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THE SELENODONT ARTIODACTYLS

OF THE

UINTA EOCENE

BY W. B. SCOTT

WAGNER FREE INSTITUTE OF SCIENCE OF PHILADELPHIA

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INTRODUCTION

THE selenodont artiodactyls found in the various Tertiary horizons of North America may be roughly grouped into two somewhat heterogeneous assemblages: (1.) The first group comprises those which are generically identical with, or are clearly related to, Old World forms, such as the anthracotheres and the true ruminants (Pecora), and which reached this continent by migration. (2.) The second group includes the forms indigenous to America, the successive stages of whose descent may be traced, more or less completely, through several of the Tertiary formations.

Within this second group are found such peculiar and characteristically North American forms as the *Oreodontidæ*, the *Agriochœridæ*, the *Leptomerycidæ*, *Protoceras*, and *Poebrotherium*. These forms have greatly puzzled nearly all the palæontologists who have studied them, and the most diverse opinions have been expressed with regard to the systematic position and genetic relationships of the various genera. Only concerning the poebrotheres has there been any general consensus of opinion; they have been well-nigh universally regarded as representing the main line of tylopodan descent, leading directly to the camels and llamas of the modern period. For the other groups we have been accustomed to seek various European connections and analogues: the anthracotheres, the tragulines, the giraffes, and the deer have all been called upon to explain the position of these problematical American forms, though few students of the subject have been able to reach conclusions which were altogether satisfactory even to themselves.

The principal difficulty in dealing with these peculiar American families has hitherto lain in the extremely incomplete and fragmentary phylogenetic series by which they have been represented in the collections. Owing to this absence of well-defined phylogenetic series, it has been almost impossible to unravel the complicated tangle of resemblances and differences between the American and the European groups of selenodonts, and to determine which of these resemblances are to be ascribed to actual relationship, and which of them have been independently acquired as the result of a more or less parallel or convergent course of development.

To a considerable extent this difficulty has been removed by the explorations of the last few years. The collections made in the White River and Uinta formations by Messrs. Hatcher and Gidley for the museum of Princeton University, and by Dr. Wortman and Mr. Peterson for the American Museum of Natural History, in New York, have brought together a great number of new and finely preserved fossils, which shed new and welcome light upon the problem. For the opportunity of studying the collections belonging to the American Museum I am indebted to the kindness of Morris K. Jesup, Esq., President, and of Professor H. F. Osborn, and gladly take this opportunity of expressing my cordial thanks to these gentlemen.

The material to be described in the present paper consists principally of fossils from the Uinta Beds, supplemented by some White River specimens of *Leptomeryx* and *Hypertragulus*, which add in an important way to our knowledge of those genera.

The Uinta is the most ancient of the American Tertiary stages in which the artiodactyls began to play an important rôle in the life of the times. Indeed, the most striking and characteristic feature of the Uinta fauna, as distinguished from that of the preceding Bridger stage, is in the very marked increase of the artiodactyls in general and of the selenodonts in particular. In the Bridger beds selenodonts are very rare as fossils, and not more than two genera have been described from this horizon, while in the Uinta the selenodonts are individually the most abundant fossils, and not less than nine genera of them may be distinguished. More important than this mere increase in numbers and variety is the fact that the Uinta selenodonts are so obviously ancestral to those of the succeeding White River stage. It is hardly an exaggeration to say that the forerunner of every White River selenodont, except those of Old World origin, may be indicated, with more or less confidence, in the Uinta fauna. This addition to the phylogenetic series is of the utmost morphological significance, because of the help which it gives in working out the real taxonomic position of the problematical American families. That the problems cannot even now be solved in all respects is due to the fact that the record of most of the lines breaks off with the Uinta, and cannot yet be traced back into the Bridger in any satisfactory way. This interruption leaves the question regarding the position of certain families to some extent an open one, families which had already become distinctly differentiated as such in the Uinta epoch.

The most interesting and striking result to which the study of the Uinta selenodonts has led is the very unexpected conclusion that, *with the possible exception of the oreodonts and agriochœrids, all of the strictly indigenous North American selenodonts are derivatives of the tylopodan stem.* Paradoxical as this conclusion may appear, I believe it to be fully justified by the evidence which will be laid before the reader. The Tylopoda are thus seen to be a very ancient and highly diversified group, comparable in this respect to the Pecora, or true ruminants, which they so closely resemble in many features. The Pecora are an Old World group, which underwent great expansion and diversification in Eurasia, but did not reach this continent till late Miocene times, and never attained the importance here that they have so long had in the Eastern Hemisphere. Their place was to a very great extent taken in America by the Tylopoda, which ran a course of development in many ways parallel to that of the Pecora and Tragulina, but with a variety and diversity of structure, habit, and appearance such as are not attained in either of the latter groups.

It is this very parallelism with the Pecora which has led most students of the American selenodonts astray. We have constantly been endeavoring to find relationships between these forms and the European ruminants or tragulines, where no such relationships existed, but only analogies, parallelisms, or convergences. The truth appears to be that the indigenous American selenodonts make up a natural assemblage of forms, which, with much diversity of size and structure, are yet all quite closely related among themselves, and only distantly with the European forms which more or less resemble them. Just as the Pecora are typically Old World, both in origin and development, so the Tylopoda are typically New World, and did not reach the Eastern Hemisphere till the end of the Miocene or beginning of the Pliocene, and then only in very limited numbers, *Camelus* and its immediate forerunners being the only known Eurasian representatives of the group.

It is an admirable example of the keen insight which characterized Rütimeyer that he had practically reached this conclusion at a time when the White River fauna was very imperfectly known, and that of the Uinta not at all. In a passage which has not attracted the attention it deserves he says of *Leptomeryx:* "Die Merkmale des Schädels mit Einschluss namentlich des Unterkiefers, scheinen weit eher auf eine nahe Beziehung von *Leptomeryx* zu den in Nordamerika so stark vertretenen Vorläufern der Camelina (Oreodon, Procamelus, Leptauchenia, etc.), hinzudeuten und denjenigen von Tragulina und Cervina sehr fern zu stehen. . . . . Nach jeder Richtung scheint mir also *Leptomeryx* den hornlosen Wiederkäuern des europäischen Miocens sehr fern zu stehen." ('83, pp. 98–9.)

The Uinta beds are confined to the comparatively small basin in Northwestern Colorado and Northeastern Utah which lies to the south of the Uinta Mountains. They directly overlie the strata of the upper Bridger (Washakie substage), and according to Peterson are divisible into two horizons, which he calls B and C. (See Osborn, '95, pp. 72–76.) The lower horizon, B, is transitional from the Bridger, while the upper beds, C, constitute the typical Uinta. Peterson says of them: "We now reach the *true Uinta*, or Brown's Park, beds of a fine-grained, soft material, much the same in appearance as the characteristic Bad Lands of South Dakota, with the exception of the color, which is a brick red; in fact, the reddish tinge holds good throughout the Uinta sediment. . . . . These uppermost strata of the Uinta basin have hitherto been reported (by C. A. White) as resting unconformably upon the underlying Bridger sediment, but no observable breaks were found to distinguish the true Uinta from the underlying Bridger sediment." (Loc. cit., p. 74.)

On the other hand, Hatcher believes that there is a distinct angular unconformity between the horizons B and C. In favor of this opinion is the unquestioned fact that the upper beds (C) overlap the lower (B) towards the north, extending over upon the upturned Cretaceous and older rocks, which form the flanks of the Uinta Mountains.

The north to south extension of the beds is not great at present, but, doubtless, has been very much reduced by denudation along the southern edge.

The position of the Uinta formation in the geological column is perfectly clear, both upon stratigraphical and palæontological grounds; it succeeds the Bridger and precedes the White River in time. It has been customary to call the Uinta beds Upper Eocene, but much may be said in favor of regarding them as Lower Oligocene. The Uinta, White River, and John Day form three successive stages, whose mammalian faunas are most closely connected, and were the American time-scale constructed without reference to that of Europe, no student of these horizons would think of distributing them among different periods. Clearly, the natural arrangement is to make them three stages of one period or system. In the interests of palæontology it is fortunate that the French observers have reached much the same conclusion regarding the corresponding horizons in France, and are tending to enlarge the boundaries of the Oligocene. The White River beds correspond very closely indeed to the horizon of Ronzon, which is so generally taken as the type of the Middle Oligocene, while the Uinta corresponds, somewhat less accurately, to the Paris Gypsum (Lutetian); the latter is now referred by many to the Lower Oligocene, and the Uinta should receive the same reference, for the two are so nearly synchronous that they cannot well be separated into different periods.

[Before taking up the principal subject of this paper, the Uinta selenodonts, it will be serviceable to give a revised account of certain White River genera, especially *Leptomeryx* and *Hypertragulus*, which will be found necessary for the full comprehension of the Uinta forms. The new material, which necessitates the revision and modification of several statements in my former papers ('91, *a, b, c;* '95, *a, b*), was obtained at various times by Messrs. Hatcher, Gidley and Wells in the White River beds of Nebraska and South Dakota.]

Geological Museum, Princeton, N. J.,
December 1, 1898.

A. White River Selenodonts.

Family LEPTOMERYCIDÆ.

Leptomeryx Leidy.

Plate I., Figures 1, 2.

IN this genus the dental formula is: $I\frac{?}{3}$, $C\frac{0}{1}$, $P\frac{3}{4}$, $M\frac{3}{3}$. The number of upper incisors is uncertain; so far, only a single specimen has been found in which part of the premaxillary is preserved, and in this there is the alveolus for the lateral incisor, but whether the others were present also is not determinable. The upper canine is wanting, at least in the only two specimens which would show this tooth if it were present, for in the immense majority of the skulls which have been collected the delicate muzzle is broken across in front of p^2. It is possible, though it seems unlikely, that the absence of the upper canine is a sexual character, and that the two specimens mentioned are of females. On the other hand, no fragment of a tusk-like canine has ever been found associated with the numerous individuals so far discovered. The number of upper premolars is three, p^1 having disappeared; the others are quite complex, each having a well-developed deuterocone, which is conical on p^2 and p^3, crescentic on p^4. Viewed from the outer side, these premolars have a sharp and trenchant form, while the prominence of the median external rib and of the anterior and posterior buttresses gives them a trifid appearance. The upper molars have incompletely formed internal crescents, and are remarkable for the large size of the anterior and median external buttresses (or styles), and especially for the great prominence of the rib upon the antero-external crescent, which is of very unusual degree; that on the postero-external crescent is far less prominent.

The lower incisors are procumbent and almost horizontal in position; the median incisor is remarkably long and straight, and is also the broadest of the three; $i_{\overline{2}}$ is much shorter and more everted, and $i_{\overline{3}}$ is still shorter. The lower canine has become an incisor in form and function and is considerably shorter than $i_{\overline{3}}$, which it follows without a diastema. The first lower premolar is isolated by a long diastema in front of and a shorter one behind it; it is very small and shaped like a canine, and its form immediately suggests that it once functioned as a canine, but has dwindled because of the loss of the upper tooth which it opposed. The other premolars increase successively in size and complexity backward; they are long, low, trenchant, and acutely pointed, with sharp basal cusps; $p_{\overline{3}}$ (and more distinctly $p_{\overline{4}}$) has an internal ridge, which incloses a fossette. The lower molars have narrow, compressed crowns, and display the traguline character of ridges upon the anterior crescents. Indeed, the entire dentition bears considerable resemblance to that of the tragulines.

The skull (Plate I., fig. 1) is very much more like that of *Poebrotherium* and the typical Tylopoda than the mutilated specimens hitherto figured would lead one to suppose; it has the same elongate, triangular shape, and the same very long, slender, and tapering muzzle. It is really surprising to see how the whole character and appearance of the skull are changed, and how its traguline resemblances are removed by the addition of the muzzle. While the skull of *Leptomeryx* is in general very much like that of a minute *Poebrotherium*, yet there are many noteworthy differences. The orbit is placed much farther forward, its anterior border being over m^1; the zygomatic arch is relatively stouter, and the glenoid cavity presents a curiously notched appearance when seen from the side; the auditory bulla is small and is not filled with cancellous bone, but simple and hollow, and is provided with a long, tubular meatus; a small facial vacuity is present between the lachrymal, frontal, nasal, and maxillary. The horizontal ramus of the mandible is very slender and the angle is very broad, extending much behind the condyle, but does not form the great, hook-like process which occurs in *Poebrotherium;* the masseteric fossa occupies a very elevated position upon the ascending ramus of the jaw.

In addition to these obvious and striking differences in skull-structure between the two genera, there are numbers of minor discrepancies which it is not necessary to point out.

The neck in *Leptomeryx* is short, and the odontoid process of the axis is peg-shaped. The other cervicals are of the normal artiodactyl type, not like those of the *Camelidæ.* The back is much curved, owing to the elongation of the hind-limbs.

The fore-limb is short and lightly constructed. The scapula is broad and triangular, and ruminant rather than tylopodan in shape, though not unlike that of *Poebrotherium.* The humerus has no very definite characteristic, and while quite like that of *Poebrotherium,* its small size gives it a traguline appearance. The ulna is reduced and very slender, but uninterrupted and entirely free from the radius, which has a broad, antero-posteriorly compressed and oval shaft. The carpus is quite traguline in appearance, the magnum being so shifted as to have only a lateral contact with the lunar; it is also coōssified with the trapezoid, which is very unusual in this group. The manus contains four complete digits, though the lateral metacarpals (mc. ii. and v.) are exceedingly slender. No anterior cannon-bone is formed.

The hind-limb greatly exceeds the fore-limb in length and stoutness. The pelvis is like that of *Poebrotherium* and altogether different from that of the tragulines in shape, and much the same statement applies to the femur, though the distal end of this bone is remarkable for the narrowness and length of its rotular trochlea. The proximal end of the fibula is a short spine anchylosed with the tibia; the shaft is wanting, and the distal end is a malleolar nodule, wedged in between the tibia and the calcaneum. The navicular and cuboid are coōssified, which, like the union of the trapezoid and magnum, is very rare in this group of selenodonts. A cannon-bone is formed by the coōssification of the median metatarsals (mt. iii. and iv.), to which are attached the splint-like proximal ends of the lateral pair (mt. ii., v.). The distal end of the cannon-bone (Plate I., fig. 2) in uninjured specimens is quite deeply cleft, and shows in a slight but unmistakable way the eversion of the metatarsal trochleæ which is so characteristic of the Tylopoda; the carina is confined to the palmar aspect of the trochleæ. The phalanges are like those of *Poebrotherium*, and the unguals are elongate, slender, and pointed.

That the whole appearance of the skeleton of *Leptomeryx* and many details of its structure closely resemble those of the tragulines is not to be denied, and I formerly referred it to that group with much confidence ('91*c*, p. 360), in this following Cope's example ('89, p. 121). The new material just described has convinced me, however, that this reference is erroneous, and that Rütimeyer was right in regarding it as essentially tylopodan ('83, p. 98), a conclusion which Wortman has also reached in his latest paper ('98, p. 100).

Hypertragulus Cope.

PLATE I., FIGURES 3, 4.

This genus is a remarkable variant of the *Leptomeryx* type, to which it is obviously allied, though departing less from the main tylopodan stem, as represented in *Poebrotherium* and the John Day *Gomphotherium.*

The dental formula is: $I\frac{?}{?3}$, $C\frac{1}{1}$, $P\frac{4}{3}$, $M\frac{3}{3}$. From the material at present available it is extremely difficult to work out the homologies of the incisors and canines, but the arrangement appears to be as follows: The upper incisors, if present at all, are quite unknown, for no specimen has yet been found with uninjured premaxillaries. The upper canine was preserved, as is indicated by the alveolus in one individual. The lower incisors are small and very delicate and somewhat less procumbent than those of *Leptomeryx*. The lower canine is not incisiform, and is separated from $i_{\overline{3}}$ by a very short diastema; it has a high, slender, pointed, and recurved crown, which is distinctly larger in some specimens than in others, a difference which is doubtless sexual. The premolars are much simpler than in *Leptomeryx*. $P^{\underline{1}}$ is a simple, sharp, compressed cone, implanted by two widely divergent fangs. $P^{\underline{2}}$, which follows $p^{\underline{1}}$ after a considerable diastema, is similar but somewhat smaller; $p^{\underline{3}}$ is supported upon three fangs and bears a small internal cusp (deuterocone); $p^{\underline{4}}$ is, like that of *Leptomeryx*, composed of two crescents, internal and external. Unless what seems to be the lower canine should prove to be a caniniform premolar, which is extremely improbable, then $p_{\overline{1}}$ has disappeared; $p_{\overline{2}}$ is simple, compressed, and conical, implanted by two fangs, and isolated by a long diastema in front of it and a much shorter one behind; $p_{\overline{3}}$ is high, acutely pointed, and simple, but $p_{\overline{4}}$ has anterior and posterior basal cusps and a small though distinct deuteroconid. The premolars of *Hypertragulus*, both upper and lower, are distinguished from those of *Leptomeryx* not only by their greater simplicity of structure, but also by their much smaller extension in the antero-posterior direction. The molars are much like those of the last-named genus, and the superior ones have the same extraordinarily prominent median rib upon the antero-external crescent, but the outer buttresses are smaller and project less.

The skull (Plate I., figs. 3, 4) has quite as characteristically a tylopodan appearance as that of *Leptomeryx*, though in a somewhat different fashion. The cranium is well-rounded and capacious, with low and short sagittal crest, and the forehead is broad; the face narrows anteriorly more abruptly than in *Leptomeryx*, so as to give it a more llama-like appearance. On the other hand, the muzzle is not nearly so long and tapering, which makes quite a difference in the general look of the two skulls. The orbit is left rather widely open behind, because of the absence of a postorbital process from the jugal, and the facial vacuity between the frontal, nasal, lachrymal, and maxillary is larger than in *Leptomeryx*. The top-view of the skull is of strikingly tylopodan character. (Plate I., fig. 4.) The mandible has a shorter horizontal ramus than that of *Leptomeryx*, and the angle approximates much more to the great hook-like shape seen in *Poebrotherium*.

The ulna and radius are coössified, but the manus, so far as it is known, does not differ in any important way from that of *Leptomeryx*. There is no cannon-bone in the pes, the two functional metatarsals (iii. and iv.) remaining separate; vestigial splints representing mt. ii. and v. were probably present also, but they have not yet been recovered.

That *Hypertragulus* is nearly connected with *Leptomeryx*, and at the same time is a member of the Tylopoda, appears from its entire structure and from a comparison with the typical members of that group which preceded or accompanied it in time. It must be remembered, in considering the systematic position of these genera, that the early tylopodans differed in many important respects from the modern representatives of the suborder.

Hypisodus Cope.

The little animals comprising this genus are the smallest known members of the family. They differ from all the others in having hypsodont molars and in the peculiar character of the anterior lower teeth, the canine and first premolar having taken on the form and function of incisors, which thus appear to be ten in number in the mandibular series. Very little is known of the skeleton, but that little leads us to infer that the foot-structure was very similar indeed to the condition found in *Leptomeryx*, except that there was no cannon-bone in the pes.

Protoceras Marsh.

Professor Marsh ('91, p. 82) has proposed the formation of a separate family for the reception of this extraordinary genus, but this seems hardly necessary, for in essentials *Protoceras* does not differ more from *Leptomeryx* or *Hypertragulus* than they do from each other, despite its bizarre appearance.

The dental formula is: $I\frac{0}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. The upper incisors have entirely disappeared, but the canine is, in the males, a large curved tusk of D-shaped section and abraded upon the posterior face; the lower canine has gone over to the incisors, and its place is taken, in the males, by $p_{\overline{1}}$. $P^{\underline{1}}$ is isolated by diastemata in front of and behind it; the other premolars, both upper and lower, are much as in *Leptomeryx*, but their great elongation antero-posteriorly gives them a strong resemblance to those of *Poebrotherium*. The molars also resemble those of *Leptomeryx*, and in the upper jaw they are characterized by the same great prominence of the external buttresses and ribs, while in the mandible they are broader and lower.

The skull is very remarkable, not only for its bizarre appearance, but also for its extreme modernization in certain respects, and for the great difference between the males and females. This skull retains the tylopodan form only in a very modified way, this form being shown in the prominent sagittal and occipital crests and in the long, slender, and tapering muzzle. The cranium is much shortened, the orbit being shifted almost entirely behind the teeth, and the face is bent down upon the basi-cranial axis, as in the Cavicornia, a feature which has not been found in any other White River mammal. The auditory bulla is hollow and very small. The zygomatic arch is short, but quite heavy, and the orbit is completely enclosed by bone. The nasals are extremely short, making the anterior narial opening exceedingly large, much as in the Saiga antelope. The premaxillaries are edentulous and their alveolar portion is thin and depressed, but the spines are broad and the incisive foramina very narrow. The mandible is quite pecoran in appearance, with a long, slender, horizontal ramus, and a rather low and broad ascending ramus, with the angle hardly projecting at all behind the condyle. This latter feature is in marked contrast to most of the tylopodan genera. A resemblance to the oreodonts is found in the shape of the coronoid process, which is very low and tapers abruptly to a blunt point.

The sexual differences are very striking. In the male skull we find a pair of compressed, club-shaped, and somewhat horn-like processes on the parietals, short spines on the frontals, while the free margins of the maxillaries rise into massive and everted bony plates. In the females these various protuberances are very feebly indicated.

In the vertebral column the neck is moderately elongate and the vertebræ are not of the characteristically tylopodan structure, but the axis is elongate, with a broad, flattened odontoid process, like that of *Poebrotherium*, and a great hatchet-shaped neural spine, like that of *Leptomeryx*.

The scapula is, in general, like that of *Poebrotherium*, but is narrower and has a very much smaller prescapular fossa, a somewhat shorter acromion, and a less prominent coracoid. The ulna and radius are separate, except that in old individuals they may unite distally. The head of the radius has a broad intercondylar convexity, somewhat as in the oreodonts; distally it has no contact with the pyramidal. In the carpus the trapezoid and magnum are separate, and the carpal elements, especially those of the proximal row, are high vertically. The metacarpus has four members, of which the laterals are still well developed, much better than in *Leptomeryx*.

The hind-limb is considerably longer and stouter than the fore-limb. The pelvis is like that of *Poebrotherium* and *Leptomeryx*, and the femur is a good deal like that of the former, but is shorter and heavier, its rotular trochlea is broader, and the suprapatellar fossa less distinct. The tibia is long and the fibula completely reduced, its proximal end a short spine anchylosed with the tibia and its distal end a malleolar bone. The cuboid and navicular are separate, as are the metatarsals. The latter are reduced to two functional members, while the lateral pair are reduced to splints. The phalanges are like those of *Poebrotherium*, though rather shorter and heavier.

Aside from the extraordinary peculiarities of the skull, especially in the male sex, *Protoceras* displays an unmistakable likeness to *Leptomeryx* and *Hypertragulus*, a likeness which is apparent in the vertebral column, the limb-bones, the feet, and the dentition. Combined with these are certain resemblances to *Poebrotherium*, fewer and less striking ones to the oreodonts, and a number to the Pecora. It should be remembered, however, that the pecoran characteristics, which are almost exclusively confined to the skull, are such as are found only in the *higher* Pecora, the Cavicornia, and do not occur in the deer. It may seem quite absurd to regard *Protoceras* as an aberrant member of the Tylopoda, but, as will be shown in the sequel, it is highly probable that such is the correct view of its relationships. I am glad to find myself in agreement with Dr. Wortman on this point, for in the paper already cited he speaks of "the early cameloids, *Protoceras* and *Leptomeryx*." ('98, p. 102.)

B. Uinta Selenodonts.

FAMILY I. CAMELIDÆ.

Protylopus Wortman.

PLATE II., FIGURES 5–9.

Bull. Am. Mus. Nat. Hist., vii., p. 104. (April 9, 1898.)
Paramerys Scott (*non* Marsh), Proc. Am. Phil. Soc., xxxvii., p. 74. (April 15, 1898.)

IN my preliminary paper (loc. cit.), which was printed but a few days after that of Dr. Wortman, I referred this genus to *Parameryx* Marsh, with the extremely vague and unsatisfactory descriptions of which it seemed to agree. Dr. Wortman, who has seen the type specimens of the so-called *Parameryx*, is satisfied that the present genus is distinct from it. He has given ('98, pp. 104–110) an excellent outline description of this animal, the phylogenetic importance of which it is difficult to exaggerate, but a somewhat more detailed account is necessary for the purposes of this paper. As this genus almost certainly represents the main line of tylopodan descent in Uinta times, the line which has led to the modern camels and llamas, it will serve as an admirable standard of comparison by which to test the divergences of its contemporaries. *Protylopus* is of very great interest as being the most ancient undoubted member of the tylopodan line, though it sheds less light than could be desired upon the relations of that line to the other artiodactyl series, for the peculiar differentiation which is so strongly marked in the White River genus, *Poëbrotherium*, is already distinct in the Uinta form.

I. *The Dentition.* The dental formula is unreduced, $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$, and in both jaws the teeth form straight and almost continuous series, slightly spaced apart, it is true, in the anterior region, but without anything that can be fairly called a diastema.

A. *Upper Jaw.* (Plate II., figs. 5, 6.) The incisors are small and are arranged in a nearly straight fore-and-aft line, curving inward but very slightly at the anterior end; they increase somewhat in size from the first to the third, and are separated by moderate interspaces, with a rather longer space between

i^3 and the canine. The crowns are small, laterally compressed and acutely pointed, of a somewhat hastate shape, and very slightly recurved. The canine is very small and looks like one of the incisors, which it resembles in form, exceeding i^3 in size hardly more than the latter does i^2. Thus, at a superficial glance, the animal appears to have four upper incisors on each side. The crown of the canine is of somewhat more distinctly hastate shape than that of i^3, expanding below the neck and then tapering to a very acute point; it is also laterally compressed and its edges are trenchant. It is possible that the small size of the canines is a sexual character, and that the two finely preserved specimens upon which this description is founded are both females, but the analogy of *Poebrotherium* would lead us to infer that the size of the canines did not differ materially in the two sexes.

The premolars are small and very simple, increasing in size and complexity posteriorly. P^1, the smallest and simplest of the series, is separated by short spaces from the canine and p^2, which, however, do not deserve the name of diastemata, as they hardly equal the fore-and-aft diameter of the tooth itself. In unworn condition the crown of p^1 is a simple, compressed cone, without cingulum or basal cusps, elongated antero-posteriorly and terminating in an acute point; the edges are sharp, and, as the front edge is convex and the hinder edge concave, the tooth seems to be somewhat recurved. P^2 is a little larger, but is otherwise very similar, as seen from the outer side; its transverse diameter is, however, considerably greater and its external face more strongly convex. In some specimens this tooth has no cingulum, but in others the cingulum is indicated on the front and hind edges. P^2 is separated by a very short space from p^1 and by a still shorter one from p^3, while p^3 and p^4 are in contact, or may even overlap. P^3 resembles p^2, except for its somewhat larger size, the presence of a faint inner cingulum, and its slightly greater transverse width; its anterior edge is suddenly narrowed, so as to become trenchant, making a shallow depression upon the external face, and very feebly marked indications of the basal cusps may be seen. Sometimes the basal cusps, though small, are quite distinct. P^4 is of nearly the same fore-and-aft length as p^3, but is decidedly broader, owing to the development of the deuterocone, which, as in the selenodonts generally, is of crescentic form. This inner crescent is much better developed in some individuals than in others, as are also the basal cusps and the external cingulum. In the latter case these cusps are not more conspicuous than on p^3, while in the former they are much better developed on p^4. The crowns of all the premolars are low vertically, extended antero-posteriorly, and provided with sharp edges and acute points.

The upper molars are of the strictly tetraselenodont pattern, and unworn specimens demonstrate the truth of Wortman's conclusion that the intermediate tubercles were absent. ('98, p. 106.) These molars differ quite markedly from those of the contemporary genus, *Protoreodon*, not only in the absence of the unpaired cusp (protoconule), which the latter still retains, but also in the form of the external crescents, which in *Protylopus* are but slightly concave on the outer side and have a very prominent median rib, especially the anterior crescent. The median buttress, which is formed by the junction of the two external crescents, does not contain a prolongation of the median valley. In the oreodont, on the other hand, the outer crescents are much more concave externally and the median rib is less prominent; the outer median buttress is broader and does contain a narrow prolongation of the median valley.

The molars of *Protylopus* increase in size from the first, which is the smallest, to the third, which is the largest of the series, and they are all slightly different from one another in the details of construction. Differences between the molars of various specimens may also be observed. In one case m^{1} has very small anterior and median external buttresses, and the two outer crescents are of similar size and shape, with equally prominent median ribs. In m^{2} the buttresses are very much larger, and the rib of the postero-external crescent much less prominent than that of the antero-external one. The buttresses of m^{3} are still larger, enclosing small fossettes, and the posterior buttress appears. On m^{2} and m^{3} a small pillar occurs between the two inner crescents. In another specimen the anterior buttress on m^{1} is much larger, while the median buttress is much less prominent in all the molars.

B. *Lower Jaw.* (Plate II., figs. 5, 7.) The incisors are small, especially i_{1}, while i_{2} and i_{3} are much larger and of nearly equal size; they are set *en echelon* in the jaw. The crowns are chisel-shaped, slightly spatulate, and antero-posteriorly compressed, while those of the upper jaw are laterally compressed. The canine succeeds i_{3} with hardly any interval; it is not much larger than i_{3}, which it somewhat resembles in shape, but it is more pointed and continues to function as a canine, opposing the upper canine, which it slightly exceeds in size. The premolars follow the canine almost without a break, and are set more closely together than the upper series. P_{1} is almost caniniform; it is implanted by a single fang and has a compressed, acute, conical crown, without accessory cusps. The other premolars are much more elongate antero-posteriorly than $p_{\overline{1}}$, and are inserted each by two roots; they have simple, compressed crowns, with trenchant edges and acute apices, and are slightly convex on the outer side. $P_{\overline{4}}$ has small fore and hind basal cusps, but these are not present on the others. The lower premolars of *Poebrotherium* are in general like those the Uinta genus, but they are relatively much more elongate and have distinct basal cusps.

MEASUREMENTS.

	No. 11,222	No. 11,228
Upper dentition, length	0.060	
" incisor series, length	.008	.008
" premolar-molar series, length	.047	
" premolar series, length	.025	.023
" molar series, length	.0215	
" P-1, length	.005	.005
" P-2, "	.006	.006
" P-3, "	.006	.006
" P-4, "	.006	.005
" P-4, width		.005
" M-1, length	.0065	.006
" M-1, width		.006
" M-2, length	.0075	.007
" M-2, width		.008
" M-3, length	.0085	
" M-3, width		.009
Lower dentition, length	.060	
" premolar-molar series, length	.049	
" premolar series, length	.024	.0245
" molar series, length	.025	
" P-1, length	.004	.004
" P-2, "	.005	.006
" P-3, "	.0065	.0065
" P-4, "	.0065	.0065
" M-1, "	.006	.005
" M-2, "	.008	.0065
" M-3, "	.011	

The molars require no very particular description. They are of the ordinary selenodont pattern and increase in size posteriorly; the crowns, though entirely brachyodont, are relatively quite high, and the outer crescents are strongly convex externally, with a strong cingulum between them, while the inner ones are thick and but little compressed. $M_{\overline{3}}$ has a very large fifth lobe which quite equals the outer crescents in height and length; on its inner side is a small separate cusp.

