Article VII.—THE EXTINCT CAMELIDÆ OF NORTH AMERICA AND SOME ASSOCIATED FORMS.

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PLATE XI, AND TWENTY-THREE TEXT CUTS.

Among the living selenodont Artiodactyla the Camels and Llamas of the Old and New World represent a very aberrant group. Even if one were not familiar with the wonderful record of their past history as revealed in the Tertiary deposits of this country he would be quite justified, from the number of anatomical peculiarities which they exhibit, in placing their origin far back in the Tertiary, at a time when the primitive divergence of the various lines of the Selenodonts was taking place.

The evidence is not yet sufficiently complete to trace the phylum with absolute certainty below the upper Eocone or Uinta stage, but from this point on to the present time there is very little to be desired, in the way of intermediate species, to form a compact and closely connected series, reaching to the modern types.

More or less elaborate studies of this group have been made by Cope[1] and Scott,[2] to whom we are especially indebted for much knowledge concerning the extinct forms, and while it would be difficult to add anything to their statements from the specimens known to them, yet the acquisition of a large amount of new material bearing upon this subject by the various Museum expeditions within the past few years has rendered it especially desirable to review the whole subject, with a view to defining, if possible, the exact limits of the various genera and species of the extinct North American representatives. The object of the present paper, therefore, is: (1) A review of the genera and species of the North American Tylopoda, with descriptions of

[1] 'Phylogeny of the Camelidæ,' Amer. Nat., 1886, p. 611.
[2] 'On the Osteology of Poëbrotherium,' Journ. of Morph., 1891. 'The Mammalia of the Uinta Formation,' Trans. Amer. Phil. Soc., Aug. 20, 1889.

additional materials of known types, as well as of new allied forms; (2) a careful consideration of the various steps in their evolution; and (3) a study of certain osteological characters of the higher selenodont Artiodactyla in its direct bearing upon the transmission of acquired characters.

The oldest members of Tylopoda which we can determine with certainty are found in the Upper Eocene deposits of the Uinta Basin, which strata, it may be noted, contain the first remains of true selenodont Artiodactyla in this country, a fact originally pointed out by Marsh, who was the first to explore this region for fossil remains. In the preceding deposits of the Bridger Basin the remains of Artiodactyla are found, but are very rare, no truly selenodont types being known. It is true that in several genera, such as *Homacodon* and *Helohyus* of Marsh, we have a distinct foreshadowing of the selenodont molar, yet it is not until the Uinta is reached that the true Selenodonts appear.

Mr. O. A. Peterson, to whom we are largely indebted for the beautiful collection now in the Museum from this horizon, divides these beds into three stages,[1] which he designates as the lower, middle, and upper Uinta Beds, or, to use his own field designation, Horizons *A*, *B*, and *C*. A large part, if not the entire lot, of these remains were obtained from the lower part of Horizon *C*, or the upper part of Horizon *B*, so that their stratigraphical position would be correctly stated to be at least 300 to 400 feet below the top, and at least 800 feet from the bottom of the Uinta formation. No fossils are known from the upper levels of Horizon C, nor do we know any Artiodactyla from the Brown Sandstones, 800 feet in thickness, constituting Horizon A. If, therefore, close connections between these Uinta forms and the preceding Bridger species, on the one hand, and the succeeding White River, Oligocene species, upon the other, are not shown to exist, the fact is, in all probability, due to our lack of knowledge of the species which lived during the time of deposit of these intermediate strata.

The identification of these Uinta Cameloids is attended with more or less difficulty, owing in part to the fragmentary condition

[1] See Osborn's 'Fossil Mammalia of the Uinta Basin,' Bull. Am. Mus. Nat. Hist., Vol. VII, p. 74.

of some of the material, and in part to other lines which resemble them in certain points of skull and limb structure. These resemblances are, no doubt, due to the close proximity to the point at which the respective phyla began to diverge.

For the purpose of bringing into stronger relief the characters of the Cameloids of this horizon, it is necessary to compare them accurately with the cotemporary Selenodonts, and, since several of them apparently represent new genera, they are herewith described.

Leptoreodon marshi,[1] gen. et sp. nov.

