fused together. The thigh-bone was not flattened, but had the normal cylindrical shaft and a conspicuous third trochanter. The feet, in which the digits were already reduced to three, were extremely small in comparison with the size of the animal; in structure, they were almost identical with those of †*Toxodon*, but were far narrower and more slender. The heel-bone (calcaneum) articulated with the other bones of the tarsus in a normal manner. The digits were well separated and the hoof-bones quite strongly developed, indicating that the hoofs were functional, supporting most of the weight. In short, the difference in the external appearance of the feet between the two genera was much the same as between the tapirs and rhinoceroses.

The species of †*Nesodon*, of which many have been named on very questionable grounds, differed but little in size and were of such variable and fluctuating character that a proper discrimination of them is exceedingly difficult. One of these species (†*N. cornutus*) gives indications of having possessed a small dermal horn on the forehead and was thus a possible ancestor of †*Trigodon*.

A second phylum of the suborder was represented in the Santa Cruz stage by the genus †*Adinotherium*, the species of which, not equalling a sheep in size, were very much smaller animals than those of †*Nesodon*, but closely like them in other respects. The dentition, including the pre-lacteal series, and the skull were almost identical in the two genera, with the exception that a large proportion of the individuals of †*Adinotherium* had the small frontal horn, while others had no trace of it. While it is quite possible that the presence or absence of the horn, which was always inconspicuous, may have been a matter of specific distinction, a more probable explanation is that it was a sexual character, the males horned and the females hornless. Much the same thing is to be observed in the modern Javan Rhinoceros (*R. sondaicus*) in

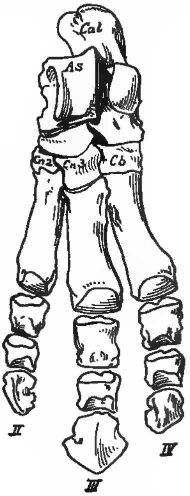

FIG. 239.—Left pes of †*Nesodon*, Princeton University Museum. Letters as in Fig. 238 and scale of reduction the same.

which the females have a very small horn, or none at all, and the males a large one.

In the skeleton also there were few differences, other than those of size, between †*Adinotherium* and †*Nesodon;* the former was not only smaller, but also lighter and more slender proportionately, and there was no hump at the shoulders, the spines of the dorsal and lumbar vertebræ all reaching the same level, so that the back must have been nearly straight in the living animal. From the more general and constant presence of the frontal horn, †*Adinotherium* was more probably the ancestor of the horned †*Trigodon* than was †*Nesodon,* but until the intermediate forms shall have been recovered, no definite decision can be made.

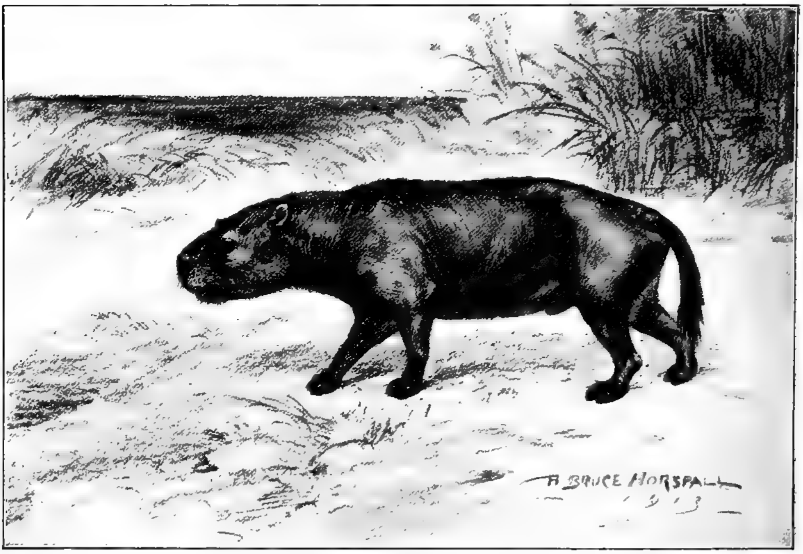

Fig. 240. — †*Adinotherium ovinum*, small, horned †toxodont of the Santa Cruz. Restored from a skeleton in the museum of Princeton University. — Note the minute horn on the forehead.

The same or very nearly the same genera of the family †Toxodontidæ lived in the Patagonian and Deseado stages, but there the record breaks off and can, for the present at least, be followed no farther. It remains to be determined whether the series originated in regions farther to the north, or whether the ancestral types will be found in Patagonia.

The other two families are still very incompletely known, but sufficiently to justify their inclusion in the present suborder. In the †Leontiniidæ, which are known only from the Deseado stage (†*Leontinia*), we have a curious variant of the †toxodont type. The tusks were decidedly smaller than in the Santa Cruz members of the preceding family, the grinding teeth with lower crowns and simpler structure. The skull was much like that of †*Nesodon*, but the anterior nasal opening was of quite a different shape, being carried much farther back on the sides, so that the nasal bones had a far longer portion which was freely projecting and unsupported; these bones were shorter and much thicker than in the Santa Cruz genera and, to all appearances, supported a small, median horn on their anterior ends. The feet, so far as they have been recovered, did not differ in any significant manner from those of the preceding family.

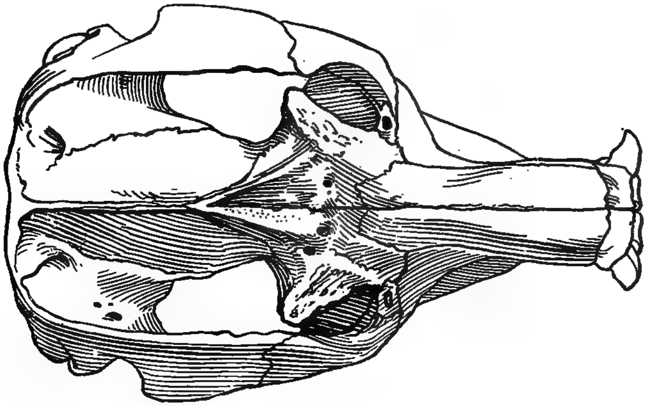

Fig. 241.—Skull of *Adinotherium*, top-view, showing the rugosity on the forehead for the small frontal horn.—Princeton University Museum.

Another imperfectly known family, that of the †Notohippidæ, occurred in the Patagonian stage, but was most abundant in the Deseado, where several genera of it have been found.

These animals had mostly hypsodont teeth, forming roots in old age, and the teeth were in closed series, but there was no tusk-like enlargement of the incisors. In the later genera, those of the Patagonian stage (†*Notohippus*, †*Argyrohippus*), the crowns of the grinding teeth had a thick covering of cement, and those of the lower jaw had some resemblance, though not at all a close one, to the teeth of horses. The skull also had a certain suggestion of likeness to the horses and Dr. Ameghino was persuaded that these animals were ancestors of the horses. The family went back to the Astraponotus stage, but can be traced no farther.

SUBORDER †TYPOTHERIA. †TYPOTHERES

This suborder was composed of much smaller animals than the †Toxodonta and contained no large forms; some, indeed, were exceedingly small, no larger than rabbits. It was much the most diversified of the suborders, as is made evident by the table of families and genera. Two of these families, the †Typotheriidæ and the †Hegetotheriidæ, continued into the older Pleistocene. Of the former there was the genus first named and described, †*Typotherium*, which has given its name to the family and suborder, and the species of which were much the largest of the entire group, almost equalling a large pig in size. At the first glance this genus might easily be mistaken for a large rodent, and indeed it has actually been referred to that order, but the resemblance was a purely superficial one and involved no relationship.

In †*Typotherium* the teeth were considerably reduced in number, the formula being: $i\,\frac{1}{2}$, $c\,\frac{0}{0}$, $p\,\frac{2}{1}$, $m\,\frac{3}{3}$, $\times 2 = 24$. The first incisor in each jaw was a broad, scalpriform, persistently growing tooth, which much resembled the corresponding tooth in the rodents, but was not, as it is in the latter, worn to a sharp chisel-edge by attrition, but was abruptly truncated. There was a second similar, but much smaller, tooth in the lower jaw; the other incisors and all the canines had been lost and the premolars reduced to two in the upper and one in the lower jaw. The molars were large, persistently growing and thoroughly hypsodont; in pattern they were very similar to those of †*Toxodon.* The skull without the lower jaw was low and the cranial portion broad and flattened, but retaining a long sagittal crest. The eye-sockets were nearly, but .not quite, closed behind by the very long and slender post-orbital processes of the frontal bones. In front of the eyes the face was suddenly constricted into a long, narrow rostrum, and it is this shape of the skull which, together with the persistently growing, scalpriform incisors, gave such a rodent-like appearance to the head. The auditory region had the same remarkable structure as in the †Toxodonta. The lower jaw had a short horizontal portion and very high vertical portion, which gave the head great vertical depth.

The skeleton, so far as it is known, was decidedly more primitive than that of the contemporary †*Toxodon,* as is shown by the presence of collar-bones (clavicles) and by the larger number of digits, five in the front foot and four in the hind. The hoof-bones, or ungual phalanges, were narrow, pointed and nail-like, though in the hind foot they were broader and more hoof-like.

Little can be done as yet in tracing back the history of this family, the Santa Cruz beds having yielded no member of it. In the Deseado stage, the genus †*Eutrachytherus* differed surprisingly little from †*Typotherium,* in view of the long hiatus in time between them. The Deseado genus already had thoroughly hypsodont and rootless teeth, and the molar pattern was quite the same as in †*Typotherium,* but the teeth were much more numerous, the formula being: $i\,\frac{3}{2},\ c\,\frac{1}{1},\ p\,\frac{4}{4},\ m\,\frac{3}{3},\ \times 2 = 42.$ Nothing is known of the skeleton. The family arose probably from one of the Eocene families (†Archæopithecidæ or †Acœlodidæ) with low-crowned teeth, but the connection cannot be made out. Presumably, the development of this family ran its chief course in some part of South America far to the north of the fossil-beds of Patagonia.

The second family which was represented in Pampean times was that of the †Hegetotheriidæ, and the sole genus of it which survived so late was †*Pachyrukhos*, a little creature no larger than a rabbit. The genus went back without any noteworthy change to the Santa Cruz stage of the Miocene, from which complete skeletons have been obtained. The dental formula was nearly as in †*Typotherium:* $i\,\frac{1}{2}$, $c\,\frac{0}{0}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 30$, and the enlarged, rootless and scalpriform incisors were similar. The grinding teeth were thoroughly hypsodont and had a thin coating of cement; the molar-pattern was fundamentally like that of †*Nesodon*, in simpler form, but can be seen only in freshly erupted and unworn teeth.

The skull was very rodent-like in appearance, its flat top and narrow, tapering facial region, and the gnawing incisors adding much to the resemblance. The very large eye-sockets and the enormously developed auditory region suggest nocturnal habits, and, no doubt, the timid, defenceless little creatures hid themselves by day, perhaps in burrows. The enlargement of the accessory auditory chambers, which all of the †Toxodontia possessed, reached its maximum in †*Pachyrukhos*, and the chambers formed great, inflated protuberances at the postero-external angles of the skull. The neck was short, the body long and the tail very short, much like that of a rabbit. Collar-bones were present, as they probably were in all of the other members of the suborder †Typotheria, though this has not been definitely ascertained in all cases. The limbs were relatively long, especially the hind legs, and very slender; the bones of the fore-arm were separate, but those of the lower leg were coössified at both ends. The feet, which had four digits each, were of unequal size, the posterior pair being much longer than the anterior, and the hoofs were long, slender and pointed, almost claw-like. The entire skeleton suggests a leaping gait and its proportions and general appearance were remarkably like those of a rabbit-skeleton. In the restoration (Fig. 300, p. 639) Mr. Knight has followed these indications and drawn an animal which might readily be mistaken for a curious, short-eared rabbit; and there is every justification for doing this, though the character of the fur and the form of the ears are, of course, merely conjectural. Perhaps the ears are too small.

Associated with †*Pachyrukhos* in the Santa Cruz stage was another genus of the family, †*Hegetotherium,* which, though it cannot possibly have been ancestral to the former, yet serves to indicate, in general terms, what the ancestor must have been. This is another example of the long-continued survival of the more primitive together with the more advanced and specialized form. †*Hegetotherium* persisted into the Pliocene, but is not known from the Pleistocene. In this genus one upper and two lower incisors were already enlarged, rootless and scalpriform, but none of the teeth had been lost; it is interesting to note, however, that the teeth which were lacking in †*Pachyrukhos* were all very small and ready to disappear. The Santa Cruz species of †*Hegetotherium* were considerably larger and more robust animals than those of †*Pachyrukhos.*

Both of these genera were preceded by very similar, almost identical forms in the Patagonian, Deseado and Astraponotus stages, but the family cannot be definitely traced farther back than the lower Oligocene, but it very probably arose from some one of the groups, with low-crowned teeth, of the Casa Mayor stage.

The family †Interatheriidæ was, in most respects, more conservative and underwent less change than either of the preceding groups. A persistently primitive type was the genus †*Protypotherium,* which appeared for the last time in the Pliocene of Monte Hermoso, but was much more abundant and better preserved in the Santa Cruz. The animal was small and had the full complement of teeth, which were arranged in each jaw in a continuous series, and were fully hypsodont and rootless, except incisors and canine, which were rooted. None of the incisors was specially enlarged, but there was a gradual

FIG. 242.—Santa Cruz †typothere (†*Protypotherium australe*) and armadillo (†*Stegotherium tesselatum*). Restored by C. Knight from skeletons in the museum of Princeton University.

transition of increasing size and complexity from the incisors to the molars. A remarkable feature of this genus was the deeply cleft form of the lower incisors, giving them a fork-like shape, somewhat as in the modern Hyracoidea. The ulna and radius in the fore-arm and the tibia and fibula in the lower leg were separate, but the digits were already reduced to four in each foot. This was one of the few Santa Cruz ungulates which possessed a long and heavy tail. The limbs were relatively long and the feet were armed with such slender hoofs that they looked almost like claws. The restoration shows the animal to have had, like nearly all of the †Typotheria, a very rodent-like appearance, a likeness which may, perhaps, be unduly increased by the form given to the ears.

In the allied genus, †*Interatherium*, from which the family is named, the head was short, broad and deep, almost bullet-like; the first incisor was enlarged and chisel-shaped, and the other incisors and the canines were much reduced in size. It is an interesting fact, observed as yet only in this genus, but probably true also of all the smaller members of the suborder which had hypsodont teeth, that the milk-premolars were rooted and comparatively low-crowned, while their permanent successors were completely hypsodont and rootless. The limbs were considerably shorter than those of †*Protypotherium* and the tail long and thick, except for which, the general appearance of the skeleton suggests that of the modern "conies" or "klipdases" (Hyracoidea) of Africa and Syria, a suggestion which Mr. Knight has followed in the drawing (Fig. 297, p. 636).

This family was represented in the Deseado stage by a genus (†*Plagiarthrus*) in which the teeth developed roots in old age, but is not known from more ancient formations. Their probable ancestors of the Eocene were very small animals, with brachyodont teeth, the premolars smaller and of simpler pattern than the molars. The upper molars had a continuous external wall, with indication of separate cusps, and two transverse crests, as in the †Toxodonta, and the lower molars were composed of two incomplete crescents. The teeth were present in undiminished number and the anterior incisors were but little enlarged. Nothing is known of the skeleton.

SUBORDER †ENTELONYCHIA. †HOMALODOTHERES

This third suborder of the †Toxodontia was in some respects the most peculiar of all; no representatives of it have been found in formations later than the Santa Cruz, and the group attained its culmination in the still older Deseado stage, in which there were very large members of it. These most extraordinary beasts are still incompletely known, and little can be done as yet in the way of following out the steps of change which led up to their exceptional characters, though the suborder itself may be traced back to the Eocene by means of jaws and teeth alone.

The Santa Cruz genus labours under the portentous name of †*Homalodontotherium*, which may be shortened to the vernacular form of †homalodothere. In this genus the dentition was unreduced in number, and the teeth, though having rather high crowns, were all rooted and placed in continuous series, with a gradual transition in shape from the incisors to the molars. The canines were tusks of very moderate size, which projected but little above and below the plane of the other teeth; the premolars, except the last, which was nearly molariform, were smaller and simpler than the molars, which had a pattern fundamentally the same as in the †Toxodonta. Those of the upper jaw were, however, less complicated by spurs and accessory crests, and they had a somewhat stronger resemblance to the rhinoceros pattern, though the resemblance is demonstrably superficial and not indicative of relationship.

The skull was very like that of the Santa Cruz †toxodonts, †*Nesodon*, etc., and had the same unusual structure of the auditory region as was found throughout the order, but differed in many details, which it is not worth while to enumerate, though it may be said that the nasal bones were so much shortened that some kind of a proboscis or prehensile upper lip was probably present. The head was quite small in proportion to the size of the animal as a whole. Such of the vertebræ as are known were quite similar to those of †*Nesodon*, but the limbs were far longer and quite stout, though not massive. The humerus was remarkable for the great development of the ridges for the attachment of the deltoid and supinator muscles and for the prominence of the epicondyles, all of which gave to the bone the appearance of the humerus of a huge burrower, yet it is impossible to believe that so large an animal could have had burrowing habits. The fore-arm bones were separate and very long, the ulna almost as heavy as the radius; the latter is not known from a complete specimen, but there would appear to have been some power of rotation, a power which is conditioned by the shape of the upper end of the radius, and its mode of articulation with the humerus in the elbow-joint. The thigh-bone was long and heavy and its shaft was much flattened, having lost the normal cylindrical shape, but retained a small third trochanter. The bones of the lower leg were separate and relatively short, and the fibula was uncommonly heavy.

So far, there was nothing very unusual, save in the shape of the humerus, about the skeletal structure of the †Entelonychia, the remarkable characters having been confined to the feet. Were it not for these, the group might be included in the suborder †Toxodonta without difficulty. The feet, which were five-toed, differed notably in size, the manus being more than twice as long as the pes. In the former the metacarpals were very long and, though actually stout, were slender in proportion to their length; there was also a very unusual feature in an ungulate foot, that the heaviest of the digits was the fifth, or external one. The mode of articulation of the metacarpals with the first row of phalanges was very exceptional, indicating an extraordinary mobility of the toes, and the hoofs had been transformed into large, bluntly pointed claws, somewhat like those of the †chalicotheres, those aberrant perissodactyls (see p. 354), but not so large or so sharp. In the pes, the ankle-bone had hardly any groove for the tibia, and its lower end was hemispherical, as in the †Condylarthra and the clawed mammals generally. The toes were quite grotesquely short in comparison with those of the fore foot, and, as in the latter, the fifth was the heaviest of the series. The hind foot was apparently plantigrade, the heel-bone and the entire sole being applied to the ground in walking, while the fore foot was probably digitigrade, the wrist being raised and the metacarpals vertical. The weight was carried upon the metacarpals and one or more pads under the phalanges, as in the digitigrade carnivores, such as dogs and cats. In describing the †chalicotheres, it was pointed out that it was uncertain whether each foot had a single large pad, or whether there was a separate one under the phalanges of each digit, and a larger one, the "ball of the foot," under the metacarpals collectively. The same doubt applies to the manus of the †homalodotheres.

This is the third instance to be cited of the acquisition of claws by a hoofed mammal and, as in the other two cases, the †chalicotheres and †agriochœrids (p. 383), we are confronted by the seemingly incompatible association of teeth which could have masticated only soft vegetable tissues with feet like those of a beast of prey. As in the other two groups, the problem as to the habits and mode of life of the †homalodotheres is an unsolved one, chiefly because no mammal now living is at all like these extraordinary creatures and one can therefore form but vague conjectures as to the use of such feet to herbivorous animals. Possibly they subsisted largely upon roots and tubers and used the great claws for digging up food, the principal employment that bears now make of their claws. This remarkable transformation of hoofs into claws took place in three unrelated groups of hoofed animals and must have occurred independently among the Artiodactyla, the Perissodactyla and the †Toxodontia. By no possibility, so far as we are able to comprehend the course of evolutionary change, could this common characteristic have been due to inheritance from a common ancestry.

The †homalodotheres were among the largest of Santa Cruz mammals, but they were then already approaching extinction, while in the Deseado stage they were more numerous and varied and some of them very much larger. This is an exception to the more common rule, according to which the successive members of a phylum increased in stature until the maximum was reached and this, in many cases, was followed by extinction. The rule is, however, by no means without exceptions and several have already been referred to. The largest of American proboscideans was the †Imperial Elephant (*Elephas †imperator*) of the upper Pliocene and Pleistocene and in many other phyla the Pleistocene species were much larger than the Recent. So with the †homalodotheres; they reached their culmination in size and importance in the Deseado stage, fewer and smaller forms surviving into the Santa Cruz, after which the entire suborder vanished. The family may be traced back to the Eocene, where it is represented chiefly by a genus (†*Thomashuxleya*) which had larger canine tusks and much more brachyodont teeth, but there is no way of determining when the transformation of the hoofs took place. The other two families (†Notostylopidæ, †Isotemnidæ) flourished chiefly or exclusively in the Eocene and were small animals still very imperfectly understood.

SUBORDER †PYROTHERIA. †PYROTHERES

This suborder was a remarkable group, still incompletely known, of elephant-like animals, which reached their culmination and died out in the Oligocene, their last appearance being in the Deseado stage. The genus †*Pyrotherium* from the

Deseado (also called the Pyrotherium Beds) was the latest, largest and best known of the suborder. The dentition was much reduced as is shown by the formula: $i\,\frac{2}{1}$, $c\,\frac{0}{0}$, $p\,\frac{3}{2}$, $m\,\frac{3}{3}, \times 2 = 28$. The upper incisors were two downwardly directed tusks, the first quite small, the second considerably larger; the single lower incisor of each side was a stout, but not very long, horizontally directed tusk, with the enamel confined to a longitudinal band; the other incisors and the canines had disappeared. The premolars, except the foremost one, had the molar-pattern, which very rarely occurred among the indigenous South American ungulates. The grinding teeth were similar above and below and each had two elevated, transverse crests, which, when quite unworn, carried a row of bead-like tubercles. These teeth are decidedly reminiscent of the dentition of the aberrant proboscidean †*Dinotherium*, from the Miocene and Pliocene of Europe (p. 435), and this resemblance, together with the form of the tusks, has led to the reference of

FIG. 243. — Head of †*Pyrotherium*, showing the two pairs of upper tusks. Restored from a skull in the museum of Amherst College.

this group to the Proboscidea, but the assignment is undoubtedly erroneous, as is shown by the character of the skull and skeleton.

The skull, hitherto unknown, was obtained by the Amherst College Expedition to Patagonia and its description by Professor F. B. Loomis is anxiously awaited. In advance of that, he has published a brief account, with a figure. This skull was long and narrow, with very short facial region and nasal bones so shortened that the nasal canal passed almost vertically down through the head, as in the elephants, and there must have been a considerable proboscis. Despite this great modification, the skull was plainly of the †toxodont and not of the proboscidean type. The legs were extremely massive and the fore legs were considerably shorter than the hind, with such a difference in length that the head must have been carried low, as in the Pampean †*Toxodon*. The upper arm and thigh were much longer than the fore-arm and lower leg respectively. The humerus was immensely broadened, especially the lower end, and the processes for muscular attachment were extremely prominent. The femur was long, with broad and flattened shaft, and had no trace of the third trochanter, quite strongly resembling the thigh-bone of an elephant, which, as we have repeatedly seen, is the type more or less closely approximated by all of the very heavy ungulates. In the standing position, the femur was in nearly the same vertical line as the tibia and the whole leg must have been almost perfectly straight, with the knee-joint free from the body. The short and massive fore-arm bones were coössified, at least in some individuals, as were the equally heavy bones of the lower leg, the fibula being exceptionally stout. Little is known of the feet, but that little renders probable the inference that they were short, columnar and five-toed.

The Eocene representatives of the Pyrotheria are known only from very fragmentary material. †*Propyrotherium*, of the Astraponotus Beds, was smaller than the Deseado genus and still smaller was †*Carolozittellia* of the Casa Mayor, which was not so large as a tapir. In the latter the molars were of the same type as in the succeeding forms and small tusks had already begun to develop. The older Eocene genus †*Paulogervaisia* was probably a member of this suborder; if so, it shows that the molars with transverse crests were derived from quadritubercular teeth, just as happened in the Proboscidea and several other ungulate groups.

CHAPTER XIII

HISTORY OF THE †LITOPTERNA AND †ASTRAPOTHERIA

Besides the four well-defined groups which make up the †Toxodontia (or †Notoungulata) there are two other extinct orders of indigenous South American ungulates, which remain to be considered. These did not have the exceptional development of the auditory region of the skull which characterized the †Toxodontia. The best known and most important genera of the †Litopterna are listed in the following table:

†LITOPTERNA. †Litopterns

I. †Macrauchenidæ.
  †*Macrauchenia*, Plioc. and Pleist. †*Scalibrinitherium*, Paraná. †*Theosodon*, Santa Cruz. †*Cramauchenia*, Patagonian. †*Protheosodon*, Deseado.

II. Proterotheriidæ.
  †*Epitherium*, Monte Hermoso. †*Diadiaphorus*, Santa Cruz and Paraná. †*Proterotherium*, do. †*Thoatherium*, Santa Cruz. †*Deuterotherium*, Deseado. †*Prothoatherium*, do.

III. Didolodidæ.
  †*Didolodus*, Casa Mayor. †*Lambdaconus*, do. †*Notoprogonia*, do. †*Proectocion*, do., etc., etc.

Only one of the families of this suborder survived into the Pampean stage, where it was represented by a single genus, †*Macrauchenia*. Like all the other large Pampean mammals of distinctly South American type, this was a grotesque creature, from the modern point of view. The genus was first discovered by Darwin, who says of it: "At Port St. Julian, in some red mud capping the gravel on the 90-foot plain, I found half the skeleton of the Macrauchenia Patachonica, a remarkable quadruped, full as large as a camel. It belongs to the same division of the Pachydermata with the rhinoceros, tapir, and palæotherium; but in the structure of the bones of its long neck it shows a clear relation to the camel, or rather to the guanaco and llama."[1] The views upon classification and relationship here expressed have been superseded, but the passage is an important one in the history of scientific opinion.

†*Macrauchenia* (Fig. 120, p. 216), as Darwin says, was as large as a camel; it had an unreduced dentition of 44 teeth and in each jaw the teeth were arranged in continuous series and were quite decidedly hypsodont. Both in the upper and the lower jaws the incisors formed a nearly straight transverse row and have a "mark," or enamel pit, like that seen in the horses; the canines were but little larger than the incisors and did not form tusks. The premolars were smaller and simpler than the molars. The upper molars had two concave and crescentic external cusps, connected by a median ridge, as in several families of perissodactyls; two transverse crests and several accessory spurs and enamel-pockets gave to the grinding surface, when somewhat worn, the appearance of considerable complexity. The lower molars had the two crescents, one behind the other, which recurred in almost all the South American types of ungulates; the vertical pillar which so generally in these types arose in the inner concavity of the posterior crescent was wanting in the permanent teeth of †*Macrauchenia*, but present in the milk-premolars.

No part of this remarkable animal was more curious than the skull, which was quite small in proportion to the rest of the skeleton. It was long, narrow and low, sloping and tapering forward to a blunt point at the end of the muzzle, though there was a slight broadening here to accommodate the transverse row of incisors. The sagittal crest was replaced by a short, narrow and flat area; the cranium was shortened and the face elongated, the orbits, which were completely encircled in bone, having been shifted behind the line of the teeth, as in the

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[1] Darwin, Voyage of a Naturalist, p. 172.

modern horses. The nasal bones were reduced to a minimum, a mere vestige of their original length, the anterior nasal opening being directly over the posterior, making the nasal passage vertical. Such an arrangement is an almost positive proof that in life the animal had a flexible proboscis, a conclusion which is confirmed by the presence, on the top of the head and behind the nasal opening, of deep pits for the attachment of the proboscis-muscles. A very curious feature of this skull was that the bones of the upper jaw, the maxillaries and premaxillaries of the opposite sides, united in the median line, making a long, solid, bony rostrum in front of the nasal opening, a character not found in other land mammals.

The neck was almost as long as in a camel and its vertebræ agreed with those of the latter in the very exceptional character of having the canal for the vertebral artery passing longitudinally through the neural arch, instead of perforating the transverse process. As Darwin says in the passage quoted above, "it shows a clear relation to the . . . guanaco and llama," but this is founded on the postulate that such a likeness must, of necessity, imply relationship. As was shown in the chapters on the Artiodactyla and Perissodactyla, it is the general rule among long-necked ungulates that the odontoid process of the axis assumes a spout-like shape, but †*Macrauchenia* was an exception and had an odontoid which retained its primitive and peg-like shape; it was, however, relatively very short and in cross-section was no longer circular, but oval. This may be regarded as a step toward the assumption of the spout-like form, but the extinction of the family put an end to further changes in that direction.

The body was rather short and the limbs very long, giving the animal a stilted appearance, while the feet were relatively short. The proportionate lengths of the different limb-segments was unusual; the upper arm was short, the fore-arm very long, the thigh long and the lower leg quite short. The humerus was very heavy; the ulna and radius, which were firmly coössified, formed a very long compound bone, which was broad transversely and thin antero-posteriorly. The long femur had only a small and inconspicuous third trochanter and the shaft was broad and thin, being flattened, or "compressed" antero-posteriorly. The tibia and fibula were united at both ends; the former was very heavy at the upper end, but diminished downward in width and thickness, and the fibula articulated with the calcaneum, as in the artiodactyls. The feet were tridactyl and had mesaxonic symmetry; that is to say, the median digit, or third of the original five, was symmetrical in itself and was bisected by the middle line of the foot, while the lateral toes (second and fourth), each of which was asymmetrical, formed a symmetrical pair. It is this perissodactyl character of the foot to which Darwin refers when he says that †*Macrauchenia* "belongs to the same division of the Pachydermata with the rhinoceros, tapir and palæotherium." On the other hand, the very significant structure of the ankle-joint was radically different from that of the Perissodactyla; not only did the calcaneum have a special facet for articulation with the fibula, but the lower end of the astragalus was a convex "head," resting only on the navicular, as in the †Toxodontia, †Condylarthra, Hyracoidea and other very primitive groups of hoofed animals and in clawed mammals generally. Such a combination of characters is not known in any of the perissodactyls and precludes the reference of the †Litopterna to that order, though such a reference is strongly maintained by several authorities. The ungual phalanges were small and appear to suggest the presence of pads on the feet.

The appearance of †*Macrauchenia* in life must have been sufficiently strange. The small head with its proboscis and the long neck and legs should probably be regarded as indicative of browsing habits, though the hypsodont teeth show that grazing was at least an occasional mode of feeding. The long limbs and short feet gave to the extremities an appearance unlike that of any existing hoofed animal. The form and size of the ears and the character of the hairy coat are, of course, conjectural.

In the later Pliocene the family was represented by forms which differed so little from the Pampean †*Macrauchenia* as to call for no particular notice, but in the presumably lower Pliocene of the Paraná stage, occurred several genera, all unfortunately but imperfectly known, which are of interest as being less specialized than †*Macrauchenia* and as showing the way in which some of the peculiarities of the latter were acquired. In †*Scalibrinitherium*, which may be taken as an example of these genera, the teeth were brachyodont; the upper molars were rather less complex than those of †*Macrauchenia*, while the lower molars had the pillar in the concavity of the posterior crescent, which the Pampean genus retained only in the milk-teeth. As we have repeatedly found, the milk-dentition is often conservative and retains primitive or archaic features which have been lost in the permanent teeth, and †*Macrauchenia* is another illustration of the same principle. In the skull of †*Scalibrinitherium* the nasal bones, though very short, had not suffered such extreme abbreviation as in the succeeding genus, the nasal opening was farther forward and the maxillaries united in the superior median line for only a short distance, while the premaxillaries were fused together for their whole length. The orbit had not been shifted entirely behind the teeth, but was above the third upper molar.

Next in the ascending series, to use the genealogist's term, came the genus †*Theosodon* of the Santa Cruz, of which almost all the skeletal parts are known and thus make possible a full comparison with †*Macrauchenia*, which assuredly was its direct descendant. In view of the great lapse of time involved, the differences between the two genera were less than might have been expected, though the more ancient animal was in all respects the more primitive. †*Theosodon* was, in

FIG. 244.—Santa Cruz †macrauchenid (†*Theosodon garrettorum*) and predaceous marsupial (†*Borhyæna tuberata*). Restored by C. Knight from skeletons in the museum of Princeton University.

the first place, considerably smaller, not much exceeding a llama in size; the teeth had lower crowns than even those of †*Scalibrinitherium* and the incisors were arranged in line with the grinding teeth, not in a transverse row, but curving inward slightly, so that those of the opposite sides nearly met in front. The incisors, canine and first premolar were simple, sharply pointed, conical teeth, which gave an almost reptilian expression to the anterior part of the skull. The upper molars were on the same fundamental plan as those of †*Macrauchenia*, but in a less advanced stage of development, the transverse crests being incomplete and the internal cusps had a certain degree of separateness from the crests and from each other. It is evident that the upper molars were derived from the quadritubercular type. The lower molars had the vertical pillar in the concavity of the posterior crescent very prominently developed.

The resemblance of the skull to that of †*Macrauchenia* is obvious at the first glance, but it was less specialized and departed less from the ordinary ungulate type. The cranium was longer and the face shorter, the orbit, which was incompletely closed behind, extending over the second molar. There was a sagittal crest, the length of which differed much in the various species; the nasal bones were already very short, though decidedly longer than in the subsequent genus †*Scalibrinitherium*, and the anterior nasal opening was extended forward as a long, narrow slit, because the maxillaries did not come into contact with each other in the superior median line, and the premaxillaries touched each other, but were not coossified. The nasal canal, though very short, was horizontal, not vertical. The skulls of the three genera thus displayed three successive stages in the backward shifting of the orbit and of the anterior nasal opening, in the shortening of the nasal bones and in the formation of a solid rostrum by the fusion of the upper jaw-bones. No doubt also the living animals exhibited a corresponding gradation in the development of the proboscis.

The neck of †*Theosodon* was even longer proportionately than in †*Macrauchenia* and the transference of the canal for the vetebral artery from the transverse processes to the neural arch had already taken place, except in the first, sixth and seventh vertebræ, and was thus less complete than in the Pampean genus, in which all the vertebræ of the neck, save the seventh, had the canal in its exceptional position. The odon-

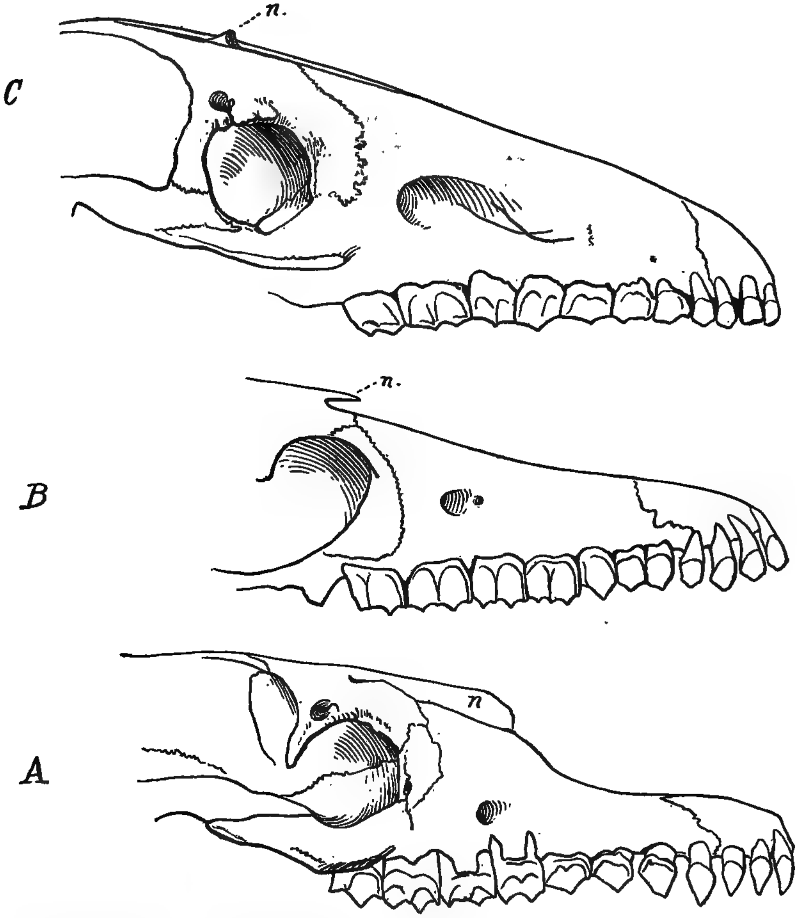

Fig. 245. — Development of the skull in the †Macrauchenidæ, side views. *A*, †*Theosodon*, Santa Cruz. *B*, †*Scalibrinitherium*, Paraná. (After Ameghino.) *C*, †*Macrauchenia*, Pampean. (After Burmeister.) *n.*, nasal bones.

toid process of the axis was less modified than in the latter, being relatively longer and more conical. The body was rather short, and the spines of the trunk-vertebræ were proportionally higher and more prominent. No caudal vertebræ

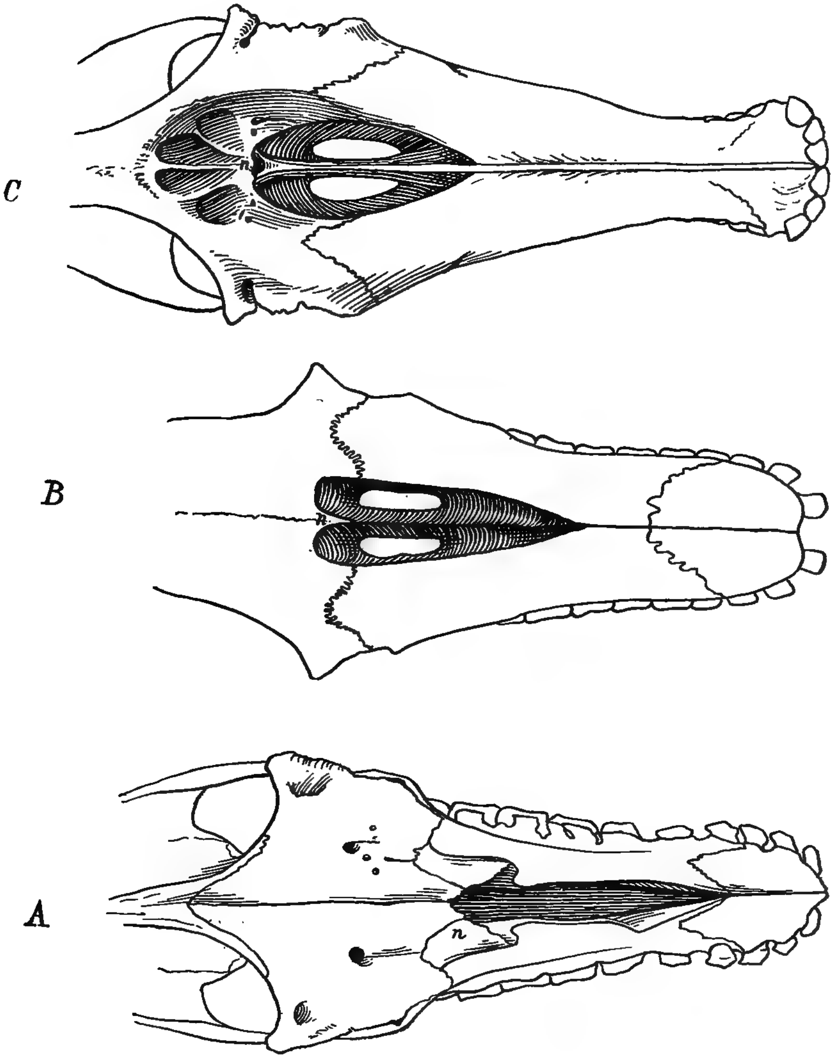

Fig. 246.—Development of the skull in the †Macrauchenidæ. *A*, †*Theosodon.* *B*, †*Scalibrinitherium.* (After Ameghino.) *C*, †*Macrauchenia.* (After Burmeister.)

have been found, but, from the shape of the sacrum, it is evident that the tail was short.

The limbs were long, but more slender and less elongate than in †*Macrauchenia,* in which the growth of the neck did not keep pace with that of the limbs, the lengthening of the proboscis probably compensating for this. The shoulder-blade had two conspicuous metacromia, very much as in the contemporary †toxodont, †*Nesodon,* but shorter and more widely separated. The humerus was short and quite slender and the fore-arm bones, which were much longer, did not coössify. The femur had a more slender and rounded shaft than in †*Macrauchenia* and a much larger third trochanter; the leg-bones were also separate from each other. The tridactyl feet were so like those of the Pampean genus, that no particular account of them is necessary, and the proportions of the limb segments were similar in both genera, short upper arm and lower leg, very long fore-arm and thigh, and short feet.

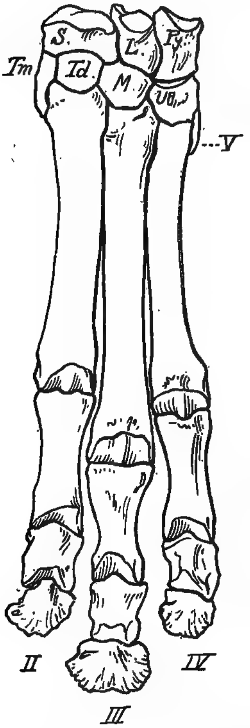

Fig. 247. Left manus of †*Theosodon.* *S.*, scaphoid. *L.*, lunar. *Py.*, pyramidal. *Tm.*, trapezium. *Td.*, trapezoid. *M.*, magnum. *U.*, unciform. *V.*, rudimentary fifth metacarpal.