As a whole, the dentition of *Protylopus* is closely similar to that of *Poebrotherium*, and just what we should expect to find in a genus ancestral to the latter. The incisors and canines are very much alike in the two genera, but in the White River form the diastema between $p^{\underline{1}}$ and $p^{\underline{2}}$ in both jaws is increased in correspondence with the elongation of the face, and the other premolars have become much elongated antero-posteriorly and have enlarged their accessory cusps; the molars display a decided tendency to assume the hypsodont structure, and on those of the upper jaw the external buttresses are reduced in size. It is of interest to observe that in *Poebrotherium* the upper milk-premolars, especially $dp^{\underline{4}}$, are more like the true molars of *Protylopus* than are the true molars of the White River genus.

II. The *Skull* (Plate II., fig. 5) is very like that of *Poebrotherium*, though with many obvious differences. In the first place, it is very much smaller than in the smallest species of the latter; secondly, the face, and especially its anterior portion, is much less elongated, while the cranium is narrower and less capacious. The orbit is smaller and much more widely open behind, and the auditory bulla has not attained such an exaggerated size. On the other hand, there is the same short sagittal crest, the same broad, lozenge-shaped forehead, narrow, tapering face, and slender jaws. *Protylopus* has already acquired the tylopodan physiognomy in a very marked degree, and the skull immediately recalls that of the llama to the observer, though, of course, the peculiarities are much less accentuated than in the later members of the series. So closely does the present genus approximate the contemporary members of certain other artiodactyl series, that, in the absence of the intermediate forms, it would be difficult to establish its connection with the modern Tylopoda.

The skull is, in some respects, of quite an advanced type of structure. The cranium is short and, for an animal of so early a date, capacious and well rounded; it supports a short and inconspicuous sagittal crest; the occiput is low, broad at the base, narrow and rounded at the top, and its crest likewise is weakly developed. The face is rather long, the orbit being shifted far back, so that its anterior margin is placed above $m^{\underline{3}}$. While remaining of nearly uniform vertical height throughout, the face narrows much anteriorly, but does so gradually, not displaying the sudden constriction at p^4 which is so characteristic of the modern members of the group.

Unfortunately, the base of the skull is so crushed and concealed in matrix that very little can be made out concerning its structure. The exoccipitals are broad and low, forming a very broad projection above the foramen magnum, with a shallow fossa on each side of the prominence; the paroccipital processes are quite long and are compressed antero-posteriorly, tapering to a blunt point. The supraoccipital is rather narrow and its posterior face is made up entirely of the median prominence, which extends upward from the exoccipitals, the lateral fossæ being cut off by the narrowing of the occiput. The supraoccipital appears to extend over upon the dorsal side of the cranium, but as the sutures in this region are mostly obliterated, it is not possible satisfactorily to make out the limits of the bone. The mastoid would seem not to be exposed upon the surface of the skull.

The parietals are relatively very large and roof in nearly the whole of the cerebral fossa; the sagittal crest is short, low, and thin, soon bifurcating into two long, low, and curved temporal ridges, which terminate at the frontal suture near the postorbital processes. Anteriorly the parietals are deeply and broadly notched to receive a median prolongation of the frontals.

The tympanic is not very well preserved in any of the specimens, but enough remains to show certain important differences from that of *Poebrotherium.* For ease of comparison, I shall quote the account of this bone in the latter genus, which I have given elsewhere ('91*b*, p. 15): "The tympanics are inflated into enormous bullæ, which in both species of *Poebrotherium* are relatively much larger than in the recent genera and are more rounded. In the small species, *P. Wilsoni,* they are larger and less compressed than in *P. labiatum,* and in both the long diameter is directed nearly parallel to the cranial axis. . . . . As in the Tylopoda generally, the bulla is filled with cancellous bony tissue. The external auditory meatus is a closed ring, opening slightly upward and backward; its rim does not project at all beyond the surrounding parts of the squamosal." To this description it may be added that the bulla abuts against the paroccipital process, with which it unites suturally for the greater part of its length, extending also considerably in advance of the postglenoid process. The auditory meatus is not a tube, but a mere opening, with a raised lip, into the bulla. In all these respects the bulla of *Protylopus* is different from that of the White River genus, the first and most obvious difference being its very much smaller size. It does not come into contact with the paroccipital process at all, but is entirely contained within the notch between the postglenoid and posttympanic processes of the squamosal, and does not extend beneath or in front of the former process. All of the bulla that is visible in the best preserved specimen is a short, transversely placed, and slightly swollen tube, which projects somewhat below the level of the postglenoid process. Whether this tube really represents the entire bulla, as it appears to do, it is not yet possible definitely to decide. The meatus is relatively large and does not form a complete ring, only the anterior half of the lip being made by the tympanic, while the posterior half is made by the posttympanic process of the squamosal. So far as I can make out, there is no cancellous tissue within the bulla.

Undue stress has been laid upon the fact that among existing artiodactyls only the Pecora have the auditory bulla free from cancelli, which occur in the Tylopoda, Tragulina, and Suina. It is altogether probable that this structure has been independently acquired by each of the three last-named groups, for in White River times only *Poebrotherium* has the cancellous bulla, all the other known artiodactyls of the time, even the peccary-like *Perchœrus*, having hollow tympanics free from cancelli. The condition of the bulla found in *Protylopus* seems to indicate that in the main tylopodan series also the cancelli were developed after the series had become well established as such. Concerning the traguline series we have as yet no information, but if the peccaries and camels acquired the structure independently, there can be no reason to doubt that the chevrotains did so likewise.

The squamosal is large and makes up much of the sidewall of the cranial cavity; inferiorly it forms a shelf which is continuous with the occipital crest, overhangs the auditory meatus, and in front passes into the zygomatic process. The glenoid cavity is a smooth, slightly convex, and indistinctly marked surface, but the postglenoid process is large, thick, and prominent, forming a high, transverse ridge. The posttympanic is also well developed, extending down nearly as far as the postglenoid and enclosing with it a deep notch, which receives the tympanic. The zygomatic process is slender and rather short, extending outward but moderately from the side of the skull.

The jugal is quite long, reaching posteriorly almost to the glenoid cavity, and is but slightly notched to receive the zygomatic process of the squamosal. The inferior edge of the orbit is prominent, but the postorbital process is quite low and is widely separated from that of the frontal. The masseteric ridge and surface are quite well marked and extend for a short distance upon the maxillary. As a whole, the zygomatic arch is rather short, though relatively somewhat longer than in *Poebrotherium*, decidedly slender and almost straight, arching outward but little.

The lachrymal is quite largely exposed upon the face in front of the orbit, but its exact limits cannot well be determined, since only the suture with the frontal is visible.

The frontals are nearly as elongate in the antero-posterior dimension as the parietals, though they take little part in roofing the cerebral chamber (as is also the case in the modern Tylopoda); they are quite broad, the width exceeding the length. The forehead is broad, smooth, lozenge-shaped, and very slightly convex, both transversely and longitudinally. Anteriorly the frontals are deeply notched to receive the nasals, but also send forward a short, narrow tongue between the divergent ends of the latter; the nasal processes are short and blunt. Behind, the frontals give off a broad, triangular process, which extends into the notch of the parietals already described. The postorbital processes are quite long and distinct, but are shorter than in *Poebrotherium* and much less decurved, leaving the orbit more widely open behind. The orbit is also conspicuously smaller than in the White River genus, and not nearly so deep, so that it is well separated from its fellow of the opposite side, and not, as in *Poebrotherium*, *Leptomeryx*, and the tragulines, divided from it by a mere septum. The supraorbital canal opens much nearer to the margin of the orbit than in *Poebrotherium*, in which it has shifted farther towards the median line, and the groove which runs forward from the foramen is much less deeply impressed than in the latter. The supraorbital notch, which in the White River form is very deep, is much shallower in *Protylopus*. A small vacuity appears to be formed between the frontal, nasal, lachrymal, and maxillary. I speak thus hesitatingly, because the fontanelle is not shown in Wortman's figure and because it may be due to distortion in the Princeton specimens, though its shape is so symmetrical that such a mode of origin seems improbable. This opening is sometimes present in *Poebrotherium*.

The nasals are very long and narrow; they are broadest just in advance of the nasal processes of the frontals, narrowing both anteriorly and posteriorly from that point. The hinder ends diverge somewhat and receive between them the short, narrow median processes of the frontals; anteriorly the nasals taper gradually to the free ends, which project somewhat beyond the edges of the premaxillaries. In general, the nasals of *Protylopus* are much like those of *Poebrotherium* and of nearly the same relative length; they extend, however, much farther back than in the White River genus, reaching nearly to the middle of the orbit, while in the latter the fronto-nasal suture is some distance in advance of the orbit. This posterior extension, in *Protylopus*, compensates for the elongation of the anterior part of the muzzle which characterizes *Poebrotherium*. Another difference between the two genera may be seen in the shape of the free ends of the nasals, which in the Uinta type are bluntly pointed and extend beyond the edges of the premaxillaries, and in the White River form they are emarginated into a semicircular notch, of which the lateral edges extend farthest forward, but not beyond the premaxillæ. In short, in *Poebrotherium* the frontals have been elongated, pushing the nasals before them, as it were; at the same time, the whole anterior part of the face has grown longer, so that, in spite of their less extension backward, the nasals are relatively as long as before.

The maxillary is much the largest bone of the face, of which it forms the greater portion; it is very long, but of only moderate vertical height, which, except in the orbital region, is nearly uniform throughout its length. In correspondence with the very brachyodont character of the teeth, the alveolar portion of the maxillary is very low. The masseteric ridge and surface are carried over for a short distance upon the maxillary. The anterior border, formed by the premaxillary suture, is nearly vertical, but inclines backward a little at the upper end. In addition to the vacuity or fontanelle already mentioned, there appears to be another, of narrow, slit-form, between the maxillary and the nasal. Less uncertainty attaches to this opening, though it also may possibly be due to dislocation. The infraorbital foramen is small, narrow, and inconspicuous, and is widely removed from the orbit, opening above p^3, the same position that it occupies in *Poebrotherium*. From the general shape of the skull it is plain that the palate was shaped much as in the latter genus, quite broad behind and contracting very much in front, where the whole muzzle becomes exceedingly slender. This contraction is gradual, not abrupt, as it is in the recent Tylopoda.

The premaxillary has a very broad ascending ramus, but in spite of this extension upon the face, it has but a relatively short contact with the nasal, because of the absence of any distinct nasal process. For the same reason, the premaxillary is very widely removed from the frontal, of which the nasal process is very short. The alveolar portion is short and low, and very narrow transversely, because the incisors are arranged in nearly the same fore-and-aft line, in consequence of which the premaxillary has but a slight lateral curvature. The anterior nares, as in *Poebrotherium*, have the narrow form and terminal, vertical position which recurs in nearly all of the primitive selenodonts, and which is so different from the long, obliquely placed opening characteristic of the modern Tylopoda.

The mandible is, on the whole, very much like that of *Poebrotherium*, but with several minor differences, which tend away from the extreme tylopodan type as exemplified by the recent members of the series. The horizontal ramus is long, shallow, compressed, and very slender, with a slightly sinuous ventral border; it is less elongate than in *Poebrotherium*, having no edentulous portion, and is not bent downward at the symphysis, as in the latter. The symphysis is quite long, extending back to $p_{\overline{1}}$, or even to $p_{\overline{2}}$. From the hinder end of the symphysis the chin rises gently and regularly to the incisive alveoli, whereas in *Poebrotherium* it is depressed and nearly horizontal. The two halves of the mandible are not coössified, even in aged individuals. The ascending ramus is low, even lower than in *Poebrotherium*, the condyle being raised less above the level of the molars. The masseteric fossa differs from that of the latter in being broader and less deeply impressed, in having less conspicuous borders, and in descending lower upon the ramus. The coronoid process differs from that of *Poebrotherium* much as the latter does from that of the recent genera of the group. In the White River type the process is more recurved and pointed, shorter and more inclined backward, than in the camels and llamas. In *Protylopus* it is still shorter, more inclined, and recurved, and is altogether like that of a true ruminant. The condyle is small and transversely extended, not having begun to acquire the peculiar, knob-like shape which is so characteristic of the recent Tylopoda. The angle is prolonged into a great hook, very much as in *Poebrotherium*, but as the posterior border is broken away in all the specimens, I cannot determine whether it is so large as in the White River genus.

Three mental foramina are present in each ramus of the mandible; the anterior one, which is the largest and quite conspicuous, is placed beneath $p_{\overline{2}}$, while the others, which are mere pin-holes, are situated, one beneath the hinder border of $p_{\overline{3}}$, and the other under the interval between $p_{\overline{4}}$ and $m_{\overline{1}}$. In *Poebrotherium* the foramina are much more conspicuous and have a somewhat different position; one is beneath $p_{\overline{1}}$, the second beneath $p_{\overline{3}}$, and the third under $m_{\overline{1}}$, nearly the same situation which they occupy in *Auchenia*.

MEASUREMENTS.

	No. 11,222
Skull, basal length	0.111
Cranium, length to anterior border of orbit	.060
Face, length	.052
Sagittal crest, length	.015
Zygomatic arch, length	.040
Mandible, length	?.088
" depth at $m_{\overline{3}}$	.013
" " $p_{\overline{3}}$	.010
" height of condyle	.026
" " coronoid	.039

III. The *Vertebral Column*, and especially the cervical region, is but imperfectly represented in any of the specimens. The only cervical vertebra which I have seen is a somewhat imperfect atlas. This, so far as it is preserved, is quite like that of *Poebrotherium;* it is short and broad and has a very convex neural arch, with hardly any more than an indication of the neural spine. The arch is perforated by foramina for the first pair of spinal nerves. Anteriorly the transverse processes extend out more widely from the sides of the vertebra than they do in *Poebrotherium*, but whether they are carried so far backward as in the latter I am unable to say.

The Princeton collection contains no thoracic vertebræ, and I shall therefore quote Wortman's account of them: "The vertebræ resemble those of the modern llamas closely in their general proportions. The bodies of the anterior dorsals are but moderately keeled, and towards the posterior end of the series strongly keeled; they increase gradually in size from before backward. The neural spine of the fifth is long and recurved, those of the succeeding dorsals decreasing in length posteriorly. The neural spines of the last two are considerably shorter and broader, having an almost vertical direction. The rib facets in the anterior region have their usual relations and positions, the ribs articulating with the vertebræ by two distinct facets, but in the last two the capitular and tubercular facets appear to be fused together as in these dorsals of the llama." ('98, pp. 107-8.)

The lumbars, which, according to Wortman, are seven in number, are relatively large. The first three have rather short but progressively elongating centra; those of the next three (4th, 5th, 6th) are of nearly the same size and shape; they are long, narrow, and depressed, with prominent ventral keels. The centrum of the last lumbar is shorter, broader, and more depressed than those of the preceding three, and has no distinct keel. The transverse processes increase in size up to the penultimate vertebra, while the last one has much shorter and straighter processes; they are long, broad, depressed, and curved strongly forward. The neural spines are rather low; they incline forward decidedly, except that of the last lumbar, which is nearly erect. The zygapophyses are of the usual cylindrical, interlocking type, and I can discover no indication of the additional, or episphenial, processes which from the faint beginnings in *Poebrotherium* have become so well developed in the existing camels. The sacrum is long and very much depressed and is composed of three or four vertebræ. The anterior one has a broad, heavy centrum and large pleurapophyses; the posterior vertebræ are broad, flat, depressed, and thin, with low, backwardly directed neural spines, and broad transverse processes.

The two anterior caudals, which are preserved in connection with the sacrum, indicate a tail of moderate length; they are short, but have complete neural arches and spines, prominent zygapophyses, and very large transverse processes, which have a backward curvature. Except for the greater size of the transverse processes, these vertebræ are much like the corresponding ones of *Poebrotherium*, and doubtless the tail was of similar proportionate development in the two genera.

IV. The *Fore-Limb* is short and slender, decidedly more so than the hind-limb. The scapula is high and narrow, much narrower than in *Poebrotherium;* the neck is slender but not abruptly contracted; the coracoid border, so far as it is preserved, inclining much less strongly forward, in consequence of which and of the position of the spine the prescapular fossa cannot be nearly so wide as in the White River genus; similarly, the glenoid border inclines but little backward in its course above the neck. In *Poebrotherium*, on the contrary, both borders pursue a very oblique course, which gives great breadth to the proximal portion of the blade. The spine is high and somewhat recurved, making the anterior side convex and the posterior concave; the acromion is both long and high, projecting somewhat outward as well as downward, but does not descend nearly to the level of the glenoid cavity, and terminates in a blunt and very slightly recurved point. The acromion is thus very much smaller than in *Poebrotherium*, in which the process is far longer, descending to the level of the glenoid cavity, and is much broadened and thickened at the end. The glenoid cavity is quite deeply concave, and, as in the White River type, of nearly circular outline. The coracoid is quite well developed and forms a stout, incurved hook, roughened at the tip; this process is less prominent and massive than in *Poebrotherium*, just as in the latter it is smaller than in the existing camels and llamas.

The humerus is, unfortunately, not preserved entire in any of the specimens, the most complete one lacking the proximal end. It may be seen, however, that the bone is long, slender, and laterally compressed, very much resembling the humerus of *Poebrotherium*, though decidedly narrower when viewed from the front; seen from the side it has the same sigmoid curvature as in the latter genus. The proximal portion of the shaft has a considerable fore-and-aft diameter, which gradually diminishes downward, while the distal portion has but a moderate transverse expansion. The deltoid ridge is very low and inconspicuous, even less prominent than in the White River genus, and is in very marked contrast to the great ridge and hook of the modern tylopodans. The supinator ridge is likewise feebly developed and adds little to the breadth of the shaft. The anconeal fossa is small, narrow, and deep, perforating the shaft and forming a minute supratrochlear foramen. The trochlea is very narrow and set quite obliquely to the long axis of the shaft, nearly as much so as in *Poebrotherium*. Considering the geological date of *Protylopus*, the humeral trochlea shows quite an advanced type of structure; it has a considerable vertical diameter and is hour-glass shaped, grooved in the middle for the corresponding ridge on the head of the radius; the intercondylar ridge, which is placed on the outer half of the trochlea, is very weak, but quite distinct nevertheless.

The bones of the fore-arm are in ordinary adults separate throughout, although the radius has already begun to increase and the ulna to diminish, and, as Wortman has shown, coössification takes place in aged individuals at the middle of the shaft, leaving the proximal ends free. Of the radius I have no well-preserved example.

The ulna has undergone considerable reduction, and its articulation with the humerus is altogether posterior. The olecranon is long, narrow transversely, but thick antero-posteriorly, with the free end somewhat thickened and club-shaped. The coronoid process is prominent, but the sigmoid notch is rather shallow, for its distal part is incomplete. The shaft is long and quite slender, tapering rapidly towards the distal end, and has a decided anterior curvature. For most of its length it is trihedral, with sharp postero-external and antero internal edges, but the distal portion loses the trihedral form and becomes laterally compressed and very slender.

The manus (Plate II., fig. 9) is highly characteristic and quite different from that of *Poebrotherium.*

Of the carpus only the pyramidal, pisiform, magnum, and unciform are preserved, but these suffice to show some of the more important features of carpal structure. In the existing Tylopoda the carpus as a whole is broad and low, which is due to the shortening of the distal elements, the proximal row retaining considerable proximo-distal height. Already in *Poebrotherium* this modification makes itself apparent, but in *Protylopus* it has hardly begun, the magnum and especially the unciform being quite high in proportion to their width. The pyramidal is high, narrow, and thick, and has much the same shape as in *Poebrotherium;* it is highest on the radial side, descending steeply towards the ulnar side. In the last-named genus this carpal is quite extensively covered by the radius, and in the existing Tylopoda nearly the whole proximal surface is so occupied. So far as I can make out, this change has already begun in *Protylopus*, but if so, the contact with the radius is much smaller than in the White River genus. While the ulnar facet is of the usual saddle-shape, that for the pisiform is small and confined to the postero-external angle of the bone.

The pisiform is shaped much as in *Poebrotherium*, but is longer, more slender, and less thickened at the free end. Its proximal facets for the ulna and pyramidal are not well preserved in the only available specimen, but they meet at a more acute angle and make the proximal end more pointed than in the White River form.

The magnum is a small bone, low, broad, and thick, but its breadth does not exceed its height so much as in the later Tylopoda, and, compared with the other carpals, it must be regarded as rather narrow; the head is small and does not rise above the level of the dorsal portion. The scaphoid facet is larger and more entirely proximal than that for the lunar, while in *Poebrotherium* the lunar facet is relatively larger and less oblique than in the Uinta genus. A comparison of the wedge-shaped space between the magnum and unciform in the two genera shows that in *Protylopus* the lunar must have had a narrower distal beak, which descended almost to the head of the third metacarpal. On the radial side the magnum bears a small facet for the trapezoid, but I can discover none for the second metacarpal.

The unciform is quite a large bone, exceeding the magnum in every dimension; it is relatively higher and narrower than in *Poebrotherium*, though the difference is not very striking. Most of the proximal end is occupied by the large, convex facet for the pyramidal, while the lunar facet is relatively smaller and more oblique than in the White River genus. A large facet receives the projection of the third metacarpal; it is relatively larger than in *Poebrotherium* and vertical, not inclined downward and outward as in the latter. Another difference is seen in the proportions of the distal facets, that for the fourth metacarpal being relatively smaller, and that for the fifth much larger than in the White River type.

One of the features which most clearly distinguish *Protylopus* from *Poebrotherium* is the character of the metacarpus. In the latter it is reduced to two functional digits (iii., iv.) and two small nodules representing the proximal ends of ii. and v. In the Uinta genus, on the other hand, there are four functional digits, though the median pair are considerably enlarged and the lateral pair much reduced. Wortman's conjecture as to the composition of the manus is thus demonstrated to be correct.

In the only manus which the collection contains (No. 11,222) the distal ends of all the metacarpals are missing, so that their length can be ascertained only approximately; it is clear, however, that these bones are much shorter than in *Poebrotherium*, in proportion both to the length of the metatarsus and to that of the other limb-bones.

The first metacarpal may have been present, but if so, it must have been in a rudimentary condition, and no trace of it is preserved in the specimen.

Metacarpal ii., though apparently not much shorter than mc. iii., is very slender, but is far more robust than the corresponding metatarsal. The proximal end is narrow but quite thick in the dorso-palmar dimension, and bears a narrow, plain facet for the trapezoid, but appears not to come into contact with the magnum. The shaft is straight, very slender, and laterally compressed; its proximal half is closely applied to mc. iii. and is thus flattened on the ulnar side, having a trihedral section; below this it becomes more rounded. At the distal end the shaft is slightly expanded and is probably a little wider than the trochlea.

Metacarpal iii. is longer, much heavier, and in every way differently shaped from mc. ii.; the proximal end is but little broader than the shaft and its increased width is principally due to the unciform process. The magnum facet is quite strongly concave transversely, much more so than in *Poebrotherium*, in which this facet is nearly plane. The head of mc. iii. rises considerably above that of mc. iv., and sends a process which, though not long and not extending much across mc. iv., has yet a large contact with the unciform, relatively larger than in the White River genus. Though mc. ii. appears to have no contact with the magnum, mc. iii. does not reach the trapezoid. The present genus, apparently, and certainly its White River successor, are thus in a stage of transition between the modes of reduction which Kowalevsky has named the "adaptive" and the "inadaptive;" mc. ii. is cut off from its connection with the magnum, but mc. iii. has not yet acquired any articulation with the trapezoid. The shaft of mc. iii. is straight and relatively broad, but much compressed antero-posteriorly and of transversely oval section, though flattened on the ulnar side by the approximation to mc. iv. Distally the two are slightly separated, but with no marked appearance of that divergence which is so characteristic of the later *Camelidæ*.

Metacarpal iv. is the counterpart of mc. iii., but is a little shorter, the head not rising so high as that of the latter, though this difference is compensated for by the height of the unciform, which descends below the level of the magnum; the shaft is also a little broader proximally and more flattened on the dorsal face; the head is narrow, no wider than the shaft.

Metacarpal v. is the counterpart of mc. ii., with which it forms a symmetrical pair. The proximal end is very narrow, though it bears a small tubercle for ligamentous attachment on the ulnar side; the shaft is slightly curved, with the convexity towards the radial side, while that of mc. ii. is unusually straight and stiff looking.

MEASUREMENTS.

Scapula, breadth of neck	0.010
" antero-posterior diameter of glenoid cavity	.0095
Humerus, antero-posterior diameter of shaft, proximal	.014
" breadth of trochlea	.0095
" height of trochlea	.008
Ulna, length of olecranon	.013
Metacarpal ii., breadth of proximal end	.003
" iii., " " " "	.006
" iv., " " " "	.005
" v., " " " "	.004

V. The *Hind-Limb* is proportionately long and robust, much more so than the fore-limb. The pelvis is as characteristically tylopodan as the other parts of the skeleton, and, so far as the material admits of a comparison, it much resembles that of *Poebrotherium*. The ilium is short, but has a relatively elongate peduncle, which is deep dorso-ventrally and, though compressed, is quite thick; anteriorly the ilium expands into a broad, everted plate, with rounded and simple crista. The acetabulum is large and deep. Both ischium and pubis are broken away, but the section of the former shows that the spine or crest was low and inconspicuous.

The femur is likewise very tylopodan in appearance. It is considerably longer and stouter than the humerus, equalling the tibia in length. Proximally, the bone is broad and carries a large, ovoidal head, set upon a short neck, and a rather low great trochanter, which does not rise quite so high as the head. The shaft is heavy, elongate, arched forward, and of nearly uniform diameter, except at the distal end, where it is somewhat broadened and thickened. The condyles are rather small and unequally developed, the external one projecting more behind the plane of the shaft. Above the outer condyle is quite a deep pit for the attachment of the plantaris muscle. The rotular trochlea is asymmetrical, owing to the prominence of the inner border, and above the trochlea the dorsal face of the shaft is grooved. In *Poebrotherium* the femur is very much like that of the Uinta genus, but has a somewhat higher great trochanter, a larger pit for the plantaris, a wider trochlea, and much more prominent condyles. In *Leptomeryx* also the proximal end is similar, but broader.

One of the most characteristic bones of *Protylopus*, and the one which can most readily be distinguished from contemporary genera of similar stature, is the tibia. This is stout and quite long, though less elongate than in the later genera of the series, for it hardly exceeds the skull in length. The proximal end is narrow and the femoral surfaces rather small and placed very obliquely, with a low and bifid spine, which is divided by a broad sulcus; the cnemial crest is very large and prominent and projects forward as a great keel, but is thinner than in *Poebrotherium* and does not extend so far down the shaft as in that genus, but its proximal end is thickened and rugose, and it is deeply grooved by the sulcus for the extensor longus digitorum. The shaft, which is almost of uniform breadth throughout, is made trihedral by the cnemial crest, but where that ceases it becomes transversely oval. The distal end is moderately expanded and very slightly thickened, giving it, when viewed from below, a rectangular outline; the malleolus is long and heavy and pointed. The external astragalar facet is somewhat the larger of the two, and the intercondylar ridge is prominent, ending dorsally in a conspicuous tongue-like process. No sulci invade the articular surface. The fibular facet is partly external and partly distal, the tibia extending slightly over the distal end of the fibula.

Of the fibula only the distal half is preserved in the most complete specimen, but that displays some interesting transitional characters. In *Poebrotherium* only the ends of the bone are retained, the proximal end as a short spine anchylosed with the tibia and the distal end as a malleolar bone. In the Uinta genus, except, perhaps, in aged individuals, there is no anchylosis, and the shaft, though reduced to a mere thread of bone, was apparently complete. At all events, fully half of its length is present in the specimen before us, and from the appearance of the tibia I should infer that it was uninterrupted. The filiform shaft is closely applied to the tibia and its distal portion expands considerably in the dorso-plantar dimension, though remaining extremely narrow. The distal end forms a stout malleolus, which is partly overlapped by the tibia; its facet for the calcaneum is narrow and almost plane.

The pes (Plate II., fig. 8) has more nearly attained the condition found in *Poebrotherium* than has the manus, though certain more primitive features are still to be found. The tarsus is high and narrow, higher and narrower than in the White River genus, but with similar elements arranged in a similar way. A small bone, probably the tibiale, is attached to the tibial side of the astragalus.

The astragalus, like the whole tarsus, is high and narrow; its proximal trochlea is deeply and narrowly grooved and is quite asymmetrical, the external condyle exceeding the internal somewhat in height and very considerably in breadth. The sustentacular facet is rather narrow and short, and occupies an oblique position. The distal surface has a narrow facet for the cuboid and a broad, hour-glass shaped facet for the navicular. In *Poebrotherium* a few changes in the character of the astragalus may be noted; its proximal trochlea is more broadly grooved, and in the distal trochlea the cuboidal facet has become relatively wider.

The calcaneum is quite elongate and has a slender tuber; it is remarkable for the broad and deep depression which runs for nearly the entire length of the bone, broadening and deepening distally. On the plantar border the calcaneum is nearly straight, except that the distal end of this border rises steeply towards the cuboidal facet. The dorsal border of the tuber rises gradually to the fibular facet, which forms a prominent convexity, rising steeply on both proximal and distal sides. The cuboidal facet is narrow and so warped that its plantar portion presents inward as well as distally. The sustentaculum is of only moderate prominence and bears a simply concave facet; it is separated from the tuber by a deep sulcus, which runs for a short distance along the dorsal side of the latter. In *Poebrotherium* the calcaneum has become somewhat more elongate, and has lost all but a trace of the great external depression, as well as the small sulcus which runs between the tuber and the sustentaculum.

The cuboid is quite strikingly high, narrow, and thick, much resembling that of *Poebrotherium*, but with its proximal facets differently proportioned. In the White River form the astragalar facet is nearly as broad as that for the calcaneum, while in the Uinta genus it is decidedly narrower; its dorsal border is raised high above the calcaneal surface, giving a deeply notched appearance to the cuboid. On the tibial side the bone is invaded by a sulcus, which is shallower than in *Poebrotherium*, and which separates the navicular facet into dorsal and plantar portions. The calcaneal facet overhangs somewhat, projecting beyond the fibular face of the cuboid; it is strongly convex in the dorso-plantar direction and is quite complexly warped. The distal end is almost entirely occupied by the large surface for the fourth metatarsal, that for the fifth being very small. The plantar hook is long and massive.

The navicular is much shorter vertically than the cuboid, but quite as broad and thick; its proximal surface for the astragalus is hour-glass shaped, and the ridge, with its dorsal projection, has a more external position than in *Poebrotherium;* the plantar hook, which in the latter is very much reduced, is of moderate size and quite conspicuous; it projects down over the ento-cuneiform, but does not touch it. On the distal end of the navicular are the usual three facets, of which that for the ecto-cuneiform is very much the largest and occupies the whole breadth of the bone, while that for the ento-cuneiform is pushed to the postero-internal angle.

The ento-cuneiform is flat and scale-like, quite high vertically and thick antero-posteriorly, but very narrow transversely. It articulates with the navicular by means of a narrow, convex facet, and has a long, oblique surface which bears against the head of the second metatarsal, while its distal end is closely applied to the plantar process from the head of the third.