This genus and species is represented in the collection by an almost perfect skull in good state of preservation, a number of vertebræ, and a few fragments of the limbs (No. 2064), which I use as the type. There are several other specimens of a more fragmentary character which are probably to be referred to the same

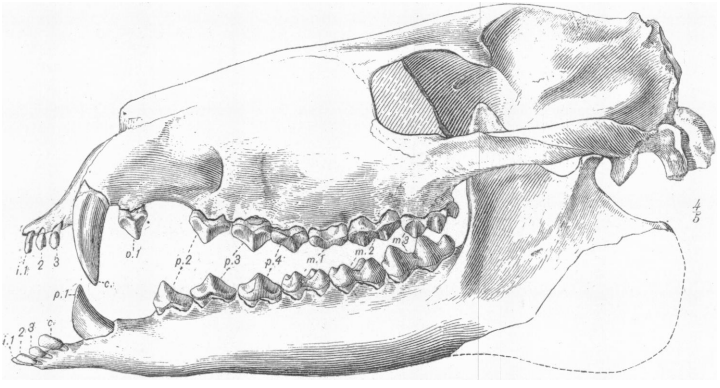


Fig. 1. Side view of skull of *Leptoreodon marshi*.

genus and species, but they contribute little additional information to the knowledge of the skeleton. The genus differs from all the Oreodonts hitherto described in the possession of a short diastema in front of, and a longer diastema behind, the first superior premolar, together with a considerable diastema between the first and second premolar in the lower jaw. The incisors are

[1] This species is dedicated to Prof. O. C. Marsh, in recognition of his numerous contributions to American palæontology.

present in full in both jaws; the inferior canine is small and incisiform; the superior canine is large, with the characteristic D–pattern of the Oreodonts on cross section, and the first inferior premolar is enlarged and caniniform as in the Oreodonts. The first superior premolar is two-rooted with a high, compressed cutting crown, the second is similar but somewhat larger, the third has a principal broad, lunate external cusp and a faint internal cingular ledge. The fourth premolar crown is composed of a single external and internal cusp, much as in the Oreodonts.

The superior molars closely resemble those of *Protoreodon* (*Eomeryx*) in the composition of the crown, so far as can be determined in their advanced stage of wear in the type specimen. It is impossible to say whether or not there were anterior intermediate cusps present, but judging from certain appearances in this region of the crown, I am inclined to think that less worn teeth would show them. The mesostyle consists of a vertical pillar as in the Oreodonts generally, and not of a wide open loup as in *Agriochœrus*.

In the lower jaw the incisors and canines are of the typical oreodont pattern, but they are unusually procumbent in position. The first premolar is enlarged and caniniform, the second simple, the third with a small internal cusp and posterior heel, and the fourth similar in pattern, except that the internal cusp is smaller and the heel more pronounced. The lower molars are almost identical in structure with those of the early Oreodonts.

The whole skull differs from that of the Oreodonts in its more slender proportions. This is particularly noticeable in the lower jaws, which are relatively long and shallow, especially in the region of the symphysis, in marked contrast with the deep and abrupt chin of the Oreodonts in general. There does not appear to have been a preorbital pit present, and the orbit was not enclosed by bone posteriorly. The present genus may be distinguished from its contemporaries in the following dental characters, viz.: from *Protoreodon* (*Eomeryx*) in the possession of diastema in both jaws and the full number of incisors in the upper jaw.[1]

[1] 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 pumilis* 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 Musuem 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.

From *Hyomeryx* it is readily distinguished by the full number of superior incisors and by the diastema, although it resembles this latter genus, which is described by Marsh[1] as having more slender jaws than *Protoreodon* (*Eomeryx*). From the cameloid, *Leptotragulus*, it is easily separated by the numerous oreodont characters which the skull exhibits, although the symphyseal region is strikingly similar in the two genera.

Of the hind foot, the cuboid, navicular and the head of the third metatarsal are sufficiently preserved to afford characters for identification. These bones indicate an animal with far more slender limbs and feet than any of the Oreodonts with which I am familiar. The navicular has an inconspicuous posterior hook unlike that of the Oreodonts, and, judging from the much reduced facet on the cuboid, the fifth digit was considerably diminished in size if not entirely rudimental. The limb-bones are not well enough preserved to confirm or negative this conclusion of the slender and delicate proportions of the animal, but, 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.

The second genus to be described in this connection contains species somewhat smaller in size and less perfectly selenodont.

Bunomeryx montanus, gen. et sp. nov.

There are two specimens in the collection which I classify under this head, viz.: an anterior portion of a cranium somewhat crushed, containing the maxillary dentition complete upon one side, together with the greater part of the left mandibular ramus of the left side having all the true molars and the last premolar in good preservation (No. 2071). The second specimen consists of a portion of a lower jaw with a few teeth, the posterior part of the cranium, a nearly complete fore foot, portions of the hind limbs and other parts of the skeleton (No. 2070). The first of these specimens may be taken as the type, but there can be very

[1] 'Descriptions of Tertiary Artiodactyles,' Amer. Jour. Sci., Vol. XLVIII, Sept., 1894, p. 268.

little doubt that the second specimen is identical with the first and can be regarded as a collateral type.