The appearance of the living animal, as shown in the restoration, was no doubt somewhat like that of †*Macrauchenia,* but less bizarre. That there must have been some sort of a proboscis or prehensile upper lip, is indicated by the greatly shortened nasal bones, but this may not have been longer than in the existing Moose or Saiga Antelope. The long neck, short body and tail and long limbs suggest an animal not unlike a Guanaco, but larger and heavier. The hair may or may not have had the woolly character given to it in the drawing; upon such a point there can be no certainty.

In the older formations preceding the Santa Cruz, the †macrauchenids are known only from fragmentary material, though something of their history may be made out even from these fragments. †*Protheosodon*, of the Deseado stage, was considerably smaller than the Santa Cruz genus and had more primitive upper molars, in that the internal cusps and intermediate cuspules were isolated and conical, not forming transverse crests. Still smaller were the several genera (†*Lambdaconus*, etc.) related to the †macrauchenids found in the Casa Mayor Eocene, which have been referred, perhaps correctly, to the †Condylarthra. In these the formation of the external wall of the almost bunodont upper molars was in progress, by the fore-and-aft extension and transverse thinning of the external cusps; the internal pair of cusps and the cuspules were separate and conical. With much confidence, it may be inferred that in these little animals the skull was normal, the nasal bones were long and that the feet were five-toed, but demonstration is lacking.

The second family of the †Litopterna, the †Proterotheriidæ, were remarkable for their many deceptive resemblances to the horses. Even though those who contend that the †Litopterna should be included in the Perissodactyla should prove to be in the right, there can be no doubt that the †proterotheres were not closely related to the horses, but formed a most striking illustration of the independent acquisition of similar characters through parallel or convergent development. The family was not represented in the Pleistocene, having died out before that epoch, and the latest known members of it lived in the upper Pliocene of Monte Hermoso. In the still older Paraná formation more numerous and varied forms occurred, but only from the Santa Cruz have materials been obtained of sufficient completeness to furnish a full account of the structure of these extraordinary animals. Not that this remarkable character was due to grotesque proportions; on the contrary, they looked far more like the ordinary ungulates of the northern hemisphere than did any of their South American contemporaries; it is precisely this resemblance that is so notable.

In Santa Cruz times the family was represented by a large number of species, which have been grouped in four or five genera, which differed sufficiently to require generic separation, yet were closely similar. In all of them the dental formula was: $i\,\frac{1}{2}$, $c\,\frac{0}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 36$. Except in one genus (†*Thoatherium*) a pair of small tusks was formed by the enlargement of the second upper and third lower incisors, as in the †toxodonts, but the first upper and lower and the third upper incisors, which were retained in the †toxodonts, were lost in this family, as was also the upper canine, and the lower canine was very small, of no functional use. The teeth were brachyodont and, except the small tusks, displayed no tendency at any time toward the acquisition of high crowns. The premolars were less complex than the molars, though the last one approximated the molar-pattern. The upper molars had two crescentic outer cusps, meeting in a vertical ridge and together forming the outer wall; the transverse crests were imperfect, especially the hinder one which was often merely the intermediate cuspule, and did not fuse with the external wall. The lower molars had the two crescents, one behind the other, which recur in the †macrauchenids, all the suborders of the †Toxodontia, except the †Pyrotheria, and other South American ungulates, but the pillar in the posterior crescent, which was so characteristic of the groups named, was reduced to very small proportions and sometimes suppressed altogether. It should be noted, however, that this was the loss of an element which was formerly present.

The skull had a long cranium and rather short face, with long, high sagittal crest. The neck was short, the odontoid process of the axis peg-shaped, and the canal for the vertebral artery was in its normal position. The body was rather short, like that of a deer or antelope; the number of trunk-vertebræ is not definitely known in any of the genera, but was very probably 19 or 20, and the tail must have been short.

The limbs were slender and of moderate length; there was no coössification between the bones of the fore-arm or the lower leg. The feet were three-toed, except in one genus (†*Thoatherium*) in which they were single-toed, and nearly or quite the whole weight was carried upon the median digit, the laterals being mere dew-claws. The shape of the hoofs and the whole appearance of the foot were surprisingly like those of the three-toed horses, but there were certain structural differences of such great importance as, in my judgment, to forbid the reference of these animals, not merely to the horses, but even to the perissodactyls. In studying the †Litopterna, one is continually surprised to note the persistence of archaic and primitive characters in association with a high degree of specialization.

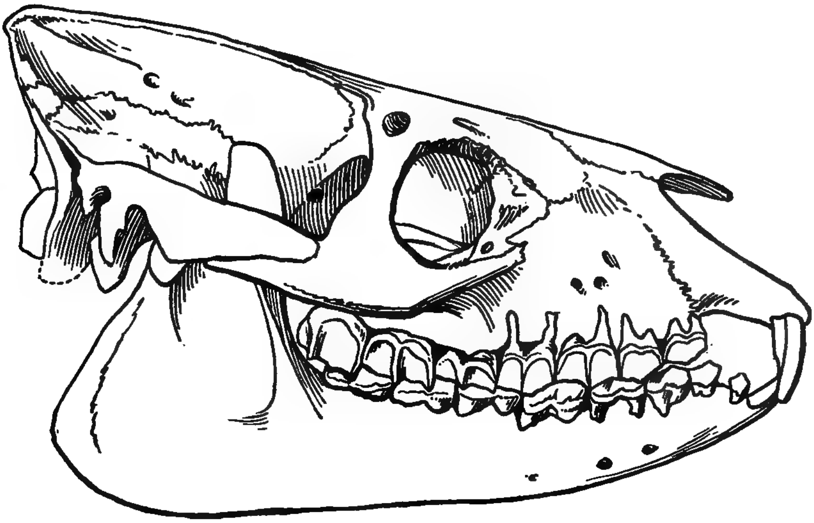

FIG. 248. — Skull of †*Diadiaphorus*, Santa Cruz. American Museum.

The largest Santa Cruz representatives of the family were

FIG. 249. — Three-toed †proterothere (†*Diadiaphorus majusculus*), Santa Cruz. Restored by C. Knight, from skeletons in the American Museum and Princeton University.

the species of †*Diadiaphorus*, animals considerably taller than a sheep and of heavier build. Their appearance was not unlike that of a short-necked, hornless antelope, but with the feet of the three-toed horses! These feet were, however, merely superficially like those of the horses, differing in points of fundamental significance. In the horses, the reduction of the digits was accompanied by a readjustment of the carpal and tarsal articulations, so that, in proportion as the median toe was enlarged and the laterals reduced, the weight was shifted more entirely upon the former. This is the method of digital reduction which Kowalevsky called "adaptive" and is exemplified in all existing artiodactyls and perissodactyls and by none more perfectly than by the monodactyl horses. In "inadaptive reduction," the method followed by †*Diadiaphorus* and the other genera of this family, there was no readjustment, or a very imperfect one, of the articulations, the lateral digits, however small and rudimentary, retaining the connections which they had when they were of full size and function. This distinction may seem to be unimportant, but its significance is shown by the fact that not a single ungulate with inadaptively reduced feet has survived to the present time.

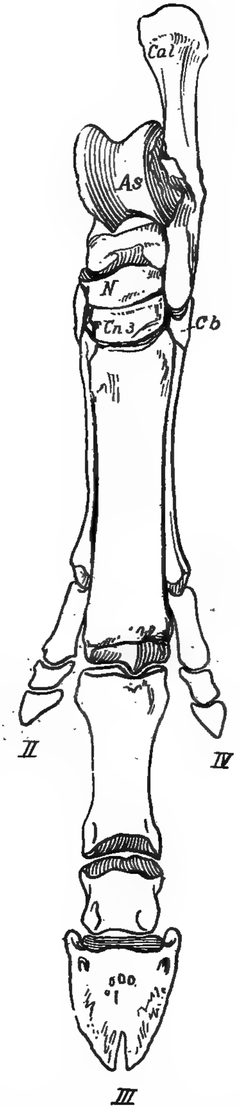

FIG. 250. — Left pes of †*Diadiaphorus*, from specimens in Princeton University and the American Museum. *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn. 3*, external cuneiform. *Cb.*, cuboid.

In still another respect the feet of †*Diadiaphorus* deviated markedly from those of the horses, viz. in the great proportionate length of the phalanges, especially of the first one, and the shortness of the metapodials, the three phalanges of the median digit together exceeding in length the metacarpal or metatarsal, while in the horses this proportion is reversed. The skull of this genus was short, deep and with an anterior taper; it had a long sagittal crest, but a brain-chamber of good capacity, considering its geological date. The nasals were quite short, though the degree of shortening was not such as to suggest the existence of a proboscis. In general appearance the skull recalls that of one of the larger †oreodonts (p. 372) of the North American Oligocene.

To the genus †*Proterotherium*, the type of the family, belonged a great number of Santa Cruz species, for at that time the genus was in a state of most vigorous development and the species were so variable that satisfactory discrimination of them is exceedingly difficult. They were all much smaller and slighter animals than the species of †*Diadiaphorus*, but did not differ from them in any important structural character. The skull in this genus closely resembled that of the one last named, save for its smaller size and lighter and more slender proportions; the nasal bones were considerably longer and the occiput was somewhat wider.

A more isolated position was held by the genus †*Thoatherium*, which was very clearly demarcated from all of the other genera of the family. Its species were the smallest of the commoner Santa Cruz members of the order and were of very light and graceful form. The dental formula was the same as in the other genera, but there were no tusks; the single upper and two lower incisors were of nearly the same size and simple, chisel-like form. The upper molars had the same elements as in the preceding genera, but somewhat differently connected, the two internal cusps and the anterior intermediate cuspule being united into a nearly longitudinal ridge. The skull was light, slender and pointed; the nasals were shortened, though less than in †*Diadiaphorus;* the sagittal crest was shorter than in the latter and the occiput was far narrower. The neck was short, the body of moderate length and the tail short. The limbs and especially the feet were proportionately more elongate and slender than in any other known genus of the family, giving quite a stilted appearance to the skeleton. The fore-arm bones were not coössified, but the ulna was much more reduced than in any of the other genera of the family, and the same is true of the fibula, which, though very slender, showed no tendency to unite with the tibia. The limb-bones, especially the femur, had a decided resemblance to those of †*Mesohippus*, the lower Oligocene tridactyl horse of North America, with the smaller species of which, †*M. bairdi*, †*Thoatherium* agreed well in size. Most remarkable of all were the feet, *which were more strictly monodactyl than those of any other known mammal.* The single functional digit, the third, had on each side of its upper end a very small, scale-like nodule of bone, the last vestiges of the lateral digits, corresponding to the immensely larger splints of the horse. Despite the unrivalled côompleteness of digital reduction which †*Thoatherium* displayed, the mode of reduction was inadaptive and the rudimentary metapodials retained the same carpal and tarsal

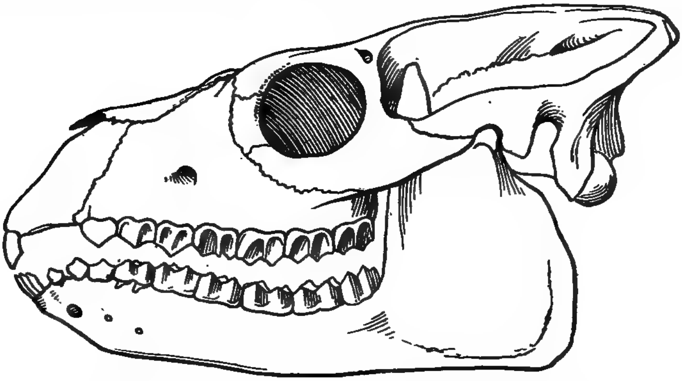

FIG. 251. — Skull of †*Thoatherium*, Santa Cruz. Princeton University Museum.

FIG. 252. —Single-toed †proterothere (†*Thoatherium minusculum*), Santa Cruz. Restored by C. Knight from a skeleton in the museum of Princeton University.

connections that they originally had in the pentadactyl manus, a very great difference from the horses. The ankle-joint also was of the same primitive character as in the other †Litopterna. The feet were relatively longer and more slender than in the other †proterotheres and the metapodial of the single functional digit longer in proportion to the phalanges.

The appearance of the living animal, aside from the character of the hair, colour-pattern, etc., may be closely inferred from the skeleton. It was a much smaller and more graceful animal than its contemporary and relative †*Diadiaphorus*, as light and agile as a gazelle. The head had some resemblance to that of a small horse, but the neck was much shorter than in the horses; the body also was shorter than in the latter, and the proportions of the trunk and limbs were quite as in the smaller antelopes. But these likenesses to horses and antelopes were, it must again be emphasized, superficial; the fundamental characteristics of structure were more primitive than in the most ancient known artiodactyls and perissodactyls.

With the aid of the fragmentary material which alone represents the †proterotheres in the formations preceding and following the Santa Cruz in time, it is not practicable to trace the development of the various phyla in a satisfactory manner. Two of the Santa Cruz genera, †*Diadiaphorus* and †*Proterotherium*, continued into the lower Pliocene (Paraná), and two additional ones have been named,

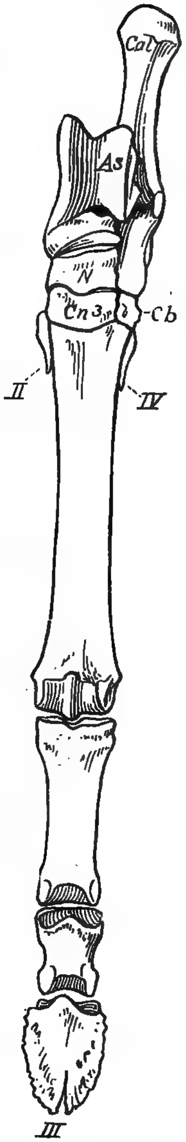

Fig. 253.—Left pes of †*Thoatherium*. Princeton University Museum. Letters as in Fig. 250.

but little is known about them. The latest known member of the family so far discovered is a genus (†*Epitherium*) from the upper Pliocene of Monte Hermoso, a tridactyl form like †*Diadiaphorus.* It is a noteworthy fact that the most advanced and specialized genus of the entire family ended with the Santa Cruz, while the less differentiated types survived till a considerably later period. Possibly, it was the incoming of the highly efficient Carnivora from North America that led to the extermination of the last †proterotheres.

Turning backward from the Santa Cruz, the family may be traced without any question to the Deseado stage of the Oligocene, though nothing but teeth has yet been obtained, while in the Eocene it would appear to have become merged in the same group of small, †Condylarthra-like animals with quadritubercular molars, as those which are regarded as the probable ancestors of the †macrauchenids. However likely this conclusion may seem to be, its confirmation must await the discovery of much more complete specimens than are now available.

ORDER †ASTRAPOTHERIA. †ASTRAPOTHERES

In the Santa Cruz another group of peculiar South American ungulates, the †Astrapotheria, made its last recorded appearance. Though not at all uncommon in that formation, no complete or even partial skeleton has yet been found, but merely the skull and a few bones of the limbs and feet. For this reason there is much doubt as to the systematic position and relationships of these animals, which were among the most curious of the many strange mammals which made up the Santa Cruz fauna. They were mentioned in connection with the †Amblypoda (p. 456) as possible representatives of that order in South America, but, as will be seen later, this is an improbable conclusion, and the group appears to have been indigenous in the southern continent, in which, at all events, it had a very long history. It has not been found in any formation later than the Santa Cruz, unless the Friasian fauna, which contains it, should be removed from that stage, of which it apparently forms the latest division.

I. †ASTRAPOTHERIIDÆ.
  †*Astrapotherium*, Santa Cruz and Patagonian. †*Astrapothericulus*, Patagonian. †*Parastrapotherium*, Deseado. †*Astraponotus*, Astraponotus Beds. †*Albertogaudrya*, Casa Mayor.
II. †TRIGONOSTYLOPIDÆ.
  † *Trigonostylops*, Casa Mayor. †*Edvardocopeia*. Astraponotus Beds.

The genus †*Astrapotherium*, which was the only well-defined representative of its family and order in the Santa Cruz stage, contained several species, some of them the largest animals of their time, as well as the most grotesque in appearance. The dentition differed in some important respects from that of all the other South American ungulates, the formula being: $i\,\frac{0}{3}$, $c\,\frac{1}{1}$, $p\,\frac{2}{1}$, $m\,\frac{3}{3}$, $\times\, 2 = 28$. The upper incisors had completely disappeared, but the lower ones were large and, what was an exceptional character, they were partially divided into two lobes, somewhat as in the Eocene †uintatheres of North America (p. 446). The canines were very large and formidable tusks, which grew throughout life and apparently formed no root; the upper tusk was nearly straight and was obliquely truncated by the strongly curved and sharp-pointed lower tusk. This arrangement was very unusual among South American hoofed mammals, many of which had no tusks at all; and in those which possessed them, such as the †toxodonts (p. 468), they were mostly incisors. Only in the †astrapotheres and †homalodotheres were there canine tusks, and in the latter group they were small and of limited growth. All the teeth, except the canines, were brachyodont and, though rather high-crowned, formed roots before coming into use. The premolars were small and greatly reduced in number ($\frac{2}{1}$), and in pattern were simpler than the molars. The upper molars were constructed on essentially the same plan as in the †Toxodonta;

indeed, the first specimen of this genus collected was referred to a large species of †*Nesodon* by Owen. On the other hand, the resemblance to the rhinoceros teeth is very decided, and has led several writers to postulate a relationship between the †astrapotheres and the rhinoceroses. The lower molars were of the bicrescentic pattern so frequently met with already; these teeth were very narrow in proportion to their length and strongly suggest those of †*Metamynodon*, the supposedly aquatic rhinoceros of the North American Oligocene (p. 346). It may be confidently inferred that so small a number of premolars was due to reduction from a full series, and this is confirmed by the milk-dentition, in which the premolars were $\frac{4}{3}$.

FIG. 254.—Head of †*Astrapotherium magnum*. Santa Cruz. Restored from a skull in the museum of Princeton University.

The skull was extremely peculiar, more so than in any other of the contemporary genera of hoofed animals. The toothless premaxillaries were quite small, but thick, and must have supported an elastic pad, against which the lower incisors could effectively bite in cropping herbage. The nasal bones were extremely short and there must have been a proboscis or greatly inflated snout, probably the former; the immense development of sinuses in the frontal bones elevated the whole forehead into a great, dome-like convexity, a feature which is not equalled in any other known mammal. The orbits were open behind and the brain chamber was small, so that the sagittal and occipital crests were very high and strong, to afford sufficient surface for the attachment of the great temporal muscles. The horizontal portion of the lower jaw was shallow vertically, but very thick and massive, and the symphyseal region was broad and depressed.

Unfortunately, the skeleton is still very incompletely known. Of the vertebræ, only the atlas and axis have been recovered, and these resembled those of the Santa Cruz †toxodont †*Nesodon*, on a larger scale. The scapula had a very thick spine, without the projections which were found in most of the Santa Cruz ungulates. The limb-bones were long and comparatively slender, and the processes for muscular attachment were singularly small and weak; the bones of the forearm and lower leg did not coössify and were proportionately elongate, the tibia being but little shorter than the femur. The latter had the flattened shaft which recurs in nearly all of the very heavy ungulates, but retained a remnant of the third trochanter. If the feet found isolated in the Santa Cruz and Deseado stages have been correctly referred to this order, then the genus was five-toed and the feet were broad, short and heavy, quite elephantine in appearance, especially the fore foot. The ankle-joint was very peculiar and the calcaneum had no articulation with the fibula, which it had in all the other indigenous South American ungulates.

Incomplete as the material is, it is yet possible to form some general conception of this extraordinary animal when in life. The head was short, broad and deep, rounded and very probably furnished with a proboscis; the neck was of moderate length, so that the mouth could not reach the ground without a straddling of the fore legs. The body was no doubt long, the limbs long and rather slender, giving the animal a stilted appearance, the feet very short, broad and columnar. Several species of the genus are known, which differed much in size, the largest (†*A. giganteum*) probably exceeding any modern rhinoceros in height and length, and the smallest (†*A. nanum*) not much larger than a Wild Boar.

†*Astrapothericulus*, of the Patagonian stage, was smaller than the average species of the Santa Cruz genus, and had teeth of the same number, but the canines were not capable of indefinite growth, and the lower molars had the pillar in the posterior crescent so characteristic of the South American hoofed animals. In the Deseado stage, on the contrary, the †astrapotheres were of larger size, and in the commonest genus, †*Parastrapotherium*, the grinding teeth had lower crowns and the premolars were more numerous, at least $\frac{3}{2}$. In the still more ancient †*Astraponotus*, which gives its name to the upper Eocene (or lower Oligocene) of Patagonia, the premolars were present in full series. In the Casa Mayor the order was abundantly represented by still more primitive genera, which assuredly had an undiminished number of teeth, though this has not been proved. One of these genera, †*Albertogaudrya*, was the largest animal of its time and the highly probable ancestor of the series leading to the Santa Cruz †*Astrapotherium.*

The second family of the order, the †Trigonostylopidæ, did not survive beyond the Eocene and is so imperfectly known that any account of it would be to small profit.

As stated above, the †Astrapotheria were an isolated group and their relationships are problematical and are likely to remain so pending the discovery of much more complete specimens of the various genera which made up the series. I am inclined to the opinion, however, that all of the indigenous groups of South American ungulates, which inhabited that continent before the great immigration from the north, were derivatives of the same stock and more nearly related to one another than to any of the orders which lived in other regions.

In looking over the labyrinth of ungulate history, as recorded by the fossils, certain facts stand out clearly, while others are still very obscure. It is like trying to trace the plan of vast and complicated ruins, which here are deeply buried in their own débris, there are fully exposed and in another place are swept away so completely that hardly a trace remains. But the problem is far more complex than any which can be presented by buildings, for the factor of repeated migrations from continent to continent comes in to obscure the evidence. Had each of the great land areas received its original stock of early mammals and then been shut off from communication with any other, many of the difficulties would be removed, but the story would lose half its interest.

Within the limits of the family, giving to that group the broad and elastic definition which has hitherto been employed, we have repeatedly found it feasible to construct a phylogenetic series which very nearly represents the steps of structural modification as they occurred in time. Much less frequently is it possible to trace allied families to their common starting point, and, so far as the hoofed animals are concerned, in no case have we yet succeeded in doing this for the separate orders. The obstacle lies in the fact that the ordinal groups were already distinct, when they made their first appearance in the known and accessible records, and the hypothetical ancestors common to them all, or to any two of them, are to be sought in regions of which we know little or nothing. Nevertheless, certain legitimate inferences may be drawn from the available evidence. It remains to be proved whether the assemblage of hoofed mammals, as a whole, was of single or multiple origin. Have all ungulates been derived from a common stock, or did they arise independently from several groups of clawed mammals? While the records cannot be followed back to the point, or points, of origin of the various orders, yet it is a noteworthy fact that, between several of them, the differences grow less marked as the more ancient members are reached, as though they were converging to a common term; others again show little such approximation, and the most probable conclusion from the evidence now at hand is that the ungulate assemblage is composed of several independent series.

One such series is that of the Hyracoidea and Proboscidea, to which Dr. Schlosser has given the name "Subungulata," and has pointed out its relationship to the †Condylarthra, which, however, is not a close one and may be illusory. Another apparently natural group is that of the peculiarly South American forms, the †Toxodontia, with its four suborders, the †Litopterna and the †Astrapotheria, which all appear to be traceable to closely allied families in the Eocene, whose teeth strongly suggest derivation from the †Condylarthra; but the material does not permit any positive statements. The Artiodactyla and Perissodactyla have so many similarities that they have always been regarded as closely related groups, but the distinction between them was almost as sharply drawn in their most ancient known members as it is to-day, and there was no distinct tendency to converge back into a common stem. Their mutual relationships are thus obscure, but the Perissodactyla, at least, seem to be derivable from a †condylarthrous ancestry.

The †Condylarthra, as a whole, were by far the most primitive of the ungulates, which they connected with the clawed mammals. None of the genera yet discovered can be regarded as ancestral to any of the higher orders, but it is entirely possible that in the upper Cretaceous period the †Condylarthra were spread over all the continents, except Australia, and that from them the other ungulate orders arose in different regions. At all events, the †Condylarthra show how the transition from clawed to hoofed types may have occurred and perhaps actually did so, but it would be premature to affirm this.

CHAPTER XIV

HISTORY OF THE CARNIVORA

The story of the hoofed mammals, as sketched in brief outline in the preceding chapters (VIII–XIII), is a curious mixture of relatively full and satisfactory paragraphs, with scanty, broken and unintelligible ones, not to mention those which have not yet been brought to light at all. With all its gaps and defects, which inhere in the nature of things, the history of the various ungulate series is the best that the palæontology of mammals has to offer and constitutes a very strong and solid argument for the theory of evolution. For the Carnivora the story is less complete and for obvious reasons. Individual abundance was a very large factor in determining the chances of preservation in the fossil state for any given species, and, as a rule, whole skeletons are found only when the species was fossilized in large numbers. In any region the Carnivora are less numerous than the herbivora upon which they prey, and while most ungulates live in larger or smaller herds, the carnivores are mostly solitary.

The Carnivora are divisible into three well-marked suborders, called respectively the Pinnipedia, Fissipedia and †Creodonta. The Pinnipedia, seals, walruses, etc., which are almost purely marine in habitat, are not dealt with in this book, since so little can be learned of them from the fossils, and the †Creodonta, an extremely ancient and primitive group, will be treated separately. The Fissipedia are chiefly terrestrial, though they include the otters, and their subdivisions, so far as the American forms are concerned, are shown in the following table, which, it should be observed, omits several genera. Unless otherwise noted, the genera are North American.

Suborder FISSIPEDIA. Land Carnivora

I. Canidæ, Dogs, Wolves, Foxes, etc.

Canis, Wolves, Pleist. and Rec. *Vulpes*, Red Fox, do. *Urocyon*, Grey Fox, do. *Cerdocyon*, fox-like wolves, S. A., do. *Icticyon*, Bush-Dog, S. A., do. ?*Cyon*, Dhole, mid. and up. Mioc. †*Dinocynops*, S. A., Pleist. †*Ælurodon*, up. Mioc. and low. Plioc. †*Tephrocyon*, mid. Mioc. to low. Plioc. †*Borophagus*, up. Mioc. to mid. Plioc. †*Ischyrocyon*, up. Mioc. †*Amphicyon*, mid. Mioc. to low. Plioc. †*Daphænodon*, low. Mioc. †*Enhydrocyon*, up. Oligo. †*Temnocyon*, up. Oligo. †*Mesocyon*, up. Oligo. †*Cynodesmus*, low. Mioc. †*Daphænus*, Oligo. †*Cynodictis*, Oligo. †*Procynodictis*, up. Eoc.

II. Procyonidæ, Raccoons, etc.

Procyon, Raccoons, N. and S. A., Pleist. and Rec. *Nasua*, Coatis, S. A., Pleist. and Rec., now extending to Calif. †*Cyonasua*, S. A., up. Plioc. *Bassariscus*, Cacomistle, low. Plioc. to Rec. †*Phlaocyon*, low. Mioc. †*Leptarctus*, up. Mioc. *Potos*, Kinkajou, Neotropical, Recent.

III. Ursidæ, Bears.

Ursus, true Bears, Pleist. and Rec. *Tremarctos*, Spectacled Bear, S. A. †*Arctotherium*, †Short-faced Bears, N. and S. A., Pleist.

IV. Mustelidæ, Martens, Weasels, etc.

Mustela, Weasels, mid. Mioc. to Rec. *Grison*, Grisón, S. A., Pleist. to Rec. *Tayra*, Tayra, do. *Martes*, Martens, up. Mioc. to Rec. *Gulo*, Wolverene, Pleist. and Rec. †*Canimartes*, mid. Plioc. †*Brachypsalis*, up. Mioc. †*Megalictis*, low. Mioc. †*Ælurocyon*, do. †*Oligobunis*, up. Oligo. and low. Mioc. †*Bunælurus*, low. Oligo. *Mephitis*, Skunk, Pleist. and Rec. *Spilogale*, Spotted Skunk, do. *Conepatus*, S. A. Skunk, Pleist. and Rec., N. A., Rec. *Taxidea*, Badger, Pleist. and Rec. *Lutra*, Otters, up. Mioc. to Rec., S. A., Pleist. and Rec. *Latax*, Sea-Otter.

V. Felidæ. Cats.

Felis, true Cats, N. A., low. Plioc. to Rec., S. A., Pleist. and Rec. *Lynx*, Lynx, Pleist. and Rec. †*Pseudælurus*, mid. and up. Mioc. †*Smilodon*, Sabre-tooth Tiger, N. and S. A., Pleist. ?†*Machairodus*, mid. Mioc. to Plioc. †*Nimravus*, up. Oligo. †*Archælurus*, do. †*Hoplophoneus*, Oligo. †*Dinictis*, do. †*Eusmilus*, low. Oligo.

Two families, the hyenas (Hyænidæ) and civet-cats (Viverridæ), are omitted from the table because they apparently never reached the western hemisphere. The bears, of Old World origin, invaded America at a very late period and are not certainly known here before the Pleistocene. The other four families were well represented in North American history, though the great weasel tribe (Mustelidæ) went through the greater part of its history in the Old World. None of the families is indigenous in South America, and all of the five families which it now shares with North America came in in the series of immigrations, of which the first recorded effects are found in the Pliocene and continued into the Pleistocene.

The Fissipedia are adapted to a great variety of habits and modes of life and consequently there is considerable diversity of structure among them, though they all form a homogeneous, natural group. The dogs (Canidæ) are terrestrial, neither swimmers nor climbers; some, like the foxes, are solitary, others, like the wolves, hunt in packs and nearly all are strong, swift runners. The cats (Felidæ) which have a remarkable range of size, are terrestrial or arboreal; they take their prey by stalking and leaping upon it, not by running it down. The bears (Ursidæ) are mostly omnivorous, not very often killing prey, and largely vegetarian in diet. The raccoons (Procyonidæ) are chiefly arboreal and omnivorous. The very large and varied weasel family (Mustelidæ) have different habits, though nearly all are fierce and bloodthirsty. Otters and sea-otters are aquatic and prey chiefly on fish; minks and fishers are semi-aquatic; martens are arboreal, skunks terrestrial and badgers fossorial.

While there is thus much diversity of habit with corresponding differences of structure among the Fissipedia, there is a certain unity of plan recognizable among them all. With but few exceptions, the incisors are present in full number and the canines are formidable lacerating weapons. Especially characteristic of the dentition are the "sectorial" or "carnassial" teeth, always the fourth upper premolar and first lower molar, which form a pair of shearing blades, the premolar biting outside. In the bears and most of the raccoons the teeth are tuberculated, in adaptation to the omnivorous habit, and the carnassials have lost the shearing form, though clearly derived from that type. The skull has powerful jaws, and the crests and ridges for the attachment of the jaw muscles are prominent except in very small animals, and the stout, boldly outcurving zygomatic arches are very characteristic. The face may be elongate, as in the dogs, or extremely short, as in the cats, or of intermediate length; the brain-case is relatively capacious, and the orbits, except in the cats, are widely open behind. The neck is never very long, but the body often is, and the tail varies greatly in length, as do also the limbs. There is great difference, too, between the various families in the prominence of the processes on the limb-bones for the attachment of muscles, as expressive of the muscular development of the limbs, and also in the extent to which the fore foot can be rotated and used for grasping. In all existing Fissipedia the femur has no third trochanter, but many extinct genera possessed it. The bones of the fore-arm and lower leg are always separate and uninterrupted.

In the wrist (*carpus*) there is always a large bone, the *scapholunar*, which is made up by the coalescence of three elements, the scaphoid, lunar and central, a feature which, though recurring in a few other mammals, is essentially characteristic of the modern Carnivora. The feet are armed with claws more or less sharp, which in some families, notably the cats, are retractile and may be folded back into the foot. The gait may be plantigrade, as in the raccoons and bears, or digitigrade, as in the dogs and cats, or intermediate in character.

Throughout the Paleocene and most of the Eocene, there were no Fissipedia, the flesh-eaters all belonging to the extinct †Creodonta, and the first clearly recognizable fissipedes occurred in the upper Eocene or Uinta.

1. *Canidæ. Dogs, Wolves, Foxes, etc.*

This family, which may with convenience be called simply dogs, is at present the most widely distributed of the families of Fissipedia, occurring in every continent, even Australia, and ranging through all climates almost from pole to pole. They are a singularly homogeneous family and show few differences of structure; such differences as there are affect chiefly the number and size of the teeth and external characters, such as the size of the ears, length and colouring of the hair, etc. The many domestic breeds are not here considered. Almost alone among the Fissipedia the dogs capture their prey by running it down, and they are endowed with remarkable speed and endurance. The entire organism, especially the limbs and feet, are adapted to cursorial habits.

For the purpose of comparison with the extinct genera of the family, some account of a wolf will suffice. The wolves, like most other members of the family, have a larger number of teeth than is usual in the suborder, as appears from the formula: $i\frac{3}{3}, c\frac{1}{1}, p\frac{4}{4}, m\frac{2}{3}, \times 2 = 42$, that is to say, only the third upper molar has been lost from the typical number, though the third lower is very small and seemingly on the point of disappearance (Fig. 44, p. 93). The upper sectorial tooth, the fourth premolar, has its shearing blade made up of two sharp-edged cusps, one behind the other, and there is a small internal cusp carried on a separate root; the upper molars are triangular and tritubercular and are used for crushing. The lower sectorial, the first molar, has an anterior blade of two shearing cusps, with the remnant of a third, and a low, basin-like posterior "heel."

The skull is characterized by the long face and jaws and by the structure of the auditory region; the tympanic bones are inflated into large oval bullæ, which are hollow and undivided, and the external opening of each is an irregular hole, without tubular prolongation. There is an alisphenoid canal for the passage of the internal carotid artery. The neck, body and tail are of moderate length and the vertebræ of the loins are not conspicuously large and heavy. There is no collar-bone. The limb-bones have a distinct, though superficial, resemblance to those of hoofed animals; the humerus has no very prominent ridges for the attachment of muscles and no epicondylar foramen, and the femur no third trochanter. The fore-arm bones are separate, but are so articulated together and with the humerus as to give the fore foot no power of rotation. The manus in all existing wild species has five digits, though the pollex or first digit is very small, a mere dew-claw; the four functional digits are arranged in two symmetrical pairs, very much as in the artiodactyls, a longer median pair, of which the metacarpals have a nearly square cross-section, and a shorter lateral pair (2d and 5th) of more trihedral form. All the metacarpals are closely appressed and almost parallel. The pes has four digits arranged in similar fashion. The claws are blunt and non-retractile, and are of little use in seizing or lacerating prey, but are useful in digging. The ungual phalanges have no bony hoods reflected over the base of the claw. All modern forms are digitigrade.

Materials are lacking for the construction of any such detailed phylogeny of the dogs as has been accomplished for many ungulates. Many of the extinct genera are known only from skulls, or even jaws, and the well-preserved skulls are too few to form distinctly defined and continuous series. On the other hand, there is every reason to believe that the canine genera of the successive geological stages did approximately represent the successive steps of development within the family, though it is difficult to distinguish between the phyla.

The Pleistocene dogs, for the most part, differed little from the Recent ones; there were some very large species like the *Canis †dirus* (Frontispiece) of the Mississippi Valley and the Pacific Coast. Two very peculiar genera have been reported.

One (†*Pachycyon*), from a cave in Virginia, had remarkably short, stout and strongly curved limb-bones, which suggest otter-like habits; the other (†*Hyænognathus*), from California, had a very short face and extremely massive lower jaw and very heavy teeth; it was probably like a hyena in appearance.

As far back as the Blanco stage of the middle Pliocene, remains occur which are assigned to the modern genus *Canis*, though better preserved specimens would probably require their removal from that genus. In the lower Pliocene the phylum of the true wolves was represented by †*Tephrocyon*, which, so far as it is known, differed only in minor details from *Canis*, and †*Tephrocyon* went back to the middle Miocene. What would appear to be its direct ancestor is †*Cynodesmus*, of the lower Miocene, which, in view of the long lapse of time involved, differed less from the modern wolves than one would have supposed, but the differences are significant, as pointing back to a far more primitive type of structure. †*Cynodesmus* was a small animal, intermediate in size between a Red Fox and a Coyote. The dental formula was the same as in *Canis*, but the teeth were relatively smaller and more closely crowded, as the face and jaws were shorter and the cranium, though longer, had a less capacious brain-chamber. The cast of this chamber, which very perfectly reproduces the form of the brain, shows that the latter was not only smaller but less

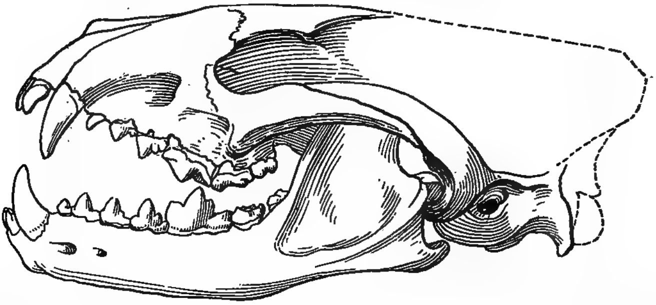

FIG. 255.—Skull of †*Cynodesmus thoöides*, a lower Miocene wolf. Princeton University Museum. Compare with Fig. 7, p. 62.

convoluted than in the modern animals, and this, in turn, denotes a lower grade of intelligence. The limb-bones were like those of wolves, but the feet were quite different. In the manus the first digit, or pollex, was much less reduced, though considerably shorter than the other digits, which were not in two symmetrical pairs, but were all of different lengths, not closely appressed, but arranged in radiating fashion; the metacarpals had not yet acquired the quadrate or trihedral form, but were more oval in cross-section. The pes was more modernized, but had five digits, which is not true of any existing member of the family. The claws were thin and sharp and were slightly retractile, a power which has been completely lost in all the modern canids. Such an animal could hardly have been preëminently cursorial.

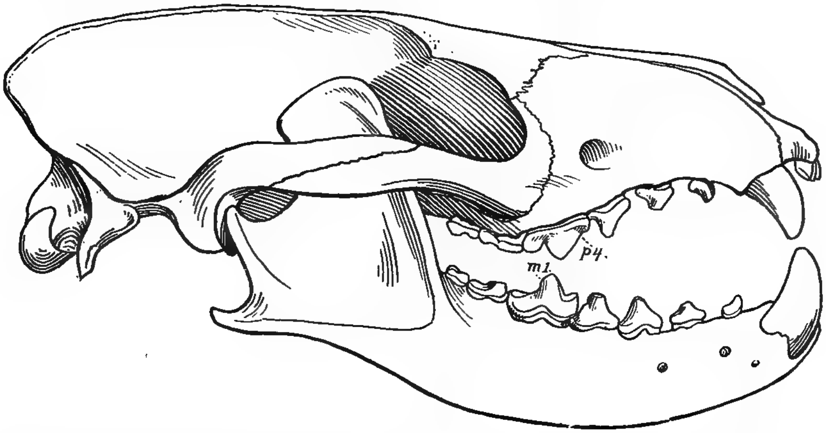

FIG. 256. — Skull of primitive "bear-dog" (†*Daphænus felinus*). White River stage. (After Hatcher.)

Out of the crowd of dog-like creatures in the John Day Oligocene, it is not yet practicable to select one which is to be taken as the ancestor of the Recent wolves through †*Cynodesmus*, nor can this be done with better assurance of success in the White River, though the beginning (†*Daphænus*) of the †bear-dogs in that formation probably closely represents the ancestral stage sought for. It is likely that several of the phyla into which the family was divided became blended in a common stock at that stage.

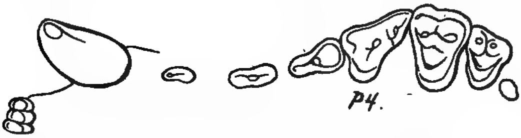

FIG. 257.— Upper teeth of †*Daphænus felinus*. *p. 4* = fourth premolar. (After Hatcher.)

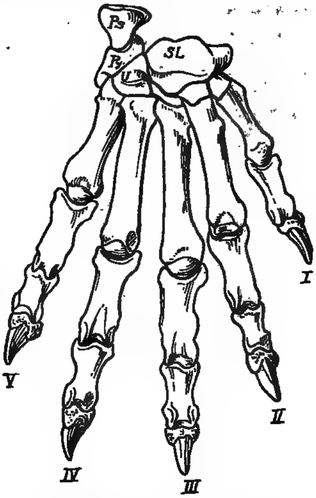

FIG. 258.—Right manus of †*Daphænus felinus*. *Sl.*, scapho-lunar. *Py.*, pyramidal. *Ps.*, pisiform. *U.*, unciform. (After Hatcher.) Compare with Fig. 32. p. 82.

A second phylum, now entirely extinct, is that of the †bear-dogs, which is not certainly recorded later than the middle Pliocene, though some have been doubtfully reported from the older Pleistocene of the Great Plains and the remarkable Californian genus, †*Hyænognathus*, may have been an offshoot of the same stock. The phylum was characterized by the unusually large size of the molars and by certain other features, which, however, are not known to have persisted through the entire series from first to last. In the middle Pliocene lived some very large bear-dogs, of the genus †*Borophagus*, the teeth of which had a strong likeness to those of the hyenas and probably the animals had hyena-like habits, feeding largely upon carrion and crushing the stoutest bones with their massive teeth. The same, or a very similar, genus lived in the lower Pliocene, but none of the species of that date is at all well known. In the upper Miocene occurred several species which have been referred to the European genera, †*Amphicyon* and †*Dinocyon*. The latter was an enormous canid, equalling in size the largest of living bears, the great Kadiak Bear of Alaska, and, though probably having a long and heavy tail, was much like a bear in appearance. The teeth indicate a more exclusively carnivorous habit than that of the bears and these may well have been savage and terrible beasts of prey.