As in most artiodactyls, the meso- and ecto-cuneiforms are coössified, but their limits may still be made out; the middle cuneiform is much the smaller of the two elements. The ecto-cuneiform is a large bone, almost as wide as the cuboid, though its breadth is exceeded by its height, while the dorso-plantar diameter is relatively hardly equal to half of the same dimension of the navicular. Apparently, the ecto-cuneiform articulates only with the third metatarsal and does not touch the second, though it is possible that a minute contact with the latter is still retained.

The metatarsus is composed of four members, two of them (iii. and iv.) enlarged and functional, and two (ii. and v.) greatly reduced and filiform.

Metatarsal ii. has undergone great reduction; its proximal end is very narrow and compressed, but has a considerable dorso-plantar thickness and is so wedged in between the ento-cuneiform and mt. iii. as to be hardly visible when the foot is viewed from the dorsal side. It articulates with the ento- and meso-, but, so far as I can determine, not with the ecto-cuneiform. The shaft rapidly tapers to a mere thread of bone, which in one specimen is preserved for a length equal to two-thirds of the large mt. iii. and is there broken. It is therefore impracticable to determine whether the bone was a mere style, or was furnished with a trochlea and phalanges, as in the tragulines. On the whole, the former suggestion appears the more probable.

Metatarsal iii. is relatively long and quite heavy, though it has by no means attained such a proportionate degree of elongation as we find in *Poebrotherium.* The head is rather narrow, but very thick in the dorso-plantar diameter, which is further increased by a prominent projection from the plantar side. This projection and a similar one on mt. iv. are closely pressed together and held in place by the ento-cuneiform and the great hook of the cuboid, between which they are wedged. The head has a broad, almost plane facet for the ecto-, but appears not to touch the meso-cuneiform, though in *Poebrotherium* the latter is covered by mt. iii. and excluded from contact with mt. ii. In *Protylopus* the pes, like the manus, is in a state transitional to the adaptive method of reduction, a method which is fully attained in *Poebrotherium.* The shaft is long, slender, of nearly uniform breadth, though narrowing to some extent distally, broadening and thickening again just above the trochlea. In cross-section the shaft is more trihedral and less distinctly quadrate than in *Poebrotherium.* The trochlea is shaped almost exactly as in the latter; it is narrow and low, but well rounded and provided with a prominent carina, which is confined to the plantar face, and a shallow pit demarcates the trochlea from the shaft.

Metatarsal iv. is in all respects the counterpart of mt. iii., and in the best specimen the two are of almost exactly equal length, their proximal ends lying in the same transverse plane. Save for the proximal facet, which is quite flat, this bone is not sufficiently different from mt. iii. to require a separate description.

Metatarsal v. is rudimentary, but as in the only specimen which retains a part of it it is broken a short distance below the head, I am unable to say whether it was elongate and filiform, like mt. ii., though there seems to be no good reason to suppose that it was not. The proximal end is a little broader and more club-shaped than that of mt. ii., but is less thickened in the dorso-plantar diameter, and bears a small, slightly convex facet for the cuboid. What remains of the shaft is excessively slender and thread-like.

MEASUREMENTS.

Tibia, length	0.117
" thickness across cnemial crest	.024
" breadth of distal end	.013
" thickness of distal end	.0095
Calcaneum, length	.033
Astragalus, length	.017
" width of proximal end	.008
" " " distal end	.009
Cuboid, height	.012
" breadth	.005
" thickness	.012
Navicular, height	.007
" breadth	.005
Ecto-cuneiform, height	.0055
Metatarsal iii., length	.061
" " breadth of proximal end	.006
" " " " distal end	.007
Metatarsal iv., length	.062
" " breadth of proximal end	.005
" " " " distal end	.007
Proximal phalanx, fourth digit, length	.020
Second " " " "	.011
Ungual " " " "	.0115

The phalanges much resemble those of *Poebrotherium*, though they are more slender in proportion to their length. The proximal phalanx is elongate, narrow, and thin, and is slightly curved, making the approximate side concave; the surface for the metatarsal is narrow, concave, and notched on the plantar border for the carina. Towards the distal end the bone contracts in breadth and especially in thickness; the distal trochlea is less notched in the median line than in *Poebrotherium*, and its articular surface is reflected much less upon the dorsal side than in the latter. The second phalanx is much shorter than the first and very slender, especially transversely; its proximal trochlea is less distinctly divided into two facets than in *Poebrotherium*, but the distal trochlea is much as in that genus, describing a semicircle and extending as far upon the dorsal as upon the plantar face. The ungual also has its proximal trochlea less clearly divided into two facets than in the White River genus, and it is rather shorter and less tapering. Another difference from the latter is the fact that the ungual is not quite so straight, but is slightly curved, with the concavity directed towards its fellow of the adjoining digit.

The Systematic Position of Protylopus.

In my preliminary paper I said of this genus (there called *Parameryx*): "There can be very little doubt that *Parameryx* is the direct and immediate ancestor of the White River *Poebrotherium*, which it so much resembles, and thus it holds an important place in the main line of tylopodan descent." ('98, p. 75.) Wortman had independently reached exactly the same conclusion ('98, p. 110), and the foregoing description should render the point sufficiently clear. In every detail of its structure the Uinta genus is just what we should expect to find in the ancestry of the White River form.

In many discussions of phylogenetic problems the reasoning proceeds upon the assumption, expressed or implied, that the steps of evolutionary change keep equal pace in the various organs, and that, consequently, if a given ancestral genus differs from a descendant by a certain amount in the structure of the teeth, it will also differ by an equivalent amount in the structure of the feet. Sometimes this assumption is justified, but quite as frequently it is not, and we find that a genus may have its teeth much more modernized than its feet, or vice versa, or that the manus and pes represent different stages of phylogenetic advance, which will be equalized at a later time in a succeeding genus. Bearing these facts in mind, our examination of *Protylopus* completely confirms the suggestion that *Poebrotherium* is its direct descendant, an interpretation which requires no straining of the facts to make them fit it.

In the first place, we observe that there is marked increase in size in the descendant genus, an increase which is a very common occurrence in evolutionary advance. Not that a reduction in size may not occur, but in the well-understood phyla an increased stature in each succeeding genus appears to be the rule.

In the second place, the relative length of the limbs and feet is augmented even more than the enlargement of the head and body.

In addition to these general facts, which are apparent at the first glance, a detailed comparison of the two genera brings out very many more correspondences:

(1.) The dentition of *Protylopus* has nearly reached the stage of development found in *Poebrotherium*, but there are many minor though significant differences, all of which are in the direction of that greater simplicity of structure which should characterize an ancestral form. Thus, the incisors have already attained almost the same condition as in the White River type; there are no diastemata in the dental series, but what may be called incipient diastemata are visible in the short interspaces between the canine and p. 1, and between p. 1 and p. 2. The premolars are of the same type as those of the succeeding genus, low, elongate, acutely pointed, and trenchant, but they have not yet acquired such great antero-posterior elongation, and the lower ones are made simpler by the absence of the basal cusps. The molars are extremely brachyodont, while those of *Poebrotherium*, though still short crowned, show a distinct tendency towards hypsodontism. We may also observe changes in the proportionate development of the molar cusps. Thus, in *Poebrotherium* the upper molars have become more elongate antero-posteriorly and narrower transversely; the external crescents are thinner and more compressed, the ribs and buttresses much less prominent, and the valleys narrower and deeper. In the lower molars, the cusps are less conical, more compressed and plate-like, and the valleys deeper. *Protylopus* departs from its White River successor in approximating to the other Uinta selenodonts and to the still earlier Bridger types.

(2.) The skull of *Protylopus* is so like that of *Poebrotherium* that the resemblance strikes the observer immediately. The skull has the triangular shape and long, slender, tapering muzzle which is so characteristic of all the Tylopoda, but the muzzle is decidedly less elongate than in *Poebrotherium*; the cranium is narrower, less capacious, and the sagittal crest, though relatively no longer, is higher and more prominent. The postorbital processes of the frontal and jugal are shorter, leaving the orbit much more widely open behind, while the auditory bulla is very small, not reaching the paroccipital process, and is hollow and free from cancellous tissue. Among the less obvious differences may be mentioned the following: In *Protylopus* the nasals extend farther backward and in front they are pointed, reaching beyond the premaxillaries; the supraorbital foramina have not shifted so far towards the median line, and the grooves leading from them are much shallower, as are also the supraorbital notches. The mandible has a shorter horizontal ramus and a lower ascending ramus, but a higher, more recurved, and more ruminant-like coronoid; the peculiar shape of the angle is much the same in both genera.

It would be interesting in the highest degree to compare the cervical vertebræ of the two forms, but, unfortunately, only the atlas of the Uinta genus is known, and that is not sufficiently characteristic for the purpose. The other vertebræ in the latter are somewhat more slender and delicate than in *Poebrotherium*, but are essentially like them.

The scapula of *Protylopus* is higher, narrower, and more slender than that of its White River successor. The spine is lower and the acromion very much shorter and more pointed. The humerus is lighter, but otherwise very similar, but the fore-arm bones remain separate, except in aged individuals, and though the radius is enlarged and the ulna reduced, the change is less than in *Poebrotherium*, in which anchylosis is complete. The manus is farther removed from that of the White River genus (in which both fore- and hind-foot have attained the same stage of reduction) than might have been expected from the advanced development of the dentition, skull, and pes. The carpus is very much as in the White River genus, except that the distal elements have not yet been so much shortened proximo-distally. Four functional members compose the metacarpus, though the lateral elements are very slender and are more reduced than in other Uinta selenodonts, but in *Poebrotherium* they are mere vestigial nodules. The carpo-metacarpal articulations are in a state transitional to the "adaptive" mode of reduction; mc. ii. still clings to the trapezoid, which mc. iii. has not yet reached, but the former has lost its connection with the magnum. The whole manus is relatively very short.

It is a suggestive fact that the fore-limb of *Leptomeryx* has many resemblances to that of *Protylopus*, and that almost the only important difference between them is the coalescence of the trapezoid and magnum in the former.

Pelvis and femur differ very little from those of *Poebrotherium*, and the tibia is also much the same, except that it is proportionately shorter and more slender, and the fibular shaft, though reduced to a mere thread, appears to be still complete. The tarsus differs so little from that of the White River type that it might almost be described as that of *Poebrotherium* in miniature; the metatarsus is much less elongate than in the latter, but in the extreme reduction of the lateral digits, which are long, filiform splints, the pes is more advanced in differentiation than the manus. The phalanges are more slender than they afterwards became, while the unguals are rather shorter and more curved.

Hardly an instance has yet been discovered in which the relationship between two genera of successive geological epochs is more clearly that of ancestor and descendant than in the case of *Protylopus* and *Poebrotherium*, yet when we inquire concerning the forerunners of the Uinta type, the answer must remain doubtful. I see no reason, as yet, to modify my former conclusion ('91*b*, p. 46) that the Bridger genus *Homacodon* should be regarded as the probable ancestor of *Protylopus*, but the gap between the two genera is so wide that the inference as to their connection must remain largely conjectural. We need to recover the connecting links, which will doubtless be found in the Washakie and in the overlying transitional beds, before a definite conclusion can be reached. The starting-point of the tylopodan line is, probably, as Cope long ago suggested, the Wasatch *Trigonolestes* (*Pantolestes*), a form whose exceedingly primitive dentition might be either oreodont or lemuroid. It seems highly probable that this genus will prove to be ancestral to all of the indigenous North American selenodonts.

If the conclusion that *Poebrotherium* and *Protylopus* are the real, if remote, ancestors of the modern Tylopoda be well founded, certain inferences of far-reaching significance for the philosophy of evolution will necessarily follow.

(1.) Schlosser's dictum ('87, p. 42) that a closed dentition without diastemata indicates the end of a phyletic series is proved not to be tenable, at least for all cases. *Protylopus* is without diastemata. In the smaller species of *Poebrotherium* they are very inconspicuous, but they become longer and longer in the later species of that genus and in *Gomphotherium*, not to mention the succeeding genera. This growth of the diastemata is, it should be observed, not due to any loss of teeth, for the John Day genus retains the full number, but to an elongation of the jaws. The case of the oreodonts is also in point: the Uinta representative of this family (*Protoreodon*) has no diastema, and yet the group flourished abundantly and became highly diversified throughout the whole of Oliogocene and Miocene times. Schlosser's principle, though doubtless true of the cases to which he applied it, is thus seen not to be of general application.

(2.) In discussing the modes in which evolution acts it has often been disputed whether development is always by a series of direct and unswerving changes in a phylum, each step coming in every detail just so much nearer to the final result. A study of the horses led me to conclude that while, as a rule, development is remarkably unswerving in a large sense, yet in minor details it may pursue a more or less zigzag course. ('94, p. 120.) This conclusion is strengthened by what we believe to be the facts of tylopodan evolution. No difference between the earlier genera of this series and its modern representatives is more obvious and striking than in the character of the canine teeth. In *Protylopus* and *Poebrotherium* the canines are very small and may almost be called incisiform, but from *Gomphotherium* onward these teeth become larger and larger until the formidable lacerating apparatus of the modern type is reached. Even though we should exclude *Homacodon* and *Trigonolestes* from the series, the analogy of all the ungulate groups, condylarth, amblypod, perissodactyl, and artiodactyl, would justify us in assuming that the ancestors of *Protylopus* possessed canines which were of fairly large size and effective as weapons. If this be true, then the canines first dwindled to very small proportions, only again to enlarge and become formidable.

Another instance of much the same kind is afforded by the history of the premolars. In *Protylopus* these teeth are very moderately elongated in the antero-posterior direction, and in general form resemble those of the contemporary selenodont genera and of the White River *Leptomeryx*. In *Poebrotherium* the premolars have become greatly elongated, accompanying the elongation of the muzzle, and, as it were, preventing the formation of diastemata. In their antero-posterior length the premolars of *Poebrotherium* recall those of *Xiphodon*. In the John Day, however, this tendency is changed, and the premolars of *Gomphotherium*, in their form, revert almost to the Uinta type, while *Procamelus* and the subsequent genera of the phylum are remarkable for the reduction of their premolars both in size and number. These facts are very significant and have a wider bearing than merely upon the phylogeny of the Tylopoda.

(?) **Leptotragulus** Scott and Osborn.

? *Parameryx* Marsh, Amer. Journ. Sci., 3d Ser., xiv., p. 364 (*nomen nudum*).
Leptotragulus S. and O., Proc. Amer. Phil. Soc., 1887, p. 258.
? *Parameryx* Marsh, Amer. Journ. Sci., 3d Ser., xlviii., p. 269.
Parameryx Wortman, Bull. Amer. Mus. Nat. Hist., x., p. 103.

In view of Wortman's recent attempt to rehabilitate the name "*Parameryx*," it will be necessary to say a few words concerning the terms which have been applied to this genus. In what follows I assume that Dr. Wortman's identification of *Leptotragulus* with "*Parameryx*" is correct, for he has seen the type specimens, and that my use of the latter name for *Protylopus* is a mistake. ('98, p. 74.) At the same time I cannot but feel some doubts as to the correctness of the identification, the reasons for which doubts will be explained below.

Professor Marsh (loc. cit.) proposed the name "*Parameryx*," in the course of an address upon the "Introduction and Succession of Vertebrate Life in America," without any definition, without any figures, not assigning any species to the proposed genus, and not indicating in any way that he was establishing a new genus, or that the name was used for the first time. The only references made to the animal in the course of the address are as follows: "With this genus is another (*Parameryx*) also closely allied to *Homacodon*, but apparently a straggler from the true line, as it has but three toes behind." ('77, p. 364.) "A most interesting line, that leading to the camels and llamas, separates from the primitive selenodont branch in the Eocene, probably through the genus *Parameryx*." (Ibid., p. 365.) From such vague allusions as these it is obviously impossible to identify the genus referred to, and according to all the codes of nomenclature the term must be regarded as the baldest nomen nudum, and has no standing whatever. This is especially true because the single hint of a diagnostic character which is given in the account, namely, the alleged presence of three toes in the pes, is probably erroneous. When the name *Leptotragulus* was proposed the authors had no means of determining whether or not it was the same as "*Parameryx*," and thus were compelled to employ a new term. Seventeen years after his first use of the term Professor Marsh published a very vague and meagre description of "*Parameryx*" ('94, p. 269), together with figures of an isolated upper molar and of the astragalus. So far as it goes, this description will apply quite as well to *Protylopus* as to *Leptotragulus*, and hence my use of the name for the former in my preliminary paper. ('98.)

It was stated above that I do not feel entirely satisfied that the two generic terms, *Leptotragulus* and *Parameryx*, actually refer to the same genus. Professor Marsh's figure of the astragalus ('94, p. 268, fig. 21), if correctly referred to the same animal as the upper molar (fig. 20), indicates a form of totally different proportions from those of *Protylopus*. While the molar is of about the same size as in the latter genus, the astragalus is far larger and equals that of *Protoreodon* in size. It seems unlikely that the astragalus can be correctly associated with the tooth, and if they belong to different individuals, no indication is given as to which should be regarded as the type. In view of these doubtful matters, the question as to the synonomy of *Paramerуx* and *Leptotragulus* is not even yet altogether clear.

The dentition of *Leptotragulus* is still quite imperfectly known, but it may readily be distinguished from that of any other Uinta selenodont; it is, on the whole, most like that of *Protylopus*, but differs markedly from the latter in the presence of a long diastema in front of $p_{\overline{2}}$ and in the large caniniform tooth in the mandible. It is still a matter of considerable uncertainty whether this caniniform tooth is a transformed premolar or the true canine, because in no specimen yet found is the crown of this tooth or of the incisors preserved. However, the course taken by the fang and the shape of the remnants of the crown render it more likely that the tooth is a true canine. In this case the number of inferior premolars is reduced to three. The other mandibular teeth very much resemble those of *Protylopus*, and thus are easily to be distinguished from those of *Leptoreodon* and the other contemporary genera.

The caniniform tooth is large, erect, and slightly recurved, its fang running upward and forward; so much of the crown as is preserved is of compressed oval section. As already mentioned, the number of lower premolars is perhaps reduced to three through the loss of the first, though better preserved specimens than any which have yet been found may show $p_{\overline{1}}$ to be present and caniniform. Between this tooth and $p_{\overline{2}}$ is a considerable diastema, much as in *Leptoreodon*. The second premolar is a much compressed, simple cone, with acutely pointed apex and trenchant edges, and having no accessory cusps of any sort; in its antero-posterior elongation it resembles $p_{\overline{2}}$ in *Protylopus* rather than that of *Leptoreodon*. The third premolar has a crown of similar form, but is provided with a minute antero-internal basal cusp, and on the posterior half is a low internal ridge, which encloses a very narrow fossette, almost exactly as in *Protylopus*. The fourth premolar is hardly at all larger than the third, which it resembles, except for the larger size of its accessory elements; it has a high and very sharply pointed principal cusp (protoconid) and a small, acute, anterior basal cusp, which arises on the inner side of the crown. From the apex of the protoconid a thin ridge runs downward and backward, enclosing a narrow, deep fossette between itself and the outer wall of the crown. *Protylopus* has an extremely similar $p_{\overline{4}}$, but the anterior basal cusp is smaller and so completely internal as hardly to be visible from the outer side.

The molars also are very like those of *Protylopus*, though they are narrower and somewhat more like those of *Poebrotherium* in form. In size they increase from $m_{\overline{1}}$, the smallest, to $m_{\overline{3}}$, the largest of the series; all of the cusps are high and pointed, while the valleys are narrow and deep. The inner cusps are already laterally compressed and are less conical than in the other Uinta genera of selenodonts. The two external crescents are widely separated, while the internal pair are more closely approximated, though with a deep cleft between them; a transverse valley is thus formed across the breadth of the crown. Both internally and externally the gap between the fore and hind crescents is spanned by a cingulum, which has a minute pillar arising from it, best developed on the outer side. The third molar has a large basin-like heel, but with a separate cusp on the inner side, which is low and ridge-shaped, but very distinct. This cusp also recurs in *Protylopus*, but in none of the other Uinta selenodonts which have been named. However, a third genus with the same peculiarity is probably indicated by some specimens in both the Princeton and New York collections, which are too imperfectly preserved for definite generic reference.

Of the milk dentition only $dp_{\overline{4}}$ is known, and this is preserved in a specimen (No. 2509) belonging to the American Museum, in which the crown of the permanent successor ($p_{\overline{4}}$) is already almost completely protruded. The milk-tooth is of the usual selenodont pattern and is composed of three pairs of crescents, but a primitive feature is to be seen in the comparatively small size of the anterior pair.

MEASUREMENTS.

	No. 11,500*	No. 2509†	No. 1803†
Lower P-2, length	.006		
" P-3, "		.006	
" P-4, "	.0065	.006	
" Dp-4, "		.007	
" M-1, "	.007	.006	.006
" M-2, "		.0065	.006
" M-3, "			.0115

The foot-bones which I referred to *Leptotragulus* in a former paper ('89, p. 482) were not found with the type specimen, which is a fragment of the mandible; the reference was made on the strength of the tylopodan char-

* Type specimen of genus, Princeton Museum.

† American Museum of Natural History.

acter of these bones, and is so uncertain that no dependence can be placed upon them in attempting to decide the nature of the genus. Wortman ('98, p. 104) has described a remarkable pes which he attributes to *Leptotragulus* (*Parameryx*), but the reference is very problematical.

The single well-defined species is *L. proavus* S. and O.

The Systematic Position of Leptotragulus.

The difficulty in making a satisfactory reference of this genus lies simply in our very imperfect knowledge of it, and until we have learned the character of the anterior teeth and of the feet the difficulty will remain. The similarity of the lower teeth to those of *Protylopus* is so very close, even in minor details, that the genus is included in the same family as the latter, though with a question, for should the caniniform tooth eventually prove to be a transformed premolar, it would be necessary to remove *Leptotragulus* from that family. In this case the connection of the main tylopodan phylum with *Leptoreodon*, and through that genus with the oreodonts, would be made all the closer.

In my former account of *Leptotragulus* ('89, p. 483) I pointed out that the presence of only three inferior premolars would, if confirmed by other specimens, render the known species, at least, ineligible for a place in the direct line of tylopodan descent. By the discovery of *Protylopus*, *Leptotragulus* is made to take its place as a side-branch of that stem. Among the White River genera *Hypertragulus* seems to be the one most likely to have descended from the Uinta form, which would serve to explain its many resemblances to *Poebrotherium* and its intermediate position between the latter and *Leptomeryx*. If the lower caniniform tooth of the Uinta genus should prove really to be a canine, then its position, here suggested as ancestral to *Hypertragulus*, would be much strengthened. However, until much more complete material of the Uinta genus has been collected its taxonomic position must remain an open question.

Family II. LEPTOMERYCIDÆ.

Leptoreodon Wortman.

Plate II., Figures 10–14.

Bull. Amer. Mus. Nat. Hist., N. Y., x., p. 95. (April 9, 1898.)
Merycodesmus Scott, Proc. Amer. Phil. Soc., xxxvii., p. 75. (April 15, 1898.)

The following description is founded upon two specimens, one of which, the type of *Merycodesmus* (Princeton Museum, No. 11,225), consists of the skull and an imperfectly preserved fore-foot, and the other is a block (No. 11,223) containing parts of two skulls, several vertebræ, the pelvis, and hind-limb nearly complete. While the parts of the skull preserved in the second specimen are not sufficient to put the reference of it to the present genus beyond all question, yet there is little room for doubt in the matter. It certainly cannot pertain to *Leptotragulus*, *Protylopus*, or *Oromeryx*, and must belong to some form either identical with or very closely allied to *Leptoreodon*.

The dentition is exceedingly peculiar, and seems to unite the characteristics of several distinct families. The formula is: $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$.

A. *Upper Jaw.* (Plate II., figs. 10, 11.) The incisors are small, conical, pointed, and slightly recurved; they are much smaller than in *Protylopus*, but have a similar shape, and, as in that genus, they are separated by short interspaces and arranged in almost the same fore-and-aft line. A longer space intervenes between $i^{\underline{3}}$ and the canine. The canine is large, very much larger than in *Protylopus*, and though laterally compressed, is yet quite stout and thick; the anterior border is thickened and rounded, with a deep, narrow groove running down the external face; in cross section the tooth is D-shaped, much as in the oreodonts, but thinner and more compressed laterally. As the upper canine is opposed by the caniniform $p_{\overline{1}}$, it is the posterior face that shows abrasion.

The premolars are quite simple. The first is placed near the canine, but is separated by a long interval from $p^{\underline{2}}$; it is implanted by two roots and has a small, but high, thin, pointed, and trenchant crown, which in shape and position resembles that of *Hypertragulus*. The second premolar is like the first, but is larger, especially in the fore-and-aft dimension; it is somewhat thickened transversely. The third closely resembles the second when seen from the outer side, but internally there is a marked distinction, for this tooth is carried upon three fangs, and in *L. gracilis* has a small but distinct deuterocone; in *L. marshi* this is "a faint internal cingular ledge." (Wortman, '98, p. 96.) The fourth premolar is of the well-nigh universal selenodont pattern, composed of two transversely placed crescents. It remains only to note that the external wall of the tooth is quite markedly concave, with a low median rib, and that the inner cingulum is prominent.

The molars are composed of four cusps only, and Wortman was mistaken in supposing that the anterior intermediate cusp was probably present, as unworn specimens clearly show. They bear considerable resemblance to those of *Protylopus*, and, indeed, it is a difficult task to identify scattered molar teeth of any of these genera in which the unpaired cusp has been suppressed. In size the molars increase successively from m^1 to m^3; they are considerably wider transversely than long antero-posteriorly, and are of nearly regular quadrate outline, though the front half of the crown is slightly broader than the hinder half. The first molar is small, its external crescents have more concave outer faces than in *Protylopus*, and the external buttresses are but little larger. On the second and third molars the antero-external buttress has become very large, much more so than in *Protylopus*, but the outer crescents are more concave than in that genus, and the median rib of the anterior one is rather less prominent.

B. *Lower Jaw.* (Plate II., figs. 10, 12.) The incisors are quite procumbent, and in length diminish slightly from $i_{\overline{1}}$ to $i_{\overline{3}}$, while in breadth the relation is reversed, $i_{\overline{3}}$ being slightly broader than $i_{\overline{1}}$; the crowns are simple and chisel-shaped, broadest at the cutting edge and tapering to the root. The canine resembles a fourth incisor, and follows upon the third after an interval no greater than that between $i_{\overline{2}}$ and $i_{\overline{3}}$; the crown is a little shorter and wider than that of the latter.

The premolars are rather complex for an Uinta artiodactyl and are of highly characteristic form. The first is isolated by a short diastema in front of and a much longer one behind it; it is a large caniniform tooth, implanted by a single fang, and stands much higher than any other of the mandibular teeth; the crown is simple and quite thick, and is worn obliquely on the anterior face by the attrition of the upper canine, which it opposes. In shape and function this tooth is like the caniniform premolar of the oreodonts; but this peculiar transformation is not confined to the latter family; it is repeated in the males of *Protoceras*, and in *Leptomeryx* $p_{\overline{1}}$, although very small and almost rudimentary, is in form a canine, and irresistibly suggests that it must once have functioned in that capacity.

The second premolar is short antero-posteriorly and is carried upon two fangs; the crown is perfectly simple, high, compressed, trenchant, and acutely pointed. The third premolar resembles $p_{\overline{2}}$, except that it is more extended antero-posteriorly and has on the inner side of the crown a short, compressed, plate-like ridge, which runs a short distance back from the central apex and partially encloses a fossa, that is, however, open behind, very much as in $p_{\overline{4}}$ of *Leptotragulus.* The fourth premolar has a large, conical, internal cusp (deuteroconid) in place of the inner ridge, a feature which clearly demarcates this genus from *Leptotragulus.*

The molars considerably resemble those of *Leptomeryx*, but the cusps are more conical and less compressed, as well as somewhat smaller, which makes the transverse valleys wider and separates the two external crescents more; the external cingulum is quite conspicuous. On $m_{\overline{3}}$ is a large fifth cusp, which has a continuous rim enclosing a narrow fossette.

MEASUREMENTS.

Upper dentition, length	0.070	Lower dentition, length	0.072
" incisor series, length	.007	" incisor series, length	.0075
" canine, fore-and-aft diameter	.005	" canine, fore-and-aft diameter	.002
" " transverse diameter	.003	" premolar-molar series, length,	.058
" premolar-molar series, length,	.054	" premolar series, length	.032
" premolar series, length	.033	" diastema between $p_{\overline{1}}$ and $p_{\overline{2}}$,	.0085
" diastema between p^1 and p^2,	.009	" P-1, length	.005
" P-1, length	.004	" P-1, width	?.003
" P-2, "	.007	" P-2, length	.005
" P-3, "	.0075	" P-3, "	.007
" P-4, "	.006	" P-4, "	.0065
" P-4, width	.0065	" P-4, width	.004
" molar series, length	.022	" molar series, length	.026
" M-1, length	.0065	" M-1, length	.0065
" M-1, width	.0085	" M-1, width	.0055
" M-2, length	.008	" M-2, length	.0075
" M-2, width	.010	" M-2, width	.006
" M-3, length	.009	" M-3, length	.0115
" M-3, width	.011	" M-3, width	.0065

The *Skull* (Plate II., fig. 10) is in general appearance and character a good deal like that of *Protylopus*, but is somewhat heavier and stouter, and the muzzle is more elongate, especially in the anterior region where the diastemata in the dentition occur. The tylopodan characteristic of a triangular skull with its broad cranium and forehead, and slender, tapering muzzle, is very distinctly displayed. The cranium is relatively well-rounded and capacious and the sagittal crest is short, though quite prominent, at least in old individuals, while the temporal ridges are long and converge backward quite gradually into the short crest. This arrangement prolongs the forehead well behind the orbits and gives it much the same shape as in *Protylopus*, but the temporal ridges are far more prominent than in the latter, and separate the forehead from the brain-case in a more conspicuous way. The orbit is small, with its upper margin rising somewhat above the general level of the forehead, and in *L. gracilis* is placed quite far forward, the anterior border being above the line between m^1 and m^2, while in *L. marshi* this border is above the hinder half of m^2. Despite the long, decurved postorbital process of the frontal the orbit is quite widely open behind.

In the skulls which I have had the opportunity of examining, most of the sutures are obliterated, so that it is difficult and often impossible to make out the limits of the individual bones. The occiput is rather low and is bounded by a prominent crest; the condyles are large and extend conspicuously behind the plane of the occiput, and the paroccipital processes also are curved strongly backward. The coronal suture is not visible in any of the specimens, but assuming that it occupied the same position as in *Protylopus*, then, as in that genus, the temporal ridges must extend for some distance over upon the parietals, but for a shorter distance and converging more rapidly to the sagittal crest than in the latter. The sagittal crest is short, as is the whole postorbital part of the cranium. The parietals are broad and gently arched and are suddenly and deeply constricted at the postorbital notch, which follows immediately behind the orbits. Above the orbits the frontals are broad and slightly concave, but they narrow rapidly towards the front end. The postorbital process is very long and prominent, much more so than in *Protylopus*, but this length is partly due to the great depth of the postorbital constriction; the process is broad and heavy and bent downward, so as to form a partial hinder boundary to the orbit, though the enclosure is very far from complete. The supraorbital foramina are shifted much nearer to the median line than in *Protylopus*, and broad, well-defined grooves lead forward from them. No supraorbital notch is present. The nasals are long, narrow, and slender, and are slightly convex both transversely and longitudinally, but they are truncated in front and cease at the line of p^1. In consequence of this the anterior nares, though rather small, are much more steeply inclined than in *Protylopus*, and their oblique position suggests that here we find the beginnings of the transformation which led to such remarkable results in *Protoceras*. The premaxillaries have quite stout, though depressed, horizontal rami, in which the incisors are inserted; the ascending rami, on the contrary, are very narrow, much more so than in *Protylopus*, and seem not to reach the nasals, though this is difficult to determine positively.