This genus most nearly resembles *Homacodon* Marsh, from the Bridger Beds, although it presents some dental characters similar to *Dichobune* of the European Eocene. The more important generic characters may be stated as follows :

Dentition, $I\frac{1}{3}$, $C\frac{1}{1}$, $Pm\frac{4}{3}$, $M\frac{3}{3}$. Superior molars, having well-defined crescentic outer cusps and a distinct mesostyle and parastyle ; first molar provided with two conic internal cusps (protocone and hypocone), with anterior and posterior subcrescentic intermediates; second molar having anterior subcrescentic intermediate, subconic protocone, a posterior subcrescentic intermediate and no hypocone ; third molar similar to second. The superior premolars are present in full number ; the two anterior have simple cutting crowns, while the crowns of the third and fourth are made up of single external and internal conic cusps well developed. In the lower jaw the structure of the molars is intermediate between the bunodont and selenodont pattern ; there are only three premolars, the anterior two of which have simple compressed crowns, while the last or fourth of which is provided, in addition to the principal cusp, with anterior and internal cusps, together with a well-defined heel.

As compared with *Homacodon*, *Bunomeryx* is readily distinguished (1) by the possession of three premolars in the lower jaw ; (2) by the crescentic character of the external cusps of the superior molars ; (3) by the presence of a well-developed parastyle and mesostyle ; (4) by the absence of the hypocone on the second superior molar, and (5) by the subcrescentic character of the intermediates. (6) The internal cusp of the third superior premolar is, moreover, better developed in *Bunomeryx* than in *Homacodon*, and (7) the fourth inferior premolar is much more advanced in structure. The structure of the inferior molars is much more selenodont in *Bunomeryx* than in *Homacodon.*

From *Dichobune* the present genus is readily distinguished by the absence of all traces of the anterior cusp of the trigon in the lower molars as well as the more crescentic character of the outer cusps of the superior molars, and the possession of well-defined mesostyle and parastyle. The complete adult dentition of *Dichobune* is apparently not known, but there can be but little doubt that it had the full number, forty-four teeth, in which case *Bunomeryx* would be sharply distinguished by the inferior premolar formula. I cannot at present say in what manner *Bunomeryx*

differs from the European *Deilotherium*, *Spaniotherium*, *Metriotherium*, *Mouillacitherium* and *Oxacron* of Filhol, which are placed by Zittel in the subfamily Dichobuninæ. On account of the very imperfect knowledge we have of these forms, no comparisons are at present possible.

In specimen No. 2071, the upper and posterior portion of the cranium is sufficiently preserved to indicate a relatively high overhanging occipital and a strong sagittal crest, the latter dividing into two well-marked lateral postorbital branches. In advance of the point of division of these two branches a strong ridge is continued forward upon the frontals in the median line as in many of the lower forms of the Selenodonts. The postorbital process is well developed, but it does not join the molar, so that the orbit is not enclosed by bone posteriorly. There is no evidence of the presence of any long horn-cores.

Of the fore limb, the distal ends of the ulna and radius are preserved, but they are considerably crushed. There is apparently little or no tendency to coössification of the bones, although the shafts are closely applied to each other in the lower third of their extent. The articular end of the radius shows distinct facets for scaphoid and lunar, but does not touch the cuneiform. The distal end of the ulna articulates solely with the cuneiform.

The carpus is of the typical artiodactyl pattern, and especially resembles that of the earlier Selenodonts. In the proximal row the cuneiform rests exclusively upon the unciform, the lunar about equally upon magnum and unciform, while the scaphoid is supported below by magnum, trapezoid and trapezium. In the distal row the unciform articulates distally with Mt. III, and to a slight extent with Mt. II. In the modern Suillines, the Cameloids and the later Oreodonts, the second metacarpal has lost all connection with the magnum, but in the early Oreodonts Mt. II still retains a contact between these two bones. In *Protoceras* of the Oligocene a very minute contact is observable.