†*Amphicyon,* which had three upper molars, continued down through the middle Miocene, but was replaced in the lower by †*Daphœnodon,* which may or may not have been its direct ancestor. The uncertainty as to the exact relationship between the two genera will remain until more complete material shall have been obtained from the middle Miocene.

FIG. 259. — Lower Miocene "†bear-dog" (*Daphœnodon superbus*). Restored from a skeleton in the Carnegie Museum, Pittsburgh.

†*Daphœnodon* was the largest dog of its time, the contemporary wolves (†*Cynodesmus*) having been hardly half so large, but was much inferior in size to the huge †bear-dogs of the middle and upper Miocene. The skull resembled that of a large wolf, but the tympanic bullæ were smaller and more loosely attached and the molar teeth were relatively much larger, a persistent characteristic of this phylum. The very long and heavy tail was a cat-like feature. The limbs were comparatively short and stout; the humerus had the epicondylar

foramen and the femur retained a trace of the third trochanter, both of which are lost in the modern members of the family. The feet were not at all canine in type, but rather resembled those of the ancient and unspecialized flesh-eaters. There were five digits in manus and pes and were not arranged in parallel pairs, but diverging; the metapodials were of oval cross-section, not squared, and their lower ends, which articulated with the first row of phalanges, had hemispherical surfaces, not semicylindrical. The claws were sharp and a remnant of former retractility was to be observed. Such an animal could hardly have been a strong and enduring runner and its structure suggests that it captured its prey by stalking and leaping upon it. The wolf-like head, with cat-like body, tail and limbs, made a strange combination, not closely paralleled by any existing carnivore.

Through the Oligocene the phylum was carried back by the several species of †*Daphœnus*, assuredly the ancestor of †*Daphœnodon* and decidedly more primitive in many respects. The Oligocene genus was a much smaller animal than its lower Miocene successor, the larger species hardly equalling a Coyote; the teeth were smaller and more closely set, but the molars were proportionately large, while the carnassials were less finished and effective shearing blades. The skull was less distinctively dog-like and had a smaller brain-case, with very prominent sagittal and occipital crests, a longer cranium and shorter face; the tympanic bones were very small and so loosely attached to the skull that they are rarely found, a very striking difference from all existing dogs. The backbone was remarkable for the unusually large size of the lumbar vertebræ, a point of resemblance to the cats and suggesting that †*Daphœnus* had great powers of leaping; there was a long, heavy, leopard-like tail, and the caudal vertebræ were very like those of the long-tailed cats. The limbs and feet were similar in character and proportions to those of †*Daphœnodon*, but the astragalus was less grooved for the tibia, the claws were rather more retractile and the gait was probably more plantigrade. There were so many cat-like features in the skeleton of †*Daphænus*, that the observer cannot but suspect that these resemblances indicate a community of origin, but, until the Eocene ancestors of the cats are found, the question of relationship must remain an open one.

The most ancient member of the bear-dog phylum yet discovered appears to be one of the †creodont family of the †Miacidæ, found in the Uinta Eocene.

A short-lived branch of the canine stock was that of the so-called "†hyena-dogs," a peculiar American type, which abounded in the upper Miocene and lower Pliocene and then became extinct. Traced backward, this brief series of species would appear to have sprung from the true wolves (†*Tephrocyon*) of the middle Miocene. The upper Miocene and lower Pliocene genus †*Ælurodon* had several species, which differed considerably in size; the commoner of these were large wolves with very modern type of body, tail, limbs and feet, but having short and massive heads. The premolars were extremely thick and heavy, with such a resemblance to those of the hyenas, that these animals have sometimes been mistakenly regarded as ancestral to that family. The especial characteristic, however, of the series was in the form of the upper sectorial tooth, which was much more feline than canine in construction and has given occasion for the generic name which means "cat-tooth."

A fourth phylum of the Canidæ, which would seem to be represented in the modern world by the Indian Dhole, or Wild Dog (*Cyon*), and perhaps by the Brazilian Bush-Dog (*Icticyon*), was characterized by the lower sectorial molar, the heel of which was not basin-like, as in the typical dogs, but trenchant and consisted of a single sharp-edged cusp, the external one of the primitive basin. Although there is no inherent improbability in the view that the Dhole and the Bush-Dog are derivatives of this phylum, no positive statement can yet be made, for the gap in the history is too great to be bridged with any assurance. The fossil members of the series did not come down later than the middle or upper Miocene and it is quite possible that the trenchant heel of the carnassial was developed more than once. The middle and lower Miocene members of the series are still very imperfectly known and it is only from the upper Oligocene (John Day) that well-preserved skeletons have been obtained. These pertain to an aberrant member of the phylum, the genus †*Temnocyon*, in which not only does the sectorial have a trenchant heel, but the second lower molar also was trenchant, having lost the two inner cusps, while the upper molars were as large as in the †bear-dogs.

†*Temnocyon* was a comparatively large animal and its skeleton had a mixture of primitive and advanced characters, the latter predominating, so that this genus was not only the largest but also the most specialized canid of its time. There was the long, heavy tail, which all of the known Oligocene carnivores possessed, but the limbs were long and the gait was, it would seem, thoroughly digitigrade. While the epicondylar foramen was retained by the humerus and the third trochanter by the femur, those bones were otherwise very modern in form. The feet were five-toed, but the functional metapodials were parallel, appressed and with something of the quadrate shape. In very notable degree, therefore, the feet of †*Temnocyon* anticipated the characters which the true wolves acquired considerably later. The less specialized †*Mesocyon*, which was smaller, was the ancestor of the Miocene forms and was, in turn, very probably derived from the White River †*Daphœnus*.

Still a fifth phylum, that of the †short-faced dogs (†*Enhydrocyon*), is very imperfectly known and has, so far, been found only in the lower Miocene and upper Oligocene. These also may have been descended from †*Daphœnus*, but the connection is not clear, nor has the relationship of the American genus to the extremely †short-faced dogs of the European Pliocene been determined.

Finally, so far as North America is concerned, there was a phylum of very small fox-like canids, which ranged from the lower Miocene to the upper Eocene and were very abundant, relatively speaking, in the White River and John Day. The dental formula was the same as in *Canis* and the skull was narrow and slender, though the brain-chamber was proportionately capacious, and the face was quite short. The tympanic bullæ were large and inflated. The body and tail were long and the limbs quite short and weak. The humerus had no epicondylar foramen and the femur no third trochanter. The five-toed feet had the spreading arrangement of the metapodials seen in the more primitive fissipedes generally and the claws were sharp. In proportions and appearance these animals must have been more like civets or weasels than like dogs and it is evident that they were not swift runners. The series had its earliest representatives (†*Procynodictis*) in the Uinta and was doubtless derived from the †creodont family

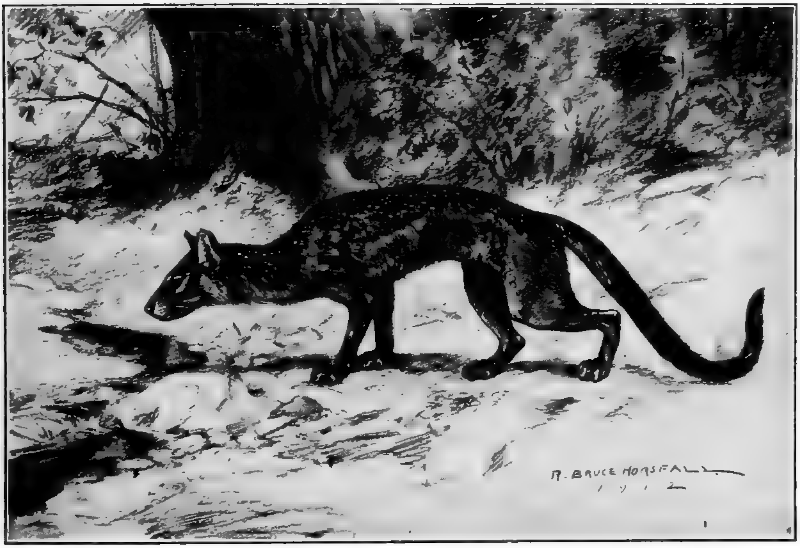

FIG. 260.—Small, fox-like dog (†*Cynodictis gregarius*) of the White River. Restored from a skeleton in the American Museum of Natural History.

†Miacidæ. The White River species are referred to the European genus †*Cynodictis,* those of the John Day and lower Miocene to †*Nothocyon,* and it has been suggested that this series gave rise to the foxes, a suggestion which may prove to be true, but the very long gap in time between these animals and the most ancient known foxes prevents any conclusion.

To determine the mutual relationships of the six phyla of Canidæ which, from the Eocene onward, inhabited North America in such numbers, is a task of great difficulty and only a tentative solution of the problem can be offered. The central stock would seem to be nearly represented by the White River †*Daphœnus,* leading through †*Cynodesmus* and †*Tephrocyon,* of the Miocene, to the wolves. A short-lived series, apparently given off from †*Tephrocyon,* was that of the †hyena-dogs, which flourished greatly in the upper Miocene and lower Pliocene and then became extinct. Another branch, that of the †bear-dogs, was derived from †*Daphœnus,* through †*Daphœnodon* to †*Amphicyon,* †*Dinocyon* and †*Borophagus,* the gigantic Miocene and Pliocene forms, ending perhaps in †*Hyænognathus* of the California Pleistocene. A third branch, represented by †*Mesocyon* and †*Temnocyon,* is believed to be continued to-day by the Asiatic Dhole and the Brazilian Bush-Dog. The †short-faced dogs (†*Enhydrocyon*) are still very obscure. The last phylum, that of †*Nothocyon,* †*Cynodictis,* †*Procynodictis,* had become distinct in the upper Eocene and possibly gave rise to the foxes, but this is highly conjectural.

2. *Felidæ. Cats*

The only other fissipede group whose development in North America may be followed for a long period is that of the †*Sabre-Tooth Tigers,* the subfamily †*Machairodontinæ,* which have been extinct since the Pleistocene; the history of the True Cats (Felinæ) is much more obscure. In most respects the two subfamilies agreed closely and, as they became separate at least in the early Oligocene, they furnish instructive parallel series. The †sabre-tooth cats were terrible beasts of prey, which in most of the Tertiary period ranged over the whole northern hemisphere and in the Pleistocene or late Pliocene extended throughout South America.

The Pleistocene genus †*Smilodon* (Frontispiece) belonged to nearly the whole western hemisphere and its various species were distributed from California and Pennsylvania on the north, to the Argentine Pampas on the south. The most obvious and striking peculiarities of †*Smilodon* were in the teeth, which were much reduced in number, the formula being: $i\,\frac{3}{3-2}$, $c\,\frac{1}{1}$, $p\,\frac{2}{2-1}$, $m\,\frac{1}{1}$. The upper canine was a great, curved, scimitar-like blade, eight inches or more in length, with broad

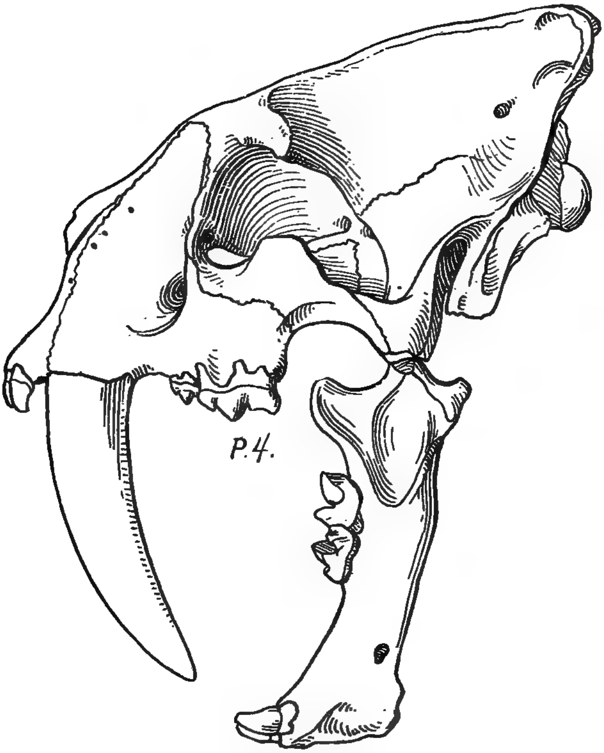

FIG. 261. — Skull of the Pleistocene †sabre-tooth tiger (†*Smilodon californicus*, after Matthew). *P. 4*, fourth upper premolar, sectorial.

inner and outer faces, but quite thin transversely, and with finely serrate posterior edge. It is difficult to understand how these great tusks, which would seem to have blocked the entrance to the mouth, could have been effectively used, unless the creature could open its mouth much more widely than any existing mammal, so as to clear the points of the tusks, and would then strike with them as a snake does with its fangs. There are great anatomical difficulties in the way of accepting this explanation and the problem, which is the same as that presented by the †uintatheres (p. 446), is still unsolved. It is, however, quite certain that no arrangement which was disadvantageous, or even inefficient, could have persisted for such vast periods of time. The lower canine was much diminished and hardly larger than an incisor. The two upper premolars were the third and fourth of the original series; the third was small, but the fourth, the sectorial, was a very large and efficient shearing blade. In addition to the two external trenchant cusps of the blade, which are present in the Carnivora generally, the cats have a third small, anterior cusp which in †*Smilodon* was large; the internal cusp had almost disappeared. The single upper molar was very small and so overlapped by the great carnassial as to be invisible from the side. The third lower premolar was small and unimportant and most specimens had lost it, leaving only the fourth, which was larger and evidently of functional value. The single molar was the sectorial, a large, thin, flattened blade, consisting of only two cusps, one behind the other, the trenchant edges of which met at nearly a right angle, and there was no trace of a heel.

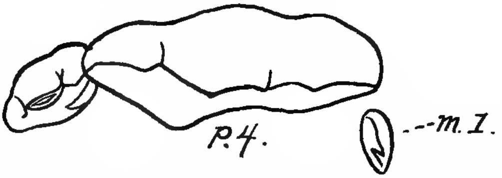

Fig. 262. — Upper teeth of †*Smilodon*, left side. *P. 4*, fourth premolar. *m. 1*, first molar. (After Matthew.)

The skull was in appearance closely similar to that of one of the great modern cats, such as the Lion or Tiger; with extremely shortened face, heavy and widely expanded zygomatic arches and very prominent sagittal crest. The tympanic bullæ were large and inflated, each divided by a septum into two chambers, but were not visible from the side, being covered externally by very large processes, which served for the attachment of some of the great muscles of the neck. The short, rounded, bullet-head of the true cats was thus repeated, but there were in the skull several interesting differences of detail, which it is not worth while to enumerate here. Suffice it to say, that some of these differences were due to the retention of primitive characters in the skull of †*Smilodon*, which have been lost in the modern felines, and others to special developments, in which the true cats did not share. The lower jaw had on each side a small, descending flange for the protection of the tusks, which, however, projected well below these flanges when the jaws were shut. The neck was heavy and the structure of its vertebræ was such as to suggest the presence of unusually powerful muscles; the back and loins were also uncommonly stout, in the larger species heavier than in the Lion or Tiger, but, in marked distinction from those modern forms, the tail was short. The limbs were shorter and much heavier in relation to the size of the body than in the great existing cats and must have been extremely powerful. The humerus usually had no epicondylar foramen, which all the true felines possess, though it was sometimes present. The feet also were very stout and armed with large retractile claws; the base of each claw was covered by a thin bony hood, an outgrowth of the ungual phalanx, which is very characteristic of the entire family. The hind foot had five digits, whereas no existing cat has more or less than four. The appearance of these animals must have been very much like that of the Lion or Tiger, aside from the unknown factors of mane and colour-markings, but differed in the great tusks, the short tail and the shorter and more massive legs and feet.

On account of the very incomplete preservation of the material so far collected, little is known of the †sabre-tooth series in North America during the Pliocene and Miocene epochs. Remains of very large cats have been found in the lower Pliocene and upper Miocene, but it is uncertain whether they belong to the feline or the †machairodont subfamily. Some of the species have been referred to the genus †*Machairodus*, which ranged from the lower Pleistocene to the middle Miocene of Europe, and the reference may be correct, but is uncertain. However, the European representatives of that genus, which are much better known, will serve to show the developmental stage from which †*Smilodon* was undoubtedly derived. The dental formula was the same as in the American genus, though there were generally two premolars in the lower jaw and in †*Smilodon* generally but one; the individual teeth were formed on the same plan as in the latter, but were relatively smaller, and the very small, rudimentary upper molar was visible externally

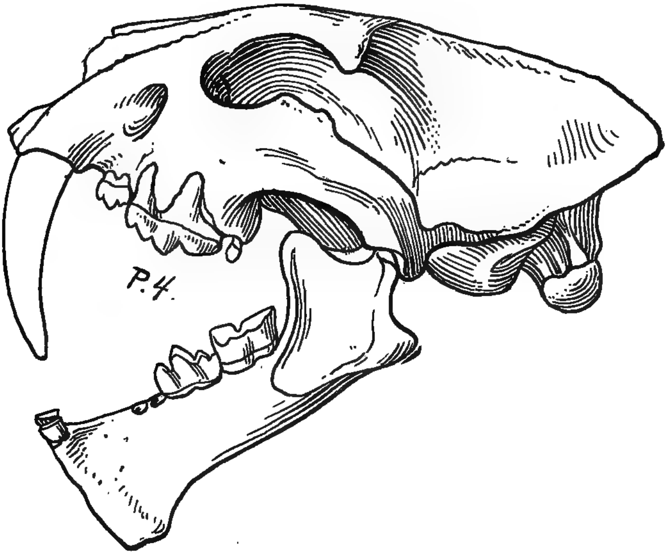

FIG. 263.—Skull of a †sabre-tooth tiger (†*Machairodus palmidens*) from the Miocene of France. (After Filhol.) *P. 4*, fourth upper premolar, sectorial tooth.

and was not overlapped and concealed by the great carnassial; the sabre-like tusk had not attained such great proportions. The skull of †*Machairodus*, the only part of the skeleton which is definitely known, was like that of †*Smilodon* on a much smaller scale, but more primitive in several respects. It was longer and had a less capacious brain-case and less prominent sagittal and occipital crests. The large tympanic bullæ were conspicuous in the side-view of the skull, as the processes for the attachment of the neck-muscles had no such development as in †*Smilodon*. The descending flanges of the lower jaw were larger than in the latter.

The upper Oligocene (John Day) contained a large variety of cat-like forms, of which no less than five genera have been described; one of them (†*Pogonodon*), nearly as large as a Lion, would seem to have died out here without descendants, and two others, to which we shall return later, so combined the characters of true felines and †machairodonts as to be of uncertain reference. Two other genera, which are much commoner and better known, from the White River, will be described from specimens of that stage.

The White River, or lower Oligocene, had three highly interesting genera of †machairodonts, two of them known from nearly or quite complete skeletons. One of these (†*Hoplophoneus*), which was, it can hardly be doubted, the direct ancestor of the later typical †machairodonts, had several species, which are found in the various levels of the White River beds. The largest of these species was considerably smaller than †*Machairodus*, and the smallest and most ancient was inferior to the modern Wild Cat. The number of teeth was variable, but normally greater than in the genera above described, being $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3-2}{3-2}$, $m\,\frac{1}{1}$, $\times 2 = 28\text{–}32$. The foremost premolar in each jaw was very small and often absent. The upper canine was a long and curved, but very thin, scimitar, finely serrate on both edges, while the lower canine was but little larger than the incisors. The carnassial teeth had a significant likeness to those of other fissipede families; the upper one, the fourth premolar, was relatively smaller than in †*Machairodus* and its blade less effectively trenchant; the accessory antero-external cusp was present, though extremely small, and the internal cusp, which in †*Smilodon* had almost disappeared, was quite large. The lower sectorial, the first molar, though already cat-like and consisting of two thin, broad and trenchant cusps in line, yet had vestiges of the heel and sometimes of the inner cusp. These vestiges were a connecting link between the highly specialized sectorial of the cats and the type usual among the Fissipedia, which is exemplified by the dogs. The small upper molar was less reduced than in the Miocene and Pliocene genera and plainly consisted of a larger external and smaller internal cusp.

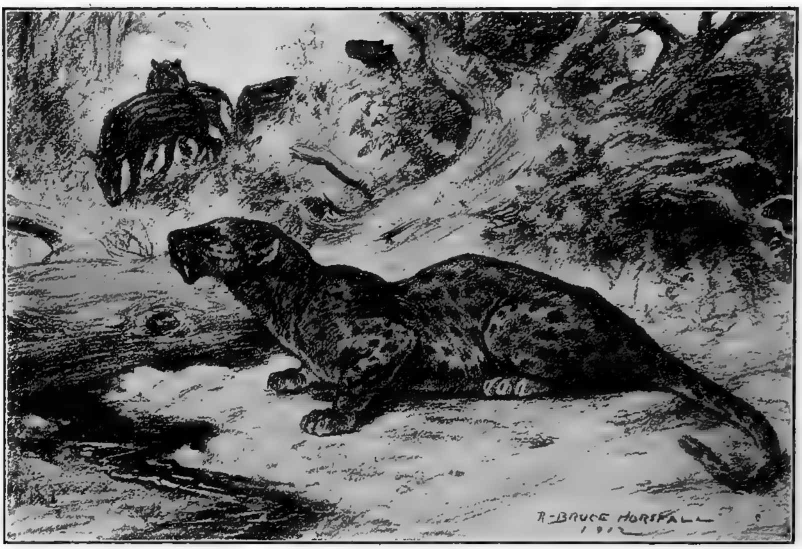

Fig. 264. — White River †sabre-tooth tiger (†*Hoplophoneus primævus*). Restored from a skeleton in the American Museum. †Oreodonts (†*Merycoidodon*) in the background.

Compared with that of other Fissipedia, the skull was short and broad, but in comparison with that of the modern cats and of †*Smilodon*, it was decidedly longer and narrower and the face was less abbreviated; the resemblance to †*Smilodon* was very marked in the form of the cranium, but, of course, the skull of †*Hoplophoneus* was distinctly more primitive in many respects. Thus, the orbit was much more widely open behind, the tympanic bullæ were but imperfectly ossified, and the perforations, or foramina, in the base of the skull, by which the nerves and blood-vessels communicated with the brain-chamber, were quite different and had more resemblance to those of the ancient dogs (*e.g.* †*Daphœnus*). In the classification of the Fissipedia much stress is laid upon the number and arrangement of these cranial foramina, and it is very significant to find the primitive dogs and cats agreeing so much more closely than do the modern members of these families. The lower jaw was relatively much stouter than in †*Smilodon* and the anterior flanges much more prominent, projecting downward so far that, when the jaws were closed, the points of the tusks did not extend below the flanges. The animal could have made no use at all of the sabre-tusks unless the mouth could have been opened so widely as to clear their points.

With close general resemblance, allowing for the very inferior size, the skeleton of †*Hoplophoneus* had many significant differences from that of †*Smilodon.* The neck was shorter and the body, especially the loins, longer, lighter and more slender and the tail very much longer, equalling that of the Leopard in relative length and surpassing it in thickness. The limbs were much less massive and somewhat differently proportioned, the upper arm being shorter and the fore-arm longer. The humerus, though far more slender than that of †*Smilodon,* was remarkable for the great development of the deltoid and supinator ridges, the latter, together with the shape of the radius, indicating very free rotation of the fore paw. The very prominent internal epicondyle was pierced by a foramen, and the femur had a distinct remnant of the third trochanter. The five-toed feet were comparatively small, but the claws were as completely retractile and as fully hooded as in any of the subsequent genera.

That †*Hoplophoneus* was a fierce destroyer, is made evident by every part of its skeleton, and, like other cats, it no doubt subsisted upon warm-blooded animals, which it killed for itself, the size of the prey being determined by the size and power of the particular species of the †sabre-toothed genus. In view of the probable extent of the Oligocene forests, the restoration (Fig. 264) gives the animal a spotted coat and the general aspect is that of one of the modern spotted cats, but the protruding ends of the tusks and the relatively long head distinguish it from any existing cat. "The presence of long, knife-like canines is correlated with powerful grasping feet possessing highly developed retractile claws. With its powerful feet the animal clung to its prey, while it struck repeatedly with its thin, sharp sabres" (J. C. Merriam).

In the latter part of the White River stage lived one of the most highly specialized of the †machairodonts, so far, at least, as the dentition is concerned, for only the skull is known. This genus, †*Eusmilus*, which also occurred in the Oligocene of Europe, was apparently an example of premature specialization which led to nothing, for none of the subsequent genera could have been derived from it. The teeth were reduced to a minimum in number: $i\,\frac{3}{2}$, $c\,\frac{1}{1}$, $p\,\frac{2}{1}$, $m\,\frac{1}{1}$, $\times\, 2 = 24$, one lower incisor and at least one premolar less in each jaw than had †*Hoplophoneus*. The canine tusk was very large and the flange of the lower jaw for its protection correspondingly elongated, being more prominent than in any other †machairodont. The American species, †*E. dakotensis*, was the largest carnivore of its time and not greatly inferior in size to the Lion.

Still another White River †machairodont, †*Dinictis*, differed in many interesting ways from its contemporary †*Hoplophoneus*, being more primitive and departing less from the ordinary fissipede type of structure. This is shown by the greater number of teeth, which was normally, $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$,

$m\,\frac{1}{2}, \times 2 = 34$. The upper carnassial had a considerably larger internal cusp and the trenchant blade did not have the accessory anterior cusp, which is present in almost all other cats and was thus more dog-like than cat-like. The lower carnassial was more feline, but retained a remnant of the heel and of the inner cusp, but the latter was variable, being sometimes present in one side of the jaw and not in the other, a sign that it was on the point of disappearance. The upper molar was plainly a reduced form of the tritubercular tooth, in plan like that of the dogs, while the second lower molar was a very small, single-rooted tooth. No other American cat has such a primitive dentition as this, and, aside from the sabre-tusk, which was not nearly so long as in †*Hoplophoneus*, and the lower carnassial, it might almost as well have belonged to a dog or musteline.

FIG. 265. — Primitive †sabre-tooth (†*Dinictis felina*) from the White River. Restored from specimens in the American Museum and Princeton University.

The skull was very like that of †*Hoplophoneus*, but was still longer and somewhat different in shape, owing to the higher forehead and lower occiput. The primitive features of the cranial base, such as the foramina, the imperfectly ossified tympanic bullæ, etc., were repeated in †*Dinictis*, but the lower jaw had much less prominent flanges for the protection of the tusks. The limbs differed considerably from those of †*Hoplophoneus* in being relatively longer and more slender and retaining more primitive features, such as the larger third trochanter of the femur. The five-toed feet were decidedly small and weak, and the claws, though retractile, were less so than in the other genus and were not hooded. The gait was probably plantigrade or semi-plantigrade.

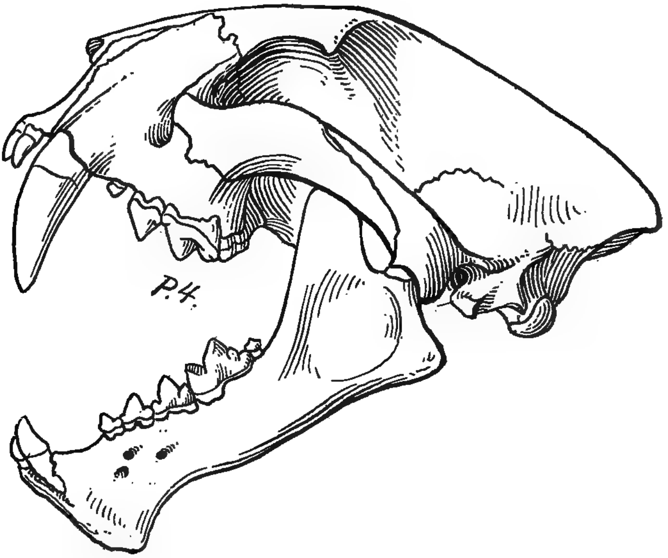

FIG. 266. — Skull of †*Dinictis squalidens*, White River. (After Matthew.) *p. 4* = fourth upper premolar, sectorial.

The relationships of †*Dinictis* and †*Hoplophoneus* are rather puzzling; none of the known species of the former could have been ancestral to the latter, for the two genera were contemporaneous. †*Dinictis* was apparently the somewhat modified survivor of the ancestral stage and represented very nearly the common starting point of both the feline and †machairodont subfamilies. Dr. Matthew has propounded the bold theory that this genus was the actual ancestor of the felines, continuing the series through †*Archælurus* and †*Nimravus* of the John Day to the unmistakable felines of the middle Miocene. This view runs contrary to the supposed "law of the irreversibility of evolution," a rule which many authorities look upon as well established. The theory postulates a different mode of development from anything that we have so far encountered in the series previously described and supposes that the upper canine first lost its original form, becoming a thin, elongate and scimitar-like tusk, while the lower canine was reduced almost to the proportions of an incisor and the lower jaw acquired a straight, flat chin and inferior flanges for the protection of the tusks. Then, after specialization had advanced so far, it was reversed and the original condition regained. This interesting hypothesis may possibly turn out to be true, though personally I cannot accept it, and, should it do so, it would necessitate a thoroughgoing revision of current opinions as to the processes of mammalian development.

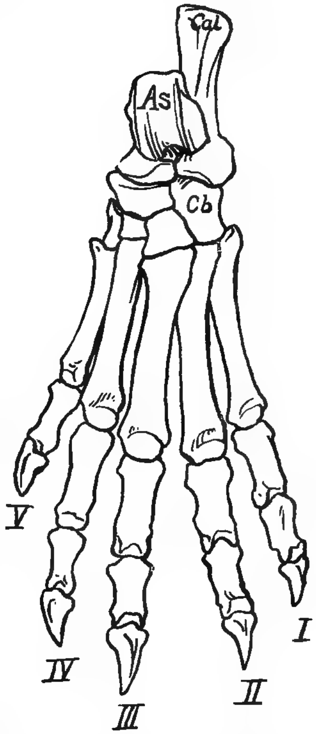

FIG. 267.—Left pes of †*Dinictis felina*. *Cal.*, calcaneum. *As.*, astragalus. *Cb.*, cuboid. Princeton University Museum.

The only John Day cat which was assuredly derived from †*Dinictis* was the large †*Pogonodon*, previously mentioned.

Also in the John Day stage lived †*Archælurus* and †*Nimravus*, which, as was noted above (p. 249), have been called the "false sabre-tooths," for in them the upper canine was not much larger than the lower and the latter, though smaller than in the felines, was yet very much less reduced than in the true †machairodonts. The skull closely resembled that of †*Dinictis*, but the lower jaw was without flanges. The limbs were long and slender and the feet long and digitigrade. The pes had only four digits, of which the median pair was elongated and the lateral pair shortened, so as to produce considerable resemblance to the pes of the dogs, and the claws were partially retractile. The proportions of the body, limbs and feet were suggestively like those of the Cheeta, or Hunting Leopard (*Cynœlurus jubatus*) of India, the generic name of which means "dog-cat," and it is quite possible that the

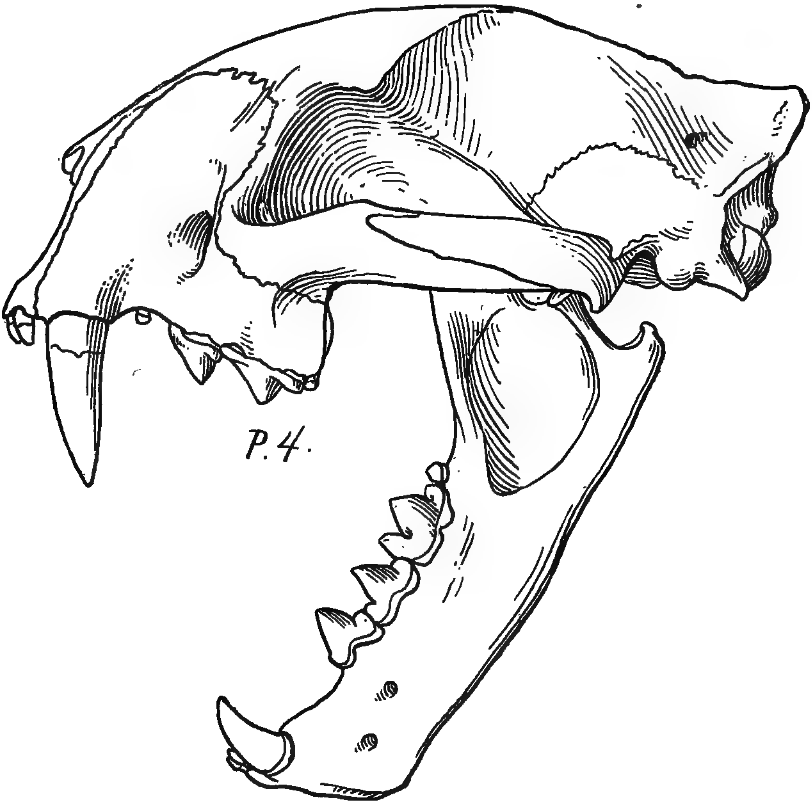

FIG. 268.—Skull of false †sabre-tooth (†*Nimravus gomphodus*) from the John Day. (After Matthew.) *p. 4* = fourth upper premolar, sectorial.

Cheeta may have been derived from some member of this "false †sabre-tooth" series, though the connecting links are unknown. These cursorial cats quite displaced the leaping †machairodonts of the †*Hoplophoneus* type, at least in the Oregon region at a time when, it will be remembered, that region had a remarkable variety of dogs. In other parts of the continent, of which we have no record, the true †machairodonts must have been thriving, as may be inferred from their comparative abundance in the later formations.

Concerning the habits of these cursorial cats, Professor Merriam says: "When the canines are not developed to the dagger-like form for stabbing, the premolar teeth serve a more definite purpose in the destruction of prey and would be less subject to reduction. The view suggested above finds support in that such evidence as we have indicates that during the deposition of the Middle John Day beds this region was in the main a country of open plains, offering advantages to running types of carnivores, and that during this epoch the *Archælurus-Nimravus* type of feline was by far the most common form [*i.e.* of cats]." The derivation of these cats is still obscure, but their likeness to certain forms of the European Oligocene suggests that they were immigrants.

The true cats of the subfamily Felinæ include the great variety of living forms, large and small, from the Lion and Tiger at one extreme to the Domestic Cat at the other. There is great difference among naturalists with regard to the nomenclature of the Recent cats; some make a considerable number of separate genera, while others include all the species, except the lynxes and the Cheeta, in the genus *Felis*. For the purposes of this book the latter practice is the more convenient and will be followed. In *Felis* the dental formula is: $i\frac{3}{3}$, $c\frac{1}{1}$, $p\frac{2-3}{2}$, $m\frac{1}{1}$, $\times 2 = 28\text{–}30$; the canines are large and strong, of oval section, and the upper one is but little larger than the lower; there are two large and functional premolars in each jaw, and an additional very small one may or may not be present in the upper jaw. The upper sectorial has a large shearing blade, with well-developed anterior accessory cusp, and the inner cusp, which in †*Smilodon* had almost disappeared, is quite large and carried on a separate root. The lower sectorial is composed of two cusps only, all traces of the heel and of the inner cusp having disappeared. The single upper molar is very small and usually concealed by the sectorial. The skull is very short and broad, and the shortening of the jaws gives great power to the biting muscles, because of the more favourable leverage. The zygomatic arches are very stout and curve out boldly, contributing much to the rounded shape of the head; the orbits are almost encircled in bone. The large tympanic bullæ are two-chambered and there is no alisphenoid canal, but in several other respects the base of the cranium differs markedly from that of †*Smilodon*. The lower jaw is without flanges and there is no angle between front and sides.

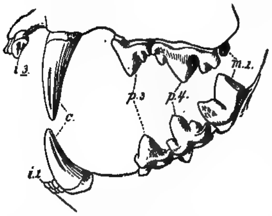

Fig. 269. — Dentition of Lynx (*L. rufus*), left side. *i. 3*, external upper incisor. *i. 1*, first lower incisor. *c.* = canine. *p. 3*, *p. 4*, third and fourth premolars. *m. 1*, first molar.

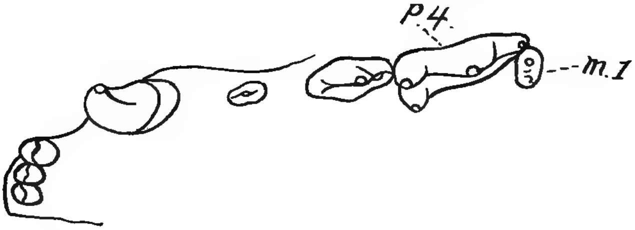

Fig. 270. — Upper teeth of Puma (*Felis concolor*), left side. *p. 4*, fourth premolar. *m. 1*, first molar.

The neck is short, the body long and the tail is long in most of the species, but short in the lynxes. The limbs are relatively longer and less massive than in †*Smilodon*, and there are five toes in the manus, four in the pes; the claws are hooded and retractile.

The western hemisphere at the present day contains none of the very large species, the Puma and Jaguar being the largest; but this was not true of the Pleistocene, where a huge cat (*Felis* †*atrox*), surpassing the Lion in size, ranged over the southern half of North America. Enormous cats also lived in the lower Pliocene and upper Miocene of the Great Plains region, but are not sufficiently well known for reference to either subfamily.

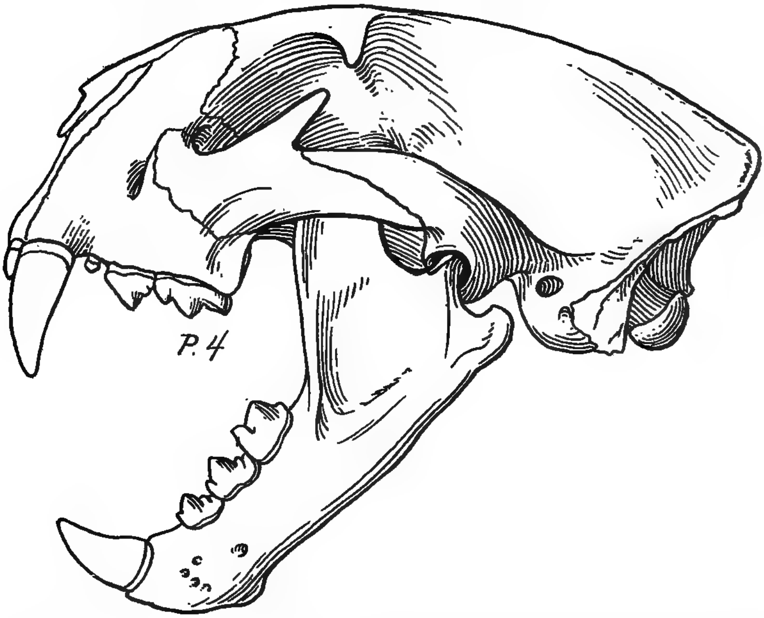

FIG. 271.—Skull of Puma (*Felis concolor*). *p. 4*, upper carnassial. The upper molar is concealed.

The history of the true felines has been but partially deciphered, and can, as yet, be traced back only to the middle Miocene, the genus †*Pseudœlurus* representing the series both in Europe and North America. In this genus the dental formula was nearly the same as in *Felis*, but there was frequently an additional small premolar in the lower jaw and the sectorials were more primitive, the upper one having the accessory anterior cusp in a merely incipient stage and in the lower one there was a vestige of the heel. The upper canine was considerably longer than the lower, thinner and more blade-like than in *Felis*, which, so far as it goes, is in favour of Dr. Matthew's theory (p. 541). What little is known of the skull and skeleton of †*Pseudœlurus* agrees with the modern cats.

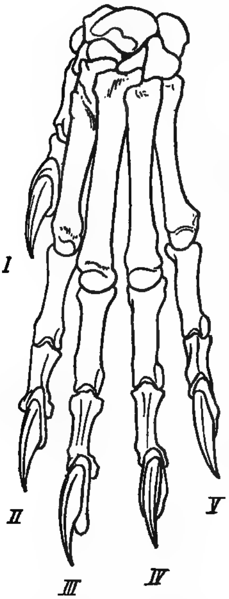

Fig. 272. — Left manus of Domestic Cat (*Felis domestica*, after Jayne). The horny claws are left in place, covering the ungual phalanges.

While it is not feasible to trace the series of true felines to an earlier stage than the middle Miocene, there can be no doubt that the subfamily was derived from the same stock as the †machairodonts and it is probable that the White River †*Dinictis* nearly represents the common starting point for both series; the resemblances between †*Dinictis* and such primitive dogs as †*Daphœnus* are suggestive of a common origin.

3. *Procyonidæ.* *Raccoons, etc.*

An almost exclusively American family of Fissipedia is that of the raccoons, which includes not only the latter (*Procyon*), but also the coatis (*Nasua*), curious animals, with long, flexible, pig-like snouts, the cacomistles (*Bassariscus*) and kinkajous (*Potos*). In addition to these American forms, there is an outlying Asiatic genus, the Panda (*Ælurus*) of the southeastern Himalayas, the last of a series which goes back to the European Pliocene.

The Procyonidæ are animals of small and moderate size, largely arboreal in habits and subsisting upon a mixed diet of fruit, eggs, insects and the like; the teeth are adapted to this diet and the sectorials have mostly lost their shearing form and the molars are tuberculated for crushing and grinding. The species generally have long tails, except in the raccoons proper, in which the tail is of medium length, and five-toed, plantigrade feet, with naked soles. Fossil members of this family are very rare in Tertiary formations and its history is therefore but scantily known; in the lower Pliocene have been found fragmentary remains with less specialized teeth, which appear to belong to the direct ancestor of *Bassariscus*. The upper Miocene genus †*Leptarctus* was an undoubted member of the family, and, while it would seem not to have been in the direct line of any of the modern forms, it was near to the common ancestry of the American genera, so far as the imperfect specimens enable us to judge.