The maxillary is quite extraordinarily elongate, and forms much the greater part of the face; the alveolar portion is very low, but in front of the orbit the body of the bone rises to considerable vertical height, though this height diminishes steadily to the premaxillary suture. The large infraorbital foramen opens above $p^{\underline{2}}$. The palatine processes of the maxillaries are long and narrow, and slightly concave transversely; a deep palatal notch separates the hinder half of the alveolus of $m^{\underline{3}}$ from the palatine bone. Along the edentulous portion of the maxillary a low ridge marks the limits of the soft palate. The palato-maxillary suture is not distinctly shown, but appears to be opposite $m^{\underline{2}}$, and the posterior nares are placed quite far back, their front margin being on a line with that of $m^{\underline{3}}$; this margin is somewhat raised and thickened and has two short median spines.

The zygomatic arch is long, despite the posterior position of the orbit, horizontal in position, and decidedly stouter than in *Protylopus.* The squamosal element of the arch is quite long and extends forward to the hinder margin of the orbit; it merely overlaps the jugal and is not received into a notch of the latter, as it is in *Protylopus.* The jugal is deep vertically, laterally compressed and elongate; it has no distinct postorbital process.

The mandible is quite like that of *Protylopus*, but displays a number of minor differences; its horizontal ramus is long, shallow, and slender, though rather stouter than in the latter, while the diastemata give it a somewhat different appearance; the symphysis is shorter and the chin rather more steeply inclined, though in Wortman's specimen the symphysis is procumbent and almost horizontal. The difference may be specific or may be partly due to crushing. Three mental foramina are visible, a large one beneath $p_{\overline{1}}$, and two small ones beneath $p_{\overline{3}}$ and $p_{\overline{4}}$ respectively. The ascending ramus of the mandible is broad and the angle is much extended behind the condyle, quite as in *Protylopus;* the masseteric fossa is placed high up, its lower border being on a line with the molars. The condyle is transversely extended and is raised relatively little above the level of the teeth; the coronoid process is high, erect, and pointed, but not recurved, and therefore quite different from the ruminant-like form seen in *Protylopus.*

The vertebral column, so far as it is preserved, is not especially peculiar; it is represented in specimen No. 11,223 by the atlas, axis, and four lumbars. The atlas is quite elongate and seems to be rather narrow, though, as the transverse processes are incomplete, the full breadth of the vertebra cannot be determined. The neural and ventral arches are both strongly curved, giving to the canal a somewhat circular outline; the neural arch bears a low but distinct spine, which arises near the anterior border. The anterior cotyles are deeply concave and are quite widely separated, both dorsally and ventrally; they are notched quite deeply on the anterior border. The surfaces for the axis are rather small and are placed very obliquely with reference to the median line. The vertebrarterial canal pierces the base of the transverse process and runs but a brief course.

The axis has a moderately elongate, broad, and depressed centrum, which bears a prominent keel upon its ventral face. The articular surfaces for the atlas project outward prominently beyond the sides of the centrum, but their principal diameter is the vertical one; deep notches separate the dorsal portions of these surfaces from the neural arch. The odontoid process is moderately elongate, peg-shaped, and bluntly pointed, but is so broad and stout as to suggest that it will eventually take on the spout-like form. The transverse process is thin and compressed, but deep vertically, and is perforated by a short vertebrarterial canal. The neural canal is narrow, but rather high, and the pedicels of the arch are short from before backward. The neural spine is quite remarkable, forming a large, hatchet-like plate; it is well extended antero-posteriorly, especially behind the zygapophyses, and overhangs both the atlas and the third cervical, but is rather low vertically, and has a strongly curved free margin.

The lumbar vertebræ which have been preserved form a series of four, probably the second, third, fourth, and fifth; they are large and strong, and indicate considerable muscular power in the loins. The centra are long and depressed, and the neural arches are low, but the transverse processes are long, broad, and heavy, and they extend outward without much anterior curvature, considerably resembling those of *Protoceras*.

Of the fore-limb the parts preserved are the distal end of the radius and an imperfect manus, associated with the skull (No. 11,225); the distal end of the humerus and the proximal end of the ulna and radius of the second specimen (No. 11,223), which is referred, though with some little uncertainty, to the same genus and species. The humeral trochlea is intermediate in character between *Protylopus* and *Protoreodon*; it is fairly high and cylindrical in form, but is divided into three portions for the corresponding facets on the head of the radius. Of these, the median or intercondylar portion is convex, the others concave; the internal facet is considerably wider than the external. The intercondylar ridge is much broader and more rounded than in *Protylopus*, but less so than in the oreodonts. The external epicondyle is small, but the inner one is large, prominent, and rugose; it is not pushed so near to the postero-internal angle as in the oreodonts, but retains an altogether internal position. The anconeal fossa is quite deep and perforates the shaft at one point, making a small supratrochlear foramen.

The bones of the fore-arm are not anchylosed at any point, at least in the specimens before me, both of which belong to adult animals with complete but unworn dentition. The ulna is represented only by a small part of the proximal end, from which a great part of the olecranon has been broken away. So far as it is preserved, it resembles that of *Protylopus;* the olecranon is thick and broad, agreeing in proportions with that of the latter, and, as in that genus and in *Poebrotherium*, the process is continued upward in the line of the shaft, not projecting back of it. Although the coronoid process is prominent, yet the sigmoid notch is not very deep, for its distal portion is not produced forward, the radius occupying the entire breadth of the humeral trochlea. On the outer side, the facet for the humerus is confined to the proximal portion of the sigmoid notch, but on the inner side it is continued downward to the contact with the radius. For the latter there are two small proximal facets, separated by a narrow sulcus. The proximal portion of the shaft is stout and trihedral, with rounded posterior border; of the distal end it can be said only that it is stouter than in *Protylopus.*

The proximal end of the radius is quite suggestive of that of the oreodonts. In correspondence with the form of the humeral trochlea, the head of the radius is narrow, not much wider than the shaft; what little expansion there is, is towards the ulnar side. The articular surface for the humerus is divided into three clearly demarcated facets, the outer one nearly plane and descending obliquely forward, the median one distinctly concave, and the inner one narrower and saddle-shaped; the dorsal border is raised into a point opposite the median concavity. Proximally, the shaft is narrow, but quite thick and of transversely oval section; distally, the shaft is slender and the distal end is very moderately expanded, covering the scaphoid and lunar, but apparently not touching the pyramidal.

The manus (Plate II., fig. 13) is but little differentiated, though not unlike that of *Protylopus.* The carpus is in such a damaged condition that many important questions regarding it must remain unanswered; it bears a general resemblance to that of *Leptomeryx*, but differs in a number of details, especially in the height of the distal elements. The scaphoid is a large bone, high, broad, and thick; distally it rests in almost equal proportions upon the trapezoid and magnum, but is too much injured to show whether or not a trapezium facet was originally present. The lunar is narrow, but quite high vertically and rests almost equally upon the magnum and unciform, a very marked difference from all known oreodonts; the junction of the two facets is at such an angle as to make a sharp distal beak. Of the pyramidal only a shapeless fragment remains. The trapezoid appears to be distinct from the magnum, though this point is somewhat uncertain; it is very small. The magnum is rather narrow, but quite high; its proximal end is divided symmetrically between the facets for the scaphoid and lunar, and distally it appears to have a very limited contact with the second metacarpal. Of the unciform it can be said only that it is broad and high, and carries a stout hook upon the plantar face. The pisiform is short and stout, laterally compressed, but deep vertically; at the free end it is moderately thickened and incurved towards the radial side; its shape is very much as in *Protylopus*, but somewhat shorter and heavier.

The metacarpus consists of four functional elements and has a general resemblance to that of *Protylopus*, but differs from it in the more uniform size of the bones, the median pair being less enlarged and the lateral pair less reduced.

Metacarpal ii. is long, straight, and quite slender, though decidedly stouter than in *Protylopus;* the proximal end is enlarged in the dorso-palmar diameter, but not transversely; the head articulates by means of a concave facet with the trapezoid and sends out a short process towards the ulnar side, which probably reaches the magnum, though the state of preservation of the bones is not sufficiently good to make this point clear. Below the proximal end the shaft is of nearly uniform size and quite straight, though with a slight curvature towards the ulnar side. The distal trochlea is low and small.

Metacarpal iii. is considerably longer than mc. ii. and distinctly heavier, though as compared with mc. iii. in either *Protylopus* or *Leptomeryx* it is still slender. The head has the usual transversely concave facet for the magnum, and sends out a prominent process to meet the unciform, which process is somewhat larger than in *Protylopus*, and beneath it the shaft is more excavated for the head of mc. iv. than in the latter. The shaft is straight and narrow, but rather thick, while the distal trochlea is narrow and very low. As always in these early selenodonts, the carina is entirely plantar in position.

Metacarpal iv. differs from mc. iii. only in the shape of the proximal end, which has but a single carpal articulation, that with the unciform.

Metacarpal v. is like the second, except that it has a narrower proximal end and a more strongly curved shaft. In correspondence with its larger size, this bone has a more extended contact with the unciform than in *Protylopus*.

A single phalanx, the proximal one of the fourth digit, is preserved in connection with the manus; it has the same general shape as in *Protylopus*, but is depressed and very slender.

The pelvis (No. 11,223), so far as it is preserved, is tylopodan in character and recalls that of *Leptomeryx*. The anterior portion of the ilium is broken, so that its length cannot be determined, but it may be seen that the plate-like expansion is broad and widens suddenly from the peduncle; the latter is rather short and stout, having a considerable vertical diameter; the pubic and acetabular borders are obscurely marked, and the iliac surface is narrow. The ischium is relatively quite long, a marked difference from *Poebrotherium*, in which this element is much shortened; it is, for the most part, narrow and compressed, but rather deep dorso-ventrally and sub-trihedral in section; the dorsal border forms a thin and prominent crest above and for some distance behind the acetabulum, drooping suddenly at the ischiadic notch. The hinder part of the ischium is expanded, depressed, everted, and plate-like; no tuberosity is preserved, but one may, nevertheless, have been present. The acetabulum is large and deep and has very prominent borders, which project far out from the sides of the pelvis. The pelvis of *Protylopus*, so far as it is known, is similar to that of the present genus, but has a little more the aspect of the innominate bone in *Poebrotherium*, while *Leptoreodon* agrees somewhat more closely with *Leptomeryx* in this regard, though the four genera are very much alike, so far as the pelvis is concerned.

Of the femur (No. 11,223) the proximal end is lost. The shaft is relatively quite long and stout, especially in the antero-posterior dimension, and is well arched forward. This arching is, however, less marked than in the White River genera, *Poebrotherium* and *Leptomeryx*, but more than in the contemporary *Protylopus*. As in all the genera mentioned, there is a pit above the external condyle for the insertion of the plantaris muscle, a feature which is absent in the modern *Camelidæ*, though in *Poebrotherium* it is deeper and larger than in the Uinta genera. The rotular trochlea is narrow but prominent, and is deeply grooved. The condyles are rather small and narrow and of almost equal size; they are larger than in *Protylopus* and extend farther behind the plane of the shaft, making the entire distal end thicker than in that genus, for both condyles and trochlea are more prominent.

The tibia (No. 11,223) is shorter, more slender, and in every way smaller than that of *Protylopus*, from which it may immediately be distinguished by the far less prominent development of the cnemial crest. The condyles for the femur are narrow, but well extended from before backward, and of nearly equal size. Despite their extension, these condyles do not project so far back of the plane of the shaft as in *Protylopus*. The proximal portion of the shaft is stout and trihedral; beneath the cnemial crest it becomes much more slender and assumes an oval section, expanding in both dimensions at the distal end. As already mentioned, the cnemial process is far less conspicuous than in *Protylopus*, a difference which especially affects its antero-posterior breadth, for in length there is little difference; distally, it dies away much less abruptly upon the shaft. The distal end of the tibia exhibits no noteworthy difference from that of the last-named genus, except that the malleolar process is somewhat longer and heavier.

In none of the specimens is the fibula quite complete, but there can be no doubt that it was uninterrupted and entirely free from the tibia. The proximal end is very narrow and compressed, though it has considerable antero-posterior extension; the shaft is much reduced and very slender, and though it has not attained the thread-like proportions found in *Protylopus*, yet it is far more slender than in any of the known oreodonts. The distal end is a narrow but thick external malleolus, which is deeply channelled on the outer side by the sulcus for the peroneal tendons, and which has shifted partly beneath the edge of the tibia.

The pes (Plate II., fig. 14) (No. 11,223) is of very considerable interest. The tarsus is of the same structural type as in *Protylopus*, but may readily be distinguished from the latter by the smaller proximo-distal height of its members, especially of the cuboid. In size, shape, and general appearance the astragalus resembles that of the last-named genus, with a few differences in relatively unimportant details. The tibial trochlea is quite deeply grooved and somewhat more asymmetrical than in *Protylopus*, the outer condyle exceeding the inner one more in width, thus bringing the deepest part of the groove nearer to the internal side. On the distal trochlea the cuboid facet is conspicuously narrow. The sustentacular facet is broad, extending to the tibial border of the bone.

The calcaneum is relatively long and slender; its actual length is almost the same as in *Protylopus*, and thus the bone is proportionately longer, as compared with the rest of the limbs and feet. On the other hand, the tuber is somewhat shorter, a difference which is due to the position of the fibular facet, and distinctly more slender, and the depression upon the external side, while large and deep, is smaller and shallower than in the last-named genus. The fibular facet is an elevated and regularly curved prominence, which is placed somewhat more proximally than in *Protylopus*, thus making the tuber shorter and the distal portion longer relatively.

The cuboid shows no tendency to coössify with the navicular, and is high and narrow, though distinctly less so than in *Protylopus*; the astragalar facet is very narrow and simply concave in the dorso-plantar direction; it rises high above the calcaneal facet in a very characteristic way, forming a tall, narrow prominence, the internal (tibial) border of which is bevelled to provide for the expansion of the navicular proximally. The calcaneal facet is very deeply incised and its dorsal margin is far below that of the navicular facet. This constitutes a very marked difference from the condition seen in *Protylopus*, and is correlated with the relatively greater length of that part of the calcaneum which lies distal to the fibular facet. The calcaneal facet differs further from that of *Protylopus* in lacking the expansion upon the plantar side, which in the latter forms an overhanging shelf. The plantar hook is narrow and bluntly pointed, very different from the massive ridge which is found in *Protylopus*. The distal end of the cuboid is mostly taken up by the large facet for the fourth metatarsal, but posterior to this is a very small one for the fifth.

The navicular is a large bone, exceeding the cuboid in every dimension save the proximo-distal one; the proximal portion is expanded transversely at the expense of the cuboid. The plantar hook is longer than in *Protylopus*, but more slender and pointed. The distal face is occupied almost entirely by the facet for the compound cuneiform; that for the internal one is very small and placed at the postero-internal angle.

The ento-cuneiform is small and flat and lies in the concavity embraced by the plantar hook of the navicular; distally it bears a small, concave facet, which suggests that at least a vestige of the first metatarsal was preserved.

As in all the members of the present series from the Wasatch *Trigonolestes* (*Pantolestes*) onward, the meso- and ecto-cuneiforms are firmly coössified, but the shape of each element may still be distinguished. The meso-cuneiform is very small and almost concealed when the pes is seen from the front, while the ecto-cuneiform is very large and occupies nearly the entire breadth of the navicular. This compound bone is quite like that of *Protylopus*, but is shorter proximo-distally.

The metatarsus is composed, so far as is definitely known, of four functional elements, for though the lateral pair are considerably reduced and are more slender than the corresponding metacarpals, they are far from being thread-like splints, such as we find in *Protylopus.*

Metatarsal i. may, perhaps, have been preserved in the form of a vestigial nodule, as is suggested by the facet on the distal end of the ento-cuneiform.

Metatarsal ii. is quite long and very slender; it is longer in proportion to the median pair than is the second metacarpal, and much more slender. But it must be borne in mind that the manus and pes here described belong to different individuals, possibly even to different genera, although the example of *Leptomeryx*, *Protoceras*, and *Protylopus* shows that such a difference in the degree of reduction between the fore- and hind-foot is not of itself unlikely. The head of mt. ii. is slightly widened and thickened, and its plantar edge is bevelled for the ento-cuneiform; the shaft is slender and nearly straight. The distal trochlea is very narrow, but has a considerable dorso-plantar thickness and bears a prominent carina.

Metatarsal iii. far exceeds mt. ii. in all of its dimensions, but is both absolutely and relatively very much shorter than in *Protylopus.* It is considerably longer and stouter than the corresponding metacarpal, though the difference is less than in the last-named genus or in *Leptomeryx.* The proximal end is narrow, the shaft moderately long and stout, straight, and of nearly uniform width throughout. For part of its length the shaft is trihedral, the fibular side being flattened by its close approximation to mt. iv., assuming a transversely oval section below. The distal trochlea resembles that of *Protylopus*, being low and subspheroidal in shape rather than cylindrical; it is demarcated from the shaft by a somewhat deeper depression than in the latter genus.

Metatarsal iv. is slightly longer than mt. iii., its proximal and distal ends standing at a little lower level than those of its fellow.

Metatarsal v. corresponds in length and thickness to mt. ii., but has a somewhat heavier and larger proximal end.

Of the phalanges of the pes only a single one is preserved, a second phalanx of one of the median digits; it closely resembles the corresponding bone of *Protylopus* and is of nearly the same actual length. It is, therefore, much longer in proportion to the length of the metapodials and decidedly more slender.

MEASUREMENTS.

No. 11,225

Length of face	0.057	Mandible, depth at $m_{\overline{3}}$	0.010
Forehead, width	.034	" " " $p_{\overline{2}}$	.012
Palate, length	.066		
" width at $m^{\underline{3}}$	.017		
Metacarpal ii., length	?.030	Metacarpal iv., length	.036
" " breadth, prox. end,	.004	" " breadth, prox. end,	
" " " dist. "	.003	" " " dist. "	.006
" iii., length	.0385	" v., length	.031
" " breath, prox. end	.006	" " breadth, prox. end,	.0035
" " " dist. "	.0055	" " " dist. "	.005

No. 11,223

Tibia, length	0.108	Metatarsal ii., length	.044
" breadth, proximal end	.011	" " breadth, prox. end,	.0025
" thickness, "	.021	" " " dist. "	.004
" breadth, distal end	.012	" iii., length	.052
Fibula, thickness, "	.008	" " breadth, prox. end,	.006
Calcaneum, length	.034	" " " dist. "	.007
Astragalus, "	.017	" iv., length	.053
" breadth, proximal end	.007	" " breadth, prox. end,	.0045
" " distal "	.008	" " " dist. "	.006
Cuboid, length	.009	" v., length	.043
" width	.005	" " breadth, prox. end	.003
		" " " dist. "	.0045

The Systematic Position of Leptoreodon.

Wortman does not express himself very definitely upon this question. In one place he speaks of "the Oreodonts other than *Leptoreodon*" ('98, p. 96, foot-note) and in another place he says: "Upon the whole, I think it may be safely concluded, from the evidence at hand, that *Leptoreodon* held the same position with reference to the American Oreodontidæ that *Xiphodon* did to the European *Anoplotheriidæ*." (P. 97.)

I have reached a different conclusion. The phylogenetic position of this genus is not so clear and definite as that of *Protylopus*, because we have as yet found no White River genus which is so obviously descended from it as *Poebrotherium* is from the former. Leaving aside for the present the oreodonts and agriochœrids, it seems highly probable that all the Uinta selenodonts are closely related to one another, and there is no reason apparent to doubt that they were all derived from the same family, possibly even from the same genus, of Bridger times. The only important differences in the dentition between *Leptoreodon* and *Protylopus* are as follows: In the former the upper canine is large and the lower canine has assumed the shape and function of an incisor, while $p_{\overline{1}}$ is caniniform and takes its place. Considerable diastemata separate the first from the second premolar in both jaws. Except in very minor details, the other premolars and the molars are alike in the two genera. We also find great similarity in the character of the skull, although in *Leptoreodon* the face is longer and of greater vertical height, and the mandible has in both the same great extension behind the condyle. In both the feet and limbs are very much the same, save that in *Protylopus* the metapodials are more elongate and the lateral digits, especially those of the pes, far more reduced. *Homacodon* may serve as well for the Bridger ancestor of one genus as of the other.

Looking forward to White River times, the descendants of *Leptoreodon* cannot be so distinctly identified, though it seems highly probable that one of these is *Protoceras*. Unfortunately, there is a wide, unbridged gap in this line between the Uinta and the upper White River, and unless the problematical *Stibarus* should belong in this series we have yet to find the successive steps that led up to *Protoceras*. The latter genus has in the structure of its skull a number of deceptive resemblances to the higher Pecora, resemblances which the rest of the skeleton does not sustain. Highly significant is the fact that in the males the upper canine is a curved tusk, abraded upon the posterior face by the caniniform $p_{\overline{1}}$. Except that they have increased in size, the limbs and feet show surprisingly little advance over those of *Leptoreodon;* almost the only changes to be noted are the reduction of the fibula and of the lateral digits of the pes, with the partial anchylosis of the ulna and radius. Comparing *Protoceras* with *Leptoreodon*, one is surprised to find that, in view of the long time interval which separates them, they should differ so little. All the facts, as we at present know them, point to the conclusion that *Protoceras* was derived from *Leptoreodon* or from some very similar genus.

In my former paper upon the osteology of *Protoceras* I called attention to the many points of resemblance between this genus on the one hand and *Leptomeryx* and *Hypertragulus* on the other: "This family represents a group of White River selenodonts, each of whose genera has become more or less specialized in a way peculiar to itself, and with a tendency to simulate the Pecora in some respect or other, yet always retaining a number of primitive features. I cannot but believe that *Protoceras* represents a divergent offshoot of the same stock, which, retaining in most respects the foot structure belonging to the common ancestor of all these genera, has, at the same time, wonderfully paralleled the higher Pecora in many features of the skull." ('95*b*, p. 365.)

The newly discovered material of *Leptomeryx* and *Hypertragulus* brings out very clearly their tylopodan affinities and confirms Rütimeyer's views concerning them. If *Leptorcodon* be the ancestor of *Protoceras*, as there is so much reason to believe, there is all the more reason to refer the latter to the Tylopoda, for it would be difficult to assign any ground for making more than a family distinction between the former and *Protylopus*, almost the only important difference between them being in the character of the canine teeth.

In my preliminary paper I suggested that *Leptorcodon* was the forerunner of *Leptomeryx* also ('98, p. 77), but since I have seen the specimens belonging to the American Museum, especially the fine skull which has been figured by Wortman, this view strikes me as less probable. The skull seems a little too large and heavy, and the orbit to have been shifted too far back, to belong to a forerunner of *Leptomeryx*. Nevertheless, the ancestor of the latter must have been some closely similar form, possibly even a smaller species of the same genus. However that may be, the significant fact remains that in the Uinta all these lines, including the main tylopodan series, are seen converging very nearly to a common term.

The relation of *Leptorcodon* to the oreodonts offers a somewhat difficult problem. Its most striking resemblance to this family is to be found in the canine teeth and the caniniform first lower premolar, but the example of *Leptomeryx* and *Protoceras* shows that this peculiar arrangement is not confined to the oreodont family. Certain other resemblances to the latter family also occur in the limbs, as in the shape of the humeral trochlea and head of the radius, but the feet are of quite a different type and approximate rather to those of *Protylopus*. I am, however, inclined to the opinion that the resemblances to the oreodonts are not accidental, but that they have a real significance and tend to connect that family with the Tylopoda. The late Professor Cope once said to me that he believed *Protoceras* to be allied to the oreodonts, though I am not aware that he published this view. It is of importance as indicating the resemblances, which, though masked, could not escape

Cope's keen observation, and as helping to unify the American selenodonts. The oreodonts have already become established as a distinct family in Uinta times, and not until we find their Bridger ancestors shall we be able definitely to fix their taxonomic position.

Camelomeryx Scott.

PLATE III., FIGURES 15–18.

Proc. Amer. Phil. Soc., xxxvii., p. 77.

This genus is very much like *Leptoreodon*, though it should, in my judgment, be separated from it. The type of the genus is a fairly well preserved skull without the mandible (Princeton Museum, No. 11,226), and I provisionally refer to it a specimen in the American Museum (No. 2070), which consists of a cranium without teeth, ulna, radius, manus, pes, and other bones. The latter may, perhaps, be referable to *Oromeryx*, though the published accounts of that genus are so vague as in the absence of teeth to render identification well-nigh impossible.

The dentition (Plate III., fig. 16) is of the same type as that of *Leptoreodon*, from which it differs only in minor points. The formula is: $I?\frac{2}{}$, $C\frac{1}{}$, $P\frac{4}{}$, $M\frac{3}{}$.

The upper incisors are small and apparently only two in number; they are separated from each other by a short space, and quite a diastema intervenes between the lateral incisor and the canine. The crowns are very small, antero-posteriorly compressed, and somewhat chisel-shaped, resembling those of *Leptoreodon marshi*, but not the conical crowns of *L. gracilis*. The very small amount of wear which the incisors have undergone, in comparison with the other teeth, indicates that they were of little functional importance to the animal.

The canine is of rather peculiar form; its crown is not very long, but is quite broad antero-posteriorly, and, though compressed, is thick transversely; the edges are sharp and the end very bluntly pointed. What little abrasion the crown shows is upon the posterior surface, from which we may infer that, as in *Leptoreodon*, $p_{\overline{1}}$ had become caniniform, and that the lower canine had gone over to the series of incisors. This tooth is smaller than that of *Leptoreodon*, its fore-and-aft breadth being especially shorter, and it has not the thickened anterior border and external grooving which characterize the latter genus.

The first premolar follows the canine after a short interval, and is separated from $p^{\underline{2}}$ by a considerable diastema; it has a small, simple, conical, and much compressed crown, which is supported upon two fangs. It entirely resembles the corresponding tooth of *Leptoreodon*, except that it is smaller, and this difference may well be sexual rather than generic. The second premolar is much larger than $p^{\underline{1}}$; its crown is low, elongate, compressed, and trenchant, ending in an acutely pointed apex, and of cordate shape in profile, like the premolars of the oreodonts. It is perfectly simple, without basal or internal cusps, and is supported upon two roots. The third premolar is externally very similar to $p^{\underline{2}}$, but is thicker transversely and is carried upon three fangs; it has a minute anterior basal cusp. This tooth has suffered so much wear that I cannot determine whether it possessed a deuterocone; if so, it must have been smaller than in *Leptoreodon*, for the breadth of the crown is notably less than in that genus. The fourth premolar is like that of *Leptoreodon*, except that the external crescent has a more concave outer face, and that the cingulum is decidedly more prominent at the outer angles of the crown, forming minute though distinct buttresses at the points where these are so prominent in $p^{\underline{4}}$ of *Leptomeryx*. On the whole, the upper premolars of *Camelomeryx* differ from those of *Leptoreodon* only in minute details.

MEASUREMENTS.

Upper dentition, length I-1 to M-3	0.062
" canine, antero-posterior diameter	.005
" " transverse diameter	.003
" premolar-molar series, length	.051
" premolar series, length	.029
" molar series, length	.021
" M-1, length	.0055
" M-1, width	.0075
" M-2, length	.007
" M-2, width	.010
" M-3, length	.0085
" M-3, width	.0115

The upper molars also closely resemble those of the last-named genus in their shape and proportions, but differ slightly in a few details of construction. They increase in size, especially in width, from the first to the third, and have quadrate outlines, forming transversely placed rectangles, though a slight degree of asymmetry is produced by the somewhat greater breadth of the anterior half of the crown, a difference which is most marked in $m^{\underline{3}}$. The first molar, the smallest of the series, is so much worn that its pattern is almost completely obliterated. The second is also much abraded, making an exact comparison with *Leptoreodon* difficult, but it is obvious that the external median buttress is distinctly larger than in the latter. The third molar may be fully compared with that of the allied genus, which it resembles closely, but differs in the larger size of the external buttresses, especially of the median and posterior ones, which are very small in *Leptoreodon;* the ribs upon the outer crescents are also more prominent than in the latter. It is interesting to observe that these differences are in the direction of *Leptomeryx.* From *Protylopus* the two allied genera differ in the greater breadth of the upper molars.

The skull (Plate III., fig. 15) in its general character closely resembles that of *Leptoreodon* and less nearly that of *Protylopus*, but has some well-defined peculiarities of its own. It has the characteristic tylopodan form which recurs so often among these Uinta genera and which is so well shown in *Protylopus*, *Leptoreodon*, *Leptomeryx*, *Hypertragulus*, and even in *Protoceras*. The cranium, measured from the occipital condyles to the anterior border of the orbit, is considerably longer than the facial region, though the brain-case proper is rather short and quite slender. Its narrowness and the great depth of the postorbital constriction are in decided contrast to the conditions found in *Leptoreodon* and *Protylopus*, in which the brain-case is broader and the postorbital notches shallower. In similar contrast to the two genera mentioned is the sagittal crest, which is high and prominent, and which occupies the entire length of the parietals, the temporal ridges being short and confined to the frontals, where they pursue a nearly transverse course, instead of converging gradually into the sagittal crest, as they do in *Leptoreodon* and *Protylopus*. The forehead is broad over the orbits, ceasing abruptly behind, but contracting gradually in front into the narrow, rounded muzzle. The orbit is quite small and has an anterior position, its front margin lying above the middle of m^1, almost the same position that it occupies in *Leptomeryx*.

In *Leptoreodon* the orbit is larger and not so far forward, and in *Protylopus* also it has shifted backward, in consequence of which the muzzle is as long as in *Camelomeryx*, despite the fact that *Protylopus* is without diastemata.

The occiput is small and low, broad at the base, but contracting rapidly towards the summit; its shape is as in *Leptomeryx*, but it is actually and relatively lower and narrower. The basioccipital is quite elongate and very broad proportionately; its ventral surface is nearly flat, but is broken near the anterior end by two low eminences, between which is a broad, shallow groove. In *Leptomeryx* this bone is as long and quite as broad, but appears to be narrower because of the convexity of its ventral surface. The exoccipitals are low and wide, narrowing dorsally; as in *Protylopus*, they form a broad prominence above the foramen magnum, with a fossa on each side of it; the condyles are quite large, expanded laterally, but depressed vertically; in the median ventral line they are separated by a broad, shallow notch. The paroccipital processes are laterally compressed and broader than in *Protylopus*, but, as in that genus, they stand well in advance of the condyles, enclosing large fossæ with them. In *Leptomeryx* the processes have the same shape as in *Camelomeryx*, but are somewhat smaller and placed farther back. The supraoccipital would seem to have resembled that of *Leptomeryx* and to have had about the same extension upon the roof of the cranium; the lambdoidal crest is quite prominent in both genera. A considerable strip of the periotic is exposed between the exoccipital and squamosal, but does not give rise to any distinct mastoid process.

The basisphenoid resembles the basioccipital in shape, save that it is somewhat narrower. The alisphenoid is quite large; its ascending process forms a considerable portion of the floor of the cerebral fossa, rising in front to make part of its anterior wall. This bone is so exactly like that of *Leptomeryx* in shape that I may apply to it the description elsewhere given of the latter: "The alisphenoid is directed nearly horizontally, but there is a curious angulation or ridge in it, from which a portion of the bone passes upward, bounding the anterior edge of the temporo-sphenoidal lobe of the cerebrum." ('91*c*, p. 346.) However, in *Leptomeryx* this angulation is slightly more pronounced. In none of the specimens is the tympanic preserved, and the periotic is thus exposed to view; the fossa shows, however, that the bulla must have been very small, smaller even than in *Leptomeryx*, and the contracted space between the postglenoid and posttympanic processes of the squamosal indicates an auditory meatus of small size, much smaller than in *Protylopus*.

The parietals are very long and narrow, forming almost the entire roof of the cerebral fossa. For their entire length they unite to form a thin but prominent sagittal crest, which is far longer than in *Leptomeryx*, in which the temporal ridges are continued over upon the parietals, thus shortening the crest. In this respect both *Leptoreodon* and *Protylopus* are more like the White River genus. The parietals are even longer and narrower than in *Leptomeryx*, and differ from those of the latter in not diverging anteriorly to receive the median prolongations of the frontals; the narrowness of these bones is due both to the slenderness of the cranium and to the large size of the squamosals.

The squamosal is a very large bone, both longitudinally and vertically, and makes up the greater part of the cranial side-wall; it is highest behind, its suture with the parietal running quite steeply downward and forward. The posttympanic process is short, but quite thick, and is made conspicuous by its separation from the paroccipital; the notch between the posttympanic and postglenoid processes is narrower than in *Leptomeryx* or *Protylopus*. The root of the zygomatic process forms a much narrower and more horizontally directed shelf than in the White River genus, and the glenoid cavity is of quite a different form. In *Leptomeryx* the articular surface is larger and nearly flat or slightly convex; from the external side it is invaded by a large, deep concavity, which is visible as a broad sulcus when the skull is seen in lateral view, and which intervenes between the articular surface and the postglenoid process; internally the two are continuous. In *Camelomeryx* the surface is broad and simply convex, and only a slight indication of the external sulcus is visible; the postglenoid process is high, broad and thick, even larger than in *Protylopus*, and much larger than in *Leptomeryx*. The zygomatic process is broken away, but the form of the jugal shows it to have been longer than in the last-named genus.

The jugal is long, quite heavy in front, especially in the vertical dimension, and tapering posteriorly; it is largely expanded upon the face, both in front of and beneath the orbit; the masseteric surface is broad and distinct and is bounded by a prominent masseteric ridge; the postorbital process is exceedingly small and is widely separated from that of the frontal. This jugal differs in several important respects from that of *Leptomeryx;* it is longer, shallower vertically, but thicker and less plate-like; the masseteric surface and ridge are much better developed and the postorbital process much smaller, leaving the orbit far more widely open behind; the inferior boundary is flat and not flared out into a prominent lip, as it is in the White River genus. As a whole, the zygomatic arch is longer than in the latter, both because the glenoid cavity is farther behind the molar series and because the orbit does not extend so far back. In both genera the anterior boundary of the orbit occupies the same position, above m^1, but in *Leptomeryx* the orbit is larger and its hinder margin is well behind the molars, while in the Uinta genus it extends only to the posterior edge of m^3.

It is impossible to make out the limits of the lachrymal, or to determine whether a vacuity was present between it and the frontal.

The frontals are relatively very large bones; they are both long and broad, but take almost no share in the formation of the cranial roof, for they cease abruptly at the line of the postorbital processes. The temporal ridges thus follow an almost straight transverse course, curving backward very slightly as they approach the median line. The forehead is broad and triangular, contracting anteriorly; it is almost flat, or slightly concave, with a prominent median ridge. The postorbital processes, properly so called, are not very long and but little decurved, but they have the effect of great length, because the forehead and orbits project out widely beyond the sides of the narrow cranium, which is in marked contrast to the condition found in *Protylopus* and much more extreme than that in *Leptoreodon.* In *Leptomeryx* a remnant of the same condition may be observed, but the broader and more capacious cranium renders it much less conspicuous.

The nasals are long, narrow, and convex, slightly so in the longitudinal direction, and strongly so in the transverse. For most of their length they remain of nearly uniform width, and in front their emarginate tips project freely for a short distance beyond the premaxillæ. So far as they are preserved, these nasals agree very well in shape with those of *Leptomeryx*, but probably do not extend so near to the orbits.

The premaxillaries are evidently in a state of incipient reduction; the alveolar portion is very low and short, shorter than in *Leptoreodon* and much shorter than in *Protylopus*, and the ascending ramus forms, when seen from the side, a narrow strip along the front of the maxilla, widening a little at the nasal suture. Transversely, however, the ascending ramus is quite broad and contracts the narial opening considerably. This opening is very small, terminal, and nearly erect in position. The palatine processes are small and the incisive foramina narrow. In *Leptomeryx* the premaxillary has an ascending ramus which is considerably broader (antero-posteriorly) than in the Uinta type, but transversely is very thin and compressed.

The maxillary is long and low, especially beneath the orbit, and even in front of the latter the facial portion is lower than in *Leptomeryx* and the edentulous region is decidedly shorter. The muzzle tapers anteriorly and is constricted in front of p^2, but is expanded again by the swollen alveoli of the large canines. The palatine processes are long, somewhat concave transversely, and almost plane longitudinally. The bony palate is of nearly uniform width throughout, because the inner or lingual borders of the premolars and molars are arranged in almost the same fore-and-aft lines, those of the two sides keeping nearly parallel. However, the total breadth of the skull, measured to the outer sides of the teeth, is far greater at m^3 than at p^1. The palate is narrowed in front of p^2, but broadens again slightly at p^1 and still more at the canines. Anteriorly the palatine plates diverge widely to receive the premaxillary spines. The posterior nares are not preserved in either of the available specimens, but enough is left to show that the opening must have been farther back than in *Leptoreodon*, and that the palatal notch, which is quite distinct in the latter, is hardly at all indicated. This character of the palate forms another approximation to the structure of *Leptomeryx*.

Comparatively few of the cranial foramina are exposed to view. The condylar foramen is large and is placed in the angle between the condyle and the horizontal portion of the basioccipital; external to it is a second small foramen. The foramen lacerum posterius is a narrow, curved slit, which bends around the periotic and is continued anteriorly into the foramen lacerum anterius, though the bulla probably separated them when it was present. A large glenoid foramen makes a conspicuous opening upon the hinder face of the postglenoid process. As in *Leptomeryx*, the foramen rotundum is separate from the foramen lacerum anterius and is placed near the foramen ovale, internal to the glenoid cavity. A small venous foramen perforates the bony palate on each side, opposite p^1. The infraorbital foramen, which is quite large, occupies the same position as in *Leptomeryx*, opening above p^2 and well in advance of the orbit. I can detect no supraorbital foramen, but the frontal is not sufficiently complete in either of the specimens to enable me to say definitely that it was lacking. If present, however, it must have held a very different position from that of *Leptoreodon*, farther forward and much nearer to the median line; the absence of vascular grooves on the forehead is a marked distinction from *Leptoreodon* and *Oromeryx*. In *Leptomeryx* the supraorbital foramen is a minute paired opening placed near the outer rim of the frontal.

In the collection of the American Museum of Natural History is a specimen (No. 2070) which apparently belongs to this genus, though in the unfortunate absence of upper teeth the reference must remain somewhat uncertain. The cranium agrees exactly both in size and in character with that of the type specimen, and this agreement is the principal reason for referring the fossil to *Camelomeryx*.

The ulna and radius are long and slender and seem to be firmly coössified, though it is difficult to determine this point. At all events, they are very closely approximated throughout their length and are anchylosed at points, but, at the same time, their limits are clearly shown by deep grooves along the line of junction. The radius is relatively well developed; its proximal end is moderately widened, but thin and compressed antero-posteriorly, and in shape resembles that of *Leptomeryx*. The humeral surface is divided into two facets of unequal size, the internal one being considerably the larger; the groove for the intercondylar ridge is shallow, but makes a distinct notch on the dorsal border of the proximal end. The shaft is long and quite broad transversely, with a well-marked curvature towards the anterior side. In general proportions it is very different from the slender, cylindrical form which is characteristic of the oreodonts and rather resembles that of *Leptomeryx*, but is of less uniform width than in the latter; it is widest proximally, gradually contracting towards the middle, whence it again expands towards the distal end. The latter is moderately broad and thick, and displays a broad and shallow sulcus for the extensor tendons upon its anterior face. The facets for the scaphoid and lunar are of nearly equal size, though the former is slightly the larger; it is also reflected farther up upon the palmar face; the lunar face is simply concave.

Despite its anchylosis with the radius, the ulna is quite stout and very little reduced. The olecranon is so broken that its exact size and shape cannot be determined, but it was evidently large and heavy. The sigmoid notch is rather shallow, though the coronoid process is prominent, and the humeral facet is almost confined to the inner side; the external radial facet forms a marked projection. The shaft is quite stout, especially its proximal third, tapering steadily towards the distal end; the inferior part is laterally compressed and plate-like. The distal end is somewhat thickened, but its internal side is deeply notched to receive a projection from the radius. The facet for the pyramidal is small and saddle-shaped, and that for the pisiform, which is quite small, is continuous with it. In *Leptomeryx* the ulna and radius are, in general, much like those of the present genus, but they show no tendency to anchylosis, though the shaft of the ulna is much more slender.

MEASUREMENTS.

Radius, length	0.067	Ulna, length	?0.080
" width of proximal end	.008	" width of proximal end	.006
" " of distal end	.010	" " of distal end	.004

The manus (Plate III., fig. 17) bears a close general resemblance to that of *Leptomeryx* both in size and appearance, save that the lateral digits are much less reduced. The carpus is broad and rather low, although the distal elements are not so much shortened as they are in the White River genus. The scaphoid is of only moderate size, low, broad, but rather thin in the dorso-palmar dimension, and, except that it is somewhat thinner, it resembles that of *Protylopus*. The distal end is divided somewhat unequally between the facets for the trapezoid and magnum, the former rather the larger of the two. Although the trapezium was probably present, no distinct facet for it is visible upon the scaphoid.

The lunar is quite high and narrow, though less so than in *Leptomeryx*; the proximal end is not so much expanded transversely as in the latter, not sending out such a prolongation towards the pyramidal; the distal end is a wedge-shaped beak, formed by the junction of the magnum and unciform facets, which meet at nearly a right angle, and of which the former is slightly the larger. This symmetry of articulation between the lunar and the distal bones of the carpus is somewhat exceptional in this group. In *Protylopus* the unciform facet is larger than that for the magnum, while in *Leptomeryx* the lunar rests almost entirely upon the unciform and has only a lateral contact with the magnum, as is also true of all the oreodonts, even of *Protoreodon*. In *Protoceras*, however, there is only a slight tendency towards this displacement and the two facets are not far from equal in size, though that for the unciform is a little larger and more distal.

The pyramidal is a relatively large bone, slightly exceeding the scaphoid in all its dimensions except in breadth. On its palmar side is developed a large and prominent rugosity, such as is but feebly indicated upon the scaphoid. Of course, the large size of the pyramidal is to be correlated with the stoutness of the ulna, and forms a decided contrast to the reduced pyramidal of *Leptomeryx*. The ulnar facet is a transverse groove, with dorsal border much elevated at the radial side, but descending steeply towards the ulnar side; the pisiform facet is small and separated by a distinct ridge from the ulnar surface, with which it forms nearly a right angle. Articulation with the lunar, so far as the dorsal side is concerned, is by means of two facets, proximal and distal, with a sulcus between them. A simply concave facet for the unciform occupies the entire distal end.

The pisiform is smaller than in *Protylopus* or *Leptoreodon* and of a different shape; its proximal end is transversely extended, which is unusual among the artiodactyls, and bears narrow, concave facets for the ulna and pyramidal. The body of the bone is compressed, of moderate vertical depth, and so curved that it presents a convexity towards the ulnar side, while the distal end is slightly thickened. In the other Uinta genera above mentioned the pisiform is much larger; it is not transversely extended at the proximal end, and is much more thickened and club-shaped at the distal end. In *Protoreodon* this bone is much broader than in *Camelomeryx.* The pisiform of *Leptomeryx* is, unfortunately, not known, which prevents a comparison with that genus.

The trapezium is not preserved in connection with the specimen, but no reason is apparent to doubt that it was originally present, as is indicated by a small facet upon the radial side of the trapezoid. As in all of the Uinta selenodonts whose carpal structure is known, the trapezoid is distinct from the magnum. *Leptomeryx* is quite exceptional as a member of the Tylopoda in having these elements united; the union does not occur in *Protoceras* or *Poebrotherium,* or in the existing camels and llamas, though it is usual in the Pecora and Tragulina. In *Camelomeryx* the trapezoid is quite a small bone, though relatively high in the proximo-distal diameter, exceeding in this respect the corresponding element of *Leptomeryx.* The proximal end is rounded and convex, fitting into the concave facet upon the distal end of the scaphoid. On the radial side is a small facet which was doubtless destined for articulation with the missing trapezium. Connection with the magnum is maintained by two facets, proximal and distal. The distal end, so far as may be judged from the specimen, appears to bear an almost plane facet for the second metacarpal.

The magnum is still quite small proportionately, for the obvious reason that the third metacarpal is not greatly enlarged nor the lateral digits much reduced. The proximal end is unequally divided between the surfaces for the scaphoid and lunar, which meet at a very open angle; the former is somewhat the larger and more completely proximal in position, while the lunar facet is more oblique. A very small facet occurs at the disto-internal angle for the head of the second metacarpal, which preserves its primitive connection with the magnum. Nearly all of the distal end is taken up by the large facet for mc. iii., which is only slightly convex. It is impossible to say definitely whether there is any dorsal contact between the magnum and the unciform; if so, it must have been very small, owing to the distal extension of the beak of the lunar. In *Leptomeryx* the magnum is much lower proximodistally than in the present genus, and has so shifted that dorsally it lies altogether beneath the scaphoid, as is also the case in *Protoreodon.* In *Protylopus* the magnum is relatively larger than in *Camelomeryx* and has a proportionately larger scaphoid surface, though that for the lunar is still well developed, and the distal surface for the third metacarpal is much more strongly convex in the transverse direction.

The unciform is relatively small, hardly exceeding the scaphoid and pyramidal in size, though in the vertical dimension it, like the other distal elements, considerably exceeds the corresponding bone of *Leptomeryx*. The lunar facet is small and oblique in position and makes an obtuse angle with the surface for the pyramidal, which is altogether proximal. Quite a large facet for the unciform process of the third metacarpal occupies the distal half of the radial side and almost meets the lunar facet, leaving between them only a very narrow area, which may come into contact with the magnum. The distal end is but slightly convex, and the facets for the fourth and fifth metacarpals lie in almost the same transverse plane. In *Leptomeryx* the unciform is broader and much lower; its surface for the lunar is more proximal in position and its connection with the third metacarpal is considerably reduced. In *Protylopus* the unciform is larger in every dimension than in *Camelomeryx*. The proportions of its various facets are not markedly different from those of the latter, except that the surface for the fourth metacarpal has somewhat increased at the expense of that for the fifth.

In the specimen before us the metacarpus has preserved but four members, but there is some reason to believe that five were present in the animal, though doubtless the pollex was in a rudimentary condition. The median pair of metacarpals are but moderately enlarged, while the lateral pair are but slightly reduced, giving to the manus an almost isodactyl appearance. The laterals are relatively little heavier, though decidedly longer than those of *Leptoreodon*, and are, consequently, much less reduced than those of *Protylopus*. In spite of its primitive appearance the manus of *Camelomeryx* bears a distinct resemblance to that of *Leptomeryx*, although in the latter the lateral metacarpals are very slender and almost splint-like. Metacarpal ii. is quite long and stout, though shorter and more slender than the median pair; the proximal end is not enlarged, except slightly in the dorso-palmar dimension, its breadth not exceeding that of the shaft, and it bears a narrow, plane facet for the trapezoid and a very minute one for the magnum. On the radial side the head is flattened and slightly excavated, doubtless for the reception of the rudimentary first metacarpal. For most of its length the shaft is closely applied to that of mc. iii., and is of uniform size and trihedral shape; its course is nearly straight, except for a slight eversion of the distal end. Near the distal end the shaft is slightly contracted, becoming more rounded in shape, but expands again just above the trochlea. The latter is sub-spheroidal in shape and has quite a prominent palmar carina; it is demarcated from the shaft by a narrow but distinct groove.

Metacarpal iii. considerably exceeds the second both in length and thickness, though not so much as is usual among the selenodonts, even of this early period. Except for the projection which abuts against the unciform, the head is not expanded and is no broader than the shaft, and even this projection, though it has quite an extensive contact with the unciform, reaches but slightly across the head of mc. iv. There is, of course, no articulation with the trapezoid, which is prevented by the articulation, small as that is, of mc. ii. with the magnum. The facet for the magnum is almost plane transversely, as it also is in *Leptoreodon*, while in *Protylopus* this surface is quite deeply concave. The tubercle for the attachment of the extensor carpi radialis muscle is larger and more rugose, though not more prominent than in the last-named genera. The shaft is straight and of almost uniform diameter throughout, though broadening slightly above the distal trochlea, and for the greater part of its length the dorsal surface is rounded and convex. The trochlea is low, of subcylindrical form, and the carina is altogether palmar in position.

Metacarpal iv. differs in a few details from mc. iii. It is a little shorter, for the proximal end does not rise so high, owing to the downward extension of the unciform; distally also it ends at a level slightly above that of mc. iii. The head, which articulates only with the unciform, is, of course, differently shaped, and the dorsal surface of the shaft is plane or very faintly concave, instead of convex. The distal trochlea also is rather more spheroidal than that of mc. iii.

MEASUREMENTS.

Carpus, breadth	0.011	Mc. iii., breadth, distal end	0.006
" height in median line	.0065	Mc. iv., length	.0345
Mc. ii., length	.033	" breadth, proximal end	.005
" breadth, proximal end	.0035	" " distal end	.0045
" " distal end	.005	Mc. v., length	.030
Mc. iii., length	.037	" breadth, proximal end	.0035
" breadth, proximal end	.005	" " distal end	.0035

Metacarpal v. is slightly shorter and more slender than mc. ii., of which it forms the counterpart. The head, which articulates by a good-sized facet with the unciform, is slightly enlarged and thickened; this is principally due to the tubercle for the insertion of the extensor carpi ulnaris muscle. The shaft is slender, laterally compressed, and almost straight, though displaying a slight lateral curvature.

No phalanges have been found in connection with the manus.

Of the tarsus (Plate III., fig. 18) only the astragalus, calcaneum, and cuboid are preserved, but these are sufficient for a satisfactory comparison with the tarsus of the other Uinta genera. The astragalus is very much like that of *Protylopus*, though a little smaller in actual size and somewhat broader and shorter proportionately. The proximal trochlea is very asymmetrical, the external condyle exceeding the internal even more than in *Protylopus*, while the deep intercondylar groove is somewhat broader and more open than in that genus. Both of these condyles, and especially the inner one, are rather more widely separated from the distal facets for the cuboid and navicular respectively. The various facets for the calcaneum, so far as they can be made out, do not differ in any important respect from those on the astragalus of *Protylopus*, save that the surface for the sustentaculum appears to be hardly so wide in proportion. The distal trochlea is very unequally divided between the facets for the cuboid and navicular; the relative breadth of the two facets is about as in *Protylopus*, but that for the navicular is of different shape, in that its convex portion is rather narrower. The whole distal trochlea lies somewhat internal to the proximal one, and this gives an oblique shape to the entire bone. In *Leptomeryx* the astragalus is suggestively like that of *Camelomeryx*, but exhibits a number of advances. Owing to the increased size of the internal condyle, the proximal trochlea is less asymmetrical and the intercondylar groove is wider; the shape of the bone is less oblique, the proximal and distal trochleæ being more nearly in line, and the cuboidal facet is distinctly broader, while the dorso-plantar diameter of the whole bone is increased. *Leptoreodon* has an astragalus almost exactly like that of *Camelomeryx*, but is a little longer and narrower, and the distal trochlea has a somewhat different shape, due to the shallowness of the concave portion of the navicular facet. In *Protoreodon* the astragalus is of the same general type, but is heavier and more oblique in shape, with more asymmetrical proximal trochlea and more rounded angles.

The calcaneum is a rather small and slender bone, with perhaps a greater resemblance to that of *Leptomeryx* than to the corresponding tarsal in the other genera which have been mentioned. The tuber calcis is quite short, narrow transversely, and thin in the dorso-plantar dimension, much as in *Leptomeryx*, except that in the latter genus the tuber is distinctly elongate. Upon the external side of the calcaneum, and running for most of its length, is a very conspicuous sulcus, broad and deep; this sulcus is most marked in *Protylopus*, less so in *Leptoreodon*, and still less in *Camelomeryx*, while in *Leptomeryx* it is obsolete, only a slight remnant of it indicating that this genus was probably derived from an ancestor which possessed it. The fibular facet is narrow and does not rise so high as in *Protylopus* or *Leptoreodon*, but is more prominent than in *Leptomeryx*. The distal end of the calcaneum is like that of the latter genus in having a considerable dorso-plantar diameter, this diameter being suddenly diminished just above the fibular facet, as it is not in either *Leptoreodon* or *Protylopus*. The cuboid facet is relatively broader, but less extended planto-dorsally than in the last-named genus, in which the facet is so warped that its plantar portion presents inwardly rather than distally, while in *Camelomeryx* this warping is much less in degree. From *Leptomeryx* the chief difference lies in the relative width of the facet, the astragalus not taking up so much of the cuboid as in the White River genus. The sustentaculum is much more prominent than in the oreodonts.

The cuboid is rather small, narrow, and light. The proximal end is divided almost equally between the facets for the calcaneum and astragalus, though the former is perhaps slightly the broader of the two, but not so much so as in *Protylopus* or *Leptoreodon*, while in *Leptomeryx* the astragalar surface is distinctly the broader one. The facets are shaped much as in *Protylopus*, except that the cuboidal one is less warped and projects less towards the fibular side. The plantar hook is quite large and heavy, but far less so than in the last-named genus or even than in *Leptoreodon*, though larger and heavier than in *Leptomeryx*. The distal end is entirely occupied by the large facet for the fourth metatarsal, which is plane in front, concave behind. It is doubtful whether any facet for the fifth metatarsal is present; if so, it is exceedingly small. In *Leptomeryx* the cuboid is coössified with the navicular, a feature which, like the anchylosis of the trapezoid and magnum, is very exceptional among the Tylopoda and has not been observed in any Uinta genus.

The metatarsus consists of a large median pair and a very reduced lateral pair, but as the latter are not preserved in connection with the specimen, it is quite uncertain whether they were retained in their entire length or only as short splints, though the former alternative seems the more probable one. Metatarsal iii. is long and quite stout, much shorter, however, than in *Protylopus* and heavier than in *Leptoreodon.* The proximal end is narrow, but is given considerable dorso-plantar extension by the large projection from the plantar side. On the tibial side of the head is a shallow groove for the reception of mt. ii. From the size and shape of this groove it is evident that the missing metatarsal was exceedingly small. On the fibular side is a round pit which receives a projection from mt. iv. The shaft is long, stout, and nearly straight; it is broad transversely, but compressed antero-posteriorly, except in the proximal portion, which is quite thick in the dorso-plantar dimension; in breadth the shaft increases gradually and uniformly towards the distal end. The distal trochlea is demarcated from the shaft by a very distinct pit; the carina is but moderately developed and hardly at all visible from the front. The shape of the trochlea shown in the drawing (Plate III., fig. 18) is probably due to the crushing which the fossil has undergone.

Metatarsal iv. differs but slightly from mt. iii., except that the shaft is a little broader. The head is narrow and the shaft widens gradually to the distal end; the plantar projection is rather small, decidedly smaller than in *Protylopus*, and the depression on the fibular side which receives mt. v. is even shorter and shallower than the groove on mt. iii. for mt. ii. In *Leptomeryx* the median metatarsals have coalesced to form a cannon-bone, while the lateral pair are reduced to short splints, which are also anchylosed with the cannon-bone.

MEASUREMENTS.

Astragalus, length	0.016	Metatarsal iv., width, proximal end	0.0055
" width, proximal trochlea	.008	" " distal end	.0085
" " distal trochlea	.008	Phalanx 1, length	.018
Calcaneum, length (est.)	.031	" width, proximal end	.006
Cuboid, height	.0115	" " distal end	.0045
" width	.006	Phalanx 2, length	.011
" thickness	.011	" width, proximal end	.0055
Metatarsal iii., width, proximal end	.0055	" " distal end	.004
" " distal end	.0065	Ungual phalanx, length	.0105
Metatarsal iv., length	.052	" " width proximal end	.005

The phalanges are very much like those of *Protylopus*, except that they are relatively longer and more slender. As compared with the length of the metatarsals, the proximal phalanx is very long and slender; its proximal trochlea is narrow and quite deeply concave; the body of the bone is elongate and very narrow, and the distal trochlea is almost confined to the plantar face. The second phalanx is very much shorter than the first and even more slender; its distal trochlea is reflected well over upon the dorsal face. The ungual is long, narrow, straight, and pointed. The phalanges of *Leptomeryx* are of similar type, but a little shorter and thicker proportionately.

The Phylogenetic Position of Camelomeryx.

The problem concerning the taxonomic position of this genus is rendered somewhat obscure by the incompleteness of our knowledge of it; the mandible and the inferior dentition are quite unknown, and the limbs and feet have not yet been certainly identified, though there is every reason to believe that the specimen above described represents very nearly the actual structure of the genus. From the foregoing description it will be sufficiently obvious that *Camelomeryx* is very closely allied to *Leptoreodon*, so much so that one cannot but feel some doubt as to the propriety of separating them generically, though if we may assume that the feet described in this and the preceding section have been correctly referred, the difference is enough for generic distinction. It is a significant fact that almost all the minor differences which separate *Camelomeryx* from *Leptoreodon* are structural features in which the former agrees with *Leptomeryx*, and suggest that the latter was derived from it. There are, however, some objections to this view. In the first place, the ulna and radius—which in the White River genus, are separate—are already coössified in the Uinta form. This may be merely individual and due to advanced age, or it may be specific, occurring only in *C. longiceps*, and again the specimen may perhaps be properly referable to some other genus. But if future research shall show that *Camelomeryx* is characterized by anchylosis of the fore-arm bones, it will undoubtedly militate against the conclusion that *Leptomeryx* was descended from it. Secondly, *Leptomeryx* is remarkable for the character of its carpus, the magnum having shifted from beneath the lunar, which rests entirely upon the unciform. We might reasonably expect to find in the Uinta ancestor of this genus some indication of this displacement, if only in the incipient stage, but in the carpus referred to *Camelomeryx* there is no such indication.

Whether *Camelomeryx* be the direct ancestor of *Leptomeryx* or not, it is highly probable that it very closely resembles that ancestor in all save a few minor details of structure. At all events, we may feel confident that in the group of Uinta selenodonts represented by *Camelomeryx* and *Leptoreodon* we shall find the forms which later diverged into the lines terminated by *Leptomeryx* and *Protoceras*. Further, this group is unmistakably related to the main tylopodan stem. *Camelomeryx* and *Leptoreodon* are already, it is true, quite distinctly separated from *Protylopus*, but the difference lies almost entirely in the anterior region of the skull and in the character of the incisors and canines. The remainder of the skull and dentition are of the same type of structure, as are also the limbs and feet, only in *Protylopus* the elongation of the manus and pes and the reduction of the lateral digits have been carried one stage farther. This near alliance greatly strengthens the conclusion already reached that the White River selenodonts, such as *Protoceras*, *Leptomeryx*, and *Hypertragulus*, are derivatives of the tylopodan stem. The latter is in some sense intermediate between *Leptomeryx* and the main tylopodan line, for in it the canines have retained or reacquired their original form and function. *Hypertragulus*, therefore, cannot have been derived from *Camelomeryx* or *Leptoreodon*, but its very close resemblance in nearly all other respects to *Leptomeryx* shows that its Uinta predecessor must have been very much like those genera, except in the character of the incisors and canines. In the White River it runs a course closely parallel to that of *Leptomeryx*, though keeping an even more markedly tylopodan physiognomy, which makes it look like a miniature *Poebrotherium*, save for the long and slender canines.

(?) **Oromeryx** Marsh.

Oromeryx Marsh, Amer. Journ. Sci., 3d Ser., xiv., p. 364 (*nomen nudum*).
Oromeryx Marsh, Ibid., xlviii., p. 269.

This genus may be distinguished from the preceding ones, *Leptotragulus*, *Leptoreodon*, and *Camelomeryx*, by the absence of diastemata in the dentition, and from *Protylopus* by the much less advanced reduction of the lateral digits in both manus and pes, and by the shape of the upper molars, in which the anterior half of the crown decidedly exceeds the posterior half in breadth, giving a curiously asymmetrical shape, which is most marked in $m^{\underline{3}}$; the external median buttress is much more prominent than in *Protylopus*. $P^{\underline{3}}$ is inserted by two fangs only. In the absence of information concerning the canine teeth it is uncertain whether *Oromeryx* should be referred to the present family or the preceding one, and for the same reason we cannot definitely point out the White River successor of the genus. In a general way it is clear that it is allied to the other Uinta selenodonts described in the foregoing pages, and it is not at all impossible that *Oromeryx* may prove, when better known, to be the forerunner of *Hypertragulus*. Both genera are characterized by simplicity of the premolar teeth, and both have very similar molars, which in *Oromeryx* and less markedly in *Hypertragulus* are distinguished by the narrowness of the posterior half of the crown and the consequent asymmetry of form. In the character of the skull, limbs, and feet nothing is known to forbid or render improbable the derivation here suggested. At the same time it must be remembered that this is only a suggestion, and quite as good reasons may be given for deriving *Hypertragulus* from *Leptotragulus*. The difficulty in deciding the question comes from our ignorance regarding much of the structure of the two genera from the Uinta, and until these are better known we shall not be able to determine with accuracy even the family or families to which they should be referred, still less to indicate their successors in the White River fauna.

Family III. HOMACODONTIDÆ.

Bunomeryx Wortman.

Bull. Amer. Mus. Nat. Hist. N. Y., x., p. 97.

This exceedingly interesting form is not represented in the Princeton collection, and I therefore have nothing to add to Wortman's account. One of the most significant facts regarding *Bunomeryx* is the structure of its upper molars, which strongly suggests, as Wortman has pointed out, that the postero-internal crescent of the selenodont upper molar is not the hypocone, as has hitherto been taken for granted, but the metaconule. This determination is of the greatest interest as showing that the elements which make up the molar crown may develop in different ways, and that cusps occupying similar positions are not always homologous. The same fact has already been established with regard to the premolars. It is confirmatory of Wortman's view that the Uinta selenodonts almost all have more or less asymmetrical upper molars, due to the fact that the anterior half of the crown is broader transversely than the posterior half. In *Oromeryx*, and especially in $m^{\underline{3}}$ of that genus, this asymmetry is most clearly shown, but it has almost entirely disappeared in the White River genera. On Wortman's hypothesis the asymmetry seen in the teeth of the earlier selenodonts is intelligible enough; it is simply due to the fact that the metaconule has not yet grown to the full size of the protocone.