FIG. 273. — Dentition of Raccoon (*Procyon lotor*), left side. *i. 3*, external incisor. *c.*, canine. *p. 4*, fourth premolar. *m. 1*, first molar.

By far the most primitive representative of the family yet discovered is the lower Miocene genus †*Phlaocyon*, which connected the Procyonidæ with the Oligocene genus of dogs, †*Cynodictis* (p. 529). The dentition resembled that of the latter, with several differences, which were all changes toward the Procyonidæ. All the cusps were lower and blunter than in †*Cynodictis;* the premolars were small, thick and closely crowded together and the upper sectorial, while still trenchant, had a postero-internal cusp, which is found in none of the Canidæ and was a first step toward the tuberculated pattern of the raccoons, and the lower sectorial had a very low cutting blade and large heel; the other molars of both jaws were low, wide and of subquadrate shape. The skull was short and broad, with the face as much shortened and the orbits as far forward as in *Procyon*, but the brain-case was narrower, less capacious, and the lower jaw had the curved form and much the same character as in the modern genus. The limbs were relatively more slender than in the latter and the five-toed feet were more canine than procyonine in the proportions of the digits.

The discovery of †*Phlaocyon* by Dr. Matthew was an event of capital importance, as showing the highly probable derivation of the raccoons from †*Cynodictis* and thus bringing another fissipede family into relationship with the dogs.

4. *Ursidæ.* *Bears*

The present distribution of the bear family is all but exclusively northern, as there is but one African species, confined to the northwestern corner of that continent, and one in the Andes of Peru and Ecuador, all the others belonging to Eurasia and North America.

Structurally, the family is very distinct and the dentition is quite peculiar. The incisors and canines resemble those of other Fissipedia; the three anterior premolars are very small, single-rooted and often shed early; the carnassials have lost their trenchant character; and the molars, which are usually longer than wide, are tuberculated, somewhat resembling those of pigs. Almost all the bears live principally upon vegetable food, and even the Polar Bear, which feeds upon fish and seals, will eat grass and berries in the brief Arctic summer; thus, the shearing teeth of the strictly carnivorous types are unnecessary to these animals. The skull is not unlike that of the dogs in shape, but the tympanic bullæ are much flattened and the entrances to them are long, bony tubes, while the cranial foramina are nearly as in the dogs. The body is very heavy and the tail always short. The limbs are short and thick; the humerus has lost the epicondylar foramen in all existing species except the South American Spectacled Bear (*Tremarctos ornatus*). The plantigrade feet have naked soles (except in the Polar Bear) and each foot has five well-developed

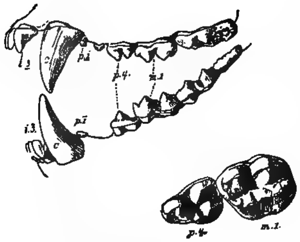

FIG. 274. — Dentition of Black Bear (*Ursus americanus*). *i. 3*, external incisor. *c.*, canine. *p. 1*, first premolar. *p. 4*, fourth premolar. *m. 1*, first molar. — Below is a view, on a larger scale, of the grinding surface of the fourth premolar and first molar, upper jaw.

and functional digits, armed with very long, sharp and non-retractile claws.

The Pleistocene representatives of the family in America included species of the true bears (*Ursus*) and of the very large †short-faced bears (†*Arctotherium*) which ranged over both North and South America. In †*Arctotherium* the dentition was less modified; the larger premolars were very closely crowded together and the molars were nearly square; the lower jaw was almost as much curved as in the raccoons. The humerus retained the epicondylar foramen. The family, which was of Old World origin, may have reached America in the lower Pliocene, but was rare until the late Pleistocene. †*Arctotherium* has not been found in the eastern hemisphere, but that, of course, is no proof that the genus was not an im-

Fig. 275. — Restored head of the †Short-faced Bear (†*Arctotherium bonæerense*). From a skull in the National Museum, Buenos Aires.

migrant from Asia. On the other hand, it may have been a peculiar American development from Pliocene immigrants. In the Old World, bears were first distinguishable in the upper Miocene, and may be there traced back to forms which were unmistakably derivatives of the early dogs.

5. *Mustelidæ. Mustelines*

The last fissipede family, which has, or has had, representatives in the western hemisphere is that which includes a great variety of small carnivores, such as minks, martens, skunks, badgers, otters, etc., and was likewise of Old World origin, though now of universal distribution, except in Australia and Madagascar. These are fierce and bloodthirsty beasts of prey, most of them strictly carnivorous and often killing in mere wantonness more than they can devour. Though now quite numerous and varied in North and South America, they are decidedly less so than in the eastern hemisphere and comparatively few peculiar types have originated here. Owing to the small size and fragility of the skeletons, they have not been well preserved as fossils, and little can be done as yet in tracing out the genealogy of the various phyla.

The mustelines have shortened jaws and a reduced number of teeth, the molars being $\frac{1}{2}$ or even $\frac{1}{1}$ and the premolars varying from four to two, though three in each jaw is the usual number. The cranium is generally very long and the facial part of the skull short, but the soft snout may add considerably to the length of the face. The tympanic bullæ are single-chambered and little inflated, and the lower lip of the entrance is extended; the hard palate is usually continued well back of the teeth. The body is very long and the tail variable and, in most of the genera, is short rather than long. The limbs are short, the feet, except in one genus, five-toed and plantigrade or semi-plantigrade, and the claws are non-retractile. Terrestrial, arboreal, burrowing, aquatic and marine forms are all represented in the family.

So far as North America is concerned, it is scarcely practicable to do more than catalogue the genera of the successive geological epochs. Pleistocene mustelines were very modern in character, differing little from those now inhabiting the continent, though in some cases with different ranges, according to climatic fluctuations. Badgers, martens, skunks and others occurred then very much as they do now and the Boreal Wolverene extended down to Pennsylvania. Little is known of Pliocene mustelines, the Blanco having yielded fragments of only one genus of uncertain affinities and though several genera occurred in the lower Pliocene, but one, a marten (*Martes*), can be identified. Unquestionably, North America had many more Pliocene members of the family, but the conditions of preservation were unfavourable.

Much the same is true of the Miocene stages. In the upper Miocene there were a marten (*Martes*), a weasel (*Mustela*) and two otters (†*Potamotherium* and the modern *Lutra*), of which the marten and the more primitive otter went back to the middle Miocene. In the lower Miocene were several mustelines quite different from any now existing. One of those, †*Megalictis*, was truly gigantic, with a skull nearly as large as that of a Black Bear and having heavy, pointed claws. This and a similar genus, †*Ælurocyon*, were related to the Ratel (*Mellivora*) of India and Africa and, more closely, to the Wolverene. †*Oligobunis*, a much smaller animal, was apparently of the same group. This genus was also in the upper Oligocene, but there represented by a larger species, which was as large as a badger.

The White River beds have yielded but a single genus, †*Bunœlurus*, which was the most primitive of American mustelines and had four premolars and two molars in each jaw, though the second upper molar was extremely small. The face was much less shortened than in the modern weasels and the tympanic bullæ were short and strongly inflated and had no tubular entrance, and were thus canine rather than musteline in form. The bony palate was not extended back of the teeth as it is in the modern genera. The same primitive group was much more abundant in the European Oligocene, migrating probably from Asia into Europe as well as into North America.

SOUTH AMERICAN FISSIPEDIA

The history of the South American carnivores is a comparatively brief one; the southern continent has representatives of the same five families as the northern, but most of the genera are different, the time since the great southward migration having been sufficient for the development of peculiar forms in the new environment. Among the dogs, there are to be noted the curious, close-haired, long-bodied and short-legged Bush-Dog (*Icticyon*) and the fox-like wolves (*Cerdocyon*), but there are no true foxes. Of the cats, the Puma differs little from that of North America, and the Jaguar (*Felis onca*) and Ocelot (*F. pardalis*) also range into the northern continent, but several small cats are confined to South America, which has no lynxes. There is but one bear (*Tremarctos ornatus*) of Andean range. Of the Procyonidæ, the northern *Procyon lotor* is replaced by the Crab-eating Raccoon, *P. cancrivorus*, while the coatis (*Nasua*) and kinkajou (*Potos*) are chiefly Neotropical. Except for the otters, the genera of Mustelidæ are nearly all different; there are no badgers and a different genus of skunks (*Conepatus*) replaces the northern *Mephitis;* the Grison (*Grison*), Tayra (*Tayra*) and the Patagonian *Lyncodon* are peculiar.

Even less can be done to trace the evolution of the South American genera than for the forms of the northern continent, whence migrated the more or less different ancestors of the former. The Pleistocene has yielded most of the modern genera, both existing and extinct species. An example of the latter was *Procyon †ursinus* from the Brazilian caverns, a truly gigantic Raccoon, as large as a bear. The †sabre-tooth tigers (†*Smilodon*) and short-faced bears (†*Arctotherium*) were shared with North America. In the Pliocene a bear, a raccoon and a dog were the only known fissipedes, and in the Miocene none have been found, their place being taken by flesh-eating marsupials.

While the history of the Fissipedia, as outlined in the preceding pages, is sadly incomplete as compared with that of many ungulates, it is nevertheless highly suggestive. In each family the advance of specialization and adaptation to a narrow range of habits may be followed; generally speaking, the teeth were diminished in number and increased in size and were either simplified by the loss of parts, as in the cats, or complicated by the addition of new elements, as in the bears and raccoons. The brain grew larger and more convoluted and the cranium more capacious; in most of the families, the face was shortened, notably in the cats and mustelines, while in others, especially the dogs, it was elongated. In all of the early types there was a long and heavy tail, but in most series it underwent more or less reduction. There was little reduction of digits, and no fissipede has less than four. In modern dogs and cats there are five digits in the manus and four in the pes and the hyenas have four in each, as has one genus of mustelines; other modern genera throughout the suborder are pentadactyl.

It is significant that the more ancient members of the various families differed less than do the modern ones; the various groups, as they are traced back in time, would seem to be converging to a common ancestry, of which the lower Oligocene dogs were the least changed representatives, and it is probable that all the families of the Fissipedia were derived, directly or indirectly, from a single Eocene group of primitive flesh-eaters. The families, none of which is extinct, are not all of equal antiquity. So far as now appears, the dogs and viverrines are the most ancient, having become distinct in the upper

Eocene; in the Oligocene were added the mustelines and cats; the raccoons branched off from the dogs in the lower Miocene, as did the bears in the upper Miocene. Finally, the hyenas appeared in the lower Pliocene, seemingly derived from the viverrines. The dogs passed through the greater part of their development in North America, where, during the Oligocene and Miocene, they were very abundant and varied, while at the same time they were comparatively rare in Europe and belonged chiefly to the phylum of the †bear-dogs. On the other hand, the remaining four families are of Old World origin, the bears and mustelines migrating to America, while the viverrines and hyenas did not.

SUBORDER †CREODONTA. †PRIMITIVE FLESH-EATERS

This group long preceded the Fissipedia in time, for they began their recorded history in the Paleocene and became extinct in the Oligocene. Through one family, the †Miacidæ, the †creodonts were broadly connected with the fissipedes, and it seems probable that that family was the ancestral stock from which all the fissipede families were derived. The other †creodont families died out without leaving descendants.

There is some difference of practice as to the number of families to be admitted; the table contains those listed in Professor Osborn's book and also adopted by Dr. Schlosser. I should prefer a somewhat larger number of family groups, but the matter is one of secondary importance. Many genera are omitted.

I. †OXYCLÆNIDÆ.
  †*Oxyclænus*, Paleoc. †*Deltatherium*, do.
II. †ARCTOCYONIDÆ.
  †*Clænodon*, Paleoc. †*Anacodon*, low. Eoc.
III. †MESONYCHIDÆ.
  †*Triisodon*, Paleoc. †*Dissacus*, do. †*Pachyæna*, low. Eoc. †*Mesonyx*, mid. Eoc. †*Dromocyon*, do. †*Harpagolestes*, mid. and up. Eoc.

IV. †OXYÆNIDÆ.
  †*Palæonictis*, low. Eoc. †*Oxyæna*, do. †*Patriofelis*, mid. Eoc. †*Limnocyon*, do. †*Machairoides*, do. †*Oxyænodon*, up. Eoc.
V. †HYÆNODONTIDÆ.
  †*Sinopa*, mid. Eoc. †*Stypolophus*, low. and mid. Eoc. †*Tritemnodon*, mid. Eoc. †*Pterodon*, low. Oligo. †*Hyænodon*, do.
VI. †MIACIDÆ.
  †*Didymictis*, Paleoc. and low. Eoc. †*Viverravus*, mid. Eoc. †*Miacis*, low. Eoc. †*Uintacyon*, low. to up. Eoc. †*Oödectes*, mid. Eoc. †*Vulpavus*, do. †*Palæarctonyx*, do.

The †Creodonta were an extremely varied assemblage, of carnivorous, omnivorous and presumably insectivorous habits, so that few statements, not subject to exceptions, can be made of them all. Only seven genera are known from skeletons, and several more from skulls, but most are represented only by jaws and teeth; limb- and foot-bones, however, give us a conception of the general structure of a considerable number. As a rule, the dentition was complete, according to the formula, $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 44$, but the first premolar or the last molar may be lost. The canines were always large, as was befitting for beasts of prey. In only one family, the Miacidæ, were the carnassial teeth confined to a single pair and those the same as in the Fissipedia, the fourth upper premolar and first lower molar; in all the other families there were either no sectorial teeth, or else there was more than one pair. In the Fissipedia the first is the largest of the lower molars, while in the †Creodonta (except the †Miacidæ) it was usually the smallest. The premolars were generally simple, compressed-conical teeth and the molars, with all their great variety, may be reduced to a common plan; those of the upper jaw were primitively tritubercular, with a triangle of two external and one internal cusps, and those of the lower jaw were in two distinct parts, an anterior, elevated triangle of three cusps and a low heel of two.

The skull was almost always very large in proportion to the size of the animal; the cranium, though long, was of small capacity and the face varied much in length in the different families. Primitively, the face and jaws were short in correlation with the small size of the teeth, and this primitive condition was modified in two opposite directions; in one the face and jaws were elongated, as the teeth enlarged, and in the other they were shortened still further. The zygomatic arches were stout and curved out strongly from the sides of the skull, making very wide openings, and, in almost all cases, the sagittal and occipital crests were very high, as would be necessary from the combination of powerful jaws and small brain-case (see p. 63). The tympanic bullæ were not ossified. The brain was extremely small, especially in the more ancient genera, and the convolutions were almost always few and simple, which indicates a low grade of intelligence and very marked inferiority to the Fissipedia.

In all the genera of which sufficient material has been obtained the body was long and had 19 or 20 trunk-vertebræ: in the lumbar and posterior part of the dorsal regions the processes by which the successive vertebræ were articulated together (zygapophyses) were cylindrical and interlocking, as in the artiodactyl ungulates (p. 360). To this general statement, the †Miacidæ formed a partial exception. The tail was very long and heavy in all the forms of which the caudal vertebræ are known, and this was probably true of all. The limbs were short and generally heavy; the femur had the third trochanter and the humerus, save in a few of the later genera, the epicondylar foramen, and the manus could, in nearly all, be freely rotated. Except in the most advanced forms of one family, the †Mesonychidæ, the feet were five-toed and plantigrade, or semi-plantigrade, and of decidedly primitive structure. The scapholunar bone of the Fissipedia (see p. 519) was not formed, its three elements, with very few exceptions, remaining separate. The astragalus nearly always had a shallow groove, or none at all. The claws were thick and blunt and the ungual phalanges cleft at the end, except in the

†Arctocyonidæ and †Miacidæ, which had sharp claws and uncleft phalanges.

From this brief description, it is obvious that the †Miacidæ occupied a very isolated position among the †creodonts and, in my judgment, it would be better to transfer that family to the Fissipedia and include the others in a separate order.

Throughout the Paleocene and Eocene epochs the †Creodonta were numerous and varied, the first of the Fissipedia appearing in the upper Eocene. Till then the †creodonts were the only predaceous mammals in North America and Europe, and they were especially abundant in the former. Most members of the suborder and all the Paleocene forms were of small or moderate size, but some of the Eocene species were very large. In the Uinta the †creodonts were greatly decreased in numbers and in the White River there were only two genera of one family, the †Hyænodontidæ, and since the Oligocene the suborder has been extinct.

1. †*Miacidæ. Fissipede-like* †*Creodonts*

It is unfortunate that no member of this family is known from a complete skeleton, but the material collected is sufficient to give a fairly adequate conception of these most interesting animals. These were the only †creodonts with a single pair of carnassials, the fourth upper premolar and first lower molar, but in some of the genera the carnassials did not differ greatly from the other teeth. In the various genera the skull differed considerably in length and in the proportions of cranium and face; the brain-case was larger than in most other †creodonts and the brain more advanced, though smaller than in the fissipedes, and the sagittal and occipital crests were very prominent; the tympanic bullæ were not ossified. The humerus had the epicondylar foramen and the femur the third trochanter; in the wrist the scaphoid, lunar and central were separate, almost the only important difference from the Fissipedia and merely the primitive stage of the latter. The feet were pentadactyl and the digits were arranged in spreading fashion; the claws were small, sharp and partially retractile and the ungual phalanges not cleft at the tip.

Within the family several different phyla may be distinguished, one of which (†*Miacis* — †*Uintacyon*) led to the dogs, another to the †bear-dogs, or †amphicyons. A third phylum (†*Didymictis* — †*Viverravus*) is by several authorities regarded as ancestral to the civet family, or viverrines, of the Old World, and a fourth (†*Oödectes*, †*Vulpavus*) as the forerunner of the kinkajous (*Potos*). Except for the connection with the dogs, the hiatus in time between the supposed ancestors and descendants is too great to permit any confident statements. It seems very probable, however, that the †Miacidæ represented the common stock, from which the fissipede families were all derived, directly or indirectly, though for most of them the details of the connection remain to be learned.

We find thus a group separating itself from the other †creodonts in the older Paleocene and gradually assuming fissipede characteristics, at the same time dividing into several phyla. In the upper Eocene this group passed almost imperceptibly into the Fissipedia, more obviously into the dog family, which, as we have seen, represents the central line of fissipede development.

2. †*Mesonychidæ*

This family displayed, in certain respects, the highest degree of specialization attained by any †creodonts, for they were the only ones which acquired cursorial limbs and feet. The †mesonychids were prevailingly, but not exclusively, a North American family and their range in time was through the Paleocene and Eocene.

The teeth, in the more advanced genera, had a curious mingling of primitive and specialized characters and none were sectorial in the proper sense of the word. The incisors were small, the canines large and bear-like and the premolars simple. The upper molars were very primitive, retaining the original tritubercular pattern, except that the two outer cusps were joined together, but the lower molars had lost all the internal cusps, which gave them a carnassial appearance; they were not sectorial, however, for their cusps wore directly against the upper teeth, not shearing past them, and were greatly blunted and worn down by use.

The last of the family was †*Harpagolestes*, of the Uinta and Bridger, one of the largest of the †creodonts. The skull, which was of disproportionate size, exceeded that of the Grizzly Bear; the upper profile of the skull had considerable resemblance to that of a bear in the steep forward descent at the fore head. The teeth were more reduced than in the other members of the family through the loss of the second premolar and third molar of the upper jaw. The skeleton is little known, but the humerus had a long and prominent deltoid crest and an epicondylar foramen.

In the middle Bridger stage were closely allied and very similar genera, †*Mesonyx* and †*Dromocyon* (Fig. 139, p. 269), which were like small, big-headed wolves, for the skull was as long as that of a Black Bear. Though the cranium was very long, the brain-chamber was very small and the sagittal crest enormously high, to afford surface for the attachment of the powerful jaw-muscles. The tympanic bullæ were ossified and had quite long, tubular entrances, a feature which has been found in no other †creodont skull. The face and jaws were also elongate, giving the head quite a wolf-like appearance. The neck and body were of moderate length, but the tail was extremely long, slender and whip-like.

FIG. 276. — Upper teeth, right side, of †*Mesonyx obtusidens*, showing the grinding surface.

The limbs and feet were more specialized than in any other †creodont and the changes were all in the direction of adaptation to swift running. The humerus was very smooth, with low ridges, and, alone among †creodonts, had in these genera no epicondylar foramen, though the femur retained the third trochanter. The radius was broad and so interlocked with the humerus as to prevent any rotation of the manus. The feet were four-toed and much resembled those of the modern dogs and hyenas. In each foot the metapodials were closely appressed and parallel, not spreading, but arranged in two symmetrical pairs, a longer median and shorter lateral pair, much on the artiodactyl plan; the ankle-bone (astragalus) also had an artiodactyl look, with its deeply grooved surface for the tibia and pulley-like lower end. The ungual phalanges were so short and broad as almost to suggest hoofs rather than claws. It is clear that the gait was as fully digitigrade as in a modern wolf and these were the only †creodonts of which this is known to be true. These were somewhat puzzling animals; the whole structure of the limbs and feet was that of cursorial types, but the broad, blunt claws do not suggest the running down and capture of prey, nor were the teeth those of savage killers. The speed may have been defensive, to escape from enemies, and the food may have been largely vegetable.

Ancestors of these Bridger genera have not been found yet in the Wasatch, a time when the family was represented by †*Pachyæna*, some of the species of which were very large, rivalling †*Harpagolestes*, which was descended from one or more of them. †*Pachyæna* had extremely massive teeth and was not improbably a carrion-feeder of hyena-like habits, and it retained the epicondylar foramen of the humerus and pentadactyl feet.

Much more primitive was †*Dissacus*, of the upper Paleocene, which was very probably the direct ancestor of both the Wasatch and the Bridger genera. The upper molars were substantially as in the latter, but the lower molars had the internal cusp of the primitive triangle, though the heel was trenchant, and had lost its inner cusps. The feet had five well-developed digits, which were arranged in spreading fashion, and the gait was plantigrade. The claws were longer, more pointed and much less hoof-like than in the Bridger genera. The Puerco genus †*Triisodon* may or may not have been directly ancestral to †*Dissacus;* at all events, it was very nearly what the desired ancestor must have been. The teeth were much less specialized than in †*Dissacus;* the tritubercular upper molars were broader and their external cusps were more separated, while in the lower molars the anterior triangle was made up of three nearly equal cusps and the heel was low and basin-shaped. The skull had an extremely narrow brain-case and a long, heavy sagittal crest.

The most interesting feature in the history of the †Mesonychidæ is the demonstrable derivation of the cursorial, digitigrade, four-toed and almost hoofed Bridger genera from the plantigrade, five-toed Torrejon genus, which had sharp claws. To all appearances, this family was the †creodont analogue of the hyenas.

3, 4. †*Arctocyonidæ and* †*Oxyclænidæ*

This second †creodont family which had no carnassial teeth has received the not very happily chosen name of †Arctocyonidæ, or "bear-dogs," though they were not related to either bears or dogs. The family was a very ancient one and has been found only in the Paleocene and lower Eocene (Torrejon and Wasatch) of North America and Europe. The molar teeth were very low-crowned and quadritubercular, with numerous small tubercles in addition to the four principal cusps, a pattern which was rather pig-like than bear-like. The Wasatch genus †*Anacodon*, known only from jaws and teeth, had reduced premolars, both in size and number, while in the Torrejon genus, †*Clænodon*, the premolars, though small, were present in full number. The skull was like that of †*Mesonyx* in the relative lengths of cranium and face, the very small size of the brain-case and the great prominence of the occipital and sagittal crests. The feet were pentadactyl and plantigrade and the claws were long, thin and pointed, and the ungual phalanges were not cleft at the tip, the only †creodont family, except the †Miacidæ, of which this was true.

Of the †Oxyclænidæ, very little is known and they may not have been †creodonts at all. They were quite small animals, with sharp-cusped tritubercular upper molars and lower molars with high anterior triangle and low heel. This is the type of dentition from which all the divergent †creodont types were doubtless derived. The family was Paleocene.

5. †*Hyænodontidæ*

This was the last of the †creodont families to survive, being quite common in the lower Oligocene of North America and Europe and in the upper Eocene of the latter also. The family became extinct in the upper Eocene of North America and the White River genera were not of native origin, but migrants from the Old World. One of the more abundant predaceous genera of White River times was the European †*Hyænodon;* it was represented by several species which ranged in size from a fox to a Black Bear. In this genus the dentition was somewhat reduced, the incisors often numbering $\frac{2}{2}$ and the molars constantly $\frac{2}{3}$; there were three pairs of carnassial teeth on each side, of which the pair formed by the second upper and third lower molar was the largest and most efficient, the other pairs being the first upper and second lower molar, the fourth upper premolar and first lower molar, the latter the smallest of the three. The upper molars had lost the internal cusp and the remaining, external portion consisted of a flattened-conical anterior cusp and a posterior trenchant ridge; the milk-teeth of †*Hyænodon,* as well as the permanent dentition of the ancestral genera, show that the anterior cusp was composed of the two external cusps of the primitive tritubercular tooth fused into one and that the trenchant ridge was a superadded element. The fourth upper premolar was a sectorial like that of the Fissipedia, but of an unfinished, ineffective sort. The third lower molar was very similar in shape to the carnassial of the cats and was composed of only two large, thin and trenchant cusps, which made a shearing blade, having lost the inner cusp of the primitive triangle and the heel. The first and second molars were like the third except in size and in retaining a vestige of the heel. The premolars were large and massive, almost hyena-like, which suggested the generic name. The canines were prominent and strong.

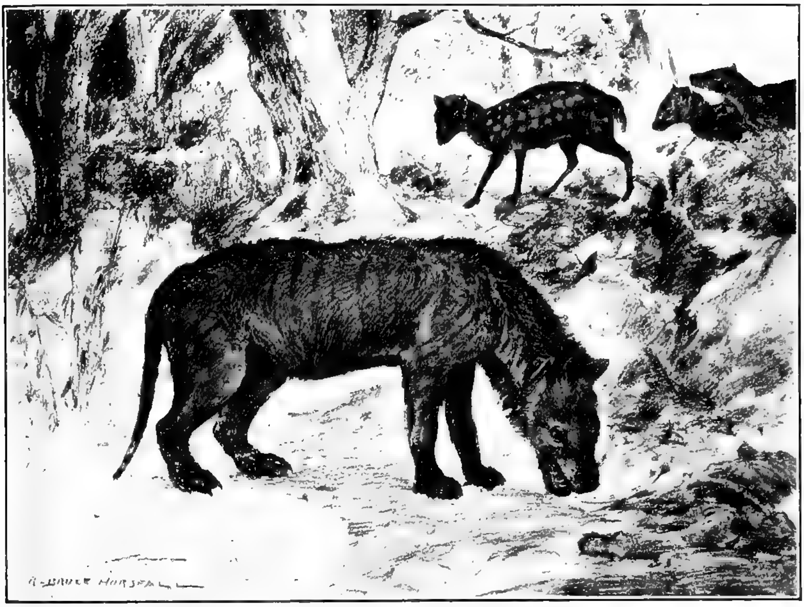

FIG. 277. — †*Hyænodon horridus*, a White River †creodont: in the background, †*Leptomeryx evansi*. Restored from skeletons in the American Museum of Natural History.

The skull, as in almost all †creodonts, was relatively very large, but in the various species there was considerable difference of shape; more commonly it was long and narrow, with elongate jaws, and was quite wolf-like in appearance, but in some of the species it was shorter and wider. The brain-case was more capacious and the brain more richly convoluted than in any other known †creodont, but the sagittal and occipital crests were very prominent. The neck was rather short, not equalling the head in length, the body elongate and the loins very muscular; the tail was fairly long and thick, but much less so than in most †creodonts. The limbs were short and, in most of the species, quite slender, though in some they were much stouter; the primitive features, such as the third trochanter of the femur, the epicondylar foramen of the humerus, the separate scaphoid, lunar and central in the carpus, were retained. The feet had five digits arranged in spreading fashion and were probably semi-digitigrade; the claws were so thick and blunt that they could hardly have served in seizing prey.

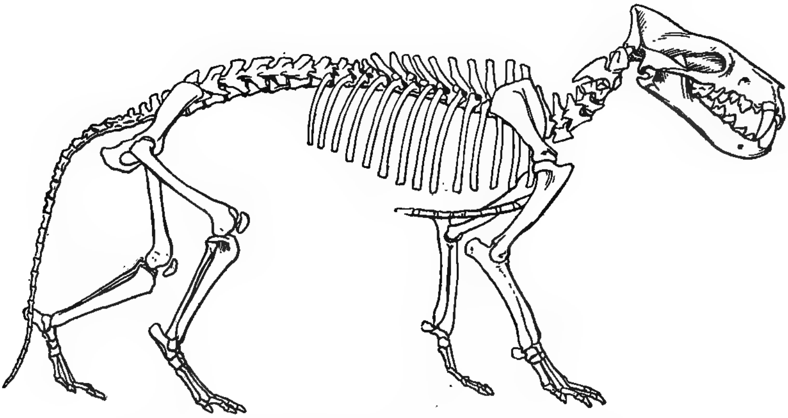

FIG. 278. — Skeleton of †*Hyænodon*. American Museum.

The restoration gives the animal quite a near resemblance to the modern hyenas and perhaps errs in making the likeness so close. From the whole structure of the skeleton and the form of the claws, it may be inferred that †*Hyænodon* was not a swift runner or very efficient in the capture of prey. While probably savage fighters, they doubtless subsisted chiefly as carrion-feeders and scavengers.

Another doubtfully distinct genus, †*Hemipsalodon,* was so closely like, if not identical with, the much better known European †*Pterodon,* that the latter may be taken in place of it. †*Pterodon* was similar in most respects to †*Hyænodon,* but distinctly less advanced, and though not the ancestor of the latter, serves to connect it with the older members of the series. †*Pterodon* did not, so far as we know, penetrate North America south of the Canadian border, occurring in the lower White River of Alberta. In this genus the upper molars retained a large internal cusp,

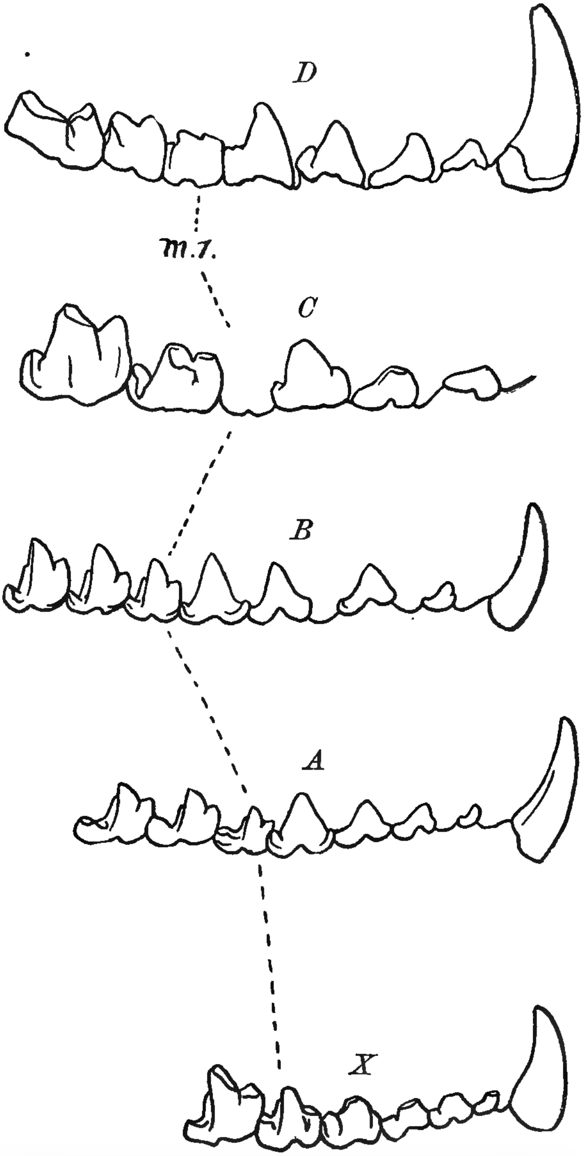

FIG. 279. — Lower teeth, right side, of †hyænodontids. *A,* †*Sinopa. B,* †*Tritemnodon. C,* †*Pterodon. D,* †*Hyænodon. X, Oxyæna.* The dotted line connects the first molar of each, lost in †*Pterodon.* See explanation of Fig. 280. (After Matthew.)

and the third molar, though small and not sectorial, had not been lost; the two external cusps were connate, but not completely fused together and the posterior ridge was not so well developed as in †*Hyænodon*, nor was the fourth upper premolar so nearly a carnassial. The lower molars were shearing blades, but distinct vestiges of the heel remained. So far as they are known, the skull and skeleton resembled those of †*Hyænodon*.

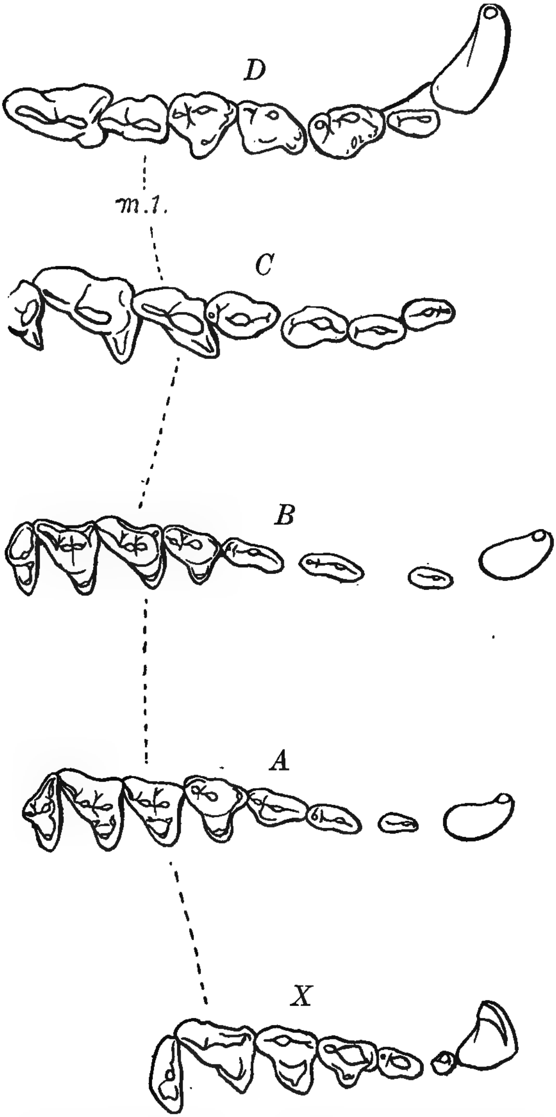

FIG. 280. —Upper teeth of †hyænodontids, right side, showing the grinding surface. *A*, †*Sinopa*, Wasatch and Bridger. *B*, †*Tritemnodon*, Bridger. *C*, †*Pterodon*, upper Eocene and lower Oligocene of Europe. *D*, †*Hyænodon*, White River. The dotted line connects the first molar of each. For comparison is added *X*, †*Oxyæna*, one of the †Oxyænidæ. *C* and *D* are much larger than the others, but all, except *X*, are reduced to the same length. (After Matthew.)

†*Hyænodon* and †*Pterodon* were evidently derived from a group of small †creodonts which, in the lower and middle Eocene, were spread

all over the northern hemisphere, but it is not yet possible to select from the crowd of allied genera those which formed the actual steps of descent. These small animals were numerous and varied and are far better known in North America than in Europe and it is not at all improbable that some of the lower Eocene genera migrated to the Old World and there gave rise, among other forms, to †*Hyænodon* and †*Pterodon*, which eventually returned to the land of their earlier ancestry. If confirmed, this will be an exceptionally interesting case of back and forth migration. However that may be, the American Eocene genera, †*Sinopa* and †*Tritemnodon*, illustrate very well the ancestry of the Oligocene genera, as they must have been similar to the actual progenitors.

FIG. 281. — †*Tritemnodon agilis*, a primitive †hyænodont, Bridger stage. Restored from a skeleton in the American Museum.

The first and most obvious difference from the Oligocene genera was the very much smaller size of the animals, few of the Eocene forms equalling a fox in height. The teeth were unreduced in number, and there were three pairs of carnassials. The first and second upper molars were not far removed from the primitive tritubercular form, but the two external cusps were close together and a small posterior cutting ridge was present; the third molar was progressively reduced in size. The three lower molars were carnassials of a rather imperfect kind and the first was the smallest of the series; the two outer cusps of the anterior primitive triangle formed the shearing blade and there was a basin-shaped heel. The skull was long, narrow and low and the cranial portion, despite the very small brain-case, was especially elongate, though face and jaws were also long; the sagittal crest was very prominent. The neck was of moderate length, the body long and slender and the tail extremely long. The short and delicate limbs were of very primitive character, but the radius had already lost the power of rotation; the feet had five spreading digits, armed with sharp claws. The †hyænodont relationships of these small animals are obvious in every part of their structure and yet, as would be expected, they were far less specialized. Probably, too, they were more active and successful hunters of prey, the smaller mammals and birds, less given to carrion-feeding. The line probably originated in the †Oxyclænidæ of the Paleocene.

6. †*Oxyænidæ*

The genera of this family had such feline characters that more than one writer has been misled into the belief that they were the ancestors of the cats. In this family there were two pairs of sectorial teeth, of which the larger pair was composed of the first upper and second lower molar, the smaller pair of the fourth upper premolar and first lower molar, as in the fissipedes. Of the three phyla within the family, the most specialized one ran a brief career, through the Wasatch, Wind River and Bridger, and then died out. The terminal member of this series, the Bridger genus †*Patriofelis*, had a skull as large as that of a lion, but the rest of the skeleton was not so large in proportion. The teeth were considerably reduced in number, the formula being: $i\frac{?}{2}, c\frac{1}{1}, p\frac{3}{3}, m\frac{1}{2}$, a loss of at least twelve from the primitive total of 44. The single upper molar was a large sectorial, which was formed much as in the †hyænodonts, the two external cusps connate, but not indistinguishably fused together, and a long, trenchant ridge behind, while the inner cusp had almost vanished. The second lower molar was very cat-like; its cutting blade was formed of two shearing cusps; of the inner cusp no trace was left, and of the heel merely a vestige. The first lower molar was smaller and less specialized, since it retained a small internal cusp and quite a large heel.

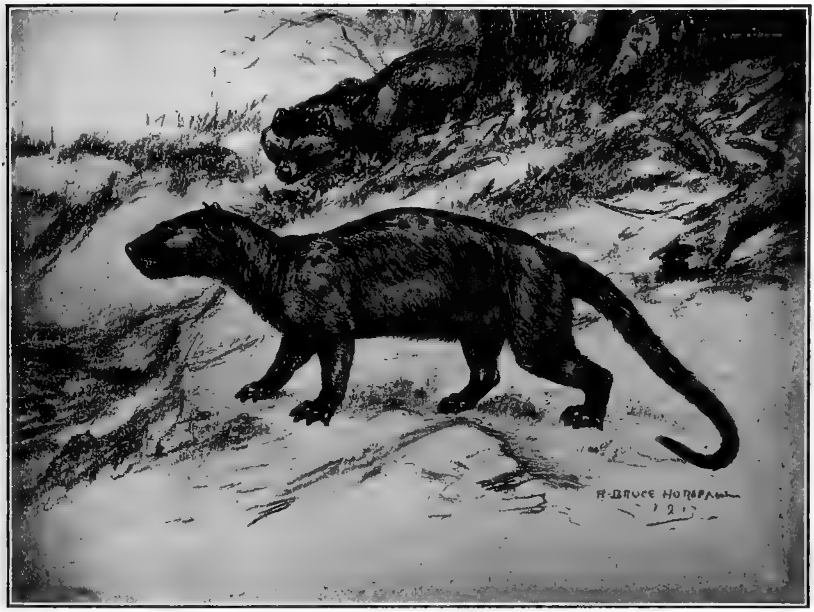

FIG. 282. — †*Patriofelis ferox*, Bridger stage. Restored from a skeleton in the American Museum.

The skull was very large and massive, with elongate cranium and shortened face, the muzzle broad and abruptly truncate, not tapering; the brain-case was exceedingly small, with very long and prominent sagittal crest; the zygomatic arches were extremely heavy and curved outward boldly, so that the head was very wide, notwithstanding the absurdly small brain-case. The lower jaw was very deep and heavy and the chin abruptly rounded, with almost vertical front. The very unusual massiveness of the zygomatic arches and the great development of the crests and ridges for the attachment of the jaw-muscles, and the short, heavy lower jaw, all indicate a degree of power in the biting and shearing apparatus such as occurred in no other known †creodont.

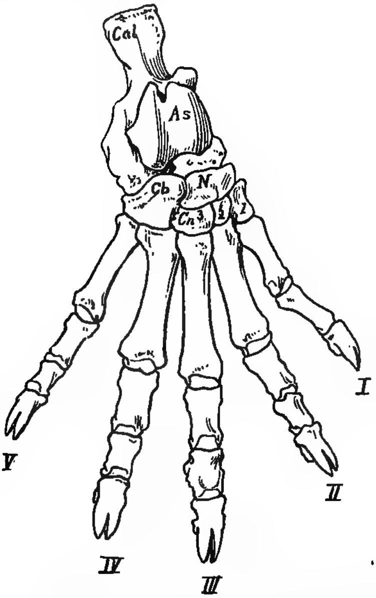

Fig. 283. — Right pes of †*Patriofelis ferox*. *Cal.*, calcaneum. *As.*, astragalus. *Cb.*, cuboid. *N.*, navicular. *Cn. 1, 2, 3*, internal, middle and external cuneiforms. (After Wortman.)

The neck was of medium length, while the body, though actually elongate, was rather short as compared with most other †creodonts; the loins were very heavy and must have been extremely powerful in the living animal; in this region the articulations between the successive vertebræ were more complex than in any other member of the suborder; resembling the structure found in certain artiodactyls. The ribs were long and thick, the chest deep and capacious. Even for a †creodont, the tail was long and uncommonly thick.

The limbs, especially the anterior pair, were short and very stout; the humerus had an immensely developed deltoid ridge, which extended down for two-thirds the length of the shaft, and a very prominent supinator ridge; the fore-arm bones, particularly the ulna, were heavy and the radius had but a limited power of rotation. The feet were short and broad, with five complete, spreading toes, ending in thick and blunt-pointed claws.

†*Patriofelis* was by far the most formidable of the Bridger Carnivora and, with the exception of †*Harpagolestes*, the largest. Its appearance must have been very curious, judged from the modern standpoint, with its disproportionately large, broad and rounded, leonine head, thick body and long, extremely heavy tail. The short, powerful limbs and broad feet must have given it something of the appearance of an otter. As in the case of so many other †creodonts, the combination of characters in the skeleton makes the question of habits a very puzzling one. The teeth had a form suited only to seizing and devouring prey, but the short legs and feet were not at all adapted to the swift movements, whether by long-continued running, or by stealthy approach and sudden leap, which are required in capturing agile prey, while the blunt claws could have rendered no service in holding a struggling creature. The form of the humerus and fore foot suggests burrowing habits, but it seems most unlikely that so large an animal could have lived in any such fashion. Terrestrial, arboreal and aquatic modes of life have all been suggested, and, all things considered, perhaps the least improbable conclusion is that †*Patriofelis* was more or less aquatic and preyed chiefly upon the fishes and turtles with which the Bridger waters abounded. This hypothesis of Dr. Wortman's is supported by the otter-like form of the animal. Whatever the principal kind of food was, it must have been something that greatly abraded the teeth, which in old animals were mere stumps.

The Wind River representatives of the series are known only from fragments, which, so far as they go, are not separable from †*Patriofelis*. On the other hand, the Wasatch genus, †*Oxyæna*, is fairly well understood. This genus was very like its Bridger successor, but differed from it in just such ways as would be expected in an immediately ancestral form, that is to say, in smaller size and less advanced specialization. The number of teeth was not so far diminished: $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{2}{2}$, $\times\,2 = 40$; the carnassial teeth were the same, but they were less effective; the fourth upper premolar and first upper molar had large inner cusps, and in the latter the postero-external trenchant ridge was shorter. The second upper molar, lacking in †*Patriofelis,* was a transversely placed ridge, which engaged the heel of the second lower molar. The latter tooth, though larger than the first molar, was much less completely trenchant than in †*Patriofelis* and retained a small internal cusp and quite large heel. The skull resembled that of the Bridger genus, but the face was not so much shortened, the zygomatic arches were not so widely expanded or so massive, the lower jaw was not so heavy, nor the chin so steep. The body was relatively longer and more slender, the ribs being thinner and the chest shallower; the tail was even longer, but not nearly so thick. The articulations of the lumbar vertebræ were less complex. Except for their greater length and slenderness the limbs and feet were nearly identical with those of †*Patriofelis.*

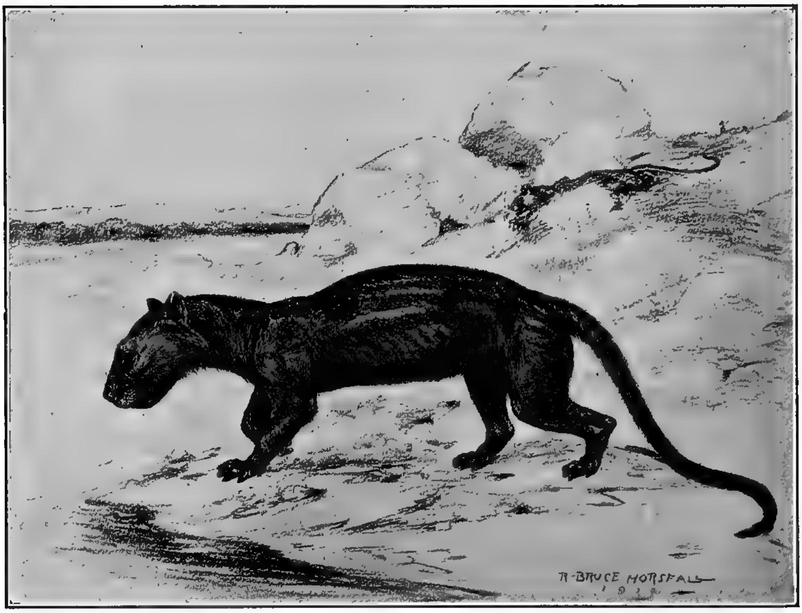

FIG. 284. — †*Oxyæna lupina,* Wasatch stage. Restored from a skeleton in the American Museum.

In appearance, †*Oxyæna* must have been merely a smaller, lighter and less powerful variant of the Bridger genus, and, no doubt, its habits of life were substantially the same; but in the details of structure were many minor differences, all of them in the direction of greater primitiveness in the more ancient animal.

The second phylum of the family was represented in the Uinta and Bridger stages by a group of small species, which were survivors of still more ancient and primitive progenitors of the family. In the typical genus, †*Limnocyon*, the dental formula was the same as in †*Oxyæna:* $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{2}{2}$, but the first upper molar had its two external cusps well separated and a much lower posterior cutting ridge, while the inner cusp was much larger. The second upper molar, though transversely placed, had all the elements of the primitive tritubercular tooth, the pattern from which all the varied types of †creodont upper molars were derived by the addition or suppression of parts. The two lower molars were very primitive, having a high anterior triangle of three cusps, forming an imperfect shearing blade, and a low heel. This dentition was on nearly the same plan as that of the small, contemporary †hyænodonts, but the emphasis of development, so to speak, was differently placed. In the †hyænodonts there were three pairs of sectorials and the best-developed pair was made up of the second upper and third lower molar; while in †*Limnocyon* the third molar was lost, and there were but two pairs of sectorials, of which the largest pair was the first upper and second lower molar, as was also true of †*Oxyæna* and †*Patriofelis.*

The skull of †*Limnocyon* had a much longer facial region, and more elongate and slender jaws than in the last-named genera, and the feet must have been quite different, with less spreading digits. †*Limnocyon* thus tends to indicate a common origin for the †oxyænids and †hyænodonts, though these common ancestors are still unknown.

A very interesting genus of this series, †*Machairoides,* of the Bridger, shows another imitation of the cats, the flanges of the lower jaw indicating sabre-like upper canines.

Another genus, †*Palæonictis,* of the Wasatch, found also in France, is sometimes referred to the †Oxyænidæ and sometimes made the type of a distinct family, but is too incompletely known for final reference. It had the same number of teeth as †*Oxyæna,* but the principal pair of carnassials was the fourth upper premolar and first lower molar, as in the Fissipedia, the first upper and second lower molar forming the subsidiary pair. The first upper molar was hardly sectorial at all; its two outer cusps were long, sharp-pointed cones, and the posterior cutting ridge was a mere tubercle. The skull had a short, cat-like face. The genus left no successors.

This concludes the long story of the Carnivora, so far as it has been recovered from the rocks. Incomplete as it is, and full of unsolved problems, it yet enables us to follow, somewhat vaguely, but with a general kind of accuracy, the development of the various modifications which characterized the different families and genera of the group.

The more ancient and primitive suborder, the †Creodonta, made its first recorded appearance in the lower Paleocene and was, no doubt, derived from Mesozoic ancestors, which cannot yet be distinguished among the very imperfectly understood mammals of that era. In the upper Paleocene, if not before, the †creodonts had spread over the northern hemisphere and had begun to diverge into a number of families, which continued to diverge more and more widely throughout the Eocene epoch, as they became more specialized and adapted to different habits of life. From the most primitive group, represented more or less accurately by the †Oxyclænidæ, may be traced the several lines of diverging adaptations incorporated in the various families, some of which had become distinctly recognizable in the lower Paleocene, others in the upper, while all were in existence in the lower Eocene. In one series, the †Mesonychidæ, the upper teeth underwent comparatively little change, while the lower ones lost the inner cusps, but no carnassials were formed. The face and jaws were elongated and the limbs and feet became adapted to cursorial habits, and the more advanced genera had four-toed, completely digitigrade feet, with blunt, almost hoof-like claws. A second series, the †Arctocyonidæ, likewise failed to develop sectorial teeth, the molars becoming quadritubercular, with many accessory tubercles, and assuming a bear-like or pig-like pattern, while the premolars were reduced in size. The pentadactyl feet had sharp claws.

In the †Oxyænidæ two pairs of carnassial teeth were formed, of which the larger and more effective pair were the first upper and second lower molar, the smaller pair the fourth upper premolar and first lower molar. The teeth were diminished in number, first by the loss of the last molar, then the suppression of the first premolar and finally by that of the third incisor and second upper molar; the remaining teeth were enlarged. The upper carnassial molar (the first) was formed by the approximation and partial fusion of the two external cusps and the addition of a trenchant ridge behind these, and by the reduction and eventual loss of the internal cusp, thus becoming more exclusively shearing in function. The second lower molar also lost the inner cusp and the heel, becoming remarkably cat-like in form; the first was similar, but less simplified. The face and jaws were greatly shortened, which, with the widely expanded zygomatic arches, gave the head a very cat-like appearance. The body and tail were long, the limbs short and thick, and the feet had spreading toes and blunt claws. Save for a notable increase in size and muscular power, the †oxyænids showed but little change within the family.

The †Hyænodontidæ differed from the †oxyænids in the retention of all or nearly all the teeth and in having three pairs of sectorials, of which the largest pair was the second upper and third lower molar, but resembled them in the mode of forming these sectorials and in the cat-like form of the inferior ones.

Although the actual line of descent was not through these genera, the series, †*Sinopa* — †*Tritemnodon* — †*Pterodon* — †*Hyænodon,* extending from the lower Eocene into the Oligocene, displays perfectly the successive steps in the transformation of the teeth. The skull underwent a corresponding series of changes, ending in long-faced, long-jawed, wolf-like forms, with larger brain-case than in any other †creodonts. The elongated form of body was retained, but the tail was reduced to moderate proportions. The limbs and feet did not change greatly, except in size and in the greater bluntness of the claws.

The †Miacidæ, if not actually referable to the Fissipedia, at least anticipated them in the mode of carnassial development. The upper molars changed very little from the primitive tritubercular plan, but the fourth upper premolar was enlarged and acquired a trenchant ridge behind the original single outer cusp. The lower molars were at first all alike, except in size, the first being the largest; they had the primitive pattern common to the earlier members of nearly all the †creodont families, of an elevated anterior triangle of three subequal cusps and low, basin-like heel. The first molar grew larger in the successive genera and, by the enlargement of the two external cusps of the primitive triangle and reduction of the inner one, gradually became an efficient sectorial, the fourth upper premolar keeping pace with it. In proportion as the first lower molar was elaborated, the second and third were reduced in size and the anterior triangle was lowered to the level of the heel, these teeth thus becoming tubercular. All the †Miacidæ were small animals, none attaining the stature of a fox, though some had heads as large. From this family, as was pointed out above, probably arose all of the Fissipedia, the history of which it is needless to repeat.

CHAPTER XV

HISTORY OF THE PRIMATES

THIS order embraces the lemurs, monkeys, man-like apes and Man, though in the general account Man will be omitted from consideration. The Primates are clothed in dense fur or shaggy hair. The teeth are always low-crowned and rooted and reduced in number, the incisors generally to $\frac{2}{2}$ and the premolars to $\frac{3}{3}$–$\frac{2}{2}$; the molars are trituberculate or quadrituberculate. The cranium is unusually capacious and the orbit is entirely encircled in bone. The tail varies much in length and may be entirely wanting. The bones of the forearm and lower leg are separate and the radius has much freedom of rotation, in correspondence with the grasping power of the hand. The pes is also a grasping organ and, with few exceptions, the thumb and great toe are opposable to the other digits; the bones of the wrist do not coössify and frequently the central is present. The feet are plantigrade and almost always pentadactyl and, with a few exceptions, have neither claws nor hoofs, but flat nails; the ungual phalanges are correspondingly modified and do not taper toward the free end, but expand at the tip. The Primates are characteristically arboreal in habit, but a few, such as the baboons, have become secondarily adapted to a terrestrial mode of life. They inhabit at present all the tropical regions of both hemispheres, Australia excepted. Extratropical North America has no existing member of the order and, so far as we know, has had none since the Eocene epoch. The most important of the genera of the western hemisphere are listed below.

Suborder LEMUROIDEA. Lemurs

I. †NOTHARCTIDÆ.
  †*Pelycodus*, low. and mid. Eoc. †*Notharctus*, Eoc.
II. †ANAPTOMORPHIDÆ.
  †*Anaptomorphus*, low. and mid. Eoc. †*Omomys*, mid. Eoc. †*Hemiacodon*, do.

Suborder ANTHROPOIDEA. Monkeys, Apes, Man

Section PLATYRRHINA

III. HAPALIDÆ. Marmosets.
  Hapale. Pleist. and Rec. *Midas*, Rec.
IV. CEBIDÆ. South American Monkeys.
  Cebus, Pleist. and Rec. *Alouatta*, Howling Monkeys, Pleist. and Rec. *Ateles*, Spider Monkeys. *Pithecia*, Sakis. *Cacajao*, Uakaris. *Nyctipithecus*, Douroucoulis. †*Eriodes*, Pleist. †*Homunculus*, Santa Cruz. †*Pitheculus*, do.

The existing Primates are divided into two suborders, Lemuroidea and Anthropoidea, which are quite clearly distinguished from each other, but the fossil forms largely efface the distinction.

SUBORDER LEMUROIDEA. LEMURS

The name *Lemur*, which Linnæus gave to a genus of this suborder, signifies in Latin a spectre or ghost and was probably suggested by the very strange appearance and nocturnal habits of these curious creatures. The term has been adopted as the English name for the group, as there was no vernacular word for it. The lemurs are very obviously the more primitive division of the Primates. Omitting for the present the extinct forms, the dental formula is usually: $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$, $\times 2 = 36$; the upper canine is a long, sharp, dagger-like tooth, but the lower one, in nearly all of the genera, is like an incisor and its place is taken by the anterior premolar; the premolars are simple, compressed and trenchant and the upper molars tritubercular. The skull usually has a long and tapering facial portion, so that the living head has some resemblance to that of a raccoon. The orbits almost always have a more or less lateral presentation, instead of being directed forward, as they are in the Anthropoidea; they are encircled in bone, but are not walled in by a bony funnel; the lachrymal bone is extended on the face and the foramen is outside of the orbit. The hind legs are longer than the fore; the humerus retains the epicondylar foramen and the femur has a third trochanter; the feet are plantigrade, almost always five-toed, with opposable thumb and great toe, and having a varying proportion of flat nails and sharp claws. The brain is of a primitive type and not much convoluted.

All the existing and most of the fossil lemurs are small animals, some quite minute, and only in the Pleistocene of Madagascar have large ones been found. They are chiefly nocturnal and arboreal in habits, and feed upon fruit and leaves, but vary their diet with insects, small reptiles, birds and eggs. Their present geographical distribution is very remarkable; more than two-thirds of the existing species are confined to Madagascar; the others are in tropical Africa, southern Asia and the Asiatic islands, as far east as Celebes and the Philippines. In the Eocene epoch they extended all over the northern hemisphere, but have not been found in any subsequent formation outside of their present range.

Lemurs occurred in the Uinta stage, but were much more abundant in the Bridger, of which the best-known genus is †*Notharctus*. These Eocene forms did not have the aberrant peculiarities of the modern lemurs, but departed less from the primitive stock common to both of the suborders. In †*Notharctus* the dental formula was: $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, $\times 2 = 40$, the dentition being reduced only to the extent of losing one incisor on each side above and below; the lower canine was not incisiform nor had the anterior premolar taken its place; the upper molars were quadritubercular, and in the lower ones the anterior triangle was hardly higher than the heel. The two halves of the lower jaw were coössified at the symphysis, and the femur had lost the third trochanter. It is not likely that †*Notharctus* was ancestral to any of the existing lemurs, but may have been to the numerous forms of the European upper Eocene.

The Wasatch genera are known from very fragmentary material, but it suffices to show that some of the genera, at least (*e.g.* †*Pelycodus*), were decidedly more primitive than those of the Bridger. The incisors had already been reduced to $\frac{2}{2}$, the well-nigh universal formula among the Primates; the upper molars were tritubercular, but with a minute fourth cusp beginning to appear, and in the lower molars the anterior triangle was elevated above the heel. The two halves of the lower jaw were separate.

The Paleocene has yielded nothing that can be positively referred to the Primates, but there was a group of genera (*e.g.* †*Indrodon*), known only from jaws and teeth, which have been variously assigned to the lemurs and the Insectivora and may have belonged to either order, or have represented the transition between them. This very uncertainty is in itself a significant fact, for it is another of the many examples of the way in which, at that early period, the mammalian orders were so approximated that it is often very difficult to distinguish them.

It was stated above that the distinction between existing lemurs and anthropoids was a very clear one, but to this statement there is one partial exception. The curious little Tarsier (*Tarsius spectrum*), an animal about the size of the Grey Squirrel, an inhabitant of the Malay Archipelago, is thus described by Mr. Beddard: "The ears are large and the eyes are extraordinarily developed. The fingers and toes terminate in large, expanded disks and are furnished with flattened nails, except on the second and third toes, which have claws. The tail is longer than the body and tufted at the end. . . . The Tarsiers are nocturnal and particularly arboreal; they live in pairs, in holes in tree stems and are mainly insectivorous in their food. . . . Like so many Lemurs, this animal is held in superstitious dread, which is the result of its most weird appearance."[1] The skull is more anthropoid in character than is that of any other lemur, the face being greatly shortened, the cranium enlarged and the orbit not merely encircled in a bony rim, but with a thin posterior wall of bone. There are also structural features in the soft parts, which are more anthropoid than lemuroid.

The particular interest which *Tarsius* possesses for the student of American mammals is its resemblance to the Wasatch genus †*Anaptomorphus*, the type of a family which was abundant and varied in the lower and middle Eocene. This genus was remarkably advanced in view of its great antiquity. The dental formula was: $i\frac{2}{2}$, $c\frac{1}{1}$, $p\frac{3}{3\text{-}2}$, $m\frac{3}{3}$, $\times 2 = 34\text{–}36$; in the upper jaw the premolars were bicuspid and the molars tritubercular, while the lower premolars were simple. The face was very much shortened; the orbits were very large and encircled in bone, but without the posterior wall. This produces a decided likeness to the Tarsier and is no doubt indicative of nocturnal habits. The cranium was remarkably large, and no other Wasatch animal had a brain-case so capacious in proportion to its size. A lemurine character was the position of the lachrymal foramen outside of the orbit. The two halves of the lower jaw were separate. It is hardly likely that these American lemurs were the actual ancestors of the anthropoids, but they closely represent what those ancestors must have been.

FIG. 285.—Head of monkey-like lemur (†*Anaptomorphus homunculus*) from the Wasatch. Restored from a skull in the American Museum.

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[1] F. E. Beddard, Mammals, London, 1902, pp. 550, 551.

SUBORDER ANTHROPOIDEA. MONKEYS, APES, MAN

The specifically human characters will be omitted in defining the suborder. The Anthropoidea are plantigrade, usually arboreal and pentadactyl, with opposable thumb and great toe and thus the pes is like a hand, hence the term "Quadrumana" formerly given to the apes and monkeys. Except in the South American marmosets (Hapalidæ) all of the digits have nails. The canines are generally more or less tusk-like, projecting above (or below) the level of the other teeth; the premolars mostly have two tubercles, like the human bicuspids, the upper molars have three, or more commonly four, cusps and the lower, four or five. Save in the baboons, the skull has a very short muzzle and a very large cranium, the capacity of which is relatively greatest in the large apes; the brain is large and complexly convoluted. The orbits present directly forward and are deep, funnel-shaped cavities for the lodgment of the eyeballs, a thin bony wall completely enclosing them externally and posteriorly. The lachrymal bone and its foramen are within the edge of the orbit; the nasal bones are short and have a nearly vertical position. The two frontal bones are early fused into one and usually there is no sagittal crest; the two halves of the lower jaw are coössified at the symphysis. The tail is extremely variable in length and may be three times as long as the body, or entirely absent. The fore and hind legs are sometimes of nearly equal length, but far more frequently the anterior pair are much the longer. The length of the legs in proportion to that of the body is very different in the different families. The humerus is much like that of Man and has no epicondylar foramen; the radius has a very complete movement of rotation; the femur never has the third trochanter and the lower leg bones are always separate. The thumb is more or less opposable to the other digits, except in the marmosets, but never so perfectly as in Man; the great toe is also opposable, but shorter than the other digits.

The Anthropoidea are divisible into two sections, the Catarrhina, characteristic of the Old World, and the Platyrrhina, confined to the New. In the Catarrhina, or Old World apes and monkeys, the dental formula is the same as in Man: $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $p\,\frac{2}{2}$, $m\,\frac{3}{3}$, $\times 2 = 32$; the nostrils are close together and the tympanic bullæ have tubular entrances. Many, but not all, have cheek-pouches opening into the mouth. The tail is never prehensile and, except in most of the large, man-like apes (Simiidæ), there are naked callosities on the buttocks. With these Old World forms we have no further concern, though it may be noted in passing that Dr. Schlosser has discovered in the Oligocene of Egypt certain monkeys (†*Parapithecus*) which he thus describes: "The number and structure of the teeth, character of the jaws and bodily size make complete the transition from the Anaptomorphids and Tarsiids to the Simiids."

Section Platyrrhina. South American Monkeys

In these animals the nostrils are separated by a broad septum, and there are always three premolars above and below ($p\,\frac{3}{3}$). The tail is frequently prehensile and serves as a fifth limb, being capable of supporting the whole weight of the body. There are no cheek-pouches and no callosities, and the tympanic bullæ have no bony tubes leading into them. The thumb is but partially, or not at all, opposable and in some genera is absent.

The New World monkeys are, in general, smaller and lighter than those of the eastern hemisphere; there are no very large ones and they are all arboreal and are confined to the forested parts of the Neotropical region, except the West Indies, which have none. The marmosets (Hapalidæ), the first of the two families into which the Platyrrhina are divided, are little creatures, no longer than squirrels, with long, non-prehensile tails. They are characterized by the dental formula: $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$, $m\,\frac{2}{2}$, $\times 2 = 32$, and are the only Primates which have no third molar above or below. The thumb is not opposable, though quite long, and the hallux, or great toe, is very small; they are thus deficient in grasping power. Instead of the flat nails common to all the other Anthropoidea, they have long, sharp claws. All other South American monkeys are included in the family Cebidæ which, in turn, is divided into four subfamilies. It is not necessary to consider these or do more than cite a few illustrative examples.

FIG. 286. — Common Marmoset (*Hapale*). — By permission of W. L. Berridge, London.

Some twenty species of the genus *Cebus* are distributed from Central America to Paraguay; they have long, prehensile tails completely covered with hair, and well-developed thumbs. The monkeys of this genus are familiar to every one, as they are largely used by organ-grinders. The spider-monkeys (*Ateles*) are so called because of the great length and slenderness of

FIG. 287. — Sapajou (*Cebus*). — By permission of the New York Zoölogical Society.

their limbs; the tail is very long and perfectly prehensile, naked on the lower side near the end, which improves its grasping power. The hand has lost the thumb, but is used very effectively as a hook. The species, ten or more in number, have a wider range than those of *Cebus* and extend from Uruguay to Mexico.

The howling monkeys (*Alouatta*, more commonly, but improperly, called *Mycetes*) are gifted with most unusual vocal powers. Mr. Bates says of them: "Morning and evening the howling monkeys make a most fearful and harrowing roar." "The brief evening chorus of animals then began, the chief performers being the howling monkeys, whose frightful unearthly roar deepened the feeling of solitude which crept on as darkness closed around us."[1] The tremendous volume of sound which these small creatures are able to produce is due to a resonating apparatus, formed by the great inflation of one of the hyoid bones (see p. 67), normally the bony support of the tongue. The tail is long and prehensile, with the end naked beneath; the thumb is well developed.

The sakis (*Pithecia*) have long and non-prehensile tail and complete thumb. The species of this genus have a remarkable kind of distribution, which is rare among mammals, though not infrequent for insects and birds. Each species is limited to a definite area of forest along the Amazon and its tributaries, which it occupies to the exclusion of the others. The uakaris (*Cacajao*) are distinguished by the tail, which is much shorter than in any other of the Cebidæ.

Finally, may be mentioned the nocturnal douroucoulis (*Nyctipithecus*), which have long, non-prehensile tail and well-developed thumb. Mr. Bates describes them thus: "A third interesting genus of monkeys, found near Ega, are the Nyctipitheci, or night apes, called Ei-á by the Indians. . . . They sleep all day long in hollow trees and come forth to prey on insects and eat fruits only at night. They are of small size,

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[1] Bates, Naturalist on the Amazons, London, 1875, pp. 32, 140.

the body being about a foot long and the tail fourteen inches, and are thickly clothed with soft gray and brown fur, . . . and the eyes are large and yellowish in colour, imparting the staring expression of nocturnal animals of prey." [1]

The Brazilian caverns have preserved the remains of many Pleistocene monkeys belonging to existing South American genera, and even several modern species are represented, while others are extinct. There is also one extinct genus (†*Eriodes*), a larger animal than any of the existing Neotropical monkeys. The Pampean deposits of Argentina, on the other hand, have yielded no remains of Primates, nor is this surprising, for the Pampas would seem to have been open plains in the Pleistocene, as they are to-day. Between the Pleistocene and the Santa Cruz Miocene there is a long gap in the history. It is true that some bones have been found in the Pliocene of Monte Hermoso which have been referred to the Primates, but they are too few and imperfect to be of any real assistance in the inquiry.

In the Santa Cruz beds fossil monkeys are very rare, but that they were present in Patagonia at all, is strong evidence that the climate was then far milder than it is at present. These were essentially members of the modern family Cebidæ. The best-known genus, †*Homunculus*, retained a few primitive characters, which the existing genera have lost. For example, the premolars were relatively smaller and of simpler form and the humerus had the epicondylar foramen, though the femur no longer had the third trochanter. The radius was very modern in form and evidently could rotate freely upon the humerus.

No monkeys have been found in the Deseado formation, though too much stress should not be laid upon this fact, because of the general scarcity of small animals in those beds. But the same is true of the still more ancient stages; despite an abundant and varied fauna of small mammals, they have

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[1] Bates, Naturalist on the Amazons, London, 1875, pp. 332, 333.

yielded no Primates, nor anything which could be seriously regarded as ancestral to them. The facts are essentially the same as we have found them to be with reference to the South American rodents and insectivores. All three of these orders appeared suddenly and unheralded in the Deseado (Rodentia) or Santa Cruz (Insectivora, Primates), and all of them were allied to African or European rather than to North American types. If we may assume the existence of a land-connection with Africa to account for the remarkable distribution of the hystricomorph rodents, the same connection will equally well explain the introduction of the Primates into South America.

Concerning the relations of the Old and New World monkeys, Mr. Beddard remarks: "Not only are these two groups of the Primates absolutely distinct at the present day, but they have been, so far as we know, for a very long time, since no fossil remains of Monkeys at all intermediate have been so far discovered. This has led to the suggestion that the Monkeys are what is termed diphyletic, *i.e.*, that they have originated from two different stocks of ancestors. It is hard, however, to understand on this view the very great similarities which underlie the divergences that have just been mentioned. But, on the other hand, it is equally hard to understand how it is that, having been separated from each other for so long a period, they have not diverged further in structure than they have." [1]

The fossil monkeys of the Santa Cruz beds show that, as a matter of fact, the South American Primates have undergone little change in the essentials of structure since that remote period, and thus is removed this objection to the conclusion that the Platyrrhina and Catarrhina were derived from a common ancestry. In a certain sense also, the discovery of †*Parapithecus* in Egypt has diminished the gap between these two sections of the Anthropoidea. The evidence, though by no means conclusive, is distinctly in favour of the derivation of the South American monkeys from Old World ancestors.

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[1] Beddard, *op. cit.*, pp. 555, 556.

The Catarrhina have developed and advanced from the point of divergence far more than have the South American forms, which have changed relatively little since their invasion of the Neotropical region. So far as has been ascertained, South America never had any of the lemurs.

MAN IN THE WESTERN HEMISPHERE

Though to most people this is undoubtedly the most interesting chapter of all the mammalian history, little space can be given to it here, for the reason that the subject belongs rather in the domain of Anthropology and Ethnology than in that of Palæontology. There can be no question that Man originated in the eastern hemisphere and at a very remote period; abundant remains of his handiwork and of himself have been found in Europe as far back as the early Pleistocene, and recent discoveries in England have increased the already known length of the human habitation of Europe. So primitive and ape-like were some of these ancient men that they have been named as species (*Homo †neanderthalensis* and *H. †heidelbergensis*) distinct from the existing *H. sapiens*. Recently discovered and very ancient remains in England have even been referred to a separate genus, †*Eoanthropus*.

As has been repeatedly pointed out in the preceding chapters, America received numerous successive waves of mammalian immigrants during the Pleistocene epoch, at a time when there was a broad land-connection between North America and Asia, where now is Bering Strait; and to this late connection is due the fact that the Boreal zone of North America (see p. 150) is zoölogically a part of the Old World and forms a division of the Holarctic region. Now, there is no known reason why Man, whose powers of dispersal are so superior to those of any other mammal, should not have accompanied these migrations, and it is entirely possible that he actually did so, but the fact has not been demonstrated. It is true that discoveries of Pleistocene Man have been frequently reported from both North and South America, but these have not stood the test of critical examination, though such examination has by no means disproved the presence of Pleistocene Man in America.

Dr. A. Hrdlička has recently concluded a series of exhaustive studies of the bones of early Man in both North and South America and of the localities where these bones were found. For both continents he has reached a negative result. As to North America he says: "Thus far on this continent no human bones of undisputed geologic antiquity are known."[1] For South America the result is the same. "A conscientious, unbiased study of all the available facts has shown that the whole structure erected in support of the theory of geologically ancient man on that continent rests on very imperfect and incorrectly interpreted data and in many instances on false premises, and as a consequence of these weaknesses must completely collapse when subjected to searching criticism." "The conclusions of the writers with regard to the evidence thus far furnished are that it fails to establish the claim that in South America there have been brought forth thus far tangible traces of either geologically ancient man himself or any precursor of the human race.

"This should not be taken as a categorical denial of the existence of early man in South America, however improbable such a presence may now appear."[2]

On the other hand, the coexistence in North America of Man with several extinct species of mammals has been made extremely probable, if not certain. One of the most striking and best authenticated cases of this was the discovery by Professor Williston in western Kansas of a flint arrowhead beneath and in contact with the skeleton of the extinct *Bison †occidentalis*. Professor Russell found in lake deposits of

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[1] A. Hrdliĉka, Smithsonian Institution, Bureau of Ethnology, Bulletin 33, 1907, p. 98.

[2] *Ibid.*, Bulletin 52, 1912, pp. 385, 386.

Nevada an obsidian spearhead in association with the bones of an elephant or †mastodon, and other such instances have been reported. In these cases the doubt is as to the geological antiquity of the "finds," for the implements are of the type made by the pre-Columbian Indians.

In brief, there is no convincing evidence that either North or South America was ever inhabited in prehistoric times by races of men different from those first encountered by the European discoverers.

CHAPTER XVI

HISTORY OF THE EDENTATA

As here employed, excluding the so-called edentates of the Old World, the Edentata form a highly variegated, but natural, assemblage of related forms. The order is at present exclusively American and almost confined to the Neotropical region, an armadillo which extends into Texas being the sole exception. These animals are so peculiar and so isolated from other mammals, that it has been proposed to treat them as a separate subclass; and there is much to be said in favour of this procedure, though it would perhaps be premature, until more is learned concerning these most curious and exceptional animals. In the subjoined table only the more important and better known genera are included.

Series PILOSA. Hairy Edentates

Suborder TARDIGRADA. Tree-Sloths

I. Bradypodidæ.
Bradypus, Three-toed Sloth, Rec. *Cholæpus*, Two-toed Sloth, Rec.

Suborder VERMILINGUA. Anteaters

II. Myrmecophagidæ.
Myrmecophaga, Ant-Bear, Rec. *Tamandua*, Lesser Anteater, do. *Cyclopes*, Tree Anteater, do.

Suborder †GRAVIGRADA. †Ground-Sloths

III. †Megatheriidæ.
†*Megatherium*, Plio. and Pleist., S. A.; Pleist., N. A. ? †*Prepotherium*, Santa Cruz. ? †*Planops*, do.

IV. †MYLODONTIDÆ.

†*Mylodon*, Plio. and Pleist., S. A.; Pleist., N. A. †*Paramylodon*, Pleist., N. A. †*Grypotherium*, Pleist., S. A. †*Pseudolestodon*, Plio. and Pleist., S. A. †*Scelidotherium*, do. †*Nematherium*, Santa Cruz. †*Analcitherium*, do.

V. †MEGALONYCHIDÆ.

†*Megalonyx*, Pleist., N. A. †*Nothrotherium*, Pleist., S. A. †*Megalocnus*, Pleist., Cuba. †*Hapalops*, Santa Cruz. †*Schismotherium*, do. †*Pelecyodon*, do. †*Megalonychotherium*, do. †*Protobradys*, Casa Mayor.

Series LORICATA. Armoured Edentates

Suborder DASYPODA. Armadillos

VI. DASYPODIDÆ.

Dasypus, 6-, 7- and 8-Banded Armadillos, Pleist. and Rec., S. A. *Cabassous*, 11-Banded Armadillo, do. *Priodontes*, Giant Armadillo, do. *Tolypeutes*, Apar, Rec., S. A. *Zaëdyus*, Pygmy Armadillo, do. *Scleropleura*, do. *Chlamydophorus*, Pichiciago, do. *Tatu*, 9-Banded Armadillo, Pleist. and Rec., S. A.; Rec., Texas. †*Eutatus*, Plio. and Pleist., S. A. †*Chlamydotherium*, do. †*Proeutatus*, Santa Cruz. †*Prozaëdius*, Deseado and Santa Cruz. †*Prodasypus*, do. †*Stegotherium*, Santa Cruz. †*Meteutatus*, Deseado. †*Sadypus*, do. †*Amblytatus*, do. †*Præuphractus*, do.

VII. PELTEPHILIDÆ.

†*Peltephilus*, Deseado and Santa Cruz.

VIII. INCERTÆ SEDIS.

†*Metacheiromys*, mid. Eoc., N. A.

Suborder †GLYPTODONTIA. †Glyptodonts

IX. †GLYPTODONTIDÆ.

†*Glyptodon*, Plio. and Pleist., N. and S. A. †*Dœdicurus*, Pleist., S. A. †*Panochthus*, do. †*Sclerocalyptus*, Plio. and Pleist., S. A. †*Glyptotherium*, mid. Plio., N. A. †*Propalæohoplophorus*, Deseado and Santa Cruz. †*Cochlops*, Santa Cruz. †*Eucinepeltus*, do. †*Asterostemma*, do.

In the section Pilosa, which includes the sloths (Tardigrada), anteaters (Vermilingua) and the extinct †ground-sloths (†Gravigrada), the skin is thickly clothed with long hair, and in the Loricata, armadillos and †glyptodonts, the head, body, tail and legs are more or less completely encased in an armour of bony scutes covered with plates of horn, but with some hairs also.

The name Edentata (toothless) is not very happily chosen, for only the anteaters are quite toothless. Almost all the genera have no teeth in the front of the mouth and the teeth are nearly always alike, so that the distinction of regions among them is entirely a matter of position in the jaws. In the tree-sloths and many †ground-sloths the foremost tooth in each jaw is a more or less enlarged, canine-like tusk. The teeth are always rootless, growing from permanent pulps, and are without enamel, made up of dentine, which is sometimes homogeneous and sometimes in layers of different hardness, and with a covering of cement, usually thin and film-like. The number of teeth varies from $\frac{4}{4}$ to $\frac{10}{10}$ or more, and their form usually approximates a simple cylinder, worn off flat at the end, though the ends may be bevelled or grooved, differences which are in no way due to pattern but simply to the mode of wear. In the †glyptodonts the teeth were divided by deep vertical grooves into two or three pillars, connected by narrow necks. In most of the edentates there is no change of teeth, the milk-dentition having been completely suppressed, but in the 9-Banded Armadillo (*Tatu*) each of the permanent teeth is preceded by a two-rooted milk-tooth, and some other armadillos have milk-teeth.

The skull varies much in form and proportions, according to the character of the food and method of feeding. The tree-sloths and †ground-sloths have short, rounded heads; in the †glyptodonts, the skull was short and remarkably deep vertically; while the armadillos have long, shallow heads, with tapering muzzle, the length and slenderness of which differ in the various genera. In the anteaters the skull is extraordinarily elongate and slender. The sagittal crest is seldom present at all and never prominent. The zygomatic arch may be complete or interrupted; in the tree-sloths, †ground-sloths, †glyptodonts and some extinct armadillos, there is a descending, plate-like process given off beneath the eye.

The backbone displays some of the most remarkable peculiarities of the order. The neck in the tree-sloths has eight or nine vertebræ, the only instances known among mammals in which the normal number of seven is departed from. In the armadillos and †glyptodonts several of the neck-vertebræ are coössified into a single piece, but the atlas is always free, so as to permit the movements of the head. In the posterior part of the dorsal and in the lumbar region the articulations between the successive vertebræ are by far the most complex and intricate known among mammals; in the tree-sloths these have degenerated, though still plainly indicated. In the †glyptodonts, which were covered with a huge, tortoise-like carapace, mobility of the backbone was needless, and so all of the dorsal vertebræ were united into one long piece and the lumbars were coössified with one another and with the sacrum. The sacrum consists, throughout the order, of a very large number of vertebræ and is attached to the hip-bones at two different points, instead of only one, as in other mammals. The tail varies much in length and thickness; in the tree-sloths it is extremely short and in the anteaters very long and bushy, prehensile in the arboreal members of the group; in the †ground-sloths, especially the gigantic forms, it was of immense thickness; while in most of the †glyptodonts a varying number of the terminal vertebræ were fused together. The sternal ribs are better developed than in any other mammals, and in the anteaters and †ground-sloths they articulate with the breast-bone by regular synovial joints, and each rib has head and tubercle like a vertebral rib.

In the limbs and feet there is great variety, according to the manner of their employment. The shoulder-blade has a very long acromion and very large coracoid, which long remains separate from the scapula; collar-bones are very generally present, though often in much reduced condition. The hip-bones have in the tree-sloths, †ground-sloths and †glyptodonts a much expanded anterior element, which in the other groups is narrow. The humerus usually has very prominent deltoid and supinator ridges and epicondylar foramen; the fore-arm bones are always separate, and there is generally much freedom of rotation of the manus. In the wrist there is no distinct central and usually there are the ordinary eight separate bones. The tibia and fibula are frequently coössified. The tree-sloths, which lead most strictly arboreal lives and are almost helpless on the ground, are unique among mammals in that the body is habitually *suspended* from the limbs, not carried upon them; the feet are curved hooks, which fit over the tree-branches and support the weight without muscular exertion. The limb-bones are very long and slender, the claws long, curved and sharp, and the metapodials of each foot, two or three in number, are fused into a single mass. In the †ground-sloths there was much change in foot-structure during the course of their recorded development; they were usually five-toed and the feet were armed with one or more great claws; the later and larger representatives of the suborder walked upon the outer edge of the feet.

The armadillos, which are largely burrowers, have five-toed feet and long, heavy, pointed claws, but in some of them the pes has a varying number of flat, hoof-like nails. The immense †glyptodonts had very short, broad feet, shod with hoofs, which, in some of the genera, were longer and more claw-like in the manus.

The recorded history of the edentates was developed almost entirely in South America. In the Casa Mayor formation there were numerous armadillos, but as only scutes of the carapace have been found, little is known of them. The †ground-sloths (†*Protobradys*) have been reported, but from such imperfect material that the reference is uncertain. The first assuredly determinable members of this suborder were in the Astraponotus beds and, associated with them, the most ancient known †glyptodonts. In the Deseado stage were many armadillos, some of them extremely peculiar, several †glyptodonts and †ground-sloths, some species of the latter very large. Edentates were far more numerous and varied in the Santa Cruz than in any of the preceding stages. Tree-sloths and anteaters have both been reported, but the evidence is insufficient, though there can be little doubt that these suborders had begun their separate existence in some part of South America other than Patagonia. The three families of †ground-sloths were already distinguishable, though much less clearly separated than they afterwards became; none of them were large animals, smaller even than some of the Deseado species and veritable pygmies in comparison with the giants of the Pliocene and Pleistocene. The †glyptodonts were likewise far smaller than their Pliocene and Pleistocene successors and in several respects more primitive, approximating the armadillos more closely; nor was there any such variety of forms as in the later stages. The armadillos were extremely numerous and varied; they all belonged to extinct genera and most of them apparently have no descendants at the present day. The tropical forests of Brazil and the Guianas must then, as now, have swarmed with mammals which did not extend their range to Patagonia and of which we consequently have no record. No doubt, it was in these forests that the ancestors of most modern armadillos, as well as of the tree-sloths and anteaters, lived in Miocene times.