The taxonomic position of *Bunomeryx* is from one point of view sufficiently clear. As Wortman points out, it is obviously the direct descendant of the Bridger *Homacodon*, and should be referred to the same family as the latter. What this family should be called is another question, and one that cannot easily be answered. The European *Dichobune* has upper molars of a very similar type, and, so far as it is known, the rest of the structure seems to agree very well with that of the American genera, which may perhaps belong to the same family. It seems more probable, however, that the two groups are distinct, the *Homacodontidæ* standing in the same relation to the Tylopoda as the *Dichobunidæ* are believed by Schlosser to occupy with reference to the *Pecora.*

FAMILY IV. OREODONTIDÆ.

Protoreodon Scott and Osborn.

PLATE III., FIGS. 19–23; PLATE IV., FIGS. 24, 25.

Agriochœrus Marsh (*non* Leidy), Amer. Journ. Sci., 3d Ser., ix., p. 250.
Eomeryx Marsh, Ibid., xiv., p. 364 (*nomen nudum*).
Protoreodon S. and O., Proc. Amer. Phil. Soc., 1887, p. 257.
Eomeryx Marsh, Amer. Journ. Sci., 3d Ser., xlviii., p. 266.
? *Agriotherium* Scott (*non* Wagner), Proc. Amer. Phil. Soc., xxxvii., p. 79.

The essential features of the structure of this genus were quite fully described in a previous paper ('89, pp. 487, ff), yet the recently made collections add materially to our knowledge of it, and for the sake of completeness an account of the skeleton will be given here, though that involves a number of repetitions. Specimens of *Protoreodon* are about the most abundant of Uinta fossils, though well-preserved ones are far from common. Even the best of them have in nearly all cases suffered more or less from crushing, and it is surprising to see how much the appearance of a fossil is changed according to the direction in which the crushing has taken place. Especially is this true of the skull.

The oreodont family had already become distinctly established as such in Uinta times, and is very clearly distinguished from the other contemporary selenodonts. The genera of the succeeding White River stage differ comparatively little from those of the Uinta, of which *Protoreodon* is the most abundant, as well as the most important.

The dentition is peculiar and of considerable morphological interest; the teeth form a closed series without diastemata, and the formula is $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$.

A. *Upper Jaw.* (Plate III., figs. 20–23; Plate IV., fig. 25.) The incisors are rather small, antero-posteriorly compressed, and chisel-shaped. These teeth would seem to vary in number; in some specimens, at least of *P. parvus*, three are present, while in *P.* (*Agriotherium*) *paradoxicus* only one or two are found. Wortman says on this subject: "In all of our material I have not yet seen a specimen among the oreodonts other than *Leptoreodon* that has a full set of incisors in the upper jaw. Marsh figures the type of *Eomeryx pumilus* with but two superior incisors, and if *Protoreodon* has the full complement, as believed by Scott, then the two genera are certainly distinct. In two specimens in the Museum collection which correspond closely with *Protoreodon parvus*, as described by Scott, there is but a single incisor on each side above, and the premaxillæ are widely separated from each other in the median line." ('98, p. 96, foot-note.) Ordinarily such a difference in the number of the incisors and in the form of the premaxillaries would certainly be sufficient ground for a generic distinction, but in the present instance, as in the titanotheres, the variability is so great that for the present at least it seems better to include them all under one term, with the exception of *Hyomeryx*, which seems to be distinct. The canine is of the characteristic oreodont form, with D-shaped transverse section and abraded upon the posterior face. It is, however, relatively a little more slender, elongate, and recurved than in the later representatives of the family.

A very short diastema succeeds the canine, but only sufficient to provide for the caniniform $p_{\overline{1}}$, which of course bites behind the upper canine. The premolars are of thoroughly oreodont type, but are somewhat simpler, more compressed, and more trenchant than those of the White River genus, though in the structure of these teeth there is considerable specific and individual variation. The first and second premolars are each carried upon two fangs and have simple, compressed, and trenchant crowns, which, when seen from the outer side, have the cordate profile characteristic of the family; $p^{\underline{2}}$ differs from $p^{\underline{1}}$ in the presence of a better developed internal cingulum. $P^{\underline{3}}$ is always implanted by three roots and is wider transversely than $p^{\underline{2}}$, but the development of the inner side of the crown varies greatly. In *P. paradoxicus* (Plate IV., fig. 25) there is only a feebly marked internal cingulum; in *P. minor* (Plate III., fig. 23) the cingulum is quite distinct and a small deuterocone makes its appearance, while *P. parvus* (Plate III., fig. 20) and *P. pumilus* display an increasing size of this element. In the latter species Marsh figures the deuterocone as being almost as large and as completely crescentic as on $p^{\underline{4}}$. ('94, p.

266, fig. 18.) $P^{\underline{4}}$ is composed, as usual, of two transversely placed crescents, of which the outer one is more concave externally than in the other premolars; in *P. paradoxicus* the inner crescent is more conical and has less clearly marked horns than in the other species.

The upper premolars of *Oreodon* are just such as might be expected in the direct successor of the Uinta genus. Leidy says of the anterior three: "Their crown is a trilateral pyramid, with a pointed apex and a broad external cordiform surface. The narrower internal surfaces appear as triangular inclined planes, separated by a median acute ridge extending from the point to the base of the crown. The anterior of the internal surfaces forms at the base a pair of shallow pouches, defined by a double festoon. The posterior of the same surfaces forms a single and larger pouch at the base of the crown, included by a single and thicker festoon. This latter in the third premolar almost assumes the dignity of an additional lobe to the crown, resembling the internal lobes of the true molars." ('69, p. 81.)

The upper molars of *Protoreodon* are primitive in a very interesting way,—viz., in the retention of the anterior intermediate cusp (protoconule), though in other respects these teeth are already well advanced in the assumption of the selenodont character. They are extremely brachyodont, and are broad in proportion to their antero-posterior length. In size they increase from the first to the third. The external crescents are more concave on their outer faces than in *Oreodon*, and the median ribs upon those faces are far more prominent, as are also the external buttresses, all of which constitutes a marked resemblance to the molars of *Protylopus* and the *Leptomerycidæ*. The inner crescents, especially the anterior one, have less extended horns than in *Oreodon*, and the median valley is thus more widely open. The unpaired cusp is very small and in worn teeth soon becomes unrecognizable; such molars considerably resemble those of *Leptoreodon* and *Camelomeryx* in a corresponding stage of wear. The cingulum is much better developed than in *Oreodon*, and is almost continuous upon the front, internal, and hinder faces of the teeth.

The molars of *Oreodon* are so very familiar that they require no description. Suffice it to say that a comparison with those of the Uinta genus is extremely suggestive of a direct genetic connection between the two.

B. *Lower Jaw.* The incisors have simple, chisel-like crowns, and the canine has become one of them in form and function; these teeth are much more erect than in *Protylopus* or the *Leptomerycidæ*. The premolars are distinctively of the oreodont type, but they are simpler and much more compressed and trenchant than in the White River genus. The first premolar is caniniform and is more slender and pointed than in *Oreodon;* it is succeeded by $p_{\overline{2}}$ after an interval which, though very short, is distinctly longer than in the latter genus. $P_{\overline{2}}$ is a small, simple, and much compressed cone; $p_{\overline{3}}$ is larger, especially in the fore-and-aft dimension, and is obtusely pointed; from the apex a quite prominent ridge runs down the inner side of the crown, partially enclosing a posterior fossette. In $p_{\overline{4}}$ this inner ridge has become a well-marked cusp, much like that in *Leptoreodon.*

Leidy's admirable description of the lower premolars of *Oreodon* will show the changes which characterize that genus: "Their crown is a broad, trapezoidal pyramid, widest behind, and with an acute crescentoid border rising in a median point. From the latter an oblique ridge descends internally, and in the third [fourth] premolar terminates in a large, trilateral, pointed tubercle, which springs from the middle of the base of the crown and rises nearly as high as the principal point. In the premolars in advance the tubercle just mentioned is nearly obsolete, and the oblique ridge appears to expand into the base of the crown. Back of the oblique ridge the crown presents a fossa more or less closed internally by a tubercle or ridge. . . . . In advance of the oblique ridge mentioned, the inner part of the crown forms a broad, sloping concavity, usually enclosed at bottom by a narrow, festooned basal ridge." ('69, p. 82.)

The molars are much more primitive than those of the upper jaw and have many points of resemblance to the lower molars of *Agriochœrus.* The internal cusps are conical rather than crescentic, and the outer ones, while crescentic, are quite thick; the valleys are very broad and shallow; the anterior pair of crescents is separated from the posterior pair by a deep depression; small basal tubercles are developed on the inner cusps. $M_{\overline{3}}$ has a very large, basin-like heel. In *Oreodon* the lower molars have become typically selenodont, almost as much so as in the deer, while *Agriochœrus* retains a structure very closely like that of *Protoreodon,*—a significant fact.

The milk dentition is only imperfectly known, but one specimen which retains $m^{\underline{1}}$ and $dp^{\underline{4}}$ displays some points of interest. The deciduous premolar is completely molariform, but has more the molar pattern of *Agriochœrus* than have the true molars of *Protoreodon.* This approximation to *Agriochœrus* is manifest (1) in the greater concavity of the external crescents; (2) in the more massive and rounded shape of the antero-external buttress; (3) in the greater breadth of the external median buttress, which is not compressed as in the true molars, but is invaded by the valley, just as in *Agriochœrus*, though the buttress is much less prominent than in the latter.

MEASUREMENTS.

	P. parvus, type.	P. parvus.	P. paradox.	P. minor.
Upper dentition, length		0.070	0.067	
" canine, ant.-post. diam.			.006	.0055
" " transv. diam.			.006	.005
" premolar-molar series		.052	.050	.0465
" premolar series, length		.030	.027	.025
" molar series, length	.026	.022	.023	.021
" P-1, length		.006	.006	.006
" P-2, length		.007	.0065	.006
" P-2, width			.003	.004
" P-3, length	.007	.007	.006	.0065
" P-3, width	.0065	.0065	.005	.0055
" P-4, length	.006	.006	.006	.006
" P-4, width	.009	.009	.009	.008
" M-1, length	.008	.0065	.008	
" M-1, width	.0095	.009	.009	
" M-2, length	.009	.0085	.0085	.0085
" M-2, width	.011	.011	.011	.0105
" M-3, length	.010	.009	.009	.009
" M-3, width	.012	.012	.012	.0115
Lower premolar-molar series		.056		
" premolar series, length		.028		
" molar series, length		.028	.028	
" P-1, length		.006		
" P-1, width		.005		
" P-2, length		.006		
" P-3, length		.008	.0075	
" P-3, width		.0035	.003	
" P-4, length		.008	.008	
" P-4, width		.005	.004	
" M-1, length		.0075	.008	
" M-1, width		.006	.0055	
" M-2, length		.0075	.008	
" M-2, width		.007	.006	
" M-3, length		.012	.012	
" M-3, width		.007	.0065	

The skull (Plate III., fig. 19; Plate IV., fig, 24) is represented by several fine specimens in the two collections, which give a much more accurate idea of its structure and proportions than did the single very imperfect individual upon which my previous description was founded. ('89, pp. 488–490.) It is now obvious that the whole appearance and character of the skull are typically oreodont, though certain resemblances to the agriochœrids may be made out, and in several respects the skull, as would naturally be expected, is decidedly more primitive than in the White River representatives of either family. The cranium is long and narrow and low, especially in *P. paradoxicus*, and the face is short; the position of the orbit is somewhat variable, its anterior border being over the front part of $m^{\underline{2}}$ or the hinder part of $m^{\underline{1}}$. The occiput is low and narrow, and is drawn out dorsally into the wing-like processes so characteristic of the family; the zygomatic arch is slender, elongate, and nearly straight, and the orbit is widely open behind. No lachrymal pit has been detected. The muzzle is short, but narrow and tapering and abruptly truncate in front. The mandible is characteristically oreodont in form.

In details the skull structure is completely oreodont, though in several respects it is more primitive than that found in the genera of the White River and succeeding stages. The basioccipital resembles that of *Oreodon*, but is somewhat narrower, as are also the exoccipitals, but the foramen magnum is relatively much larger and the condyles more widely separated. The par-occipital processes are slender and appear to be relatively less elongate than in the White River forms; they have a rather more anterior position than in the latter. The limits of the supraoccipital are not clearly shown in any of the specimens, though doubtless it extends over upon the dorsal side of the cranium as it does in *Oreodon*, and, as in that genus, it forms a pair of prominent wing-like processes which extend backward, overhanging the occiput; they are best developed in *P. paradoxicus*, in which they are quite as conspicuous as in *O. culbertsoni*. The occipital crest is not very prominently developed and does not pass so directly into the root of the zygomatic process as it does in the later genera of the family. In none of the individuals that I have examined is the tympanic well preserved; it is almost certain, however, that the bulla was very small and that it was provided with a tubular meatus, much as in *O. culbertsoni*.

As in the White River genus, the parietals are very long, roofing in nearly the whole of the cerebral fossa, and they are somewhat broader proportionately than in the former. For their entire length they support a thin but high and conspicuous sagittal crest, which is not so straight as in *Oreodon*, but is arched from before backward, much as it is in *Agriochœrus*. The squamosal is very large and forms much the greater part of the cranial wall, though, corresponding to the broader parietal, it is somewhat narrower than in *Oreodon*. The glenoid cavity and process are typically oreodont, though the process is somewhat smaller and less massive than in the White River genus. The zygomatic process, which is shorter than in *O. culbertsoni*, curves out boldly from the side of the skull, but is slender and pursues an almost horizontal course, not arching upward and then downward nearly so much as in the White River forms. The jugal, on the contrary, is longer than in the latter and extends much nearer to the glenoid cavity; it is very slender and is not notched to receive the zygomatic process as it is in *Oreodon*, and the postorbital process is so feebly developed that the orbit is even more widely open behind than in *Agriochœrus*. As a whole, the zygomatic arch is more elongate, more slender, and much more nearly horizontal than in *Oreodon*, in which the arch descends quite strongly anteriorly, a feature which is due to the increased height of the ascending ramus of the mandible.

All of the skulls which I have examined are more or less damaged in front of the orbit, rendering it impossible to make out the limits of the lachrymal, though it may be seen, at least in some specimens, that the lachrymal pit, which is so characteristic of the later members of the family, is not present. A difference from *Oreodon* may be observed in the frontals, which descend forward at the forehead and are flat, not swollen and arched by the large sinuses. The forehead is broad and lozenge-shaped, narrowing abruptly behind and gradually in front, and displaying obscurely marked temporal ridges. The postorbital processes are in *P. parvus* quite long and decurved, much shorter in *P. paradoxicus*. The nasals are long, narrow, and quite convex transversely; in front they terminate in points and project well beyond the premaxillæ. The anterior nares are small, terminal, and almost vertical in position.

The premaxillaries are small, and, as in *Oreodon*, but little of them is visible in side view; the alveolar portion is low and weak, and in such species as *P. paradoxicus*, which have reduced incisors, the two bones do not meet in the median line. The incisive foramina are quite large and the spines are long, extending back to $p^{\underline{1}}$. I can discover no indication of the curious dorsal expansion of the ascending ramus which in *Oreodon* is received into a notch in the maxilla. The maxillary is shaped much as in *O. culbertsoni*, but is somewhat lower vertically; its palatine processes are narrow and short, and quite concave transversely. The palatal notches are very shallow, and, as the jugal joins the maxillary farther back than in *Oreodon*, the alveolus of m^3 is not so bar-like as in that genus. The palatines are quite large and make up an extensive part of the bony palate, reaching forward to p^4. As in *Oreodon*, the palate is of nearly uniform width throughout. The posterior nares are intermediate in character between those of *Oreodon* and those of *Agriochœrus;* they are wider than in the latter, but extend farther forward than in the former (to m^2), and thus the fore-and-aft extent of the canal is considerably greater.

The mandible is as characteristically oreodont as the rest of the skull; the horizontal ramus is of moderate length, but deep and compressed, tapering forward to the abruptly inclined chin. The symphysis is short and very steep, and in old individuals the two rami are sometimes coössified at this point. The shape of the symphyseal region is one of the most marked differences between *Protoreodon* and the other Uinta selenodonts, such as *Protylopus* and *Leptoreodon.* The ascending ramus of the mandible is shaped very much as in *Oreodon* but is lower, the condyle being raised much less above the level of the teeth. The angle is very broad and extends well behind the condyle, decidedly more than in *Oreodon*, but less than in *Leptoreodon;* its border is thickened, as in the former. The coronoid process is higher and more recurved than in the White River genus, and the masseteric fossa extends farther down upon the jaw.

MEASUREMENTS.

	P. parvus.	P. paradox.
Skull, basal length	0.127	0.132
Cranium, length to anterior margin of orbit	.073	.081
Face, length, orbit to premaxilla	.061	.051
Sagittal crest, length	.052	.060
Zygomatic arch, length	.059	.056
Skull, breadth across zygomata	.086	.078
Mandible, length	?.112	?.109
" depth at m_3	.021	.026
" " p_4	.018	
" breadth of angle		.045
" height of condyle		.047

The brain is relatively smaller than in *Oreodon* and much more simply convoluted. The hemispheres are particularly small, leaving the cerebellum entirely uncovered and, apparently, even a portion of the corpora quadrigemina. The cerebrum is pear-shaped and narrows anteriorly, abruptly so in front of the temporo-sphenoidal lobes; the latter are proportionately quite large. The convolutions are very simple and take a longitudinal course. On the dorsal surface of the hemisphere only two sulci are visible, one of which is the lateral and the other may be the suprasylvian, though they come together in front, enclosing a pyriform gyrus between them. The shape of the hemispheres is quite as much like those of *Leptomeryx* as it is like those of *Oreodon*. The posterior region of the brain, including the cerebellum and medulla, is very long proportionately.

The vertebral column is represented only by scattered vertebræ from all the regions in a more or less favorable state of preservation and belonging to numerous individuals. Only in minor details do they differ from those of *Oreodon*.

The atlas is very similar to that of the White River genus; it is short antero-posteriorly, but broad and with widely extended transverse processes. The odontoid process of the axis is narrower and more peg-like than in *Oreodon*, and the other cervical vertebræ are rather longer in proportion and somewhat more opisthocœlous; they all, except the seventh, appear to be perforated by the vertebrarterial canal. The trunk vertebræ do not offer any noteworthy distinctions from those of *Oreodon* except that they are somewhat lighter and more slender. The tail was evidently very long and stout.

The fore-limb, so far as we have it, differs very little from that of *Oreodon*. The humerus is almost exactly as in that genus, but is more slender and has a much less conspicuous deltoid ridge. The ulna has a stouter shaft and the radius a more slender one, but the peculiar articulations of the elbow-joint are just the same in the two genera.

The manus (Plate III., fig. 21) is somewhat less modified than in the White River types, yet the difference is not great. In all the later oreodonts the lunar rests entirely upon the unciform and has only a lateral contact with the magnum, which has shifted beneath the scaphoid. In *Protoreodon* this change is in an incipient stage, and the lunar still rests partially upon the magnum, which is not entirely covered by the scaphoid. The trapezium is better developed and the pollex is a little larger relatively than in *Oreodon*.

Pelvis, femur, tibia, and fibula differ so little from those of *Oreodon* that they require no particular description, and the pes is likewise in almost the same stage of advancement, though with some significant and interesting differences. The astragalus is somewhat narrower and has a rather more asymmetrical proximal trochlea; in the distal trochlea the cuboidal facet is even narrower than in the White River types. The calcaneum has a much more slender tuber, and the sustentaculum is more prominent, though very inconspicuous, which is a characteristic of the entire family. The cuboid is higher, narrower, and more deeply incised by the calcaneal facet, while the astragalar surface rises higher proximally. The navicular also has a greater proximo-distal diameter. The meso- and ecto-cuneiforms are coössified, though their limits are still clearly visible, and, as in the White River types, the former is a little shorter than the latter. The whole tarsus is conspicuously higher and narrower than in the subsequent genera of the family, in which the tendency was continually to become short and broad, a tendency which reached its maximum in *Merycochœrus; Protoreodon* departs much less in this respect from the tylopodan stem as represented by *Leptoreodon* and *Camelomeryx.*

The metatarsus is also elongate, as much so proportionately as in *Leptoreodon.* According to Marsh ('94, p. 267) at least a rudiment of the hallux is retained, as I have also shown to be true of *Ancodus.* ('95*a*, p. 486.) The other metatarsals closely resemble those of *Oreodon* except for their relatively greater length, the median pair are enlarged, and the lateral pair (ii. and v.), though longer, are almost as slender as in the White River genus.

The phalanges are much as in the latter, but longer and more slender; those of the second row have the distal trochlea only slightly asymmetrical, showing a less degree of convergence of the hoofs than in any recent artiodactyls except the Tylopoda. The unguals are longer, narrower, more pointed, and altogether more claw-like than in the later members of the group.

MEASUREMENTS.

	P. parvus.	P. parad.	P. sp.
Astragalus, length	0.0225		0.026
" breadth of proximal trochlea .	.011		.013
Calcaneum, length		.039	.048
" dorso-plantar diameter of tuber,		.010	.013
Cuboid, height			.013
" width			.010
Metatarsal ii., length			.049
" iii., "			.060
" iv., "			.061
" v., "			.051

The species of *Protoreodon* are as follows:

Protoreodon parvus S. and O.

Proc. Amer. Phil. Soc., 1887, p. 257.

Characterized by the presence of three upper incisors and by the small development of the inner cusp on p^{3}. Size moderate. Upper molars with strongly concave outer crescents.

Protoreodon pumilus Marsh.

Agriochœrus pumilus Marsh, Amer. Journ. Sci., 3d Ser., ix., p. 250.
Eomeryx pumilus Marsh, Ibid., xlviii., p. 266.

Upper incisiors two; p^{3} like p^{4}; upper molars with less concave outer crescents.

Protoreodon paradoxicus Scott.

Agriotherium paradoxicum Scott, Proc. Amer. Phil. Soc., 1898, p. 79.

Cranium very long, face short; upper incisors one, premaxillæ not meeting in the median line. Upper molars with very concave outer crescents; p^{3} without inner cusp.

Protoreodon minor sp. nov.

Size smaller than preceding species; p^{3} with very small inner cusp.

In addition to these a large species, almost rivalling *Oreodon culbertsoni* in size, is indicated by limb and foot bones in the Princeton collection and in that of the American Museum. (See Plate III., fig. 22.)

The Taxonomic Position of Protoreodon and the Relationships of the Oreodontidæ.

There would appear to be two lines of development included within the genus *Protoreodon*, one of which is characterized by the reduction of the upper incisors, and which culminates in the genus *Hyomeryx*, which is without upper incisors altogether. In the other line the incisors are retained. The first series apparently died out at the end of the Uinta, leaving no successors in the White River. The second series, represented especially by *P. parvus*, seems without doubt to be the direct forerunner of *Oreodon* and its successors. The Uinta genus resembles the White River form in every part of the dentition, skull, and skeleton, but is, of course, less modified and in every way what we should expect the ancestral genus to be. Thus the incisors and canines have already assumed their characteristic shape, the lower canine going over to the incisors and the first lower premolar becoming caniniform. The upper molars retain the fifth cusp (protoconule) in the anterior half of the crown, but their form is already characteristically oreodont; the lower molars are less advanced and resemble those of *Agriochœrus* in the conical inner cusps and the widely open valleys. The premolars are typically oreodont but somewhat simpler in construction than those of the White River representatives of the family.

The skull is oreodont but has a longer and less capacious cranium than in the later genera of the group, with orbits widely open behind and no lachrymal pit; the mandible is likewise oreodont in shape, but has a longer and more recurved coronoid process and angle more extended behind the condyle. The vertebral column differs but slightly from that of the White River genus, the principal difference being in the more peg-shaped character of the odontoid process of the axis and in the longer and more massive tail. The entire character of the limbs is oreodont; scapula, humerus, ulna and radius, pelvis, femur, tibia, and fibula differ in no important way from those of *Oreodon* itself, only the manus and pes are distinctly more primitive than in the latter. In the manus the displacement of the lunar over upon the unciform is already indicated, but is much less extreme than it afterwards became, and the pollex is somewhat less reduced. In the pes a remnant of the first metatarsal is still (*fide* Marsh) attached to the ento-cuneiform. The phalanges are rather more slender and the unguals more pointed than in *Oreodon.*

While there is little room left for doubt that *Protoreodon* is thus the ancestral form whence were derived *Oreodon* and its successors, *Eporeodon, Mesoreodon, Merycochœrus, Merychyus,* the Uinta material gives us no help in determining the genealogy of those curious aquatic oreodonts, *Leptauchenia* and its successors. This genus suddenly makes its appearance in the upper White River (Protoceras beds), and nothing has yet been found in the Oreodon or Titanotherium beds which can be regarded as ancestral to it, or which will explain its exact relationship to the more typical members of the family. Whether this line had already begun its separate existence in Uinta times, or whether it first branched off from the main stem in the older White River, must be left for future discovery to determine.

A larger and more important question is that concerning the relationship of the oreodonts as a whole to the other artiodactyl groups. Upon this subject the most diverse possible opinions have been expressed by the various students of the problem. Leidy was the first to call attention to the manifold tylopodan features in the structure of the oreodonts, and spoke of the family as uniting characteristics of the deer, camel, and hog. ('69, p. 71.) This phrase, however, should probably be regarded as descriptive rather than as expressing an opinion upon the taxonomic question, concerning which Leidy seems to have held no decided views. Cope brought the family into relation with the tragulines ('88, p. 1084), but here again, as in so many of Cope's phylogenetic schemes, the connection seems to have been regarded as formal and technical rather than actual. Marsh ('77, p. 365) has vaguely expressed an opinion according to which the nearer allies of the oreodonts are to be sought for among the anthracotheres (*Hyopotamus* or *Ancodus*) of the Old World. Substantially the same opinion is elaborated in my monograph of the family. ('91*a*, p. 391.) Rütimeyer ('83, p. 98) in a very brief and cursory way expressed his belief that the oreodonts are nearly related to the camels, and speaks of the "in Nordamerika so stark vertretenen Vorläufern der Camelina (Oreodon, Procamelus, Leptauchenia, etc.)." Schlosser has adopted the same view; he says of the family: "Sie nehmen überhaupt eine ganz eigenthümliche Mittelstellung zwischen den Suiden und den Traguliden ein" ('87, p. 46), "Von den ältesten Oreodontiden haben sich wohl die Tylopoden abgezweigt" (p. 48). From the same ancestral stock Schlosser derives the anoplotheres, anthracotheres, hippopotamuses, and suillines. ('87, Table, p. 42.)

The testimony of the Uinta selenodonts, while not entirely conclusive, is distinctly in favor of the opinion held by Rütimeyer and Schlosser,—namely, that the oreodonts are related to the Tylopoda, or rather that that term should be employed in a broad sense, of subordinal value, and so extended as to include the oreodonts, and that the latter are an offshoot of the same stock which gave rise to the modern camels and llamas. The recovery of the Uinta fauna has for the first time made clear what a dominant position the Tylopoda long held among North American artiodactyls, and how widely ramified and diversified they became. We cannot yet, it is true, definitely trace back the oreodonts to ancestors common to them and to the main line of tylopodan descent, and until that is done the association of both groups in one suborder must remain open to some question. On the other hand, it is a highly important and significant fact that in the Uinta the gaps between the various families of characteristically American selenodonts were not nearly so wide as they afterwards became through the divergent courses of development followed by these families, and that they were then obviously converging back to a common term. Even in Uinta times, however, the oreodonts were the most isolated and therefore the most clearly defined of all the selenodont families, but such genera as *Leptoreodon* and *Camelomeryx*, in which the lower canine has become a functional incisor and the first lower premolar is caniniform (one of the most strikingly characteristic features of the oreodonts), tend greatly to diminish the gap between the oreodonts and the undoubted tylopodans. Even so highly differentiated a type as the White River *Protoceras* is in many respects continues to preserve certain resemblances to the oreodonts. *Leptomeryx* also retains recognizable traces of the same relationship, and there is a great deal to be said in favor of the opinion that it was derived from an ancestor in which $p_{\overline{1}}$ was caniniform.

If, as Wortman suggests, *Bunomeryx* represents the transitional stage of dental development for both cameloids and oreodonts, the principal difficulty in the way of connecting the two groups will disappear. This difficulty lies in the uncertainty whether the tetraselenodont upper molar of *Protylopus* and its allies was derived from a tooth which retained the anterior intermediate cusp, as is certainly true of the oreodonts. As already pointed out, the asymmetry of the upper molars in nearly all of the Uinta selenodonts favors the conclusion that they were derived from a type like that of *Bunomeryx.*

Another difficulty in the way of referring the oreodonts to the Tylopoda lies in the character of the cervical vertebræ, which in all the genera of the family are short, and show no tendency to assume any of the peculiarities which are so marked in the family *Camelidæ*, and which are usually regarded as diagnostic of the suborder Tylopoda. These peculiarities are already well defined in the White River genus *Poebrotherium* (though in several respects they are less decided than in the later genera of the line), and it may reasonably be supposed that in *Protylopus* also they were present, at least in their incipient stages. However that may be, these features of the cervical vertebræ seem to be confined to the main line of tylopodan descent, the line which in this paper has been designated as the family *Camelidæ*, for in all of the other White River selenodonts (*Oreodon*, *Leptomeryx*, *Protoceras*, etc.) the neck is either short or of only moderate length, and its vertebræ are of the ordinary artiodactyl type of construction. It is most unfortunate that the structure of the neck is still unknown in all of the Uinta genera except *Protoreodon*, and hence we are unable to trace the rise and development of the peculiar cameline cervical vertebræ and to determine how early these peculiarities first made their appearance.

From the Uinta onward the history of the oreodont family is long and for the most part clearly recorded, extending, as it does, through the Loup Fork at the top of the Miocene. During this long period they were nearly or quite the most abundant of North American mammals, but they were very conservative and underwent relatively little change, and so far as is known they never migrated to any other continent. Throughout this time they retained their characteristic form of skull and dentition, together with the same short neck, long body and tail, short limbs and feet, which we find in the Uinta *Protoreodon*. In their general appearance and proportions there is little to suggest relationship with the Tylopoda, but much to suggest a connection with the suillines, though any such connection must be exceedingly remote.

While the line of descent from *Protoreodon* is thus reasonably clear, it is not yet possible to determine the ancestors of that genus. In some respects the molars of the smaller species of the Bridger *Helohyus* suggest the derivation of the Uinta genus from it, but, on the whole, *Homacodon*, or some nearly allied form, seems to be the more probable ancestor, which is as much as to say that the oreodonts appear to lead back to the same group of Bridger artiodactyls as do the other Uinta selenodonts. If this conclusion is sustained by future discovery, it will completely justify Schlosser's opinion, already quoted, and will show that the oreodonts represent a peculiar side-branch of the tylopodan stem, standing in somwhat the same relation to the *Camelidæ* proper as the tragulines do to the Pecora. It will also serve to explain the many resemblances which are to be noted between the oreodonts on the one hand and such genera as *Leptomeryx* and *Protoceras* on the other, resemblances which are exceedingly puzzling on any other hypothesis.