Pliocene edentates were of the same suborders as those of the Santa Cruz, but far larger in size. Most of them are known only from very incomplete specimens, but the Pleistocene has yielded an enormous mass of beautifully preserved material. Of the tree-sloths and anteaters, only questionable remains have been found. That these tropical and forest-loving animals should not have occurred in the open Pampas of Argentina is not surprising, but it is difficult to account for their absence from the extremely rich cave-faunas of Brazil. Nearly all the existing genera of armadillos have been obtained, and with these were associated several extinct genera, some of them (†*Chlamydotherium*, †*Eutatus*) relatively huge, as large as tapirs. There was a wonderful variety of †glyptodonts, most of them enormous creatures, of which no less than five genera have been collected in Argentina and Brazil, and the †ground-sloths were even more numerous and varied. Nine genera, with many species, of these great beasts, which ranged in size from an elephant to a tapir, are already known and no doubt the list is still incomplete. These †glyptodonts and †ground-sloths must have been among the most conspicuous elements of the Pleistocene fauna.

Aside from certain problematical Eocene forms, the first North American edentates, which were immigrants from the southern continent, appeared probably in the middle Miocene of Oregon in the form of †ground-sloths, but the specimen, as well as a similar one from the lower Pliocene of Nebraska, is not sufficiently complete for positive reference. In the middle Pliocene the †ground-sloths and †glyptodonts were unquestionably present, and in the Pleistocene these two sub-orders were numerously and conspicuously represented. Three or four genera of the huge, elephantine †ground-sloths co-existed in Pleistocene North America. †*Megalonyx* was abundant in the forested regions east of the Mississippi, from Pennsylvania southward, and on the Pacific coast; †*Mylodon* was transcontinental in distribution; while †*Megatherium* was apparently confined to the southern states. While all three genera undoubtedly originated in South America, †*Megalonyx* has not yet been found in that continent.

This genus was originally named by President Jefferson in 1805 from an ungual phalanx found in a cave in Virginia, and he imagined that it belonged to a colossal lion which must still be living in the mountains of western Virginia. This was deduced from the assumption that no species could become extinct, and the passage is of interest as showing the prevalent belief of the time, although Cuvier had already demonstrated that many species had actually been extinguished. The passage is as follows: "The movements of nature are in a never ending circle. The animal species which has once been put into a train of motion is still probably moving in that train. For, if one link in nature's chain might be lost, another and another might be lost, till this whole system of things should evanish by piece-meal."

The †glyptodonts were also southern in distribution, and only very imperfect remains of them have yet been recovered from the North American Pleistocene, quite sufficient, however, to make the identification certain.

There were several genera of rather small †ground-sloths in the Pleistocene of Cuba. The best known of these, †*Megalocnus*, had several peculiarities of structure, but was plainly a member of the †Megalonychidæ. The ancestors of this genus probably invaded Cuba in the Pliocene, when the island was joined to Central America.

SUBORDER †GRAVIGRADA. †GROUND-SLOTHS

As the †ground-sloths would appear to have had a more central position within the order than any of the other groups, our study of development may well begin with them. In the Pleistocene there were three families of these gigantic brutes, which ranged through the western hemisphere from Pennsylvania and California to Patagonia. Unfortunately our knowledge of the developmental stages within the different families is very unequal, and it is therefore impracticable to do more than sketch the changes of the suborder as a whole and in a general way. In the successive geological stages the proportionate representation of the different phyla varied greatly; in the South American Pliocene and Pleistocene the †Mylodontidæ and †Megatheriidæ were the abundant forms, while the †Megalonychidæ were but scantily represented. In the Santa Cruz Miocene, on the other hand, the overwhelming preponderance was with the †Megalonychidæ, the other two families being comparatively rare and incompletely known. From the still more ancient formations, the material so far collected is so fragmentary that family distinctions have little meaning. After all, there was no very wide range of variation among the contemporary members of the three families, and the differences were principally in size, in the form and number of the teeth, the shape of the skull and the number of digits; in essentials they were all much alike.

The genus †*Megatherium* (Fig. 122, p. 220) included the largest and most massive members of the suborder, †*M. americanum* being as large as an elephant, but very differently proportioned, as it was much longer and lower in stature, owing to the shortness of the extraordinarily heavy limbs; some of the skeletons measure 20 feet or more in length. The teeth, which were $\frac{5}{4}$ in number, formed an uninterrupted series on each side; all had the same quadrate form and by abrasion were worn into two transverse ridges, formed by the meeting of the harder dentine with the thick coating of cement. The result was a form of tooth which much resembled the lower molars of a tapir, but it was not a tooth-pattern in any proper sense of the word, being due entirely to the mode of wear.

The skull was very small in proportion to the huge body and was low and narrow in shape; the cranium had a broad, flat roof, without sagittal crest; the orbit was completely encircled in bone, and the descending process of the zygomatic arch beneath the eye was very long and conspicuous. The nasals were short, and the slender, toothless premaxillaries projected far in front of them, which makes the presence of some sort of a proboscis likely. The lower jaw had a long, narrow, spout-like symphysis, which was abruptly rounded at the free end, not pointed; below the teeth, the lower margin of the jaw was very strongly convex, descending in a great flange. The neck was short, the body very long and enormously heavy, as was also the tail. The immense shoulder-blade had a very long acromion, which curved forward and inward, fusing with the coracoid and forming a bony loop or bridge. The hip-bones had the anterior element (ilium) enormously expanded transversely, so as to support the huge mass of viscera in the semi-erect position which the animal, it is believed, frequently assumed in feeding. Collar-bones were present.

The fore limb was very much more slender than the hind, but of nearly the same length. The humerus had a comparatively slender upper portion and extremely broad lower end, due to the great development of the internal epicondyle and supinator ridge; there was no epicondylar foramen. The radius evidently had the power of very free rotation upon the humerus. The femur was short, flattened antero-posteriorly, but excessively broad and heavy, and had no third trochanter. The tibia and fibula were likewise short and very massive and were extensively coössified at each end, leaving but a short interspace open between the bones. The very peculiar feet were so connected with the limb-bones, that the animal must have walked upon the outer edge of the foot, somewhat as the existing Ant-Bear (*Myrmecophaga jubata*) uses the fore foot. The manus had four functional digits, the first being a mere vestige; the fifth, upon which the weight rested in walking, had two very small phalanges and no claw, while the second, third and fourth had long, sharp claws. The pes had but three functional digits, for the first and second were reduced to rudiments; digit III had an enormous claw and of this digit the metatarsal was short and very heavy and the first two phalanges were fused together; the two external digits, Nos. IV and V, had no claws. The astragalus had a very peculiar shape, made necessary by the application of the external border of the foot to the ground and thus in both fore and hind feet the great claws were turned inward and, in the case of the pes, it must have been impossible to rest the sole upon the ground. The heel-bone was enormous and club-shaped and formed the hinder portion of the weight-carrying outer edge of the foot.

Almost all who have studied the structure of this extraordinary beast are agreed as to its habits. That it fed principally, if not exclusively, upon leaves, is indicated by the teeth. The general opinion as to its manner of life is well summed up by von Zittel: "The hip-bones, hind legs and tail are characterized by enormous strength. The entire structure of the extremities proves that the gigantic sloth could move over the ground but slowly and clumsily; on the other hand, the fore limbs served as grasping organs and were presumably employed to bend down and break off twigs and branches and even to uproot whole trees, while the weight of the body was supported upon the hind legs and tail."[1] It would be quite absurd to suppose that such ponderous animals could have been climbers or burrowers, hence the function of the enormous claws, especially the single one of the pes, is not obvious, though they may have been merely the weapons of the otherwise defenceless monsters. The great claw in the fore foot of the Ant-Bear is a terrible weapon, with which the creature vigorously and successfully defends itself against dogs, and it may even be dangerous to men, if incautiously molested.

†*Megatherium* had no bony scutes, or other ossifications in the skin, so far as is known, and was probably covered with long and coarse hair, as is known to have been the case in another †ground-sloth.

Less specialized in many respects than the †megatheres was †*Mylodon,* type of a family which was numerously and variously represented in the Pleistocene of South America, much less so in that of North America †*Mylodon* was smaller and lighter, being from $\frac{1}{3}$ to $\frac{1}{4}$ smaller in linear dimensions than †*Megatherium,* and the contemporary †*Scelidotherium* was no bigger than a tapir. The teeth numbered $\frac{5}{4}$ and the anterior one above and below had a somewhat tusk-like form; the others were worn off evenly, with nearly horizontal grinding surface, but a vertical groove on the inner side gave them a subtriangular, lobate form. The skull was short and broad, with flat top, and orbit only partially enclosed behind; the premaxillaries were very short and the muzzle very broad and

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[1] K. von Zittel, Handbuch der Palaeontologie, Bd. IV, p. 132.

abruptly truncated, the nasal opening very large. The lower jaw had a straight inferior border, a short, very wide and shovel-shaped symphysis and square chin. Nothing indicates a proboscis, and the head must have been very different from that of †*Megatherium.*

Within the family of the †mylodonts there was some variety in the dentition and more in the shape of the skull. In †*Lestodon,* for example, the first tooth in each jaw was a large, sharp-pointed tusk, the muzzle was greatly broadened, and the whole animal was larger. †*Scelidotherium,* the smallest Pleistocene member of the family, had a much narrower and more elongate skull than the others. In †*Glossotherium,* which also had an elongate skull, there was an arched bony bridge connecting the anterior end of the nasal bones with the premaxillaries and dividing the nasal opening into two parts.

The neck, body and tail of †*Mylodon* did not differ materially from those of †*Megatherium,* except in being smaller and less massive. The fore limb was relatively somewhat shorter and much stouter, but otherwise similar; the humerus had no epicondylar foramen and the femur no third trochanter; the tibia and fibula were separate. The manus had five digits, Nos. I, II and III carrying claws, that of III being especially large; IV and V had no claws and the outer edge of the manus rested on the ground in walking, the sole turned inward. The pes had lost the first digit, the second and third had claws, but not the fourth and fifth; the weight rested on the outer edge.

The skin is definitely known from large pieces belonging to the allied genus †*Grypotherium,* found in a cavern near Last Hope Inlet, Patagonia, where it had been preserved by burial in dry dust. Externally, the skin was thickly covered with coarse hair and in the deeper layers was a continuous armour of small ossicles, which were close set and in the Last Hope specimens show like a cobble-stone pavement on the inner side of the skin, the innermost layers of which have been destroyed; in life, these small bones were not visible. Simi-

FIG. 288. — Gigantic †ground-sloth (†*Mylodon robustus*), Pampean. Restored from Owen's figure of the skeleton.

lar ossicles have been found in association with several skeletons of †*Mylodon*. The habits, diet and mode of feeding of the latter were no doubt essentially similar to those of †*Megatherium*, but †*Scelidotherium*, which had a much shorter and lighter tail, was probably more quadrupedal and browsed upon low shrubbery.

The third family, the †Megalonychidæ, was scantily represented in the Pleistocene of South America, but relatively common in North America. †*Megalonyx* was, on the whole, less specialized than †*Mylodon* or †*Megatherium*, but had a strong resemblance to both of them. The teeth, $\frac{5}{4}$ in number, had the foremost one in each jaw separated by a considerable space from the others and more or less tusk-like in form; the grinding teeth were worn smooth, without ridges, and of somewhat trihedral shape. The skull was short, broad and deep, resembling in shape that of the tree-sloths; there was a long, but feebly developed sagittal crest, and the orbits were widely open behind, with hardly a trace of any posterior boundary. The muzzle was very short and broad and abruptly truncated and the premaxillary bones were extremely small. The lower jaw was short, thick and massive, with very broad symphysis and almost vertical chin. Neck, body, tail, shoulder and hip-bones did not differ sufficiently from those of †*Megatherium* to require particular notice.

The fore limb was shorter and more slender than the hind; the humerus had the epicondylar foramen and the very massive femur retained the third trochanter; the tibia and fibula were separate. The feet had five digits, three of which carried claws; the calcaneum was very peculiar, not at all like the massive, club-shaped bone of †*Megatherium* and †*Mylodon*, but long, comparatively thin and sickle-shaped. Nothing in the skeleton suggests that the creature's habits differed in any important way from those of the genera last named.

†*Megalocnus*, of the Cuban Pleistocene, a member of this family, was apparently peculiar to the island and was prob-

ably derived from ancestors which in the Pliocene migrated from Central America. Aside from certain remarkable peculiarities of the teeth, this animal was more primitive, as well as smaller, than any other of the Pleistocene genera.

Although remains of †Gravigrada are comparatively common in all of the fossiliferous formations between the Pampean and the Santa Cruz, the material is too imperfect to throw any useful light upon the development of the various families. From the Santa Cruz beds, on the other hand, a great wealth of specimens has been obtained, and it is possible to give some fairly adequate account of the †ground-sloths of that time. These animals were then extremely abundant individually and of extraordinary variety; evidently, they were in a state of rapid expansion and divergent evolution along many lines, for hardly any two specimens are alike and therefore the satisfactory discrimination of species is well-nigh impossible. Yet, with all this remarkable variability, the range of structural differences was not great; the group was a very homogeneous and natural one, and separation into families was not obvious. Two of the three families were, however, unequivocally present in this fauna and the third somewhat doubtfully so. The †Megalonychidæ, which in the South American Pleistocene had dwindled to such insignificant proportions, formed the overwhelming majority of the Santa Cruz †Gravigrada; the †Mylodontidæ were quite rare in comparison and are still very incompletely known; while the †Megatheriidæ, though probably present, have not been identified beyond all doubt.

All of the Santa Cruz †ground-sloths were small animals, the largest not approximating the smallest Pleistocene species, those of Cuba excepted, and many of them were no larger than the modern tree-sloths. This was a wonderful difference between the Santa Cruz and the Pampean, but a difference which involved nearly all other groups of mammals. So far as the skeleton is concerned, this is known with completeness only for the †Megalonychidæ, especially the genus †*Hapalops;* but

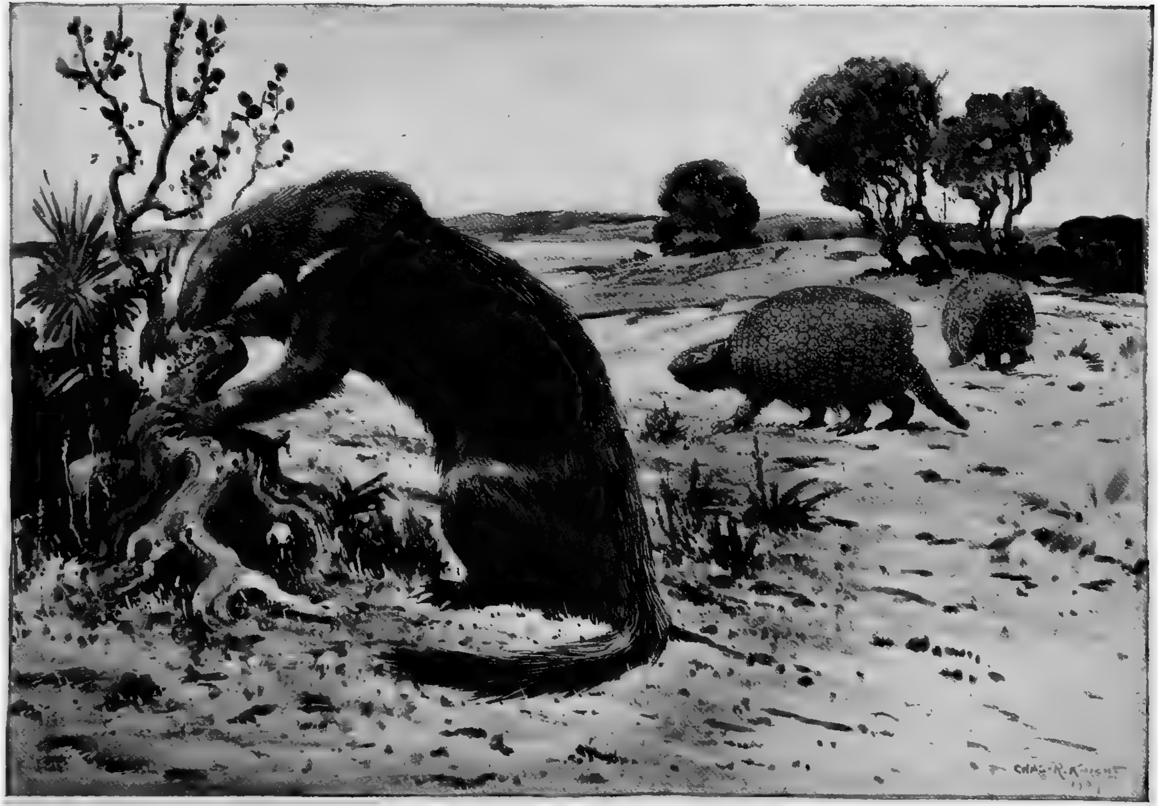

FIG. 289. — Santa Cruz †ground-sloth (†*Hapalops longiceps*) and †glyptodont (†*Propalæohoplophorus australis*). Restored by Knight from skeletons in Princeton University and the museum of La Plata.

enough has been learned of the others to show that there was far less difference between the families than had arisen in the later epochs. This backward convergence of the three groups towards a common term plainly indicates their common origin, being exactly what might have been predicted in advance of experience.

In all the genera the teeth number $\frac{5}{4}$; the teeth on each side were sometimes in continuous series, sometimes the first one was isolated and almost always more or less tusk-like, most so in †*Eucholœops*. The other teeth were usually of transversely elliptical shape and worn into two ridges, with a hollow between; the †mylodonts (†*Nematherium*, etc.) already had the triangular, or lozenge-shaped, lobate form of teeth, characteristic of the family.

The skull varied considerably in its proportions; generally, it was long and narrow, with shortened face and elongate cranium; the sagittal crest was seldom present, never prominent, and the orbit was always widely open behind, without post-orbital processes. The premaxillaries were always short and toothless and in most of the genera they were slender rods, in others (*e.g.* †*Hyperleptus*) broad and plate-like. The lower jaw had an elongate spout-like symphysis, in which the two halves were coössified, tapering forward to a blunt point and, though the length of this spout differed greatly in the various genera, in none was there a broad, abrupt chin such as †*Mylodon* and †*Megalonyx* had. In †*Prepotherium*, which is believed to be referable to the †Megatheriidæ, the lower jaw had the extremely convex inferior border, in less exaggerated degree, of its huge Pampean successor; it would be premature to say descendant.

While the long, slender skull was the prevailing type among the Santa Cruz †Gravigrada, there was a group of small animals in which the skull was shorter and more rounded and had a very suggestive likeness to that of the modern tree-sloths, as was likewise true of the teeth.

Despite innumerable variations of detail, the skeleton of the Santa Cruz †ground-sloths may be described without distinction of genera, though it should be added that the skeleton is but partially known in many of the genera, and fuller knowledge might require modification of some of the statements. The neck was of moderate length, the body long, the tail long and heavy and, in some instances, very massive. The sternal ribs were completely ossified and already had the same elaborate mode of articulation with the breastbone as in the great Pampean forms, and the vertebræ the same intricate connections. The shoulder-blade also had the same characteristics as in the latter, but the hip-bones had but a moderate transverse expansion, having no huge mass of viscera to support.

FIG. 290. — Left pes of †*Mylodon*, Pampean (after Owen). *Cal.*, calcaneum. *As.*, astragalus. *N.*, navicular. *Cn. 2*, *Cn. 3*, middle and external cuneiforms. *Cb.*, cuboid.

The limbs were stout and short, fore and hind legs of nearly equal length; the humerus had the epicondylar foramen and the broad, flattened femur retained the third trochanter. The radius had a discoidal upper end, which rotated freely upon the humerus; the tibia and fibula were always separate. The feet were five-toed, all the digits complete and functional and all provided with claws; there was no coössification between the phalanges. The astragalus was little different from the normal form, but in some genera (*e.g.* †*Prepotherium*) the highly peculiar form of this bone characteristic of †*Mylodon* and †*Megatherium* was distantly foreshadowed. The gait must have been simply plantigrade, though some of the forms had probably begun to throw the weight upon the outer edge of the foot.

No dermal armour has yet been found in association with any of the genera, and, so far as the predominant †Megalonychidæ are concerned, of which so many skeletons have been collected, this negative evidence must be allowed great weight. But the material of the other two families is so rare and incomplete, that the failure to find dermal ossicles is of no value in determining the question; probably, the †mylodonts possessed them.

These small Santa Cruz †ground-sloths were not so clumsy and slow-moving as their gigantic successors of the Pampean, and must have been inoffensive plant-eaters, some of them perhaps more or less arboreal in habits, but they could defend themselves with their long, sharp claws.

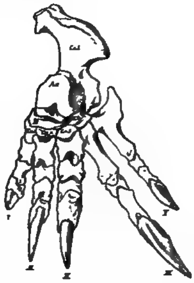

FIG. 291.—Left pes of †*Hapalops*, Santa Cruz. Princeton University Museum. Letters as in Fig. 290 and scale of reduction the same.

It would require far too much space and lead us into a labyrinth of anatomical technicalities to point out all the many resemblances to other edentate suborders which are to be noted in the skeleton of the Santa Cruz †Gravigrada, which thus justified their position as the most nearly central group of the entire order. Not only was the skeleton of these Miocene †ground-sloths very much less specialized than in their Pleistocene successors, but they were much closer to the anteaters than were the latter. Aside from the skull, all parts of the skeleton displayed this resemblance in so marked a manner that the common derivation of the two suborders seems hardly open to question. Different as was the skull in the two groups, the differences were not such as to preclude the origin of both from the same type. Even more closely connected were the †ground-sloths and the tree-sloths; the resemblance was most clear in the teeth and skull, but there were also many points of likeness throughout the skeleton. In the tree-sloths the entire bony structure has been profoundly modified in adaptation to their altogether exceptional mode of life, in hanging *suspended* from the branches of trees; but, despite this modification, there are so many notable resemblances between the Santa Cruz †Gravigrada and the existing Tardigrada as irresistibly to suggest their community of origin, and thus the former served to connect the anteaters, on the one hand, with the tree-sloths, on the other. This must not be construed as meaning that the Miocene †ground-sloths were the ancestors of the other suborders, which were probably already in existence as distinct groups, but merely that all three suborders had a common origin, from which the Santa Cruz †Gravigrada had departed less than have the sloths and anteaters.

There is evidence that at least two of the †ground-sloth families, the †Megalonychidæ and the †Mylodontidæ, were distinguishable in the Deseado stage, but materials are still lacking to give us any real knowledge of the suborder in that or the more ancient stages.

SECTION LORICATA. ARMOURED EDENTATES

SUBORDER DASYPODA. ARMADILLOS

Armadillos are still an important and characteristic element of the Neotropical fauna, ranging from Texas to Patagonia and showing a considerable variety of structure and appearance. Existing species are all of small or moderate size, and the one which is by far the largest (*Priodontes gigas*) may somewhat exceed three feet in length, exclusive of the tail, and the smallest (*Chlamydophorus truncatus*) is hardly more than five inches long. In most armadillos the hair is greatly diminished in quantity and the animal is sheathed in a conspicuous armour of bony scutes, covered with horny plates. There is a head-shield which covers the top of the skull, and the tail is enclosed in a sheath; the back and sides are protected by the great carapace and the limbs by irregular scutes and scales, leaving only the under side of the body and the inside of the legs uncovered.

In most existing genera, the carapace is in three parts, an anterior and posterior buckler, in which the plates are immovably fixed together by their edges, and between a varying number of transverse, overlapping bands, from 3 to 13, which permit sufficient flexibility of the body. The tail-sheath is made up of a series of rings. One genus (*Tolypeutes*) has the power of rolling itself into a ball, the head-shield exactly closing the anterior notch of the carapace and the tail-sheath filling the posterior notch. The animal is thus perfectly protected against attack and does not seek refuge by digging, as other armadillos do and with astonishing rapidity. In the little Pichiciago (*Chlamydophorus*) the dermal ossifications are very thin and the carapace is composed of twenty transverse bands of horny plates, without bucklers; the rump is covered with a broad and heavy shield of bone, overlaid with thin plates of horn, which is attached to the hip-bones and notched below for the short tail. In certain rare and little known genera there is a greater development of hair; in one (*Praopus*) the whole carapace is covered with a dense coat of hair, and in another (*Scleropleura*) the middle of the back has only a hairy skin and the carapace is restricted to the sides.

The teeth vary in number and size in the different genera; in some (*e.g. Dasypus*) there is one upper incisor on each side; the teeth are all simple and of nearly cylindrical form. The skull is low and flattened, with long tapering snout and orbits widely open behind; the zygomatic arches are uninterrupted. Most of the vertebræ of the neck are fused into a single piece; in the lumbar and posterior dorsal regions there are not only the usual highly intricate articulations between the vertebræ, but also high processes on each side for the support of the carapace. The fully ossified sternal ribs have movable joints with the breast-bone, but not the double articulations found in the ant-eaters and †ground-sloths. The shoulder-blade has a very long acromion, which does not form a bony loop with the coracoid, and the clavicles are complete. The anterior element (ilium) of the hip-bone is narrow, very different from the broad plate of the †Gravigrada. The humerus has prominent deltoid and supinator ridges and an epicondylar foramen, and the femur has the third trochanter. Though the fore-arm bones are separate, the radius has no freedom of rotation; tibia and fibula are coössified at both ends.

In the hind foot there is no great variety of character; it is five-toed and usually has claws, but may have broad, flat nails (*e.g. Priodontes*), but the manus, which is a burrowing organ, displays different degrees of specialization, which is carried farthest in the Giant Armadillo (*Priodontes*). *Tatu* has the fore foot of quite different type. The armadillos feed chiefly upon insects and worms, but they are omnivorous and eat roots and carrion and sometimes even capture and devour small rodents and lizards.

As in the case of the †ground-sloths, the fossil armadillos so far available are insufficient for tracing the history of the various phyla, or for doing more than making a very brief sketch of the development of the suborder as a whole. Nearly all of the modern genera have been found in the Pleistocene together with several that are extinct, some of the latter of very large size. One of these, †*Eutatus*, had a carapace without bucklers and made up of 33 movable, transverse bands. Another, †*Chlamydotherium*, as large as a rhinoceros and the largest known armadillo, had anterior and posterior bucklers, with several movable bands between; it was especially characterized by the teeth, which were divided by a vertical groove into pillars or lobes, thus approximating the teeth of the †glyptodonts. The genus went far back into the Pliocene, and the more ancient species were successively smaller.

Though remains of armadillos abound in the formations between the Pampean and the Santa Cruz, they are for the most part so fragmentary as to be of no service in deciphering the history of the group. In the Santa Cruz beds also they are very abundant and varied, and several of the genera are very completely known. As a whole, this assemblage of armadillos was very different from that of the Pleistocene, and only a few direct ancestors of the latter have been found in the Miocene of Patagonia; no doubt, like the ancestral tree-sloths and anteaters, they were then living in the warmer regions of the north. Most of the Santa Cruz armadillos belonged to aberrant types, of which no descendants have survived; but, nevertheless, they throw welcome light upon the developmental stages of the suborder.

These armadillos had the complete armour of head-shield, carapace and tail-sheath, but the carapace had no anterior buckler in any of the Santa Cruz genera, and in some there was no posterior buckler, the carapace consisting entirely of transverse, movable bands, as in the Pleistocene †*Eutatus*. In one especially peculiar genus, †*Peltephilus*, the head-shield was remarkable; it was made up of large, polygonal plates, the two anterior pairs of which were elevated into high, sharp points, which must have supported horns, that were quite large in proportion to the size of the animal. A 4-horned armadillo, like a tiny rhinoceros in armour, must have been a sufficiently bizarre object.

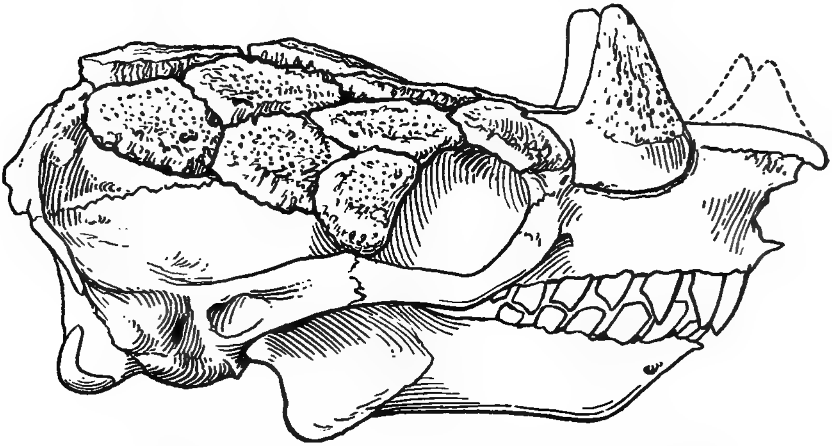

FIG. 292. — Skull of †*Peltephilus*, Santa Cruz. Ameghino collection.

As a rule, the teeth of the Santa Cruz armadillos were of the same simple, cylindrical form as in the modern genera and arranged in the same way, but there were some exceptions. In the horned †*Peltephilus*, the teeth of each jaw were so inserted as to form a continuous series around the sides and front of the mouth; and, at first sight, it would seem that this genus differed from all other known edentates in having a full set of incisors, but actually it had but one on each side above and below, as has the modern *Dasypus*, with the difference that, in the latter, the incisors of the opposite sides are widely separated and in †*Peltephilus* were brought close together. The anterior upper teeth were long and sharp and passed outside of the lower ones, when the jaws were closed, and all the teeth had an external layer of hard and shining dentine, which had almost the appearance of enamel. Another variant in dentition was †*Proeutatus*, which was the largest of Santa Cruz armadillos and larger than any existing forms except *Priodontes* and *Cabassous*. It had teeth like those of the huge Pliocene and Pleistocene †*Chlamydotherium*, of which it was a probable ancestor; the five posterior ones in each jaw were of trihedral shape, and the two kinds of dentine, of which they were composed, were so arranged as to form a rough grinding surface. Probably this animal subsisted largely upon vegetable food; at all events, the food was of such a nature as to keep the teeth worn down more than in any of the associated genera. A fourth type of dentition was displayed by †*Stegotherium* (Fig. 243, p. 480); the teeth were so few and small that they can have had no functional value and were merely minute points almost level with the gums. In all probability, †*Stegotherium* was more exclusively insectivorous than the other genera.

Among the Santa Cruz armadillos may be distinguished four well-marked types of skull. (1) That which agrees closely with the modern form, especially as exemplified by the genus *Dasypus*. (2) †*Proeutatus* had a higher and less flattened cranium and a very long, cylindrical muzzle. (3) In the horned

†*Peltephilus* the face was very short and broad, and the lower jaw was horseshoe-shaped, the two halves coössified at the symphysis, which is not true of any other armadillo. (4) Quite the opposite extreme was displayed by †*Stegotherium*, in which the face was drawn out into a very long, slender and tapering muzzle; the lower jaw was extremely weak and thin, the posterior, ascending portion low and ill-defined, the condyle and coronoid process much reduced. No other known armadillo has such fragile jaws, and there was a distinct likeness in the skull to that of the Ant-Bear.

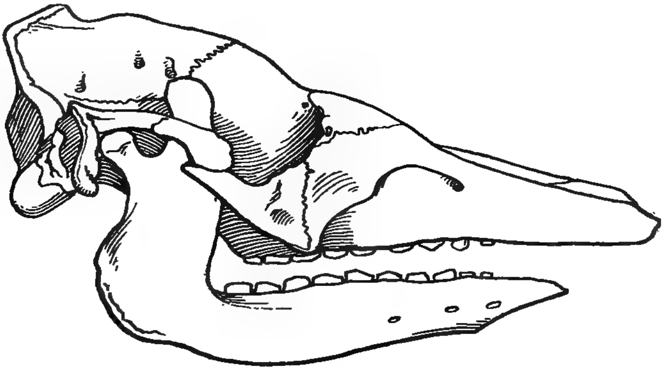

FIG. 293.—Skull of †*Proeutatus*, Santa Cruz. Princeton University Museum.

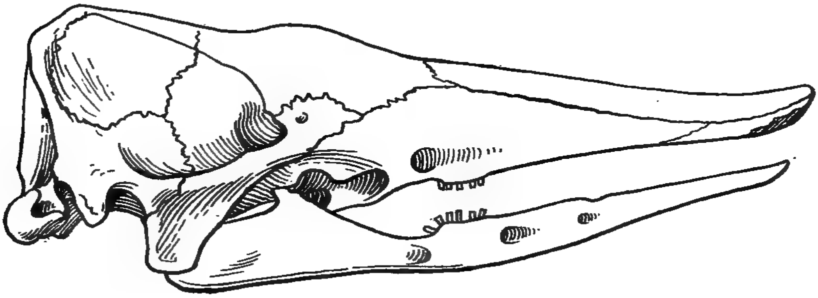

FIG. 294.—Skull of †*Stegotherium*, Santa Cruz. Princeton University Museum.

Aside from carapace and skull, the skeleton of the Santa Cruz armadillos was surprisingly modern. The vertebræ of the neck were coössified, those of the lumbar and posterior dorsal regions had the extremely complex articulations and the high processes for the support of the carapace, just as in the Recent genera. The limb-bones did not differ in any significant way from those of the latter, and the feet closely resembled those of the modern *Dasypus;* none of the genera displayed the specialization of the manus seen in *Cabassous*, *Priodontes* or *Tolypeutes*. Whether these specializations have all been acquired since Santa Cruz times, or whether they had already appeared in some other region of the continent, is a question that remains to be determined.

Little can yet be done in the way of tracing the history of the armadillos through the stages preceding the Santa Cruz times, because of the fragmentary character of the material. The suborder was abundantly represented in the Deseado stage, in which some of the Santa Cruz genera existed. Even in the most ancient of the Patagonian Tertiary formations are found scutes of the carapace essentially like those of the modern armadillos. The group is thus of very high antiquity, older than any other of the suborders is known to be.

In addition to the typical armadillos of South America, there were, in other continents, certain more or less doubtful forms, concerning which a word should be said. In the Bridger Eocene of North America was a genus (†*Metacheiromys*) of armadillo-like animals, the true relationships of which are far from clear. The teeth were mostly lost, leaving but one on each side of each jaw, and this *was covered with enamel*, which is not true of any unquestioned edentate. However, this is not an insuperable objection to the inclusion of these animals in the edentates, for there can be no doubt that these were derived from ancestors with enamel-covered teeth. Even in modern armadillos the enamel-organ is formed in the embryo, though it does not perform its functions. The skull of †*Metacheiromys* had something of the armadillo-shape, but was not especially characteristic. The vertebræ of the neck were all separate, and those of the dorsal and lumbar regions did not have the complex articulations common to all known edentates, fossil and Recent; the sacrum had on each side but one point of contact with the hip-bones, and the sternal ribs were not ossified. The shoulder-blade, hip-bones and humerus were all armadillo-like. The plantigrade feet were five-toed and the metapodials were very edentate in form. No indication of bony armour has been found. While these curious animals may very possibly have been referable to the Edentata and, at all events, had several features suggestive of relationship to that order, it can hardly be maintained that they were unequivocal members of it.

In the Oligocene of France have been obtained some very fragmentary fossils which were classified and described as armadillos, but their character is quite problematical. It is thus possible, though far from certain, that in the early Tertiary, armadillo-like edentates were spread all over the northern hemisphere.

SUBORDER †GLYPTODONTIA. †GLYPTODONTS

In the Pliocene and Pleistocene these huge armoured creatures ranged from the southern United States to Patagonia. That they were nearly related to the armadillos is clear, but they were so greatly modified and specialized as to demand recognition as a distinct suborder.

Aside from their enormous size, the most striking feature of the †Glyptodontia is the extraordinary development of their defensive armour, which was far more complete and massive than in the armadillos. The top of the head was protected by a thick head-shield, or *casque*, composed of several coössified plates; the body and much of the limbs were enclosed in the immense carapace of elongate-oval, domed shape, which covered the neck and trunk and on the sides almost reached to the ground. This tortoise-like carapace was composed of very thick, polygonal plates of bone (no doubt covered externally with horny plates) immovably fixed together by their rough edges, and ornamented with an elaborate pattern of sculpture, which varied according to the genus.

With one or two exceptions, the plates of the carapace were not arranged in transverse rows, but formed a mosaic without discernible banding. In the exceptions noted, the sides of the carapace were made up of bands, and near the margins were two or three overlapping transverse bands which permitted a minimal degree of flexibility. The tail-sheath was remarkable and differed much in appearance and make-up in the various genera. In †*Glyptodon* the tail was comparatively short and the tail-sheath was made up of a series of overlapping rings, each ring consisting of two rows of plates; those of the second row were ornamented, on the top and sides of the tail, with very prominent, conical projections, capped, in the living animal, with still longer and sharper spines of horn, so that the tail must have bristled with spikes. A more usual type of tail-sheath was exemplified by †*Sclerocalyptus*, in which there were several overlapping rings at the root of the tail, but for much the greater part of its length the plates of the sheath were fused together into a long, transversely oval tube, tapering very gently to the free end, where it was bluntly rounded. A modification of this type was the very long tail-sheath of †*Panochthus*, in which there were seven overlapping rings at the root, followed by a long, massive tube, the sides of which were set with three or more large and heavy, horn-like spines. In †*Dœdicurus* was reached the maximum specialization of this type; the very long tube had its free end greatly expanded and thickened into a huge, club-shaped mass, on the top and sides of which were fixed long and sharp horns.

The teeth, which in all the known genera numbered $\frac{8}{8}$, were all very much alike; each was divided by two broad and deep vertical grooves on each side into three pillars, connected by narrow necks. Harder dentine in the centre and on the periphery of the tooth, with a softer intermediate layer, kept the grinding surface rough through differential wear. Teeth of this character are indicative of a vegetable diet and these great creatures were, no doubt, as harmless and inoffensive as possible.

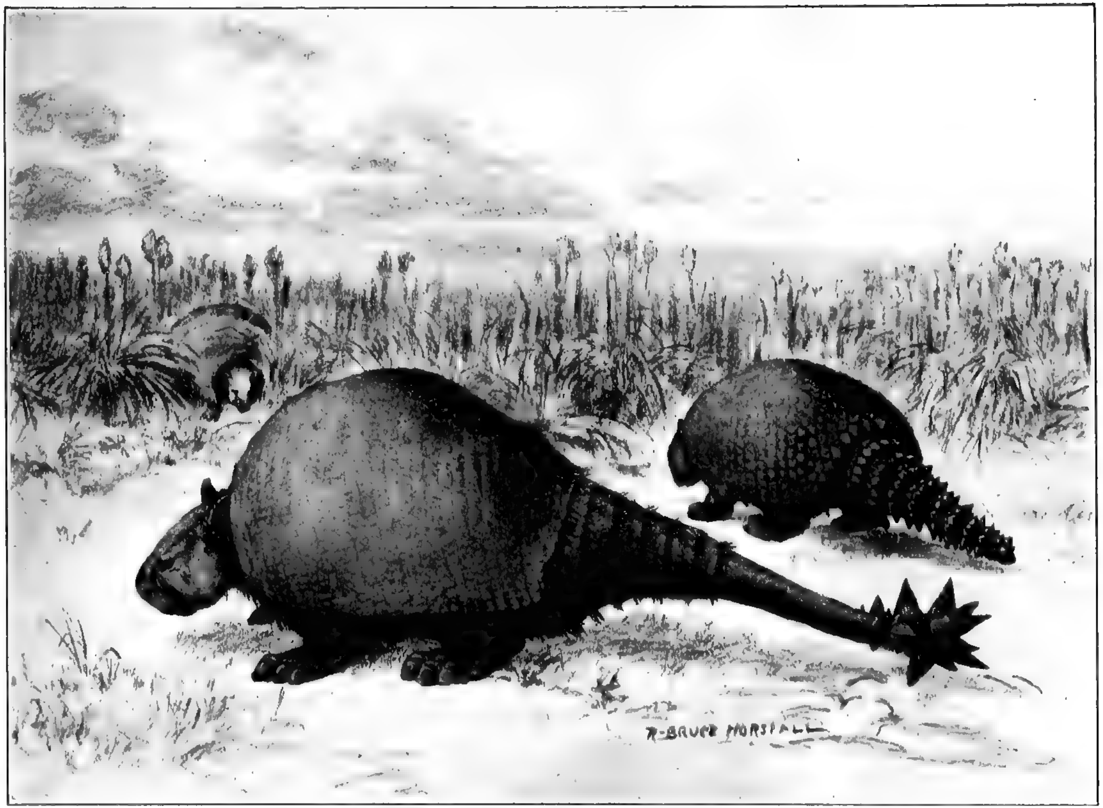

FIG. 295. Pampean †glyptodonts, †*Dædicurus clavicaudatus* and †*Glyptodon clavipes*. Restored from skeletons in the museums of La Plata and Buenos Aires.

The skull was remarkably short, broad and high, the facial region being especially abbreviated; the cranium, though forming the greater part of the skull, was yet small in comparison with the size of the animal; it had a distinct, though not prominent, sagittal crest. The occipital surface was inclined forward and had a very elevated position, the condyles being near the top of the head and raised very far above the level of the teeth. The orbits were relatively small, more or less completely encircled with bone and as near to the top of the head as they could be brought; this was to make room for the extremely high teeth, which required a great depth of jaw; the elevation of the whole cranium left unlimited space for the jaws beneath it. The zygomatic arches were strong and curved out widely from the sides of the skull; beneath each eye was given off a very long descending process which projected downward, outside of the lower jaw. In most of the species the upper profile of the skull was nearly straight, but in †*Panochthus* it descended very steeply from the forehead to the nose. The forehead was dome-like and the nasals extremely short. Sinuses were extensively developed, especially in the frontals, and in †*Sclerocalyptus* the bones around the nostrils were grotesquely inflated. The two halves of the lower jaw were fused together, and the symphysis was prolonged into a short, wide spout, which projected considerably in advance of the upper jaw, showing that the soft parts of the muzzle must have had a corresponding extension. The horizontal portion of the lower jaw, carrying the teeth, was short and very deep; the posterior, ascending portion had a forward inclination and was very high.