These conclusions are of great interest, and if sustained they will help to clear up many obscure problems of phylogeny, but it must not be forgotten that they are still only tentative; new discoveries among the artiodactyls of the Washakie and Bridger proper may at any time overthrow them. I think, however, that they are justified by the evidence now at hand.

Hyomeryx Marsh.

Amer. Journ. Sci., 3d Ser., xlviii., p. 268.

I have not seen any specimens of this genus, which is described as having lost all the upper incisors. Marsh's figure also shows that the upper molars are different from those of *Protoreodon* in having much less concave external crescents and less prominent outer buttresses.

No White River genus is known that can be regarded as a descendant of

Hyomeryx, which appears to be merely an abortive side-branch of the oreodont stem that led to nothing. At the same time this genus and the species of *Protoreodon* with reduced upper incisors would seem to have been the dominant representatives of the oreodonts in the typical Uinta horizon (horizon C). All the specimens of *P. parvus* which I have seen were found in the clays of horizon B, and while the Uinta collections are not yet sufficiently complete to give certainty upon such points, it seems exceedingly probable that in the Uinta proper the main line of oreodont development was overshadowed by the temporary abundance and importance of this short-lived group. This reasoning proceeds upon the assumption that structures once lost are not regained, and such certainly appears to be the normal course of evolution in the mammalian phyla. At the same time it must be remembered that it is an assumption, that possibly the incisors may have been partly suppressed and again redeveloped. The series *Protylopus*, *Poebrotherium*, *Gomphotherium*, etc., shows us that teeth may be greatly reduced in size and subsequently enlarge, and we cannot say with entire confidence that the process of rehabilitation may not go farther, and that teeth which are lost in the adult may not become functional again in a descendant. It is most important that we should not dogmatize concerning evolutionary processes on *à priori* grounds, and that we should await the evidence before coming to a decision upon these problems.

Family V. AGRIOCHŒRIDÆ.

Protagriochœrus gen. nov.

Plate IV., Figures 26–28.

This genus, which is represented by a species of considerably larger stature than those of any other genus of Uinta selenodonts, is founded upon a specimen belonging to the American Museum of Natural History (No. 1818). It is much to be regretted that all the known material is so very imperfectly preserved that many interesting phylogenetic questions cannot yet be settled. The dentition (Plate IV., figs. 26, 27) is of a character intermediate between the oreodonts and agriochœrids.

The dental formula is: $I\frac{?}{}$, $C\frac{1}{}$, $P\frac{4}{}$, $M\frac{3}{}$. The incisors appear to have already undergone some reduction, and in the type specimen only the fang of $i\frac{3}{}$ is visible; this fang is stout, of circular section, and is implanted quite near to and in advance of the canine. If the other two incisors were present they were probably small, as the premaxillary is so narrowed as hardly to allow space for three full-sized teeth; however, the point is not an easy one to decide. The canine is of the typical oreodont (or agriochœrid) pattern, as is plainly apparent, although both canines are broken away nearly level with the alveolus. From the broken surface several facts may be learned: the section is D-shaped, with the posterior surface nearly plane or even slightly concave, while the fang is curved, much as in *Agriochœrus.* From the characteristic form of this upper canine we may confidently infer that, as in *Protoreodon*, the lower canine had already gone over to the incisors and that $p_{\overline{1}}$ had assumed its shape and function.

The first premolar also is represented only by the roots, the crown being broken on each side. This tooth follows the canine after an interval which is relatively no greater than in *Protoreodon*, and this lack of a diastema constitutes a very marked difference from *Agriochœrus.* Another difference from the latter is in the proportionately larger size of $p^{\underline{1}}$, for though it was evidently the smallest of the series, it was not so much reduced as in the White River genus. The second premolar is larger in every dimension than $p^{\underline{1}}$, especially in the antero-posterior one; the crown is shaped much as in *Protoreodon* and has the same cordate outline, with acutely pointed and slightly recurved apex; it differs, however, in the much better development of the internal cingulum, which on the posterior half of the crown encloses a shallow fossette. In *Agriochœrus* $p^{\underline{2}}$ is very much as in the Uinta genus, except that it is less compressed and considerably thicker transversely.

Seen from the outer side $p^{\underline{3}}$ closely resembles $p^{\underline{2}}$, but when looked at from below or within it is markedly different, for it has a well developed deuterocone and is carried upon three fangs. The deuterocone is larger than in *Protoreodon*, and is even more distinct than in *Agriochœrus*, and, as in the latter, this internal cusp has an asymmetrical position near to the posterior border of the crown. The fourth premolar is a little shorter antero-posteriorly than $p^{\underline{2}}$ or $p^{\underline{3}}$, but is broader than either; the deuterocone is now a symmetrically developed crescent, the apex of which is placed opposite to that of the protocone. In *Agriochœrus* this tooth is almost molariform, having two external and in some species two internal cusps, though the postero-internal one (tetartocone) is always small and sometimes absent. From the simplicity of $p^{\underline{4}}$ in the Uinta genus it may be inferred that the corresponding lower tooth was not molariform, as it is completely in the White River genus.

While the premolars of *Protagriochœrus* are not especially suggestive of relationship with *Agriochœrus* rather than with *Oreodon*, the molars are preeminently so. They have the same low, broad crowns, with very concave external crescents, as in the White River type, though they betray their more primitive character by the presence of the anterior intermediate cusp (protoconule), as in *Protoreodon*, and even in some specimens of *Agriochœrus* a remnant of this unpaired lobe may be observed in unworn crowns of $m^{\underline{3}}$, where it is represented by a slight elevation on the anterior horn of the antero-internal crescent. In size the molars increase progressively from $m^{\underline{1}}$ to $m^{\underline{3}}$, which is the largest of the series. Between the molars of *Protagriochœrus* and those of *Protoreodon* there is considerable resemblance, but the differences are apparent at the first glance. In the former the external crescents have much more deeply concave outer faces, while the median ribs upon these faces are much less conspicuous; the antero-external buttress is larger, heavier, more rounded, and less compressed, while the median external buttress is penetrated much farther by the median valley, which thus separates the external crescents more widely; the postero-external buttress is absent except on $m^{\underline{3}}$, where it is small. The internal crescents are much alike in the two genera, though in *Protagriochœrus* their apices are somewhat higher and the unpaired cusp (protoconule) is somewhat more reduced. In both genera the internal crescents are unequally developed, the front horn of the hinder crescent reaching to the outer wall of the crown and cutting short the hinder horn of the anterior crescent.

As already mentioned, the resemblance of these molars to those of *Agriochœrus* is obvious at the first glance, and yet the latter shows a number of changes from the Uinta type in molar structure. We observe (1) that the protoconule has disappeared, or rather has become incorporated into the antero-internal crescent; (2) that the median external buttress has become more rounded and broader and is more deeply invaded by the median valley; (3) that the external crescents have become more deeply concave and their median ribs have been suppressed, as has also the postero-external buttress of $m^{\underline{3}}$. In brief, the dentition of *Agriochœrus* differs from that of its presumable predecessor, (1) in the presence of a diastema behind the canine, (2) in the greater thickness of the premolars and the more complex patterns of p^4 and $p_{\overline{4}}$, and (3) in the slight changes of molar structure which have just been enumerated. The differences between *Protoreodon* and *Protagriochœrus* are sufficiently clear to the eye and yet they are rather difficult to express in words. For this purpose the figures are more satisfactory than any description.

MEASUREMENTS.

Upper dentition, length C to M-3	0.081	Upper P-4, length	0.007
" canine, ant.-post. diam.	.0075	" P-4, width	.011
" " transverse diameter.	.007	" molar series, length	.035
" premolar series, length	.030	" M-1, length	.010
" P-1, length	.0085	" M-1, width	.011
" P-2, "	.009	" M-2, length	.0135
" P-2, width	.0045	" M-2, width	.0155
" P-3, length	.009	" M-3, length	.014
" P-3, width	.0085	" M-3, width	.0165

Of the skull very little is preserved, only the upper jaws and the occiput, but from these may be learned facts of some significance. It may be presumed that the cranium was even longer and the face shorter proportionately than in *Agriochœrus*, for not only is this the general rule in comparing earlier and later members of the same phylum, but in *Protagriochœrus* the extremely short diastema behind the upper canine points to the same conclusion. Probably the proportions of the cranial and facial regions were very much as in *Protoreodon*. The occiput resembles that of the latter genus and also that of *Agriochœrus*, being broad ventrally and narrowing much towards the dorsal side. The basioccipital is wide but tapers anteriorly, and is only moderately convex, without median keel. The condyles are large and very prominent, and in shape and proportions almost exactly resemble those of *Agriochœrus*. The exoccipitals are broad and form a wide convexity above the foramen magnum, on the dorsal margin of which they give off two processes, with a deep cleft between them. The paroccipital process is long and is curved backward; its anterior face is concave, as though it had partly embraced a small tympanic bulla; the process stands well in front of the condyle, and between the two is a large and deep fossa. Another fossa lies upon the side of the exoccipital, between the condyle and the crest of the inion. The supraoccipital is concave and its crest is on each side extended into the wing-like processes which occur in this genus, as in almost all the oreodonts and agriochœrids. Both the occipital and sagittal crests are very prominent, and the latter is quite thick and heavy. Only a narrow strip of the mastoid is exposed upon the surface of the skull, and there is no distinct mastoid process. The tympanics are not preserved, but it is clear from the shape of the basi-occipital that they cannot have been so largely inflated as in *Agriochœrus*.

The jugal is relatively stout, especially in the vertical dimension; transversely it is quite narrow and compressed; the masseteric ridge and surface are well marked, though somewhat less prominent than in *Agriochœrus.* The vertical depth of the jugal gives to the lower rim of the orbit considerable elevation above the level of the molars, though the alveolar portion of the maxillary is extremely low. The infraorbital foramen has not quite so anterior a position as in *Agriochœrus*, opening above the line between $p^{\underline{3}}$ and $p^{\underline{4}}$, while in the White River genus it lies above the middle of p^{3}. The little that is known of the skull adds no especial probability to the view that this Uinta genus is the forerunner of the White River *Agriochœrus*, but, on the other hand, it does not in any way render that view less likely.

Aside from the hind-foot, the only limb-bone preserved in connection with the specimen is the patella. This bone is quite different from that of *Protoreodon* and very like the patella of *Agriochœrus*, though it is somewhat less thickened in the antero-posterior diameter and less rugose upon the dorsal face, differences which are connected with the smaller size of the animal. The bone is of an elongate, almond-like shape, broad proximally and tapering to a blunt point distally. The dorsal surface is regularly and smoothly convex in both directions, while the surface for the femoral trochlea is obscurely divided into two facets by a low and broad median ridge. The shape of this ridge indicates that the rotular trochlea of the femur was wider and shallower than in *Agriochœrus.* This patella is broader and thinner than that of *Protoreodon*, and has a less elevated median ridge upon the femoral surface.

MEASUREMENTS.

Patella, length	0.025	Patella, maximum width	0.017

Of the pes (Plate IV., fig. 28) are preserved portions of the astragalus and calcaneum, the cuboid and navicular, and the second phalanx of one of the median digits. Of the astragalus we have the proximal half, which differs in some quite marked respects from that of *Protoreodon.* In the proportions of proximo-distal length to transverse breadth the astragalus is not very different in the two genera, and thus *Protagriochœrus* has not yet attained the broad, short, almost hippopotamus-like astragalus of its White River successor. The proximal trochlea is even more asymmetrical than in *Protoreodon*, the outer condyle much exceeding the inner one in size, though not rising so far above it proximally as in the last-named genus; the intercondylar groove is broader and more widely open than in the latter, more so even than in *Agriochœrus.*

The sustentacular facet is very broad proportionately, a point of resemblance to the White River genus, though its internal border is not so much elevated; the external calcaneal facet is more oblique and more deeply concave than in the latter, and the fibular facet somewhat broader. Though the distal trochlea is missing, yet the surfaces for it upon the cuboid and navicular show that the facet for the former was relatively broader than in *Protoreodon*, approaching the proportions seen in *Agriochœrus*.

Very little of the calcaneum is preserved, only the distal end with the fibular facet; this end has upon its external side a broad, deep sulcus, such as is found in *Agriochœrus*, but not in *Protoreodon*. The cuboidal facet is no broader—indeed, is relatively narrower—than in the latter, but has a considerably greater dorso-plantar diameter, and the distal astragalar surface is likewise more extended in the same direction. The fibular facet is narrower and rises higher and more abruptly than in *Agriochœrus* and is more regularly arched, while the proximal astragalar facet is more oblique and forms a sharp ridge by its junction with the fibular surface. The sustentaculum is badly broken, but the corresponding facet upon the astragalus shows that it must have projected more prominently than in *Protoreodon*. Between *Agriochœrus* and *Oreodon* we find similar differences; in the latter, as in all the oreodonts, the sustentaculum projects but very little from the tibial side of the calcaneum, while in *Agriochœrus* it is much more prominent.

The cuboid is decidedly lower and broader proportionately than in *Protoreodon*, though it has not yet become so low, wide, and thick as is the case in *Agriochœrus*. The difference in this respect between *Protagriochœrus* and *Protoreodon* is much the same as that between their White River successors, in both of which the tarsal bones have shortened and broadened, but far more so in *Agriochœrus* than in *Oreodon*. The calcaneal facet is quite broad, though hardly so wide proportionately as in *Protoreodon*; it is also less steeply inclined than in the latter, but descends farther upon the dorsal face of the bone. The astragalar facet is broader proportionately than in *Protoreodon* and of nearly the same relative size as in *Agriochœrus*, but its dorsal border rises higher proximally. On the tibial side of the cuboid are three facets for the navicular, a large concavity on the plantar border, and on the dorsal margin two small plane facets separated by a deep groove. Of these dorsal facets the distal one is carried upon a prominence, which also bears a facet for the ecto-cuneiform. In *Agriochœrus* the plantar facet for the navicular is much the same as in the Uinta genus, but on the dorsal side is only a single facet for the navicular and none for the ecto-cuneiform, which has become extremely short proximo-distally. The distal end of the cuboid is wider and thicker than in *Protoreodon*, and the great hook-like projection from the plantar face is shorter, but heavier; the facet for the fourth metatarsal is wider, and that for the fifth larger and more in the same plane with the fourth than is the case in *Protoreodon*. The same is true of *Agriochœrus*, but here the surface for mt. iv. is relatively more extended in the dorso-plantar dimension.

The navicular is higher and thicker than in *Protoreodon*, though this appearance of greater height is partly deceptive and due to the elevation of the dorsal border of the proximal end. The bone is shaped very much as in the last-named genus, and the only obvious difference is the greater size of the plantar hook in *Protagriochœrus*. In *Agriochœrus* the navicular has become much lower and wider, the increase in breadth being principally due to the widening of the internal portion of the facet for the astragalus, while on the distal face the surface for the compound cuneiform is more extended transversely, but less planto-dorsally, and the facet for the ento-cuneiform is smaller and more sessile.

When the cuboid and navicular are placed in their natural position with reference to each other, it may be readily seen that the cuneiforms were much higher in proportion to their breadth than is the case in *Agriochœrus*. Doubtless the meso- and ecto-cuneiforms were coössified, as in all the known oreodonts and agriochœrids.

A second phalanx of one of the median pair of digits is relatively longer and more slender than the corresponding bone of *Agriochœrus*; the proximal end is less distinctly divided into two facets by the less elevated intercondylar ridge, and the median dorsal beak is much less prominently developed. The shaft is relatively longer, narrower, and thinner, and tapers more towards the distal end. The distal trochlea is more like that of *Agriochœrus*, being reflected far over upon the dorsal face of the phalanx and distinctly cleft along the median line; it differs from that of the White River genus in being relatively narrower. The second phalanx of the pes in *Oreodon* is very similar indeed to that of *Protagriochœrus*, but with a few differences which may ultimately prove to be significant. Thus the bone is relatively shorter and heavier than in the Uinta form; the distal trochlea is not reflected quite so far over upon the dorsal side, and its plantar portion is somewhat less distinctly divided by the median cleft. In *Protoreodon* this phalanx is similar, but longer and thinner. Most unfortunately, no unguals have been found in connection with *Protagriochœrus*, but from the shape of the second phalanx it may be confidently inferred that the extraordinary claw-like form characteristic of *Agriochœrus* had not yet been developed, at least not in any such degree. It would be most important to learn whether the unguals showed any tendency towards the assumption of the claw-shape, but this must await future discovery.

In the following table measurements of *Protagriochœrus annectens* and *Agriochœrus latifrons* are given together for purposes of comparison.

MEASUREMENTS.

	Protagriochœrus.	Agriochœrus.
Astragalus, length		0.031
" width proximal trochlea	.015	.017
Calcaneum, width distal end	.006	.007
" depth " "	.014	.019
Cuboid, height of dorsal face	.014	.014
" width	.0125	.0155
" thickness	.016	.023
Navicular, height	.010	.009
" width	.011	.017
" thickness	.017	.021
Second phalanx, length	.017	.017
" " width proximal end	.009	.0095
" " " distal end	.0075	.008
" " thickness proximal end	.008	.010
" " " distal end	.0075	.008

The single species of *Protagriochœrus* at present known may be called *P. annectens*, sp. nov., and in the absence of other species with which to compare it its definition can be formal only. This may be taken, first, from the size as given in the various tables of measurements, and, secondly, from the simplicity of the premolar teeth.

The Taxonomic Position of Protagriochœrus.

This genus is not yet sufficiently well known to render its systematic position and its phylogenetic significance clear, though what little we already know concerning it is highly suggestive. The dentition, and especially the upper molars, leads us almost irresistibly to the conclusion that *Protagriochœrus* is ancestral to *Agriochœrus*, and this conclusion is further confirmed by the character of the tarsus. This differs from that of *Protoreodon* in very much the same way as the tarsus of *Agriochœrus* differs from that of *Oreodon*.

In each instance the Uinta genus has a higher and narrower tarsus than its presumable White River successor.

Certain difficulties which oppose the phylogenetic arrangement here sketched, deriving *Agriochœrus* from *Protagriochœrus*, suggest themselves, though they seem to be of no very great weight. (1) The difference between the two genera is apparently greater than that between *Oreodon* and *Protoreodon*, or that between *Poebrotherium* and *Protylopus*, and therefore it might seem that the structural gap is too great for the time interval. As a matter of fact, however, we know that development has proceeded at different rates in different phyla, and there is no known reason why change in the agriochœrids should not have been rather more rapid than in the oreodonts. (2) The lack of diastemata in the dentition of *Protagriochœrus* and their presence in the White River genus might by some be regarded as an insuperable objection to the derivation of the latter from the former. As shown in a previous chapter, this is an untenable assumption; *Protylopus* has no diastemata, in *Poebrotherium* they are very short, but in *Gomphotherium* and all the subsequent genera of the camels they are long. What has happened in the camel series may equally well have happened among the agriochœrids. (3) It would naturally be expected that the very remarkable foot-structure, and especially the ungual phalanges of *Agriochœrus*, should be more distinctly foreshadowed in its Uinta ancestor. So far as the tarsus of *Protagriochœrus* is concerned, it is just what it should be in the ancestral form, and until the ungual phalanges have been recovered we shall not know how great the difference between the two genera in this respect really is.

The available evidence thus goes to show that *Agriochœrus* is the descendant of *Protagriochœrus*, or of some very similar type, and that for all practical purposes the latter may serve to represent the actual ancestor. If this conclusion be valid, then certain interesting and somewhat unexpected corollaries will follow from it. (1) The oreodonts and agriochœrids are very closely related, and the marked differences displayed by the White River and later representatives of the two families were due to a rapid divergent evolution, especially on the part of the *Agriochœridæ*. In the latter family the skull retained most of its primitive features, such as the elongate cranium, open orbits, convex lachrymals, etc., though with an elongation of the muzzle and consequent production of moderate diastemata in the dentition. The teeth underwent a curious modification, while the limbs and especially the feet assumed a most extraordinary character, quite unique among the artiodactyls, large compressed claws taking the place of the hoofs. In the oreodonts, on the other hand, the cranium was somewhat shortened, the orbit became closed behind by the union of the postorbital processes from the frontal and jugal, and a deep pit appeared on the lachrymal; the molar teeth assumed a tetraselenodont pattern much like that of the modern deer, while the skeleton of the trunk, limbs, and feet underwent comparatively little modification, and even in long subsequent periods the changes in the skeleton never were extreme or radical.

Although the White River members of the oreodonts and agriochœrids had thus become widely separated, the Uinta representatives of the two families were still very close together, and, were it not for their subsequent history, no one would hesitate to include them all in the same group. Not only are *Protoreodon* and *Protagriochœrus* very much alike in all known parts of their structure, but the former even has a great deal about it to suggest relationship with *Agriochœrus*, and it lacks but comparatively little of being itself the common ancestor of both families. The skull is of a pattern from which both the oreodont and the agriochœrid type might readily be derived, as is also the dentition, save only the upper molars. The latter seem to have already progressed too far in the direction of the true oreodonts to be ancestral to the curious upper molars of *Agriochœrus*. The lower molars, on the contrary, are very much like those of the White River genus. The feet also would appear to have undergone changes in the same direction and away from the primitive condition which was common to the two families.

The connection between the two Uinta genera becomes all the closer when the various species of *Protoreodon* are studied with reference to this point. The species which I formerly called *Agriotherium paradoxicum*, and which I regarded as probably ancestral to *Agriochœrus*, tends to bridge the gap between *Protoreodon* and *Protagriochœrus*, and, indeed, stands almost midway between the two genera. I said of it: "The differences between *Protoreodon* and *Agriotherium* are such as strongly to suggest the inference that, while the former is the ancestor of the oreodonts, the latter stands in a similar relation to the agriochœrids. This determination can at present only be provisional until more is learned concerning the foot-structure of the present genus. At all events, if *Agriotherium* be not the desired ancestral form, we may feel confident that that form when found will prove to be of a very similar character." ('98, p. 80.) The discovery of *Protagriochœrus* renders it highly probable that this genus is the "similar form" sought for and is the actual ancestor of *Agriochœrus*, and that *Protoreodon paradoxicus* is merely a connecting link between the former and the oreodonts. Its structure thus tends to confirm the conclusion that the two families have a common origin, and that the numerous points of resemblance between them are not simply instances of parallel development.

(2.) If these conclusions are well founded, it follows that the likeness of the upper molars of *Agriochœrus* to those of the anthracotheres—a likeness to which attention has repeatedly been directed—is not due to any near relationship between the groups, but has been independently acquired. The molars of *Protagriochœrus*, despite the presence of the fifth cusp (protoconule), are less like those of *Ancodus* than are the molars of its White River successor. The peculiar arrangement of the incisors, canines, and caniniform lower premolars, which is so highly characteristic of the agriochœrids and oreodonts, is already fully established in the Uinta genera of these families. Consequently, to find a common ancestor of the agriochœrids and the anthracotheres (in which the canines are normal), we should have to go very far back indeed, so far that the peculiar features of the anthracothere dentition would probably not yet have begun to appear.

(3.) As we cannot yet point out the Bridger ancestor of the oreodonts, of course it is not yet possible to identify the common ancestor of both families. However, from the close approximation between *Protoreodon* and *Protagriochœrus*, it is altogether probable that the common ancestral form will be found in the Washakie or the Bridger proper. It is further probable that this unknown genus will prove to be very nearly related to the forerunners of *Protylopus*, *Leptoreodon*, etc., and may perhaps even be a member of the same family. Further than this it is unsafe to speculate, for the interrelationships of the various Uinta selenodonts are very complicated and difficult to unravel, their likenesses and unlikenesses being combined in such puzzling ways, but the peculiarities of the canines and premolars would indicate that *Leptoreodon* and *Camelomeryx* lead back to this common ancestor of the oreodonts and agriochœrids, and that this ancestor, while very nearly allied to the forerunner of *Protylopus*, was yet in Bridger times generically distinct. To those who are familiar with the remarkable appearance of *Agriochœrus*, with its extraordinary clawed feet, it may seem altogether unlikely that this genus can have been derived from a Bridger ancestor, common also to the oreodonts. When, however, *Agriochœrus* is carefully studied, every portion of its skeleton, not even excepting its extraordinary feet, is found to bear witness of its relationship to the oreodonts. The Uinta representatives of the latter family are still more like *Agriochœrus* and materially diminish the gap between the two groups. Even though *Protagriochœrus* should eventually prove not to be the direct ancestor of *Agriochœrus*, it certainly tends to approximate the two families very closely and to render it entirely probable that both were derived from a common Bridger ancestor. That this hypothetical ancestor was in its time nearly allied to the forerunner of *Protylopus*, and still more so to that of *Leptoreodon*, seems also very likely, whence follows the further probability that the *Oreodontidæ* and *Agriochœridæ*, like all the other indigenous North American selenodonts, should be referred to the Tylopoda.

SUMMARY AND CONCLUSIONS

1. The American Tertiary Selenodonts form two distinct assemblages: first, those derived by migration from the Old World, and, second, the truly indigenous forms. The former includes the anthracotheres and the true ruminants, while the latter has the oreodonts, agriochœrids, the *Leptomerycidæ*, and *Camelidæ*.

2. The Uinta fauna is the oldest American horizon in which the selenodonts are numerous and conspicuous.

3. The study of these Uinta selenodonts strongly suggests that all the indigenous American forms are nearly related and should all be referred to the Tylopoda.

4. The Tylopoda are a highly diversified group, filling in America the place taken in Eurasia by the Pecora and Tragulina, which they parallel in many ways.

5. The Uinta beds are confined to the basin south of the Uinta Mountains, where they overlie the upper Bridger (Washakie); they are divisible into two horizons (B and C), of which the lower is transitional from the Washakie. Apparently there is an unconformity between B and C.

6. The Uinta is to be correlated with the Lutetian of France, and belongs to the uppermost Eocene or lowest Oligocene.

7. *Leptomeryx*, a White River genus, retains some of the upper incisors, but not the canine; the lower canine is incisiform and $p_{\overline{1}}$ caniniform, but much reduced in size. The premolars are compressed and trenchant, but complicated by internal cusps; the molars are very brachyodont and have a

general resemblance to the tragulines, but the upper ones have remarkably prominent external buttresses and a development of the inner crescents which is much more tylopodan than traguline. The skull, as newly discovered specimens show, is very tylopodan in character, resembling that of a miniature *Poebrotherium*, though with small and hollow tympanic bulla, and the angle of the mandible is less produced. The neck is short, the odontoid process peg-shaped, and the vertebræ of the normal, not cameloid, type. The loins are long and much curved and the tail short. The fore-limb is short and slender; the scapula and humerus resemble those of *Poebrotherium*, but the ulna and radius are separate. The trapezoid and magnum are coössified and the lunar so shifted as to rest almost entirely upon the unciform. The manus has four complete digits, though the lateral pair are greatly reduced. The hind-limb is long; the pelvis and femur are tylopodan; the fibula is reduced to a proximal spine and distal malleolar bone. The navicular and cuboid are coössified. A posterior cannon-bone is formed, of characteristically tylopodan shape; the lateral metatarsals are short splints.

8. *Leptomeryx* should be referred to the Tylopoda.

9. *Hypertragulus* (White River and John Day) is much like *Leptomeryx*, but with many differences of detail; it has retained the canines in their original form and function and has simple premolars. The skull is very tylopodan, with abruptly contracted muzzle, which is shorter than in *Leptomeryx*, and the angle of the mandible is much more produced. The fore-limb is like that of the latter genus, but the ulna and radius have coalesced, while there is no cannon-bone in the pes.

10. *Hypertragulus* is even more obviously related to the *Camelidæ* than is *Leptomeryx*.

11. *Hypisodus* (White River) is remarkable for its prismatic molars and for the conversion of the lower canine and first premolar into functional incisors.

12. *Protoceras* (White River) has lost the upper incisors but retained a canine, which in the male is tusk-like and opposes a caniniform $p_{\overline{1}}$. The molars are like those of *Leptomeryx* and *Poebrotherium*, as are also the premolars, except for their greater elongation. The skull is of less distinctly tylopodan form than in the preceding genera, and in the backward shifting of the orbits and the bending downward of the face upon the cranial axis it resembles that of the higher Pecora. The nasals are very much shortened, and in the male great bony protuberances rise from the parietals, frontals, and maxillaries. The neck is of moderate length, the axis has a flattened odon-

toid, and the other cervicals are of normal structure. The limbs are much like those of *Leptomeryx* and *Poebrotherium;* the ulna and radius are coössified, the trapezoid and magnum separate, and the manus tetradactyl. The fibula is completely reduced, the cuboid and navicular distinct, and the pes didactyl, but without a cannon-bone.

13. *Protoceras* is clearly related to *Leptomeryx*, and if the latter is referred to the Tylopoda, the former must likewise be so classified.

14. *Protylopus* (Uinta) has an undiminished dentition without diastemata, but with the canines of very small size. The teeth are extremely like those of *Poebrotherium*, but less elongate and more brachyodont. The skull is also extremely like that of *Poebrotherium*, but has a less elongate muzzle, less capacious cranium, and a small tympanic bulla, free from cancelli; the coronoid process of the mandible is more ruminant-like. The thoracic, lumbar, sacral, and caudal vetebræ resemble those of *Poebrotherium*, as does the fore-limb, the ulna and radius showing incipient coalescence in old individuals; the manus is, however, tetradactyl. Pelvis, femur, and tibia are entirely tylopodan; the fibula is uninterrupted but with extremely slender shaft. In the pes the lateral metatarsals are elongate, filiform splints.

15. *Protylopus* seems almost certainly to be the direct ancestor of *Poebrotherium*, and thus the most ancient known member of the *Camelidæ.*

16. A closed dentition does not necessarily imply that the animal is capable of no further development.

17. The very small canines in *Protylopus* and *Poebrotherium*, and their gradual enlargement in *Gomphotherium* and the subsequent genera of the phylum, indicate that structures may first be reduced and then enlarged in a phyletic series, while the elongation of the premolars in *Poebrotherium* and their reduction in the later genera show that structures may first be enlarged and then reduced.

18. *Leptotragulus* (Uinta) is very imperfectly known; its mandibular dentition is very much like that of *Poebrotherium*, but appears to differ from it in the suppression of $p_{\overline{1}}$ and the large size of the canine.