The skeleton of the Pleistocene †glyptodonts was unique among mammals, though evidently a modification of the armadillo type. The extreme modification was conditioned by the enormous weight of the carapace, which the skeleton had to support. The neck was very short, made up of short vertebræ, which were extensively coössified; the atlas was always free, but the axis was fused with a varying number of the succeeding vertebræ; usually, the axis and the third to the sixth formed one mass, while the seventh was fused with the dorsals. The joint between the sixth and seventh vertebræ was such as to permit at least a partial downward bending of the head beneath the carapace, closing its anterior opening with the head-shield. The seventh neck vertebra and all the dorsals, except the last one, were coössified into a heavy curved rod, the "dorsal tube"; the conjoined neural arches formed a tunnel for the spinal cord and the spines made a continuous ridge. As the hind legs were very much longer than the fore, the back was strongly arched upward from the neck to the hips. The last dorsal, the lumbars and the sacrum were all fused together to form the "lumbo-sacral tube," of which the coössified neural spines made a very prominent ridge, the principal support of the carapace in the median line; the anterior half of the trunk skeleton, comprising the short, deep thorax, was free from the carapace, which in that region must have rested upon the muscles of the back and shoulders. The number of neck and trunk vertebræ combined varied in the different genera from 26 to 28, but fusion had reduced the number of separate parts to 4, or at most 5. Such greatly diminished flexibility of the back was rather an advantage. The tail differed much in length in the various genera, but was always massive; the anterior vertebræ, usually 7 in number, were free, the others were fused into a heavy, tapering rod; but for nearly its whole length the processes of the vertebræ were very prominent, each vertebra touching the tail-sheath at five points and thus giving it very effective support. In †*Glyptodon* the tail-vertebræ were all free.

In most of the genera the scapula was very broad and had the very long acromion common to all the edentates; there were no clavicles. The hip-bones were very peculiar; the anterior element (ilium) stood almost vertically, at right angles to the backbone, and formed a broad plate, facing forward, the top of which was roughened and thickened to support the carapace. The posterior element (ischium) was also much expanded, but faced outward, and its hinder end, curved upward and thickened, was another point of strong support for the carapace. The two elements together formed an inverted arch, the crown of which rested on the head of the femur.

Though less massive than those of the hind leg, the bones of the fore limb were yet very heavy. The humerus was short and had reduced deltoid and supinator ridges and no epicondylar foramen; the short fore-arm bones were separate and heavy, the ulna especially so. The femur was much the longest of the limb-bones and was extremely strong, especially in its great breadth, the antero-posterior flattening, common to nearly all very heavy mammals, being well marked. A very unusual feature was the position of the third trochanter near the lower end of the shaft. The tibia and fibula were much shorter than the femur, extremely heavy and coössified at both ends. The very short and broad feet retained five digits; in the manus the claws were sometimes comparatively long and sharp, sometimes blunt and hoof-like; those of the hind foot were always broad hoofs.

Among all the many strange and grotesque mammals which the study of fossils has brought to light, none can have been more remarkable than the Pleistocene †glyptodonts; slow-moving hillocks they must have seemed, the larger species 12 to 14 feet long and 5 feet or more in height. Those that had claws on the fore feet probably used them to dig for roots and tubers, but all were plant-feeders. When attacked by the †sabre-tooth tigers (†*Smilodon*) or the great bears (†*Arctotherium*) they needed only to squat down, bringing the edges of the carapace to the ground, and draw in the head, to be perfectly protected, while a sweep of the spiny or club-like and horned tail would have been fatal to anything in its path.

As in the case of so many other groups, little has yet been learned regarding the history of the †glyptodonts during the interval between the later Pliocene and the Santa Cruz; the intermediate formations have yielded many †glyptodonts, but not in such preservation as to be of any service in this connection. We find, as might be expected, many and very great differences between the Pampean and the Santa Cruz representatives of the suborder, the latter being in all repects less modified and less widely removed from the armadillos.

(1) The most obvious and striking distinction was in size, the Santa Cruz forms being all small and some of them very small.

(2) In all cases the carapace was made up of transverse bands, which permitted a slight degree of flexibility, and near the anterior end, at the margins of the shell, were two or three overlapping bands. The plates were thin and were but rarely coössified; the ornamentation was made by shallow grooves.

(3) The tail-sheath, which was of very uniform character, consisted of two quite distinct portions; the anterior region consisted of 5 or more freely movable, overlapping rings, each of two rows of plates, and in the posterior region the rings were closely fitted together, less distinctly marked and not movable. This posterior portion was sometimes thick and ended abruptly, sometimes slender and tapering and in one genus (†*Asterostemma*) it was very armadillo-like. In none of the genera were there any spines or horns, nor were the separate plates ever fused together to form a tube.

(4) There was considerable variety in the head-shield, which was usually made up of many separate plates, but in one genus (†*Eucinepeltus*) they were coössified into a single heavy casque.

(5) The teeth had a less extreme height and the four anterior ones of each jaw were much simpler than in the Pampean forms. An interesting survival was the retention of two minute incisors in each premaxillary bone, in one genus (†*Propalæohoplophorus*), but these were of no functional value and were early lost.

(6) The skull was much longer, narrower and lower and had a relatively longer facial portion; the occiput was higher and more erect, and the condyles had no such elevation above the

level of the teeth; the orbit was widely open behind and the descending process given off from the zygomatic arch beneath the eye had no such exaggerated length; the bones were not conspicuously inflated by sinuses. The lower jaw was shallower, the symphysis and anterior spout shorter and the ascending portion far lower.

(7) The backbone had a greater number of separate parts; the atlas, as always, was free, the axis was fused with two or three of the following vertebræ; the sixth was free and the seventh fused with the first and second dorsals to form one piece, which was succeeded by two or three separate vertebræ: the other dorsals, except the last one, were united in the dorsal tube, and the lumbo-sacral tube was already complete. Thus, instead of four or five, there were eight or nine distinct parts. None of the tail-vertebræ were fused together.

(8) There was the same disparity in the length of the fore and hind limbs, but the bones were far more slender and armadillo-like; this was especially true of the radius and humerus, the latter having well-developed deltoid and supinator ridges and epicondylar foramen; the ulna was more massive and glyptodont-like. The femur was very much more slender and rounded and the third trochanter was placed higher up the shaft; tibia and fibula were coössified at both ends and resembled those of the Pampean genera, except for their much greater slenderness.

(9) The feet were much as in the latter, but relatively narrower, and the manus had longer claws.

In short, the Santa Cruz †glyptodonts departed much less widely from the armadillos than did the Pliocene and Pleistocene genera, and, to a certain extent, bridged over the gap between the two suborders. Such backward convergence in time is very strong evidence for the community of origin of the two groups.

The †glyptodonts of the more ancient formations, so far as they are known, teach us little concerning the stages of modification in these extraordinary animals, because of their fragmentary condition. The oldest stage in which representatives of the suborder have been detected is the Astraponotus beds, which may be Oligocene or upper Eocene. On the face of the records, therefore, the †glyptodonts had no such antiquity as the armadillos.

It has long been recognized that the Edentata occupy a very isolated position among the placental mammals; their relationships to other orders and their point of departure from the main stem are unsolved problems. The South American fossils have so far thrown little light into these dark places, but they bear very cogent witness to the unity of origin of the five suborders, which were most probably all derived from a single early Eocene or Paleocene group.

In the Paleocene and through most of the Eocene of North America there lived an order of mammals called the †Tæniodontia (or †Ganodonta) which many of the foremost palæontologists regard as an ancestral type of the Edentata, and Dr. Schlosser actually includes them in that order. That the †tæniodonts had certain striking resemblances to the edentates, especially to the †ground-sloths, is not to be denied, but the interpretation of these resemblances is a very complex and difficult question. Unfortunately, no member of the order is known from an even approximately complete skeleton, and therefore a discussion of the matter here would be unprofitable. My own conclusion, however, may be stated, to the effect that the supposed relationship of the †tæniodonts to the edentates is illusory and not real. Definite decision must await the finding of more complete material both of the †tæniodonts and the most ancient South American edentates.

CHAPTER XVII

HISTORY OF THE MARSUPIALIA

THE marsupials are a group of more primitive structure and greater antiquity than any which we have yet considered, so primitive, indeed, that they are referred to a separate infraclass, the Didelphia or Metatheria. The order is one of very great variety in size, form, appearance, diet and habits, and mimics several of the higher orders in quite remarkable fashion. Herbivorous, insectivorous and carnivorous forms are all numerous, as well as arboreal, terrestrial, cursorial, leaping and burrowing genera. Some are like hoofed mammals in appearance and the Rodentia, Carnivora and Insectivora are also closely imitated in externals. With all this diversity, most unusual within the limits of a single order, there is such a unity of structure, that a division of the group into two or more orders is impracticable.

At the present time, marsupials are very largely confined to Australia and adjoining islands, where they constitute nearly the whole mammalian fauna, and it is in the Australian region that the remarkable diversity already mentioned is to be observed. There are found the phalangers, kangaroos, bandicoots, Tasmanian "devil" and "wolf," and banded anteaters, not to mention many other curious creatures. In the western hemisphere only the opossums (*Didelphis*, *Chironectes*) and one very interesting relic of a long vanished assemblage, *Cœnolestes* of Ecuador and Colombia, are in existence to-day. The opossums, of which some twenty-three species are recognized, have their headquarters in South America, to which nearly all of the species are confined, North America having but two or three.

The more important American marsupials are given in the table below:

Suborder POLYPROTODONTA

I. DIDELPHIIDÆ. Opossums.
  Didelphis, Opossum, Pleist. and Rec., N. and S. A. *Chironectes*, Water Opossum, Rec., S. A. †*Peratherium*, low. Eoc. to low. Oligo., N. A. †*Microbiotherium*, Santa Cruz. †*Eodidelphys*, do. †*Ideodidelphys*, Casa Mayor. †*Proteodidelphys*, †Cretaceous, S. A.

II. THYLACYNIDÆ. Predaceous Marsupials.
  †*Cladosictis*, Santa Cruz. †*Amphiproviverra*, do. †*Prothylacynus*, do. †*Borhyæna*, do. †*Proborhyæna*, Deseado. †*Pharsophorus*, do. †*Procladosictis*, Casa Mayor. †*Pseudocladosictis*, do.

Suborder DIPROTODONTA

III. CÆNOLESTIDÆ.
  Cænolestes, Rec., S. A. †*Zygolestes*, Paraná. †*Palæothentes*, Santa Cruz. †*Abderites*, do. †*Palæpanorthus*, Deseado.

IV. †GARZONIIDÆ.
  †*Garzonia*, Santa Cruz. †*Halmarhiphus*, do. †*Cladoclinus*, do.

Suborder †ALLOTHERIA

V. †PLAGIAULACIDÆ.
  †*Polymastodon*, up. Cretac. and Paleoc., N. A. †*Ptilodus*, do. †*Neoplagiaulax*, Paleoc., N. A.

VI. †POLYDOLOPIDÆ.
  †*Propolymastodon*, Casa Mayor. †*Polydolops*, do. †*Amphidolops*, do.

Despite all their diversity of appearance and habits, the unity of structure among the marsupials is such that the formation of groups of higher than family rank is very difficult, and it is by no means certain that the suborders currently accepted correspond to the facts of actual relationship.

Except in certain extinct South American genera, there is very little change of teeth, only the last premolar in each jaw being replaced. Sometimes the temporary tooth is long retained in function and, more rarely, it is shed very early; while in several genera no replacement of teeth has been observed. There is a difference of opinion among naturalists as to the proper interpretation of the marsupial dentition. According to one view, all except the replaced premolar belong to the milk-series and the permanent series has been lost; the alternative and more probable belief is that the milk-dentition has been almost or completely suppressed. Whichever one of these interpretations be the right one, there is strong reason to maintain that the very limited amount of change is not a primitive condition, but a secondary one, for a series of rudimentary teeth is formed before those which are to become functional. The only reasonable explanation of such a condition is that it has been derived from one in which the normal succession and replacement of the teeth took place. Something of the same sort has been observed in the simplicidentate rodents. The marsupial dentition differs from the placental one in the usual number of four molars, instead of three, and frequently also in exceeding the normal total number of 44. The incisors are almost always of a different number in the upper and the lower jaw and are frequently more numerous than in the placentals.

The skeleton has several diagnostic characters, which are present throughout the order, though one or other of these features may be absent in particular instances. The skull has a very small brain-capacity and elongate face and jaws. In the placental mammals, the sutures between adjoining bones of the skull tend to close by coössification, and the separate bones are clearly distinguishable only in young animals; but in the marsupials the sutures remain open for a much longer period. The lachrymal is expanded on the face and the foramen is outside of the orbit. The tympanic is a mere ring and permanently separate from the other bones of the cranium, while a false bulla is formed by the inflation of part of the alisphenoid. In almost all marsupials there are large openings or vacuities in the bony palate. One of the most characteristic and constant features of the marsupial skull is in the conformation of the angle of the lower jaw, which is turned inward, or *inflected,* at nearly a right angle with the body of the jaw. It is true that one existing Australian genus has lost this character; and in some of the placental orders, especially the Rodentia, a somewhat similar structure may occasionally be found, but it is never quite the same as in the marsupials, in which it goes back to a remote antiquity.

There are very constantly 19 trunk-vertebræ, of which usually 13 are dorsals. The tail differs greatly in length in the various genera, but most of them have well-developed tails. An additional pair of elements, besides the three which are found in the placentals, enter into the composition of the hip-bones; these are the *marsupial bones,* slender, flattened rods, directed forward in the abdominal wall and diverging in V-shape. Save in a few genera, clavicles are present and of full size. The humerus may or may not have the epicondylar foramen, but the femur never has the third trochanter. The feet vary greatly in form and structure, in accordance with the habits, but there is a very widespread adaptation to an arboreal life, and even in terrestrial and burrowing forms more or less distinct traces of this arboreal adaptation may be noted. This fact has led to a generally accepted inference that all existing marsupials had an arboreal ancestry.

The soft parts and more especially the organs of reproduction are likewise very characteristic, and one or two of these peculiarities may be mentioned. (1) In the female, the vagina is double and on the abdomen is the pouch, or *marsupium* (which gives its name to the order), a hair-lined bag, opening either forward or backward, which serves to carry the young and into which the teats open. A considerable number of species have lost the marsupium, while other species of the same genera retain it, and there can be little question that its absence is a secondary condition. (2) Except in one modern Australian genus, the marsupials have no true placenta, and the young are born in a very immature state, incapable of even swallowing.

The new-born young are transferred to the nipples of the mother and are attached to these and fed by the pumping of milk into their mouths by muscular action of the mother. A special, though temporary, arrangement of the gullet and windpipe is provided, so that the helpless young animal shall not be suffocated by the entrance of milk into the lungs.

Suborder Polyprotodonta

This suborder, as is indicated by its name, is characterized by its numerous incisors, which are $\frac{5}{4}$, or $\frac{4}{3}$, and none of them is especially enlarged; by the large canines in both jaws, simple premolars and tritubercular upper molars. The members of this group are carnivorous or insectivorous in habit, and all the existing ones are of small or moderate size, though some very large extinct forms are known. Except in one Australian family, the feet are not "syndactyl," a term which means the enclosure of two or more digits in one fold of skin. The only existing American representatives of the suborder are the opossums, the great majority of which are Neotropical in distribution.

1. *Didelphiidæ. Opossums*

In this family the dental formula is: $i\frac{5}{4}$, $c\frac{1}{1}$, $p\frac{3}{3}$, $m\frac{4}{4}$, $\times 2 = 50$. The incisors are small and closely crowded together, the canines large and tusk-like, the premolars simple and of compressed-conical form; in existing species, the upper molars are triangular, each of the three main cusps is V-shaped and there are additional minute cusps along the outer border; the lower molars have a high anterior triangle of three pointed cusps and a low heel with several distinct cusps. The humerus has an epicondylar foramen and the feet are five-toed; in the manus all the digits are armed with claws and the thumb is but partially opposable, while in the pes the hallux is without a claw and completely opposable, making the foot much like that of a monkey.

The division of the existing opossums into genera has caused much difference of opinion and practice among naturalists; there are five groups, which by some are regarded as genera, and by others as subgenera, all modern members of the family being very much alike. The species *Didelphis marsupialis*, which is common in the eastern United States and extends through temperate North America, Central America and tropical South America, has a complete pouch and is chiefly arboreal and insectivorous in habit. In the woolly opossums (*Caluromys*) there is no pouch, and the young, when sufficiently advanced, are carried on the mother's back, winding their tails around hers. In both of these genera the tail is long, naked and prehensile, but in the tiny species of *Peramys* the tail is short and hairy. Another Neotropical genus, *Chironectes*, the Yapock or Water Opossum, is the only existing instance of an aquatic marsupial. It has light grey fur, striped with brown, and webbed hind feet; living chiefly in the water, it feeds upon crayfish, water-insects and small fish.

The derivation of the modern North American opossums is a matter of great uncertainty. The present distribution of the family, with by far the greater number of its species confined to the Neotropical region, is certainly suggestive of a South American origin, but such considerations are very untrustworthy guides in tracing the history of animal groups. No opossum has been found in any North American formation between the Pleistocene and the lower Oligocene, though in the case of such small animals, negative evidence must be accepted with caution. In the White River Oligocene many minute opossums have been found and referred to the European genus †*Peratherium*, though it so closely resembles the modern *Didelphis* that many systematists do not make the distinction. In the Eocene, Paleocene and upper Cretaceous, opossums were represented doubtfully; the material is too incomplete for assured determination; in Europe they existed in the Oligocene and upper Eocene. In South America the family went back uninterruptedly to the oldest mammal-bearing beds of Patagonia, which may be upper Cretaceous. The opossums are thus the remnants of an exceedingly ancient group, whose beginnings are to be sought in the Mesozoic era and which was probably spread over all the continents. To all appearances, the whole group vanished completely from the northern hemisphere, but reëntered North America from the south at some time during the Pliocene or early Pleistocene and permanently established itself here.

The opossums are the most primitive of existing marsupials, especially the little South American genus, *Marmosa*, and are regarded, by some of the most competent students of the order, as closely representing the ancestral type of all the Recent families and genera, both of the Polyprotodonta and Diprotodonta.

2. *Thylacynidæ. Predaceous Marsupials*

By many naturalists this group of flesh-eating forms is included in the Dasyuridæ. The family never entered North America, but played a very important part in the Tertiary of South America. Three existing genera of the Australian region throw considerable light upon the South American types, and therefore some account of them will not be out of place here.

The largest of modern predaceous marsupials is the animal (*Thylacynus cynocephalus*) erroneously, but very naturally, called the "Tasmanian Wolf," now confined to Tasmania, but occurring also in the Pleistocene of Australia. As "wolf" applied to a marsupial is misleading, it will be less confusing to employ the anglicized form of the generic name "Thylacine." This animal is of the size of the small Prairie Wolf or Coyote (*Canis latrans*) and has very wolf-like appearance and habits. The muzzle is long and pointed, the ears erect and rather small, the tail long, very thick at the base and tapering to the end, not bushy, but covered with short, close-set hairs; the colour is greyish brown, with dark, transverse stripes on the posterior half of the back and base of the tail. Apparently the creature is in process of losing its stripes and acquiring the solid body-colour. The dental formula is: $i\frac{4}{3}$, $c\frac{1}{1}$, $p\frac{3}{3}$, $m\frac{4}{4}$, $\times 2 = 46$; the incisors are small, the canines large fangs, and the premolars simple; the upper molars are tritubercular, with large inner cusp and postero-external cutting ridge, and the lower molars are trenchant, with low heel. The whole dentition is remarkably like that of many Eocene †creodonts, such as †*Sinopa* and †*Tritemnodon* (see p. 566). The milk-premolar is small and functionless and is shed very early. The skull is very wolf-like in appearance, but thoroughly marsupial in structure, and has the large palatal vacuities common in the order. The marsupial bones do not ossify and are evidently on the point of disappearance. There are five digits in the manus, four in the pes, the hallux being completely suppressed. In habits, the Thylacine is carnivorous and so destructive to sheep that the farmers have nearly exterminated it.

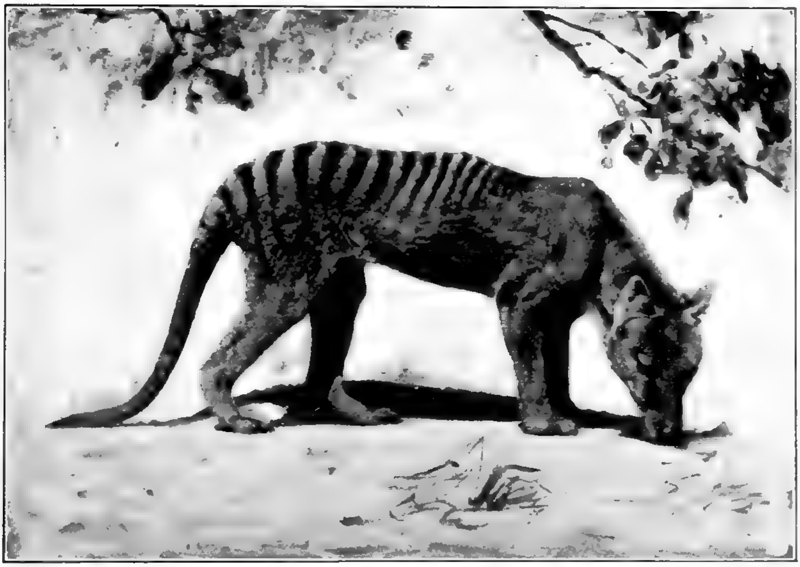

FIG. 296. — Thylacine, or "Tasmanian Wolf" (*Thylacynus cynocephalus*). — By permission of W. S. Berridge, London.

The other forms to be mentioned belong to the closely allied family of the Dasyuridæ. The "Tasmanian Devil" (*Sarcophilus ursinus*) is now, like the Thylacine, confined to Tasmania, but remains of it have been found in the Australian Pleistocene; it has one less premolar in each jaw, giving the formula: $i\frac{4}{3}$, $c\frac{1}{1}$, $p\frac{2}{2}$, $m\frac{4}{4}$, $\times 2 = 42$; there is no milk-tooth. The premolars are closely crowded and the molars resemble those of the Thylacine in construction, but are broader and heavier. The skull is disproportionately large, with shorter and wider muzzle and jaws than in the Thylacine; the tail is of only moderate length and somewhat shaggy; the hallux is wanting. In size and build, the Tasmanian Devil resembles a badger and has long and heavy fossorial claws on the fore feet; the hair is rough and shaggy, black in colour with white patches. The animal has received its name from its fierce and savage disposition and is almost as destructive to sheep as the Thylacine.

The five species of *Dasyurus* are distributed through Tasmania, Australia and New Guinea and are called "Native Cats"; they are much smaller animals than the two preceding genera, not exceeding a domestic cat in size. As the Thylacine imitates a wolf and the Tasmanian Devil a badger, the dasyures resemble the civets. In them the dental formula is the same as in *Sarcophilus*, but the teeth have higher and sharper cusps. The head has a narrow, tapering muzzle and narrow ears; the body is long and the tail of moderate length. The limbs are short and slender and a small hallux is present in some of the species. The fur is grey or brown, with numerous white spots, and the tail is covered with long hair, but not bushy. The dasyures are largely arboreal and prey upon small mammals, birds and eggs.

Until the arrival of the true Carnivora from the north, their rôle was taken in South America by predaceous marsupials, which persisted as late as the presumably Pliocene beds of Monte Hermoso. Little is known of them in that stage, however, or in the older Paraná, but abundant material representing those of the Santa Cruz has been collected. Among these there was a considerable range of size and some variety of structure, and they all differed in certain respects from the modern Australian genera, differences which have led some authorities to deny the marsupial character of all these South American forms. The differences are of three kinds: (1) there are no vacuities in the bony palate; (2) the milk-dentition is less reduced, the canines and one or two premolars being changed; (3) the enamel of the teeth, in the only genus (†*Borhyæna*) which has been examined microscopically, resembles in its minute features that of the placentals and lacks the marsupial characters. Though by no means unimportant, these differences are altogether outweighed by the thoroughly marsupial nature of all other parts of the skeleton, and I cannot but agree with Dr. Sinclair[1] in including them in the same family with the Tasmanian Thylacine.

The genus †*Prothylacynus* was especially like the latter and must have had a very similar appearance, though in the restoration (Fig. 297) the colour-pattern is changed to one of longitudinal stripes, as more probably pertaining to so ancient and primitive a form. The humerus had the epicondylar foramen, and a large vestige of the hallux was retained, though it could not have been visible in the living animal.

A more specialized Santa Cruz genus was †*Borhyæna* (Fig. 244, p. 494), an animal of about the same length and height as †*Prothylacynus* and the Thylacine, but much more massive and powerful. The skull was remarkable for the small size of the brain-case and the great spread of the zygomatic arches, which gave a rounded and almost cat-like appearance to the head, as is shown in the restoration (Fig. 244). In this genus the upper incisors were reduced to three, a very unusual thing among the Polyprotodonta, and the humerus had lost the

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[1] Reports of the Princeton University Expeditions to Patagonia, Vol. IV, Pt. 3.

FIG. 297. — Santa Cruz predaceous marsupial (†*Prothylacynus patagonicus*) and †typothere (†*Interatherium robustum*). Restored by C. Knight from skeletons in the museum of Princeton University.

epicondylar foramen. †*Prothylacynus* and †*Borhyæna* were the largest of the Santa Cruz flesh-eaters and no doubt pursued the smaller and more defenceless ungulates, but were hardly sufficiently powerful to attack successfully the larger hoofed animals, which were probably well able to defend themselves.

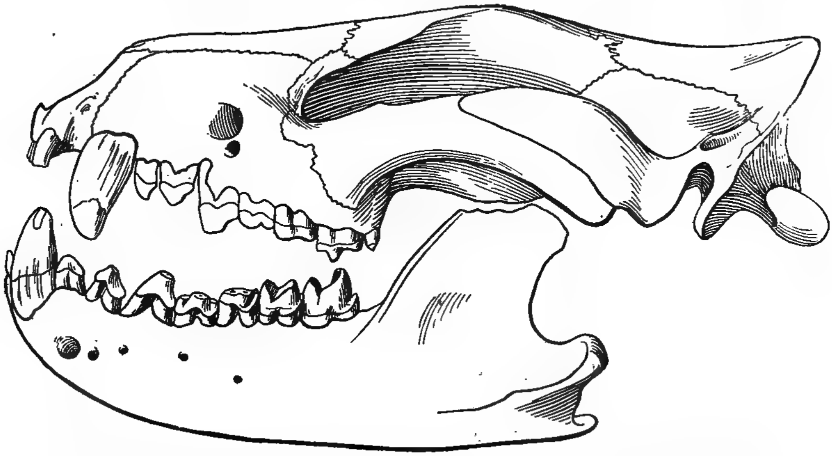

FIG. 298. — Skull of †*Borhyæna*, Santa Cruz. (After Sinclair, Reports Princeton University Expeditions to Patagonia, Vol. IV.)

Associated with these larger predaceous marsupials were several much smaller kinds, ranging in size from a fox to a weasel, which must have preyed upon the abundant rodents and other small mammals and birds. One of these (†*Amphiproviverra*) had an opposable hallux, somewhat as in the opossums, and was therefore probably arboreal. An interesting specimen in the museum of Princeton University illustrates the pugnacity of these small creatures; it is a skull in which the left upper canine was completely

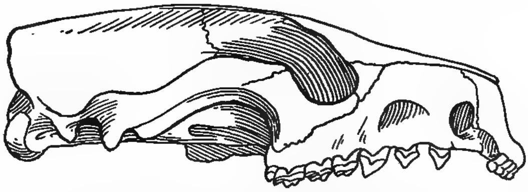

FIG. 299. — Skull of small predaceous marsupial (†*Amphiproviverra manzaniana*), showing the punctured wound from a bite. Princeton University Museum.

torn out, the circular puncture of the enemy's bite being unmistakable and the healed edges of the wound proving that the loss of the tooth was suffered during life. In structure, these smaller animals differed so little from the larger ones, that no particular description of them is needed. In the restoration of †*Cladosictis* (Fig. 300) the spotted pattern of the Australian dasyures, or native cats, has been taken as a model.

In the Deseado formation the predaceous marsupials have been less abundantly found than in the Santa Cruz and there can be little doubt that the group is very inadequately represented by the material so far collected. Only two genera, known from lower jaws, have been described, but one of these (†*Proborhyæna*) is of interest because of its enormous size, far surpassing any of the Santa Cruz forms and equalling the largest modern bears. This is another illustration of the unusual relationship between the Deseado and Santa Cruz faunas, the older stage so frequently having the larger animals.

Predaceous marsupials of small size may be traced back to the Casa Mayor formation, but very little is yet known of them. There is no obvious difficulty in the way of their derivation from opossum-like forms, such as are found in the Cretaceous of North America and probably of South America also.

The relation of the South American to the Australian marsupials offers problems of unusual interest, a discussion of which would be impracticable here. Several alternative solutions of the problem have been offered and great differences of opinion exist with regard to it. To my mind the most probable suggestion is that a land-connection, by way of the Antarctic continent, existed in early Tertiary times, by means of which the ancestors of the Australian marsupials migrated from South America, though this explanation is rejected by several eminent authorities.

FIG. 300. Small predaceous marsupial (†*Cladosictis lustratus*) and rabbit-like †typothere (†*Pachyrukhos moyani*), Santa Cruz stage. Restored by C. Knight from skeletons in Princeton University and the American Museum of Natural History.

SUBORDER DIPROTODONTA

North America never had any representatives of this suborder, but South America possessed many of them in the Santa Cruz Miocene and one genus (*Cœnolestes*) has survived to the present time. Australia, on the other hand, has three well-defined families of the suborder, the kangaroos, phalangers and wombats, but no member of any of these has ever been found outside of the Australian region. So far as we know, therefore, the suborder is and always has been confined to the southern hemisphere.

The modern South American genus *Cœnolestes* is a small, rat-like animal and very rare; it has been found only in Ecuador and Colombia. Its dentition is not at all typically diprotodont, but rather intermediate in character between the latter and the Polyprotodonta. The dental formula is: $i\frac{4}{3}$, $c\frac{1}{1}$, $p\frac{3}{3}$, $m\frac{4}{4}$, $\times 2 = 46$. The upper incisors are small and of subequal size, though the second is somewhat the largest of the series, and the canine is considerably larger and more prominent than any of them. The foremost lower incisor is long and pointed and directed almost straight forward; the other lower incisors and the canine are minute and can have little or no functional value. The premolars are small and simple and the upper molars quadritubercular, the third one triangular, and the fourth very small and apparently about to disappear. Such teeth would seem to indicate a vegetable diet, but it is reported that the animal subsists chiefly upon small birds and their eggs. The skull, which is typically marsupial in all its characters, is most like that of the smaller Australian native cats (Dasyuridæ) and the feet show no signs of the syndactyly

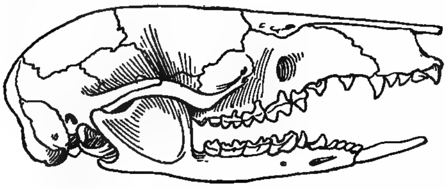

FIG. 301.—Skull of *Cœnolestes obscurus*, enlarged. (After Sinclair.)

which all the other diprotodonts display so clearly. Dr. Gregory is "inclined to regard *Cœnolestes* and its allies as an independent suborder, an offshoot of primitive Polyprotodonts which has paralleled the Diprotodonts in certain characters of the dentition."[1]

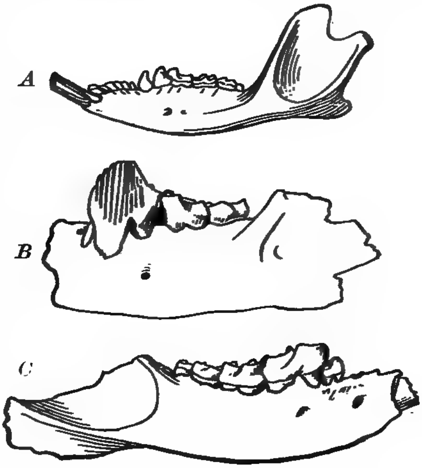

FIG. 302.—Lower jaws of Santa Cruz cænolestids, enlarged. *A*, †*Garzonia patagonica*, *B*, †*Abderites crassignathus*. *C*, †*Callomenus ligatus*. (After Sinclair, in Reports Princeton University Expeditions to Patagonia, Vol. IV.)

Evidently, the animals of this series were extremely rare or absent in the areas where the known South American deposits of the Pleistocene and Pliocene were laid down, for there is a very long hiatus in their history from the Recent to the Santa Cruz, during which none has yet been found, except one genus (†*Zygolestes*) in the Paraná. In the Santa Cruz, however, there was a great abundance of these little marsupials, to which various generic names have been given and which displayed considerable variety in the forms of the teeth. Some (*e.g.* †*Garzonia*) agreed with *Cœnolestes* in having no trenchant shearing teeth; behind the large, procumbent lower incisor, followed four or five very minute teeth, which must have been nearly or quite functionless, succeeded by the well-developed molars. Other genera (*e.g.* †*Abderites*) had a similar dentition, with the important exception that the last upper premolar and first lower molar were enlarged and trenchant, together forming a shearing pair; these teeth were vertically fluted or ribbed in very characteristic fashion. The Australian phalangers

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[1] W. K. Gregory, The Orders of Mammals; Bull. Amer. Mus. Nat. History, Vol. XXVII, p. 211.

have very similar trenchant and fluted teeth, but in that family the lower one of the pair is the last premolar, not the first molar. Marsupials of this type have not been found in formations older than the Deseado.

The relationship of these South American genera to the Australian phalangers is a very interesting question from the standpoint of mammalian distribution, but is not likely to receive a positive answer until something is learned regarding the history of the Australian family.

SUBORDER †ALLOTHERIA

This extinct suborder is still very imperfectly understood, for it is known almost exclusively from jaws and teeth; so far, the skull of one genus and most of that of another have been obtained, but hardly anything of the skeleton. The †Allotheria were small or minute marsupials, herbivorous or omnivorous, which had lost all trace of the canines and had one pair of incisors above and below, which grew from persistent pulps and had a scalpriform, rodent-like character. The molars were composed of numerous tubercles (whence the name "†Multituberculata," often applied to the group) arranged in two or three longitudinal rows, and the premolars were either like the molars, but of simpler pattern, or compressed, sharp-edged and trenchant. The †Allotheria were among the most ancient of mammals and have been found in the Triassic of Europe, the Jurassic of Europe and South Africa, the Jurassic and Cretaceous of North America and the Paleocene of both northern continents, while the South American Eocene (Casa Mayor) had certain problematical genera (†Polydolopidæ), which may be referable to the †Allotheria or to the *Cænolestes* series.

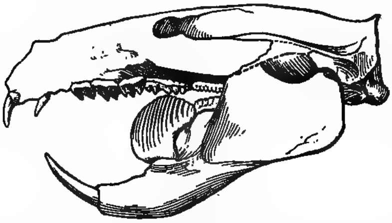

FIG. 303. — Skull of Paleocene †allothere (†*Ptilodus gracilis*), enlarged, Fort Union stage. (After Gidley.)

The suborder was thus preëminently a Mesozoic one and, with the doubtful exception of South America, it is not known to have passed beyond the limits of the Paleocene. There is not the least likelihood that any existing mammals were derived from the †Allotheria.

While the †Allotheria have an antiquity at least equal to that of any other mammals known, there were other groups in the Jurassic and Cretaceous, which, so far as may be judged from teeth alone, would seem to have been ancestral to the other marsupials and to the placentals. It would serve no useful purpose to describe these minute creatures, which are so very incompletely known, though to the specialist they are of the highest interest. The genera found in the Triassic of North Carolina may or may not represent the primitive mammalian stock.

Fig. 304. — Head of †*Ptilodus gracilis*, about natural size. Restored from a skull in the United States National Museum.

The question of the origin of the Mammalia is still involved in great obscurity, and the most divergent opinions are held concerning it. It remains an unsolved problem whether the mammals were all descended from a common stock, or have been derived from two independent lines of ancestry, or, in technical phrase, whether the class is monophyletic or diphyletic. Assuming, as seems most probable from present knowledge, that the mammals are monophyletic, the question next arises: From what lower vertebrates are they descended? A great controversial literature has grown up around this problem, one party regarding the Amphibia and the other the Reptilia as the parent group. The palæontological evidence, while not conclusive, is decidedly in favour of the latter view. In the Triassic of South Africa is found a group of reptiles which approximated the mammals very much more closely than do any other known representatives of the lower vertebrates. While it is not believed that any of these Triassic reptiles were directly ancestral to the mammals, they did, to a very great extent, bridge the gap between the two classes and show us what the reptilian ancestors of the mammals were probably like.

With perhaps the exception of certain Insectivora, the Paleocene faunas contained few, if any, ancestors of modern mammals. These originated in some region which has not been identified, but may be plausibly conjectured to be central Asia, whence they migrated westward to Europe and eastward to North America, reaching both of those continents in the lower Eocene. From that time onward they increased and multiplied, becoming more and more differentiated through divergent evolution, until the existing state of things was attained. From the lower Eocene we are on firm ground, and, though very much remains to be learned, much has already been accomplished in the way of tracing the history and development of many mammalian orders. It has been my endeavour in the body of this book to sketch the better established and more significant parts of this marvellous story.

CHAPTER XVIII

MODES OF MAMMALIAN EVOLUTION

THROUGHOUT this book the theory of evolution has been taken for granted, as it seemed superfluous to present an outline of the evidence upon which that theory rests. "Descent with modification" is now accepted among naturalists with almost complete unanimity, but, unfortunately or otherwise, this general agreement does not extend beyond the point of believing that the present organic world has arisen by descent from simpler and simpler forms. The application of the theory to concrete cases is beset with grave difficulties and gives rise to the most divergent views. The uninitiated reader who takes up a treatise upon some animal group may well be surprised to see the apparently minute accuracy with which the genealogy of the series is set forth and the complex relationships of its members marshalled in orderly array. Another treatise on the same subject, however, while agreeing perfectly with the first as to the facts, will contradict its conclusions in almost every particular. Indeed, so notorious did this become, that "phylogenetic trees" were rather a laughing-stock, and most naturalists lost interest in the problems of phylogeny and turned to fields that seemed more promising.

To some extent, this almost hopeless divergence is inherent in the very nature of the problem, which deals with the value of evidence and the balancing of probabilities, as to which men must be expected to differ; but there is another and more potent cause of the discrepancy. When the contradictory schemes are analyzed, it is seen that each is founded upon certain assumptions regarding the evolutionary process, assumptions which are generally implicit and often apparently unconscious. In the present state of knowledge, these postulates are, for the most part, matters of judgment, incapable of definite proof, and they appeal with very different force to different minds; what to one seems almost self-evident, another regards as all but impossible. It will, however, be of service to examine such of these postulates as are involved in mammalian history.

It is quite impracticable to construct a genetic series without making certain assumptions as to the manner in which the developmental process operated and the kinds of modification that actually did occur. In the preceding chapters, which deal with the evolutionary history of various mammalian groups, it was repeatedly stated that, of two contemporary genera, one was to be taken as the ancestor of some later form and the other regarded as a collateral branch, but it was also pointed out that in certain cases, palæontologists differed more or less decidedly as to the proper interpretation of the facts; it is just this lack of agreement as to the modes and processes of change that forms the root of the difficulty.

There are instructive analogies between the history, aims and methods of comparative philology, on the one hand, and zoölogy, on the other. In both sciences the attempt is made to trace the development of the modern from the ancient, to demonstrate the common origin of things which are now widely separated and differ in all obvious characteristics, and to determine the manner in which these cumulative modifications have been effected. At the present time zoölogy is still far behind the science of language with regard to the solution of many of these kindred problems and has hardly advanced beyond the stage which called forth Voltaire's famous sneer: "L'étymologie est une science ou les voyelles ne font rien et les consonnes fort peu de chose." Many of the animal genealogies which have been proposed have no better foundation than the "guessing etymologies" of the eighteenth century, and for exactly the same reason. Just as the old etymologists made their derivations upon the basis of a likeness of sound and meaning in the words compared, so the modern zoölogist, in attempting to trace the relationships of animals, must proceed by balancing their similarities and differences of structure. The etymologist had no sure test for distinguishing a true derivation from a plausible but false one, and the zoölogist finds himself in the same predicament. How much weight should be allowed to a given likeness and how far it is offset by an accompanying difference, there are no certain means of determining, and we are still in search of those laws of organic change which shall render such service to zoölogy as Grimm's law did to the study of the Indo-European languages. Doubtless, the analogy may be pushed still farther, and it may be confidently assumed that, just as sound principles of etymology were established by tracing the changes of words step by step from their modern forms to their ancient origins, so the existing animal forms must be traced back through the intermediate gradations to their distant ancestors, before the modes of organic development can be deduced from well-ascertained facts.

The evolutionary problem has been attacked by the aid of several distinct methods, each of which has its particular advantages and its peculiar limitations and drawbacks. Most of the methods suffer from the fact that they deal only with the present order of things, and thus resemble the attempt to work out the derivations of languages that have no literature to register their changes.

(1) Of necessity, the oldest of these methods is Comparative Anatomy, which had made great advances in pre-Darwinian days. It is the indispensable foundation of the whole inquiry, for an accurate knowledge of Comparative Anatomy is absolutely necessary to the use of the other methods; in the hands of the great masters it has registered many notable triumphs in determining the mutual relationships of animal groups; but finality cannot be reached by this method, because

it deals only with existing forms and possesses no sure criterion for determining the value of similarities. It is thus unable to distinguish with certainty between those resemblances which are due to inheritance from a common ancestry and those which have been independently acquired. It is a very frequent fallacy to assume that, because two allied groups, B and C, possess a certain structure, their common ancestor, A, must also have possessed it. This may or may not have been the case, and Comparative Anatomy offers no assured means of deciding between those alternatives or of confidently distinguishing primitive characters from degenerative or retrograde changes.