19. *Leptotragulus* may, when better known, prove to be the ancestor of *Hypertragulus.*

20. *Leptoreodon* (Uinta) has an unreduced dentition, with small, conical upper incisors, a stout D-shaped upper canine, and diastemata between p. 1 and p. 2. The lower canine has become incisiform and $p_{\overline{1}}$ caniniform, as in the oreodonts; the upper premolars are simple and the molars composed of four cres-

cents like those of *Protylopus*, which they closely resemble, except that the outer crescents are more concave and the outer buttresses more prominent. The lower premolars, except the caniniform $p_{\overline{1}}$ and the compressed-conical $p_{\overline{2}}$, have large inner cusps. The skull is quite like that of *Protylopus*, but somewhat more massive and with a more elongate muzzle. The cervical vertebræ are of moderate length and the odontoid process is sub-conical, but broad and blunt; the neural spine of the axis is a very large plate. The lumbar vertebræ are heavy, with large and nearly straight transverse processes. The bones of the fore-limb are intermediate in character between those of the oreodonts and those of the *Camelidæ*, and the ulna and radius are not anchylosed at any point. The carpus is quite like that of *Leptomeryx*, but the lunar rests almost equally upon the magnum and unciform. The manus is tetradactyl and resembles that of *Protylopus*, but the lateral metacarpals are less reduced and the median pair less enlarged. The pelvis, femur, and tibia are much like those of *Protylopus*, but the cnemial crest of the latter is far less prominent. The fibula has a very slender shaft, though it is not filiform, as in the last-named genus. The pes has a general resemblance to that of *Protylopus*, but the lateral metatarsals are not nearly so much reduced.

21. *Leptoreodon* may be regarded as the probable ancestor of *Protoceras*.

22. *Camelomeryx* (Uinta) has a dentition like that of *Leptoreodon*, except for the smaller upper incisors, which are reduced to two. The skull also resembles that of the latter genus, but has a narrower and less capacious brain-case, deeper postorbital constriction, and much longer sagittal crest, and the orbit is quite far forward. The skull is much like that of *Leptomeryx*. Limb-bones referred, though with some doubt, to this genus show an anchylosed ulna and radius; the tetradactyl manus is much like that of *Leptomeryx*, but the lunar rests largely upon the magnum, which is separate from the trapezoid, and the lateral metacarpals are less reduced. The pes resembles that of *Protylopus*, and has enlarged median and much reduced lateral metatarsals.

23. The taxonomic position of *Camelomeryx* is somewhat doubtful, though it is probably a form nearly allied to the ancestor of *Leptomeryx*, if not itself that ancestor.

24. *Oromeryx* (Uinta) has no diastemata in the dentition, and in the upper molars, especially m^3, the posterior half of the crown is narrower than the anterior half. The systematic position of this genus is quite uncertain.

25. *Bunomeryx* (Uinta) is interesting as tending to show that the postero-internal crescent of the tylopodan upper molar is not the hypocone but the meta-

conule, an interpretation confirmed by the asymmetrical shape of these teeth in many Uinta selenodonts. *Bunomeryx* is evidently descended from the Bridger *Homacodon* and should be referred to the *Homacodontidæ*, a family which seems to bear the same relation to the Tylopoda as the *Dichobunidæ* bear to the *Pecora*.

26. *Protoreodon* (Uinta) is already a true oreodont, the family being distinctly differentiated as such in the Uinta. The dentition resembles most that of *Oreodon* and is without diastemata, the lower canine being incisiform and $p_{\overline{1}}$ caniniform. In some species the upper incisors are reduced to two or even to one. The premolars are somewhat simpler than in *Oreodon*, and the molars broader and more distinctly brachyodont; the upper molars retain the fifth cusp (protoconule), and the lower molars are very like those of *Agriochœrus*. The skull is also like that of *Oreodon*, but resembles that of *Agriochœrus* in the narrow, elongate cranium, the incompletely closed orbit, and the absence of a lachrymal pit. The vertebral column and limbs differ from those of *Oreodon* only in minor details. In the carpus the lunar has shifted less completely upon the unciform and the pollex is somewhat larger. The pes is almost exactly like that of the White River genus, except for a rudiment of mt. i. attached to the ento-cuneiform.

27. The genus *Protoreodon* seems to include two lines of development, one represented by *P. parvus* and leading to the later oreodonts, the other composed of species with reduced upper incisors, which became dominant in the true Uinta beds, but seems to have died out without descendants.

28. The *Oreodontidæ* probably should be considered an offshoot of the Tylopoda.

29. *Hyomeryx* is distinguished from *Protoreodon* by the absence of upper incisors and by the less concavity of the external crescents of the upper molars.

30. *Protagriochœrus* has a dentition much like that of *Protoreodon*, but with somewhat more complex upper premolars, and molars with much more concave external crescents and less prominent median ribs, and the external median buttress is penetrated farther by the median valley. The skull, which is very imperfectly known, seems to agree with that of *Protoreodon*. The tarsus has considerable resemblance to that of *Agriochœrus*, and though not so broad and short, is much more so than in *Protoreodon*.

31. *Protagriochœrus* is not sufficiently well known to make its taxonomic position clear, but it seems to be the ancestor of *Agriochœrus*.

32. The *Agriochœridæ* are probably nearly related to the *Oreodontidæ*, and derived from a common Bridger ancestor, and if so, they are aberrant Tylopoda.

The conclusion that all the indigenous North American selenodonts are members of the suborder Tylopoda, though by no means demonstrated, seems to be naturally deducible from the evidence as we now have it. At all events, this hypothesis explains better than any yet suggested the complicated tangle of resemblances and differences between the various American groups, as well as those between the American and the European families. In the European *Dichobunidæ* and the American *Homacodontidæ* the Pecora and the Tylopoda nearly approximate to a common term, if they do not actually merge. *Trigonolestes*, or some similar form, may be the common ancestor of both.

Of the numerous phylogenetic lines included within the tylopodan suborder, only one—that of the *Camelidæ* proper—has persisted to the present day. The current definition of the suborder Tylopoda has been drawn from the peculiarities of the later members of this single family, and hence it is too narrowly restricted to embrace the great group of related selenodont families which flourished so abundantly in the Upper Eocene and Oligocene of North America. Indeed, so diversified is this group, that it is exceedingly difficult to frame a definition of the suborder that shall be diagnostic of it—on the one hand, embracing all its members, and, on the other, clearly distinguishing it from the Pecora and Tragulina. The difficulty arises not only from the lack of obvious characteristics which are common to all members of the Tylopoda, but also from the numerous features in which one or other member of the suborder has developed in a course parallel with that of the Pecora or the Tragulina. This difficulty of definition, however, is the inevitable result of the discovery of long and clearly marked phylogenetic series. One by one the characteristics of the terminal members of the series disappear as the line is traced back, and are replaced by more generalized features, which are repeated in many other groups. However obvious may be the relationship between a number of highly diversified families, the difficulty of expressing that relationship in a definition increases with the length and completeness of the phylogeny, because of the structural differences between the earlier and later members of the series.

In the Tylopoda the peculiarities of the cervical vertebræ, for example, are found only in the main line of descent, the *Camelidæ,* and seem to be correlated with the elongation of the neck. The reduction of the ungual phalanges to nodular form and the cancellous structure of the tympanic bullæ are also confined to the same line, and were evidently acquired within the limits of the family. In *Poebrotherium* and *Protylopus* the phalanges are of the normal selenodont type, and in the latter the tympanic is hollow. The form of the cannon-bone, when present at all, is characteristic, but, except in the pes of *Leptomeryx*, the metapodials are not coössified in any of the Eocene or Oligocene genera. In all members of the suborder, without exception, the metapodial keels are confined to the palmar (or plantar) aspect of the bones, but this is equally true of the Tragulina and the earliest Pecora (e.g., *Gelocus*). The cuboid and navicular are separate in all the genera except *Leptomeryx*, *Hypertragulus*, and *Hypisodus*, as are also the trapezoid and magnum, except in *Leptomeryx*, and perhaps the other two genera, while in the entire series from the Wasatch onward (assuming that *Trigonolestes* is properly referred to this phylum) the meso- and ecto-cuneiforms of the tarsus are coalesced. The digital formula varies between V-V and II-II.

The molars are brachyodont, save for a moderate degree of hypsodontism in the later members of the *Camelidæ*. The premolars are simple, trenchant, and often elongated, but in the more modern *Camelidæ* they become much reduced in size and number. Incisors and canines are usually present in their full number, but *Leptomeryx* has lost the upper canine and *Protoceras* all the upper incisors, which in the *Camelidæ* are also reduced, though not entirely suppressed. Except in the main line of the suborder, a very frequent characteristic is the conversion of the lower canine into a functional incisor, while the place of the canine is taken by $p_{\overline{1}}$. More or less obvious indications of this may be seen in the oreodonts, agriochœrids, *Leptoreodon*, *Camelomeryx*, *Protoceras*, and *Leptomeryx*, and the condition in *Protylopus* seems to indicate a tendency in the same direction, but the tendency was checked and the true canines were again enlarged.

It is in the structure of the skull that we find the most characteristic tylopodan features and those which are most constant throughout the suborder. Rütimeyer's summary needs but little change to apply to the newly discovered forms as well as to those which have long been known. The premaxillaries are very complete and reduced only by small incisive foramina. Nevertheless, the skull is distinguished by the very rapid tapering of the face anteriorly, which is expressed particularly in the triangular form of the palate and in the very oblique position of the molar series. The maxillary region of the skull is peculiarly limited, and mainly taken up in the formation of the nasal passage, having but a low alveolus and very limited muscular surfaces. Even the jugal, as well as the lachrymal, takes almost no share in the formation of the face. The infraorbital foramen lies far back, above the last premolar; there is no masseter crest and the masseter surface is almost obsolete. The nasal canal is high and roofed over by short nasals; the posterior nares are also high, especially in the pterygoid portion. Characteristic in the cranium is the small extent of the frontal zone as compared with the parietal zone, in the formation of which the very high squamosals take a large share. The orbits are very prominent. A consequence of these relations is the displacement of the orbits into the facial region above the molar alveoli, and the extraordinary length of the temporal fossa. Sagittal and occipital crests are prominent. The glenoid cavity is small, but has a high postglenoid process, and very generally the angle of the mandible is produced behind the condyle.

The applicability of this description is least obvious in the case of *Protoceras*, in which genus the skull is much modified, approximating it in some respects to the *higher* Pecora, the Cavicornia. This is to be seen in the edentulous premaxillaries (though the incisive foramina remain quite small), in the shifting of the orbit behind the molar alveoli, and in the downward bending of the face upon the cranial axis, the latter not recurring in any other member of the Tylopoda. Further, the angle of the lower jaw is not produced into a hook-like process behind the condyle. In spite of these deviations, the essential features even of this skull are manifestly in agreement with those of the other Tylopoda.

At the other extreme of the scale stands the skull structure of the *Oreodontidæ* and *Agriochœridæ*, but in these cases also the definition will apply. These families both retained throughout their history a very primitive type of skull, which gives quite a close and deceptive resemblance to that seen in the anoplotheres and anthracotheres.

In two respects the skull in the main phylum of the Tylopoda differs from that of all the side branches; namely, in the form of the mandibular condyle and in the cancellous structure of the tympanic bulla. The history of this phylum shows, however, that both of these peculiarities were acquired after the family *Camelidæ* had begun its separate existence. Even in *Poebrotherium* the condyle is still transverse and displays little tendency to assume the spheroidal shape, while in the earlier genus *Protylopus* the auditory bulla is small and free from cancellous bone. Were the cervical vertebræ of the latter genus known, we should probably find that the extraordinary peculiarities of these vertebræ were likewise acquired within the limits of the family.

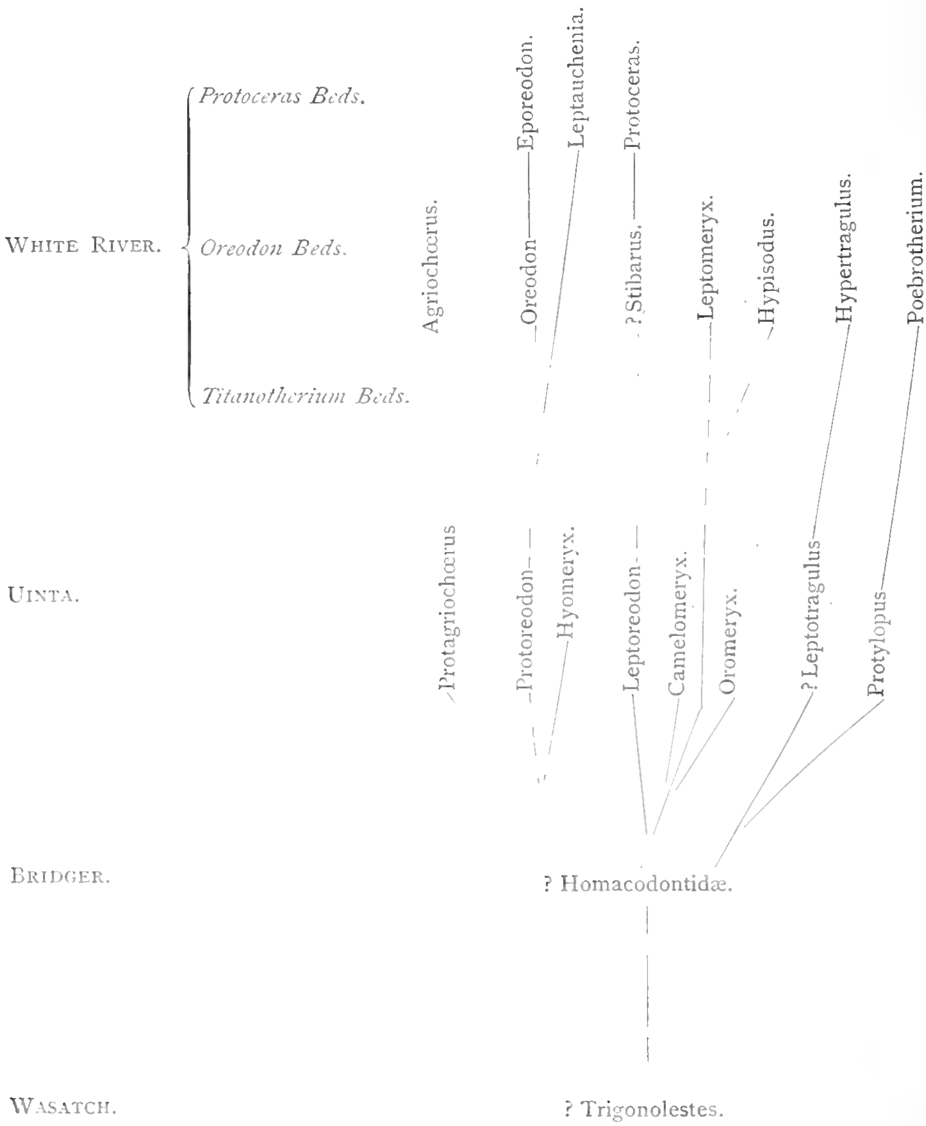
The study of the Uinta selenodonts teaches us very forcibly the importance of giving due weight to zoögeographical considerations in dealing with problems of relationship. It was considerations of this kind that first suggested to me the probability that *Protoceras* must in some way be related to *Leptomeryx* and its allies, a suggestion which now seems to be very strongly confirmed by the discovery of the new selenodonts from the Uinta beds. Migrations of terrestrial mammals have, of course, repeatedly taken place from one continent to another, as is amply demonstrated by the successive fossil faunas of Europe and North America, but the native stocks are apt to maintain their footing for long periods of time against the invasion of nearly allied forms which play similar parts in nature. It is curious to observe how long a time was required before the Pecora were able to establish themselves in North America. Not until they had reached a very high plane of organization did they succeed in overcoming the competition of the highly diversified Tylopoda, which had been developed here and which were not entirely driven from this continent until late Pleistocene times. In South America they still continue to flourish, and in that continent the only representatives of the Pecora are the deer in limited variety.

In cases of doubtful affinities the probabilities are usually in favor of reference to an indigenous group, for they almost always outnumber the immigrant forms, and it is with such indigenous groups that the most careful comparisons should be made. Neglect of this principle has led most students of the American selenodonts astray.

These considerations emphasize once more the necessity of obtaining long and fairly complete phylogenetic series for the satisfactory solution of taxonomic problems. Without such series it is exceedingly difficult, often impossible, to escape being deceived by resemblances due to parallel or convergent development. With these series, such deceptive resemblances may be exposed and allowed only their due weight, while puzzling differences may be followed out in their origin and development and given their proper taxonomic value.

This paper contains the recantation of many opinions which I formerly maintained concerning the relationships and systematic position of the various groups of peculiar North American selenodonts. I may say, however, that these opinions were not very confidently held, for they never seemed to explain satisfactorily the manifold peculiarities and the isolated position of these families and genera. It may be that the views here expressed are destined to have no longer life, but they do offer a much more satisfactory solution of the problem, and they are at least founded upon a much wider range of evidence than has been available hitherto.

The subjoined table exhibits the relationships of the various genera as conjectured in the preceding pages.



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EXPLANATION OF THE PLATES

PLATE I.

Fig. 1. *Leptomeryx evansi.* Skull, from the left side. *C.*, lower canine.

Fig. 2. *Leptomeryx evansi.* Distal end of posterior cannon-bone.

Fig. 3. *Hypertragulus calcaratus.* Skull, from the right side. (Drawn from specimens in the American Museum of Natural History.)

Fig. 4. *Hypertragulus calcaratus.* Skull, top view.

(*All figures of natural size.*)

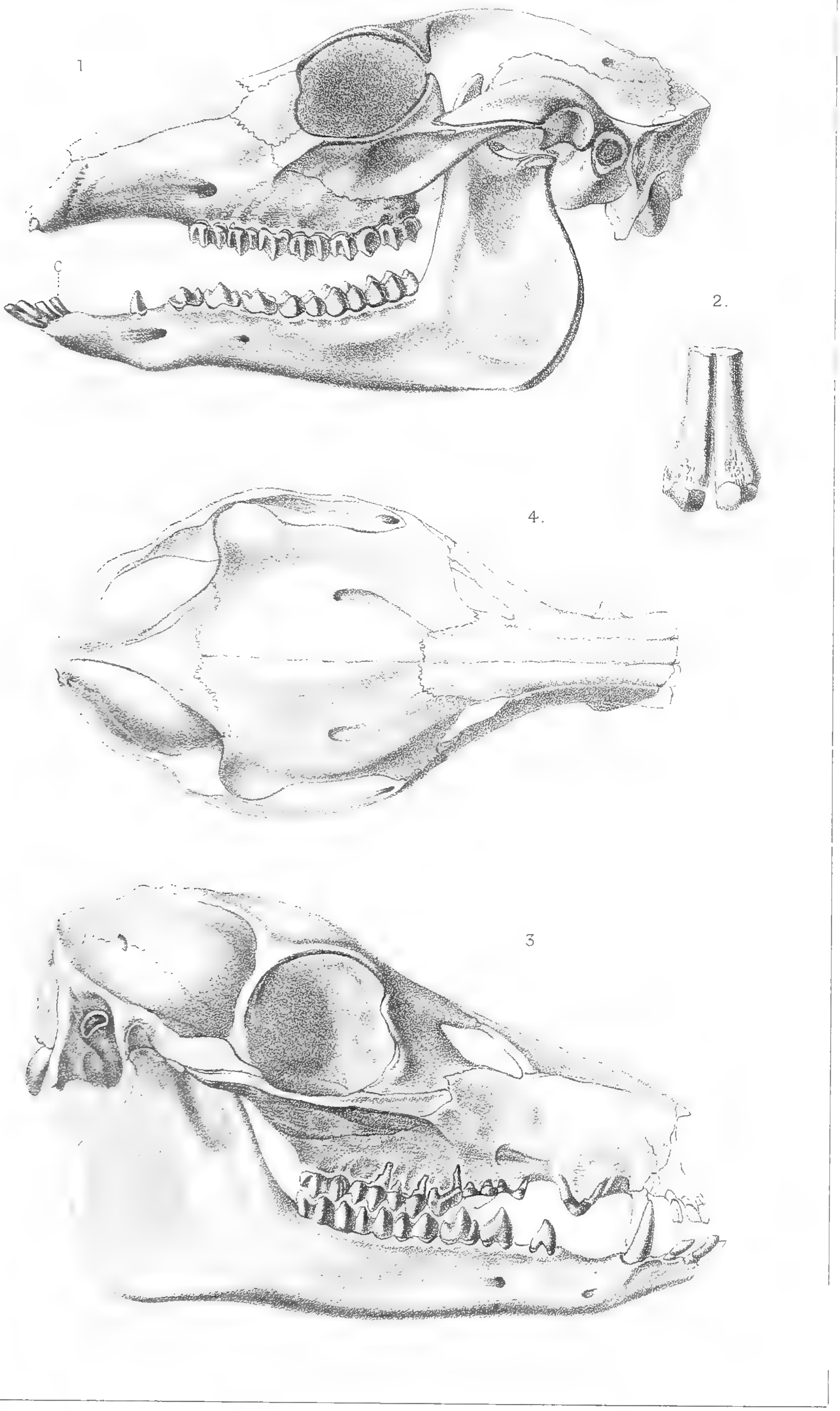

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PLATE II.

Fig. 5. *Protylopus petersoni.* Skull, from the right side.

Fig. 6. *Protylopus petersoni.* Upper molars and premolars of right side, crown view.

Fig. 7. *Protylopus petersoni.* Lower molars and premolars of right side, crown view.

Fig. 8. *Protylopus petersoni.* Left pes, front view.

Fig. 9. *Protylopus petersoni.* Left manus, front view. *M.*, magnum ; *U.*, unciform.

Fig. 10. *Leptoreodon gracilis.* Skull, from right side. *P 1*, first premolar ; *p 2*, second premolar.

Fig. 11. *Leptoreodon gracilis.* Upper dentition of right side.

Fig. 12. *Leptoreodon gracilis.* Lower dentition of right side. *C.*, canine ; *i 3*, lateral incisor ; *p 1*, caniniform first premolar.

Fig. 13. *Leptoreodon gracilis.* Right manus. *Sc.*, scaphoid ; *R.*, radius.

Fig. 14. *Leptoreodon gracilis.* Left pes, front view.

(*All figures of natural size.*)

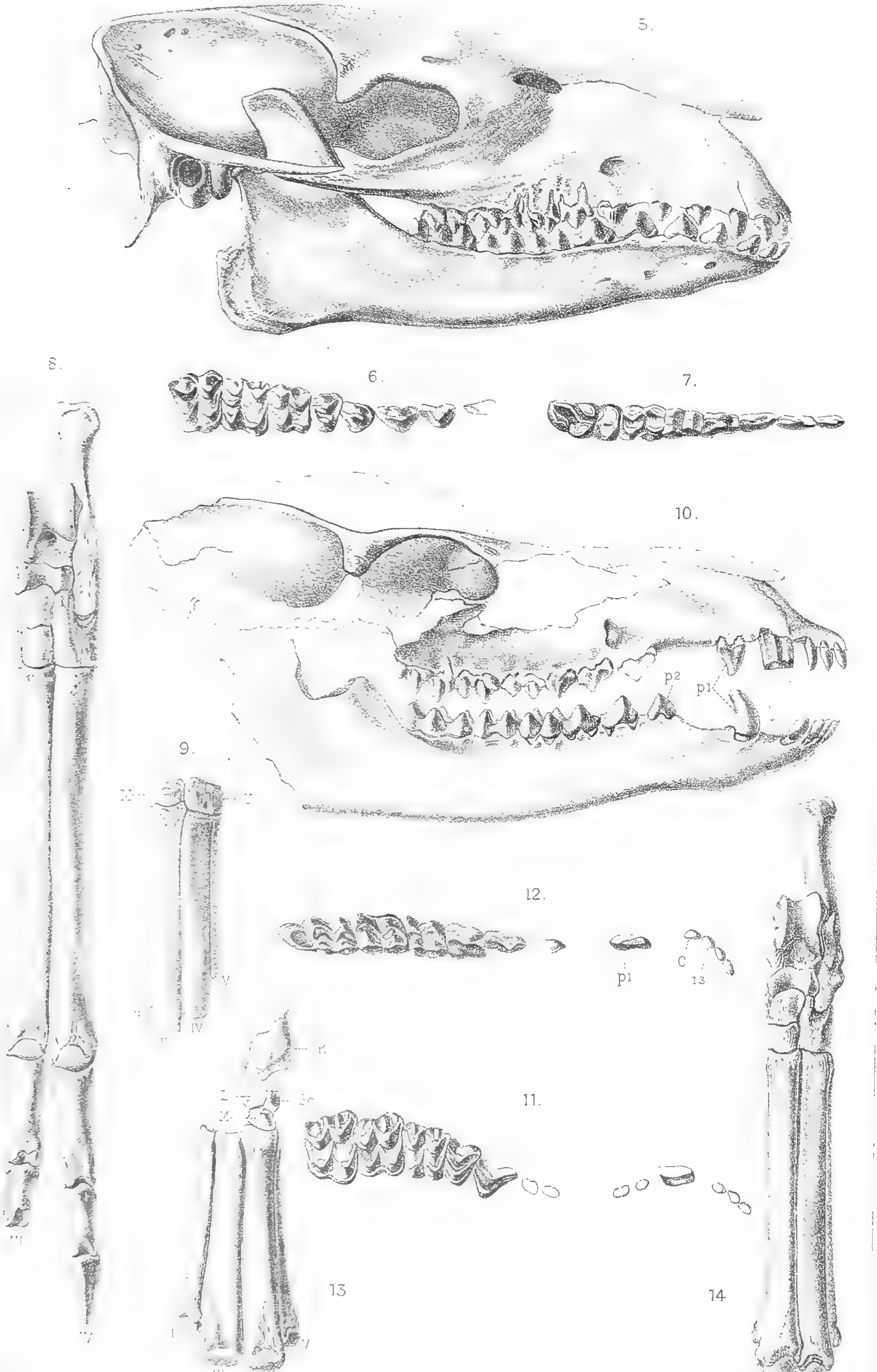

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PLATE III.

Fig. 15. *Camelomeryx longiceps.* Skull, from left side.

Fig. 16. *Camelomeryx longiceps.* Right upper dentition. *C.*, canine ; *p 4*, fourth premolar.

Fig. 17. ? *Camelomeryx longiceps.* Left manus. *Sc.*, scaphoid ; *P.*, pyramidal. Collection of American Museum of Natural History. (No. 2070.)

Fig. 18. ? *Camelomeryx longiceps.* Left pes. Collection of American Museum of Natural History. (No. 2070.)

Fig. 19. *Protoreodon parvus.* Skull, from right side.

Fig. 20. *Protoreodon parvus.* Left upper dentition, crown view.

Fig. 21. *Protoreodon parvus.* Right carpus. *Sc.*, scaphoid ; *P.*, pyramidal ; *U.*, unciform.

Fig. 22. *Protoreodon sp.* Left pes. Collection American Museum Natural History.

Fig. 23. *Protoreodon minor.* Left upper dentition, crown view.

(*All figures of natural size.*)

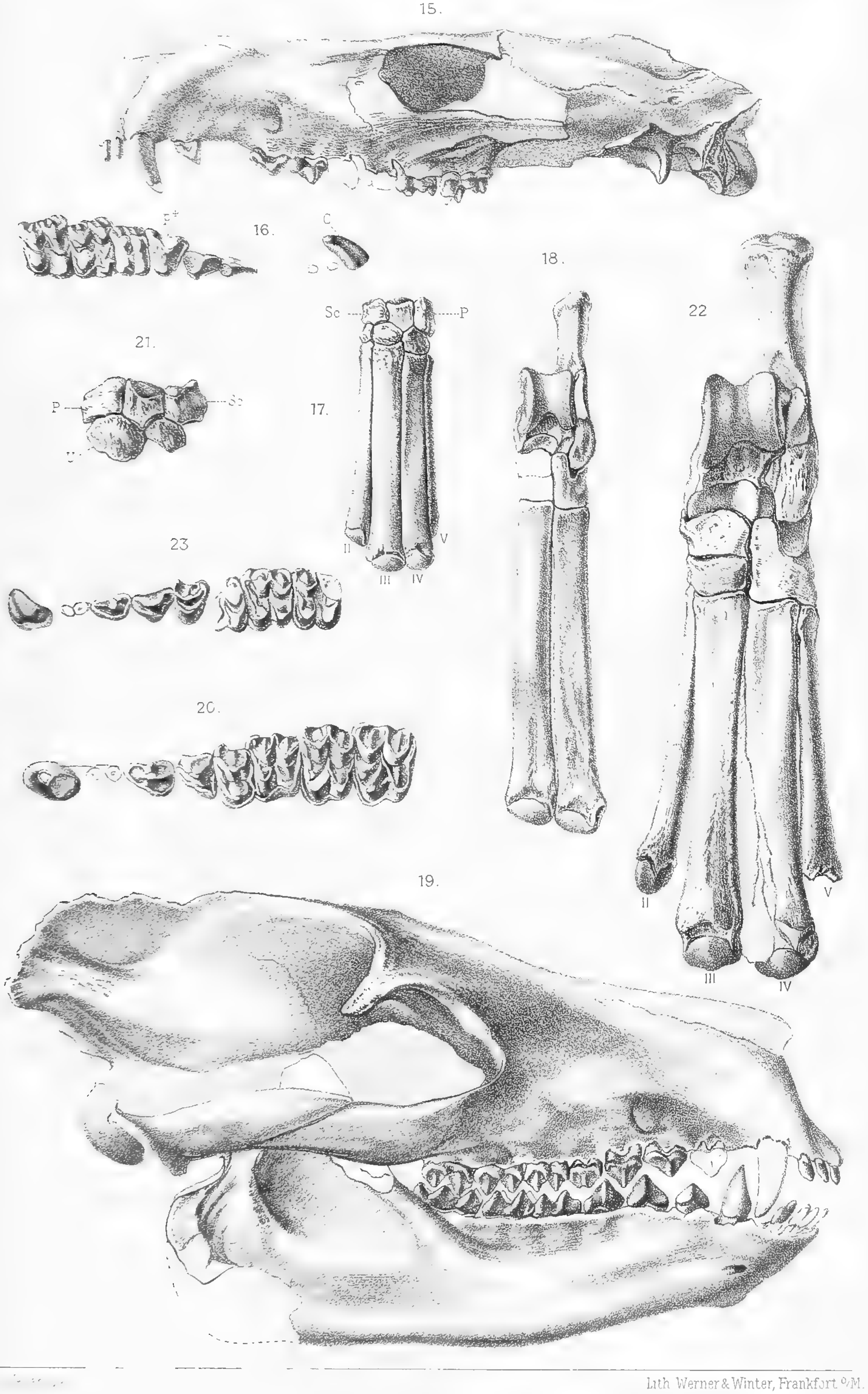
15.
16.
C
18.
Sc
P
22
21.
P
17.
II
V
III
IV
23
20.
II
V
III
IV
19.

PLATE IV.

Fig. 24. *Protoreodon paradoxicus.* Skull, from left side. (Depressed by crushing.)

Fig. 25. *Protoreodon paradoxicus.* Left upper dentition.

Fig. 26. *Protagriochœrus annectens.* Right upper dentition, side view.

Fig. 27. *Protagriochœrus annectens.* Right upper dentition, crown view.

Fig. 28. *Protagriochœrus annectens.* Left tarsus. *N.*, navicular ; *Cb.*, cuboid.

Figures 26, 27, 28 are of the same individual, belonging to the American Museum of Natural History. (No. 1818.)

(*All figures of natural size.*)

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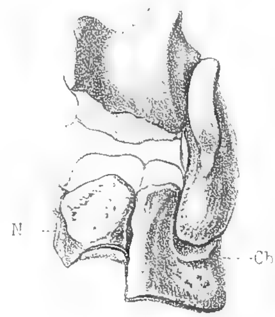

28.

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