(2) Embryology, which is the study of the development of the individual animal from the unfertilized egg to the adult condition, was long regarded as the infallible test of theoretical views in zoölogy. This was on the assumption that individual development (*ontogeny*) is a recapitulation in abbreviated form of the ancestral history (*phylogeny*) of the species, and was called by Haeckel "the fundamental biogenetic law." It was soon learned, however, that the "recapitulation theory" was not to be implicitly trusted, for structural features which could not possibly be a part of ancestral history were imposed upon or substituted for those due to phylogenetic inheritance. Now the whole theory is strongly questioned, and the absence of any universally accepted rules of interpretation, by which the contradictory embryological data may be harmonized into a consistent whole, has deprived the method of that authoritative character once so generally ascribed to it. It is like dealing with a literature which has been vitiated with many forgeries, only the grossest of which can be readily detected. Embryology has rendered many great services in the solution of zoölogical problems and will no doubt render many more, but it cannot, of itself, reach final conclusions.

(3) Experimental Zoölogy, especially that part known as "Genetics," one of the newest and most promising provinces

of the science, has already taught us much concerning the laws of inheritance and the manner in which new characters arise, and no one can venture to fix the limits of its possible results. On the other hand, it does not seem likely that the larger problems of relationship and classification can be solved by this method, because of the brief time which the shortness of human life allows for the experiments.

(4) Palæontology suffers from the drawback that much of the past history of life is irretrievably lost, and even when the record is remarkably complete, as it is for certain chapters of the history, the material is but partially preserved. With such rare exceptions as are of little practical importance, only the hard parts, bones, teeth, etc., are retained and the soft parts completely destroyed. Nevertheless, Palæontology has the preëminent advantage of offering to the student the actual stages of development, and thus, to recur to the simile of language, has preserved original documents and in the true order of succession. It is true that it is well-nigh impossible to reconstruct a phylogenetic series of ancestor and descendant, unaffected by theoretical preconceptions, and the differences which arise in the interpretation of undisputed facts are caused by divergent beliefs concerning the actual course of the evolutionary process. If final and definitive results are ever to be reached, it must be through the coöperation of all the methods of research, and such results must be able to stand the tests applied by every sound method. On the other hand, the study of those phylogenetic series which are generally accepted as well established, should furnish us with some fairly definite information as to the modes in which development has operated in the past, since the order of succession in time fixes a limit to the rearrangement of related series. Some of the conclusions thus suggested may be stated here.

I. One of the most fundamental problems concerning the course of development is that which deals with *parallel* and *convergent evolution*. The term *parallelism* implies that forms having a common origin may independently run through a similar course of development and arrive at similar results. Illustrations of this principle are given by the many phyla of horses, rhinoceroses and camels, which persisted side by side through several geological stages, following independent, but parallel, courses of change. An even more striking case is that of the two subfamilies of the cats, the true felines and the †sabre-tooths. Whatever view may be taken of the relationships of these two groups, it is clear that, at least from the upper Oligocene to the Pleistocene, they were separate, but kept remarkably even pace with each other in their advance and specialization.

By *convergence* is meant a similar result which is reached by two or more independent lines having different starting points, so that the descendants are more alike than were the ancestors, and is thus the opposite of *divergence*, the result of which is to make the descendants of common ancestors less and less alike with each succeeding stage. Either parallelism or convergence may be involved in the independent acquisition of similar characters, of which these are so many examples. It is obvious that this problem is fundamental and that little real progress is possible until a solution is reached. As to the correct solution, there is much difference of opinion among naturalists. Some deny altogether the reality and importance of these modes of development, but such are almost exclusively concerned with the modern world; others go to the opposite extreme, and looking upon every large group as polyphyletic, consider parallel and convergent development to be the rule of evolution. Few palæontologists are disposed to doubt that these modes of evolution are very frequent; their difficulty is to determine what limits can be drawn, and this difficulty can be removed only by much wider and more exact knowledge than we now possess.

So far as single structures are concerned, the fossils demonstrate unequivocally that they have been independently acquired in a great many cases. The resultant similarity may be attained through the loss, the acquisition or the modification of parts. The reduction of toes from the primitive number of five to four, three, two, or even one, has happened over and over again in the most diverse groups. There is good reason to believe that all the early and primitive placental mammals had the third trochanter on the femur and the epicondylar foramen on the humerus, but in most of the modern groups these structures are lost; and the list of such similar reductions of parts might be almost indefinitely extended.

Of much greater significance is the independent similar modification of parts and acquisition of new structures. Innumerable examples of this kind of parallel and convergent development might be given, but a few will be sufficient to illustrate the principle. (1) The odontoid process of the axis (second vertebra of the neck) was primitively a bluntly conical peg, a form which is still retained in the great majority of mammals, but in the true ruminants, the camels, the horses and the tapirs, the process is spout-shaped, concave on the upper side, convex on the lower. By tracing the development of those groups, it has been conclusively demonstrated that the change of form took place independently in each of the four. (2) The ruminants have molar teeth composed of four crescentic cusps arranged in two transverse pairs, the pattern called *selenodont.* The evidence is very strong that this highly characteristic molar pattern has been several times independently repeated, as in the true ruminants, the camels, the †oreodonts and probably other groups also. (3) The family †Macrauchenidæ of the extinct †Litopterna shares with the camel tribe the remarkable peculiarity of having the canal for the vertebral artery running through the neural arches of the neck-vertebræ. (4) A very striking instance is afforded by the three widely separated groups of hoofed animals, members of which had their hoofs transformed into claws; the †chalicotheres arose from the normal perissodactyls (p. 356), the

†agriochœrids from the †oreodonts and the †Entelonychia from the †toxodonts. From time to time attempts have been made to unite two or more of these groups, but in each case better material and fuller knowledge have demonstrated the unnatural character of such association and the separate origin of the peculiar structure.

Admitting the reality and frequency of these modes of development, a far more difficult problem is to determine the extent to which such independent acquisition of similar structures has actually been carried, and it is at this point that the widest divergences of opinion are to be found. As yet, our knowledge is far too imperfect to permit the making of positive statements, but there is no evidence which would justify the conclusion that the same genus, family or order of mammals ever arose independently from radically different ancestors. We have no reason to believe that identical groups of mammals were ever separately developed in land areas which through long periods of time had no means of intercommunication. If such a thing ever happened, it must have been the rarest of exceptions. On the other hand, parallelism, by which *related* forms pass through similar stages of development, would seem to have been so exceedingly common, as fairly to deserve being called a normal method of evolution. As more and better material has been gathered, it has grown increasingly clear that almost every large group of generic, family or higher rank, whose history is known in any adequate measure, consists of several distinct, though related phyla, which pursued more or less closely parallel courses of modification, though diverging from one another sufficiently to make the distinction of them comparatively easy. The parallelism was thus not exact, however perfect it may have been in particular structures, and the longer the phyla persisted, the more distinctly did they diverge.

A typical problem, which involves these principles, is afforded by the very curious and interesting group of South

American hoofed animals known as the †Litopterna (Chap. XIII). The many remarkable resemblances between these ungulates and the perissodactyls and, more specifically, between the family †Proterotheriidæ and the horses, have been very differently interpreted by palæontologists. Some have insisted that the †Litopterna should be merged in the Perissodactyla, on the ground that such a degree of likeness could not have been independently acquired. Others hold that this is a remarkable case of parallelism or convergence, and the latter is, in my opinion, much the more probable view. Until the ancestry of both groups, Perissodactyla and †Litopterna, shall have been definitely ascertained, it will not be practicable to make a final decision between these alternatives, nor, if the similarities were really independently acquired, to determine whether parallel or convergent evolution is involved. It is quite possible that both groups were rooted in the common ground of the †Condylarthra, and, if so, their relation is one of parallelism; but no such common ancestry has been proved, and it is equally possible that their ancestry was totally distinct. In the latter case the resemblances were due to convergence.

Assuming that the remarkable resemblances between the †Proterotheriidæ and the horses were separately acquired, it should be emphasized that these similarities nowhere amount to identity. The likenesses are not confined to a few structures, but are general throughout the skeleton and may be noted in the teeth, skull, trunk, limbs and feet, but in every single one of these parts the similarities are offset by differences of great significance. No competent anatomist would mistake any of the bones of the †proterotheres for the corresponding parts of the horses, whatever view he might hold as to the relationship between the two groups. The case is thus one of a very instructive kind, as tending to show that identity of structure in so highly complex creatures as mammals is not independently attained by widely separated or entirely unrelated forms.

Probable as this conclusion is made by all the available evidence, it cannot be regarded as demonstrated; it is proverbially impossible to prove a negative.

On the other hand, it is equally probable that nearly related forms do very frequently, perhaps normally, pass through separate, but closely similar, courses of development. It is likely that a new species is usually formed through similar and simultaneous modification of many individuals, rather than from a single individual or pair. It may be the general rule, as almost certainly has often happened, that a new genus arises by the separate assumption of the new character by several species of the ancestral genus, rather than through the rapid diversification of a single species, though, no doubt, parallel and divergent modification are both very frequent and important processes. Dr. Eigenmann concludes from his study of South American fresh-water fishes that a certain new genus is even now in process of origin through the transformation of several species of an older genus, which in different parts of the continent are simultaneously, but independently, taking on the new character.

Sometimes it is possible to assign a definite reason for the independent origin of similar structures in different groups of mammals. Except for the head, there is much similarity of appearance among the very massive hoofed animals, such as the elephants, rhinoceroses, tapirs and hippopotamuses of the present time, a fact which induced Cuvier to unite them in one order, the "Pachydermata," a term which has passed into vernacular, if metaphorical, usage. No doubt also, several extinct groups, such as the †Amblypoda and the perissodactyl family of the †Titanotheriidæ, would have been included, had they been known in Cuvier's day. In the largest and heaviest of these animals, the elephants, †amblypods and †titanotheres, there are many close correspondences in all parts of the skeleton, which are clearly due to the mechanical necessities imposed by the support of immense weight, and the developmental history of each group shows that the smaller and lighter ancestors were less similar than the larger and more massive descendants. Such subsequently acquired likenesses are thus obvious examples of convergence and were caused by adaptation to similar needs.

Fürbringer has shown that among birds size and weight of body determine many resemblances between unrelated families, the largest forms displaying a more advanced grade of specialization.

It is thus extremely probable that evolution is a highly complex process, in which divergent, parallel and convergent modes of development are normally concerned. This complexity greatly increases the difficulty of determining phylogenies, which would be very much easier could every notable resemblance be at once accepted as proof of relationship. It often renders impossible the classification of some isolated group, which seems to have several incompatible affinities. It emphasizes the necessity of founding schemes of classification upon the totality of structure and the importance of determining the value of characters, whether they are primitive or advanced, divergent, parallel or convergent, before attempting to use them in classification.

In looking over the field of mammalian evolution, so far as that is recorded by the fossils, the general impression received is that the most important process is divergent development, one line branching out into several. This process became especially vigorous and rapid at times of important change in the character of the environment, what Osborn has called "adaptive radiation." As we have repeatedly observed in the history of particular groups, *e.g.* the rhinoceroses, horses and camels, numerous parallel phyla of the same family existed together in certain geological stages, but as these phyla were traced back in time, they were found to draw together and display themselves as branches of a single stem. This favours the inference that the mammalian orders, so far as they are truly natural groups and not arbitrary assemblages, are each of single, or monophyletic, origin, and that the parallel and convergent modes of development, while very frequent and important, are subordinate to divergence.

II. A second problem is whether development among mammals is always by means of reduction in the number of parts, or whether that number may not be increased. With this is involved the so-called law of the "irreversibility of evolution," according to which organs once lost, or reduced to a vestigial condition, are never regained, or reëstablished in function. There can be no question that the usual mode of mammalian development is by reduction in the number of parts and the enlargement and elaboration of those which are retained, as, for example, in the reduction of five toes to one in the series of the horses; but there are cases which require a different explanation. The very numerous teeth of the porpoises and dolphins and of the Giant Armadillo are not a primitive feature, but must have arisen by a process of multiplication. In the very curious Large-eared Wolf (*Otocyon*) of South Africa the number of molar teeth $\frac{3}{4}$ exceeds that found in any other placental mammal. This feature has been interpreted as a proof of marsupial relationship, but, as the creature is a typical dog in all other respects, such a relationship would involve a degree of convergence in development that is quite inadmissible without the most cogent evidence. Until something is learned regarding the descent of *Otocyon*, no positive statement can be made as to the significance of its exceptional dentition, but much the most likely supposition is that additional teeth have been developed in an otherwise normal canid. However that may be, the testimony of the fossils is unequivocally to the effect that the usual mode of development among mammals is by a reduction in the number of parts, accompanied by enlargement and specialization in those which are retained.

It is equally clear that the "law of irreversibility" holds good in a very large number of cases, but whether it is always valid is very doubtful. In the Guinea Pig, as in all its family (Caviidæ), there are four toes in the front foot, three in the hind; but Professor Castle has lately succeeded in producing a race with four toes in the hind foot. To call this a "monstrosity" or "abnormality" explains nothing; the fact remains that the four-toed race has been established and no reason can be assigned why the same thing might not happen in nature. If Dr. Matthew's view concerning the origin of the American deer from †*Leptomeryx* (p. 409), should prove to be well founded, another example of the same kind would be furnished. In †*Leptomeryx* of the Oligocene the upper canine was reduced to minute, almost vestigial proportions, while in the ancestral deer, †*Blastomeryx* of the lower Miocene, it was a large, scimitar-like tusk. While I am unable to acept this derivation of the deer, it may be true nevertheless and, if so, will be a most interesting example of the rehabilitation of a vestigial organ. Decision must await the discovery of the intermediate forms. Many such cases and instances of the addition of parts may be so far undetected, but the phylogenetic series, as we have them before us, point decidedly to the conclusion that such rehabilitation or new addition is exceptional.

III. So far as we are able to follow it by the aid of the fossils, development among the mammals would appear to be a remarkably direct and unswerving process. When any long-lived phylum, made up of numerous well-preserved members, is studied, the observer cannot fail to be impressed by the straightforward course of the evolutionary process, as though the animals were consciously making for a predetermined goal, which, needless to say, they were not. A minute cusp makes its appearance on a tooth, enlarges steadily in each succeeding genus, and ultimately becomes a very important element in the pattern; and in this series of changes there is no oscillation backward and forward. In the perissodactyls and a few other groups, the premolars in each family gradually and steadily assumed the size and complexity of molars; beginning at the hinder end of the series, these teeth one by one become molariform, not in irregular and haphazard fashion, but by perfectly graded stages. The same gradual and direct process was maintained in the oft-recurring reduction of digits among the hoofed animals, differing for each group according to the symmetry of the foot. In the horses, for example, the first digit became vestigial and disappeared, and then the fifth followed, leaving a three-toed foot, in which the median digit was notably the largest and bore most of the weight. Throughout the Oligocene and Miocene epochs the horses were all tridactyl, but there was a gradual enlargement of the median digit and dwindling of the laterals, until these became mere dew-claws, not touching the ground, and the weight was carried entirely upon the median one. Finally, the laterals lost their phalanges and were farther reduced to splints, which is the modern condition. In the same gradual and unswerving manner the higher artiodactyls went through a process of digital reduction from five to two, and numberless other instances of similar sort might be adduced.

On the other hand, the direction of change long followed may be departed from, the deviation being due to the introduction of a new factor. In the earliest deer the males were hornless, but they developed effective weapons of defence by the enlargement of the upper canine teeth into long and sharp, sabre-like tusks. When antlers appeared, the work of defence was transferred to them, and the tusks began to dwindle, being eventually suppressed in those deer which had large and complex antlers, though persisting to the present time in the hornless Musk Deer and in the small-antlered Muntjaks, which can defend themselves with their sharp tusks.

It would be inaccurate to say that fluctuations in the size and effectiveness of parts never occurred; on the contrary, there is evidence that such fluctuations in details were not infrequent, and may have been even more common than we suppose. To give one instance, the very early camels of the upper Eocene and lower Oligocene had small canines, which though not at all functionless or vestigial, were yet little larger than incisors. Though the ancestral camels of the middle and lower Eocene are not yet definitely known, there is strong reason to believe that in them, as in all of their contemporaries among the ungulates, the canines were enlarged and fang-like. If so, the canine teeth in the camels underwent decided fluctuations in size, being first larger, then smaller and again enlarging. If Dr. Matthew's interesting theory as to the origin of the true felines from primitive †sabre-tooth cats (see p. 540) should be confirmed, it would furnish a very striking example of fluctuating development. The acceptance of the theory involves the admission of the following changes: (1) The upper canine was enlarged and changed into a thin, recurved, scimitar-like tusk; (2) the lower canine was much reduced, becoming little larger than the incisors; (3) the lower jaw developed a flange on each side from its inferior border, against which the inner side of the upper canine rested, when the mouth was closed, and the chin was nearly flat, meeting the outer surface of the jaw at a right angle. After these peculiarities had been fully established, the stock divided into two series; in one, the †machairodonts, the specialization continued along the same lines, assuming more and more exaggerated forms, while in the true cats it was reversed. The upper canine grew shorter and thicker, the lower canine was very greatly enlarged, the lower jaw lost its flange, and its external and anterior surfaces no longer met at a right angle, but curved gradually into each other. As previously stated, such a reversal strikes me as improbable and not to be accepted without very much more complete evidence than we now have, but it is perfectly possible that such evidence may be forthcoming.

Making the fullest allowance for all such cases of fluctuation, it remains true that in the great majority of the phyla whose history may be followed in some detail, development has been remarkably direct and unswerving. Plasticity of organization and capacity for differentiation of structure in widely different directions would seem to be limited in the mammals, especially among the more advanced groups.

IV. A question that has been much debated and is still a centre of controversy deals with continuity and discontinuity in development. In other words, does evolution proceed by the cumulative effects of minutely graded modifications, or is it a succession of leaps and sudden changes? The difference is illustrated by many breeds and races of animals and plants under domestication, the history of which is known. Some have arisen from "sports," sudden and marked deviations from the parent stock, which "breed true" from the beginning. Of this character was the Ancon breed of sheep, which was derived from a single short-legged ram that was born of normal parents in 1791 and transmitted his peculiarities to his offspring. Professor Castle's race of four-toed Guinea Pig originated from one four-toed individual, which suddenly appeared in a litter of normal ones. Other breeds have been formed by the careful and long-continued selection of minute individual variations. Which of these methods is the one that has been followed under natural conditions? or has now one method been used and now another, according to circumstances? The problem is one that has a profound and far-reaching importance for the whole of evolutionary philosophy, which largely hinges upon it.

Unfortunately, palæontology is not well fitted to give a decisive answer to these questions, for, however complete the record of any given series may be, we never can be sure that it actually is so, and interruptions in the continuity of development might be due either to progress by abrupt changes, or to a failure to preserve all the gradations. For that reason different observers have put divergent interpretations upon the facts as we have them. The general impression that is made by the study of a well-preserved mammalian phylum is that of continuity, but a closer analysis reveals numerous small breaks, and suggests, so far as the record may be trusted, that the advance was made by separate steps, though very short ones. Indeed, it has been objected that so completely recorded a phylum as that of the horses must be illusory, because there is not perfect continuity between the successive genera, it being taken for granted that such continuity is the normal mode of development.

Dr. Schlosser, on the other hand, is a disbeliever in perfect continuity. "I am of the opinion that we must reckon with development *per saltum* more frequently than is usually done. We have been decidedly spoiled by the phylogenetic series of quiet successive development, such as we meet with in the Oligocene and Miocene of North America in the titanotheres, oreodonts, camels, etc., and in the upper Eocene of Europe in *Palæotherium*, *Paloplotherium*, etc., as well as from the Oligocene into the Pleistocene, *e.g.*, in the rhinoceroses, cervids, suillines, amphicyonids. Even here we often make for ourselves artificial difficulties by balancing, with an exaggerated scrupulousness, the individual forms one against another, to see whether they really are exactly fitted to fill up any gaps. It is not the lack of suitable intermediate forms which so often renders difficult the establishment of genetic series, but, quite on the contrary, the abundance of the forms at our disposal, among which we must make a choice. If, however, the development of phyla did not take place in the same region and under constant climatic and topographical conditions, we must necessarily find apparent gaps, for adaptation to a new environment occasions rapid changes of organization, so that the immediate descendant will often deviate considerably from its ancestor. But that must not mislead us into denying the connection between such forms." [1]

Better adapted to a solution of this problem than mammals

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[1] M. Schlosser, Beiträge zur Kenntniss der Oligozänen Landsäugethiere aus dem Fayum, Vienna, 1911, p. 165.

are the fossil shells of Mollusca, the development of which may often be traced through a thick series of strata, each step of modification being represented by innumerable individuals. In very many instances it appears that each species in a series of successive modifications had many contemporary fluctuating variations, but the change from one species to the next succeeding one was by a small though abrupt mutation. The difference between two successive species may be no greater than that between two contemporary variants of the same species, but it was a constant and not a fluctuating difference. There is much reason to believe that such is at least a frequent mode of development, namely, that from species to species and genus to genus the transition has been by slight and sudden changes. The possibility that such abrupt changes, however slight, are illusory and due to small gaps in the record, must be admitted, and though this does not seem to be a very likely explanation, it is given plausibility by the almost perfect continuity between successive species which may sometimes be observed.

The extremely important and significant distinction between contemporary, fluctuating variations and successive, constant mutations was first drawn by Waagen, who says of them: "One must therefore distinguish strictly between varieties in space and those in time. To describe the former, the long-used name 'variety' will suffice, for the latter, on the other hand, I would propose, for the sake of brevity, a new term, 'mutation.' A species as such, with reference to its connection with earlier or later forms, may be conceived and regarded as a mutation. But also in regard to the value of these two concepts, just established (variety and mutation), an entirely different value is displayed on closer consideration. While the former appears extremely vacillating, of small systematic value, the latter, even though in minute characteristics, is extremely constant and always to be recognized with certainty."[1]

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[1] W. Waagen, Die Formenreihe des Ammonites subradiatus, *Benecke's Geognost.-Palæont. Beitr.*, Bd. I, pp. 185–186.

The same conception was adopted and elaborated by Neumayr: "Still other characteristics appear, which mark mutations as something different from varieties, especially that, as a rule, there is a definite direction of mutation in each series, the same characters changing in the same sense through a considerable succession of strata." [1]

Whether development was continuous or discontinuous, there is no reason to suppose that the amount and rate of modification were always constant. On the contrary, there is strong evidence that at times of great climatic or geographical changes, or when a region was invaded by a horde of immigrants, widespread readjustments were accomplished with comparative rapidity. Indeed, such periods of relatively quick changes have long seemed to be implied by the facts of the palæontological records.

It is only too clear that the principles as to the modes of mammalian development which can be deduced from the history of the various groups must, for the most part, be stated in a cautious and tentative manner, so as not to give an undue appearance of certainty to preliminary conclusions, which should be held as subject to revision with the advance of knowledge. Much has, however, been already learned, and there is every reason to hope that Experimental Zoölogy and Palæontology, by combining their resources, will eventually shed full light upon a subject of such exceptional difficulty.

[1] M. Neumayr, Die Stämme des Thierreiches, Bd. I, p. 60.

GLOSSARY

Acetabulum, the deep socket in the hip-bone for the head of the femur.

Acromion, the projecting lower end of the spine of the shoulder-blade.

Alisphenoid canal, canal in the base of the skull for the external carotid artery.

†Allotheria, an extinct suborder of Mesozoic and Paleocene Marsupials.

†Amblypoda, an extinct order of hoofed mammals.

Anconeal fossa, a deep pit on the posterior side of the humerus, near the lower end.

Anconeal process, *see* Olecranon.

†Ancylopoda, an extinct suborder of Perissodactyla.

Angle, of the lower jaw, the postero-inferior corner.

Angular process, a hook-like projection from the angle of the lower jaw.

Anterior nares, the forward opening of the nasal passage.

Anthropoidea, Monkeys, Apes, Man; suborder of Primates.

Appendicular skeleton, bones of the limbs and limb-girdles.

Araucanian, Pliocene of Argentina, including the Catamarca and Monte Hermoso.

Artiodactyl, *see* Artiodactyla.

Artiodactyla, Cattle, Deer, Camels, Pigs, etc., etc., order of hoofed mammals.

Ascending ramus, posterior, vertical portion of the lower jaw.

Astragalus, the ankle-bone.

Astraponotus Beds, upper Eocene or more probably, lower Oligocene of Patagonia.

†Astrapotheria, an extinct order of hoofed mammals.

Atlas, the first vertebra of the neck.

Auditory bulla, one of a pair of inflated bony capsules at the base of the skull; the tympanic bone.

Auditory meatus, the entrance to the bulla.

Axial skeleton, the skull, backbone, ribs and breast-bone.

Axis, the second vertebra of the neck.

†Barytheria, an extinct order of elephant-like mammals.

Biceps muscle, the large flexor muscle of the front of the upper arm; its contraction bends the elbow.

Bicipital groove, a groove between the tuberosities of the humerus for the upper tendons of the biceps.

†Extinct.

Brachyodont, low-crowned teeth, with early-formed roots.
Bridger stage, middle Eocene of N. W. America.
Bunodont, teeth composed of conical tubercles.

Calcaneum, the heel-bone.
Cannon-bone, a compound bone formed by the coössification of two or more long bones of the foot.
Cape Fairweather, marine Pliocene of Patagonia.
Carnassial, a shearing, sectorial tooth in a flesh-eater.
Carnivora, Wolves, Bears, Cats, etc., etc.; an order of placental mammals.
Carnivorous, flesh-eating, predaceous.
Carpal, one of the elements of the carpus.
Carpus, the wrist-bones.
Casa Mayor stage, terrestrial formation of Patagonia, probably Eocene.
Catamarca, a Pliocene formation of Argentina.
Caudal vertebræ, those of the tail.
Central, a small carpal, wedged in between the two rows.
Centrum, the body of a vertebra.
Cervical vertebræ, those of the neck.
Cetacea, Whales, etc.; a cohort of marine mammals.
Chelodactyla, suborder of Perissodactyla.
Chevron-bones, Y-shaped bones attached to the under side of the caudal vertebræ.
Chevrotains, "Mouse Deer," of the suborder Tragulina.
Chiroptera, Bats, an order of placental mammals.
Class, a group of the fifth order in classification.
Clavicle, the collar-bone.
Cnemial crest, a massive prominence on the front face of the tibia, near the upper end.
Cohort, division of infraclass, containing a series of related orders.
†Condylarthra, an extinct order of hoofed mammals.
Condyle, a knob-like, articular protuberance.
Convergence, or **Convergent Evolution,** similar forms resulting from two or more independent lines of descent.
Coracoid, a hook-like bone, fused with the shoulder-blade in the higher mammals.
Coronoid process, a projection in front of the condyle of the lower jaw, to which the temporal muscle is attached.
Cotyles, concavities on the atlas to receive the occipital condyles of the skull.
Cranium, the part of the skull above and behind the eyes, which lodges the brain and higher sense-organs.
†Creodonta, an extinct suborder of the Carnivora.
Cretaceous, third and last of the Mesozoic periods.
Crown, the exposed part of a tooth.

Deltoid crest, a ridge on the anterior face of the humerus for the attachment of the deltoid muscle.
Dental formula, an arithmetical expression of the number and kinds of teeth.
Dermoptera, Flying Lemur, order of placental mammals.
Deseado stage, terrestrial formation of Patagonia, probably Oligocene.
Didelphia, lower infraclass of the Eutheria.
Digit, a finger or toe.
Diprotodonta, Kangaroos, etc., a suborder of Marsupials.
Dorsal vertebræ, those which carry ribs.
Duplicidentata, Hares and Rabbits, suborder of Rodentia.

Edentata, Sloths, Anteaters, etc., an order of placental mammals.
Edentates, *see* Edentata.
†Embrithopoda, an extinct order of elephant-like mammals.
Embryo, young animal in early stages of development within the uterus.
†Entelonychia, extinct suborder of the †Toxodontia.
Eocene, second of the five Tertiary epochs.
Epicondylar foramen, perforation of the internal epicondyle for transmission of the ulnar nerve.
Epicondyle, a rough prominence on each end of the humeral trochlea.
Epiphysis, the ends of the long bones, which ossify separately and do not coalesce with the shaft until growth ceases.
Equus Beds, *see* Sheridan stage.
Eutheria, the higher subclass of mammals; viviparous.

Family, group of the third order in classification, typically containing several genera.
Fauna, the totality of animals of a given time or place.
Femur, the thigh-bone.
Fibula, the external bone of the lower leg.
Fissipedia, land-carnivores; suborder of the Carnivora.
Flora, the totality of plants of a given time or place.
Fœtus, young animal in the later stages of development within the uterus.
Foramen, a perforation in a bone for the passage of a nerve or blood-vessel.
Foramen magnum, the opening in the occiput for the passage of the spinal cord to the brain.
Formation, a general term for a group of strata, laid down continuously and under uniform conditions.
Frontal, one of a pair of bones which form the anterior part of the cranial roof; the forehead.

Genus, group of the second order in classification, typically containing several species.
Glenoid cavity, (of the squamosal) the articular surface for the condyle of the lower jaw; (of the scapula) the socket for the head of the humerus.

Hallux, the first digit of the pes, or great toe.
Herbivorous, plant-eating.
†Homalodotheres, *see* †Entelonychia.
Horizontal ramus, the tooth-carrying part of the lower jaw.
Humerus, the bone of the upper arm.
Hyoid arch, a series of bony rods, attached to the base of the cranium, for support of the tongue.
†Hyopsodonta, an extinct suborder of the Insectivora.
Hypsodont, high-crowned teeth, with late-formed roots.
Hyracoidea, Klipdases, an order of hoofed mammals.

Ilium, the anterior element of the hip-bone.
Inferior maxillary, the lower jaw.
Infraclass, division of subclass.
Insectivora, Moles, Shrews, etc., an order of placental mammals.
Ischium, the postero-superior element of the hip-bone.

John Day stage, upper Oligocene of N. W. America.
Jugal, the cheek-bone. *See* Malar.
Jurassic, the second of the Mesozoic periods.

Lachrymal, a small bone on the front edge of the orbit.
Lachrymal foramen, a canal for the tear-duct piercing the lachrymal bone.
Lemuroidea, Lemurs, suborder of the Primates.
Lemurs, *see* Lemuroidea.
Limb-girdles, the bones which attach the limbs to the body.
Lipotyphla, suborder of the Insectivora.
†Litopterna, extinct order of hoofed mammals.
Loricata, Armadillos and Glyptodonts; the armoured Edentates.
Lumbar vertebræ, those of the loins.
Lunar, the middle bone in the upper row of the carpus.

Magnum, the middle bone in the lower row of the carpus; supports the third digit or middle finger.
Malar, cheek-bone. *See* Jugal.
Malleolar bone, the lower end of the fibula, persisting as a separate bone after loss of the shaft.
Malleolus, external, the lower end of the fibula.
Malleolus, internal, process from the lower end of the tibia.
Mammal, a warm-blooded vertebrate, which suckles its young.
Mandible, the lower jaw.
Manubrium, the anterior segment of the breast-bone.
Manus, the hand or fore foot.
Marsupial, *see* Marsupialia.

Marsupialia, Opossums, Kangaroos, etc., etc.; only order of the infraclass Didelphia.

Marsupium, the hairy pouch in which the young Marsupials are carried.

Masseter muscle, a muscle of mastication, attached to the lower jaw and inferior border of the zygomatic arch.

Mastoid, that part of the periotic bone which is exposed on the surface of the skull.

Mastoid process, a spine-like outgrowth of the mastoid.

Maxillary, the upper jawbone.

Medullary cavity, the marrow cavity of a long bone.

Mesozoic, the middle era of geological time.

Metacarpal, a member of the metacarpus.

Metacarpus, the long bones of the manus, or fore foot.

Metapodial, a metacarpal or metatarsal.

Metatarsal, a member of the metatarsus.

Metatarsus, the long bones of the pes, or hind foot.

Miocene, the fourth of the Tertiary epochs.

Monodelphia, placental mammals; the higher infraclass of the Eutheria.

Monophyletic, derived from a single line of ancestry.

Monotremata, Duck-billed Mole and Spiny Anteaters; the only existing order of the Prototheria.

Monte Hermoso stage, upper Pliocene of Argentina.

Mouse Deer, chevrotains; suborder Tragulina.

Mystacoceti, Whalebone Whales; order of the Cetacea.

Nasal, one of a pair of bones, forming the roof of the nasal passage.

Navicular, central bone of the tarsus.

Neural arch, the bony arch of a vertebra.

Neural canal, the cavity in the arch, lodging the spinal cord.

Neural spine, or spinous process, the projection arising from the summit of the neural arch.

Notostylops Beds, *see* Casa Mayor stage.

Occipital condyles, a pair of knob-like protuberances from the occiput for articulation with the first vertebra.

Occipital crest, an elevated bony ridge around the margin of the occiput.

Occiput, the posterior surface of the skull.

Odontoceti, Toothed Whales; order of Cetacea.

Odontoid process, a peg-like projection from the body of the second vertebra, which fits into the ring of the first.

Olecranon, the heavy projection from the upper end of the ulna, forming the point of the elbow.

Oligocene, the third of the Tertiary epochs.

Opposable, used of the thumb and great toe, when they can be opposed to the other digits.

Orbit, the bony eye-socket.

Order, a group of the fourth rank in classification, typically including many families.

Oviparous, egg-laying.

Palate, hard, the bony roof of the mouth.

Palatine, one of a pair of bones which form the hinder part of the hard palate.

Palatine process, a shelf-like projection of the maxillary, which forms most of the hard palate on each side.

Paleocene, the oldest of the five Tertiary epochs.

Palmate, form of antler in which the tines are fused into large plates.

Pampean, Pleistocene, perhaps including the uppermost Pliocene, of Argentina.

Parallelism, or **Parallel Evolution,** similar development of related, but separate series.

Paranâ stage, lower Pliocene (or perhaps upper Miocene) of Argentina.

Parietal, one of a pair of large, vaulted bones, which form most of the sides and roof of the cranium.

Paroccipital process, a bony projection from the infero-external angle of the occiput.

Patagonian stage, marine lower Miocene of Patagonia.

Patella, the knee-cap.

Pecora, true Ruminants, suborder of Artiodactyla.

Pelvic girdle, *see* Pelvis.

Pelvis, the hip-bones.

Periotic, a small, dense bone, which lodges the internal labyrinth of the ear.

Pes, the hind foot.

Petrosal, *see* Periotic.

Phalanx, one of the joints of the fingers or toes.

Pholidota, Pangolins or Scaly Anteaters; order of placental mammals.

Phylum, a genetic series of ancestors and descendants within a family.

Pilosa, Sloths, Anteaters, etc.; suborder of Edentata.

Pinnipedia, Marine Carnivores; suborder of Carnivora.

Pisiform, an accessory bone attached to the postero-external angle of the carpus.

Placenta, a temporary structure connecting mother and fœtus, by means of which the fœtus is nourished in the womb.

Placental, having a placenta; the Monodelphia.

Pleistocene, the older of the two Quaternary epochs.

Pliocene, the fifth and last of the Tertiary epochs.

Pollex, the first digit of the manus, or thumb.

Polyphyletic, derived from two or more distinct lines of ancestry.

Polyprotodonta, Opossums, etc.; suborder of Marsupials.

Posterior nares, the hinder opening of the nasal passage.

Postglenoid process, a bony ridge behind the glenoid cavity of the squamosal to prevent backward dislocation of the jaw.

Postorbital process, a bony projection from the frontal or jugal, bounding the eye-socket behind.

Premaxillary, the anterior bone of the upper jaw, carrying the incisor teeth.

Primates, Lemurs, Monkeys, Apes and Man; cohort and order of placental mammals.

Proboscidea, Elephants, etc.; order of hoofed mammals.

Process, a distinct prominence or projection of bone for the attachment of muscle or ligament.

†Proglires, an extinct suborder of the Insectivora.

Prototheria, most primitive subclass of mammals; oviparous.

Pubis, the postero-inferior element of the hip-bone.

Pyramidal, the external bone in the upper row of the carpus.

†Pyrotheria, an extinct suborder of †Toxodontia.

Pyrotherium Beds, *see* Deseado stage.

Radius, the internal bone of the fore-arm.

Rodent, *see* Rodentia.

Rodentia, Gnawers; order of placental mammals.

Rotular groove, a broad, shallow groove on the anterior face of the femur, near the lower end, in which the knee-cap glides.

Round ligament, the ligament between the head of the femur and a pit in the acetabulum of the hip-bone.

Sacral vertebræ, those of the sacrum.

Sacrum, a bony mass of fused vertebræ, for the support of the hip-bones.

Sagittal crest, a ridge of bone in the median line of the cranial roof, running forward from the occipital crest.

Scaphoid, the inner bone in the upper row of the carpus.

Scapho-lunar, a compound bone made up of the coalesced scaphoid, lunar and central.

Scapula, the shoulder-blade.

Section, primary division of a suborder.

Sectorial, a carnassial or shearing tooth of a flesh-eater.

Selenodont, teeth composed of crescent-shaped cusps.

Shaft, the body of a long bone, comprising most of its length.

Sheridan stage, older Pleistocene of the Great Plains.

Shoulder-girdle, the bones to which the fore limb is attached.

Simplicidentata, Squirrels, Rats, Porcupines, etc., etc.; suborder of Rodentia.

Sinus, an air-cavity in one of the skull-bones.

Sirenia, Sea Cows and Dugong; order of marine mammals.

Species, the unit group in classification, made up of individuals which are most closely similar.

Spine, (of the scapula) a bony ridge on the outside of the shoulder-blade; (of the tibia) a single or double prominence from the upper end of the shin-bone; (of a vertebra) the neural spine.

Squamosal, a bone forming the posterior side-wall of the cranium.

Sternal ribs, the inferior segments of the ribs, which articulate with the breast-bone.

Sternum, the breast-bone.

Stratum, a layer of bedded rock.

Subclass, primary division of class.

Subfamily, a group of related genera within the family.

Subgenus, a group of related species within the genus.

Suborder, primary division of order.

Subspecies, a definite subdivision of a species.

Suina, swine-like animals; suborder of Artiodactyla.

Superfamily, a group of related families.

Superorder, a group of related orders.

Supinator ridge, a crest on the outer side, near the lower end of the humerus, for attachment of the supinator muscle.

Symphysis, the line of junction of the two halves of the lower jaw.

Synonym, a name improperly given to a genus or species already named.

†Tæniodontia, an extinct order of clawed mammals.

Tarsal, an element of the tarsus.

Tarsus, the bones of the ankle-joint.

Temporal muscle, a muscle of mastication attached to the side of the cranium and the coronoid process of the lower jaw.

Tertiary, the more ancient of the two Cenozoic periods.

Thoracic vertebræ, *see* Dorsal.

Thorax, the bony framework of the chest.

Tibia, the shin-bone, internal bone of the lower leg.

†Tillodontia, an extinct order of clawed mammals.

†Toxodonta, an extinct suborder of the †Toxodontia.

†Toxodontia, an extinct order of hoofed mammals.

†Toxodonts, *see* †Toxodonta.

Tragulina, "Mouse Deer"; suborder of Artiodactyla.

Transverse processes, projections from the sides of a vertebra.

Trapezium, internal bone in the lower row of the carpus; supports the first digit, or thumb.

Trapezoid, second bone in the lower row of the carpus; supports the second digit, or index finger.

Triassic, first of the three Mesozoic periods.

†Triconodonta, an extinct suborder of Mesozoic Marsupials.

†Trituberculata, an extinct order of Mesozoic mammals.

Trochanter, a projection from the femur.

Trochanter, third, a hook-like process on the outer side of the shaft of the femur, near the middle of its length.

Trochlea, the pulley-shaped lower end of the humerus for articulation with the fore-arm bones.

Trunk vertebræ, those of the body, the dorsals and lumbars.

Tubercle, an articular projection on a rib, connecting with the transverse process of a dorsal vertebra.

Tuberosities (of the humerus), heavy projections from the upper end of the bone, in front of the head.

Tubulidentata, the Aard Vark; an order of placental mammals.

Tyl'opoda, Camels and Llamas; suborder of Artiodactyla.

Tympanic, a bone forming the support of the ear-drum and usually inflated into a hollow capsule.

†Typotheres, *see* †Typotheria.

†Typotheria, an extinct suborder of the †Toxodontia.

Ulna, the external bone of the fore-arm.

Unciform, the external bone in the lower row of the carpus; supports the fourth and fifth digits, or ring and little fingers.

Unconformity, the relation between two groups of strata, one of which was deposited upon the worn surface or upturned edges of the other.

Ungual phalanx, the terminal joint of a digit, which supports the claw, nail or hoof.

Unguicúlata, clawed mammals; cohort of Monodelphia.

Ungulata, hoofed mammals; cohort of Monodelphia.

Ungulates, *see* Ungulata.

Uterus, the womb.

Vagina, the genital canal of the female.

Variety, a more or less constant group within a species.

Vertebra, a joint of the backbone.

Vertebral column, the backbone.

Viviparous, producing living young.

†Zeuglodontia, an extinct order of Cetacea.

Zygapophyses, the projecting processes, by means of which successive vertebræ are articulated together.

Zygomatic arch, a bony bridge from the eye-socket to the hinder part of the cranium.

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N. B.—The most important references are in heavy-faced type; technical names of genera and species are italicized, though most of the specific names are omitted as unnecessary. Extinct groups are indicated by a dagger (†).

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