The trapezoid is free, and shows no tendency to unite with the magnum as in *Leptomeryx*, the later Tragulines and Pecora. The trapezium is not preserved in the specimen, but judging from the well-marked facets upon the scaphoid, trapezoid and Mt. II, it is quite certain that it was not only present and of good size, but

that it supported a very considerable vestige of the first digit. It would not indeed be a matter of surprise to find this digit complete in more perfect specimens very much as in *Oreodon.*

There are four metacarpals preserved of which the median ones, Mt. III and IV, are the largest and subequal in size. Mt. II is slightly larger and longer than Mt. V, and in all of them the distal keels are confined to the palmar surfaces, as in all primitive Ungulates. The phalanges of the fore feet are not known.

Of the hind limb the materials are not so complete as of the fore limb, but enough is preserved to make out its more important characters. The fibula was much reduced, and probably incomplete in the middle part of the shaft. The distal end of the tibia displays no usual form of the more generalized Selenodonts, as do the tarsal bones. The cuboid and navicular were not coössified, and there is evidence of four complete metapodials, the lateral ones, however, being unusually slender and delicate. The first two phalanges resemble those of the early Cameloids, *Protoceros* and *Leptomeryx* in their form, as do likewise the unguals in being relatively high-pointed and flattened upon their opposed surfaces.

Bunomeryx elegans, sp. nov.

A second species of this genus is indicated in the collection by a portion of a cranium containing the last three premolars and the molars, in excellent preservation, together with both mandibular rami bearing all of the teeth with the exception of the incisors and canines.

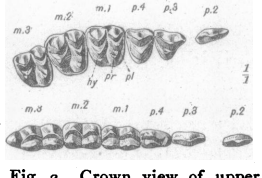


Fig. 2. Crown view of upper and lower teeth of *Bunomeryx elegans.* *hy.*, hypocone; *pr.*, protocone; *pl.*, protoconule.

The most important difference between the two species is seen in the presence of a short diastema between premolars two and three of the lower jaw in *B. elegans.* In *B. montanus* this diastema is absent, and the teeth of the lower jaw were apparently in a continuous series or closed row. *B. elegans* is smaller and more delicate than *B. montanus*, a fact that is not only indicated by all the teeth but particularly emphasized by the fourth inferior pre-

molar, which is considerably narrower and has a less development of the internal cusp. Another important distinction between the two species is found in the greater development of the vestigial hypocone of the second superior molar of *B. elegans*. In *B. montanus* this cusp has almost entirely disappeared, the only evidence of its presence being indicated by a cingulum in this portion of the crown.

One fact of great interest in connection with this genus is the probable light which it throws upon the homologies of certain cusps of the molar crown in the higher selenodont Artiodactyla. It is here that we witness the actual passage from the bunodont to the selenodont type of molar in this important group. If we can trust the evidence before us, *Bunomeryx* is a direct lineal descendant of the Bridger *Homacodon*, and it is a matter of the utmost moment to note that in the latter genus there are six fully-developed cusps upon the crowns of the first and second superior true molars ; in the third there are only five cusps present. In *Bunomeryx*, as already indicated, the full six cusps are found on the first superior molar only, while in the second molar there is but a vestige of the postero-internal cusp or hypocone. The evidence appears to be conclusive, therefore, that the true homological hypocone is in process of retrogressive disappearance, and in proportion as this cusp is reduced, the posterior intermediate is pushed out to take its place. As a further evidence of the truth of this proposition it may be stated that the true hypocone of both the first and second molars of *Homacodon*, as well as the first molar of *Bunomeryx*, exhibits no tendency whatever to develop a selenodont structure, while the posterior intermediates especially in *Bunomeryx*, exhibit very decided advances in this direction. The very position of this cusp, moreover, precludes any possibility of its entering into the formation of the single posterior internal crescent of the more perfectly developed selenodont molar of the higher types.

I believe therefore that the history of the formation of the four crescents of the superior molar crowns of the Selenodonts has been as follows, tracing it from the five-cusped *Pantolestes*[1] of the

[1] From this genus I exclude the type of *Pantolestes etsagicus* Cope as belonging to a distinct genus ancestral to and leading directly up to the bunodont Artiodactyla. It is very probably synonymous with *Eohyus distans* of Marsh, who properly placed it among the Bunodonts.

Wasatch. The primitive condition of this oldest type of the Artiodactyla was two buniform external cusps, two buniform intermediates, together with one large more or less lunate internal cusp, flanked by a rudimental postero-internal cusp which is clearly shown to be an outgrowth from the cingulum. There is no evidence that this postero-internal cusp was ever developed on the last molar, because in all the forms from *Pantolestes* to *Bunomeryx* it is persistently absent. The next step consisted in the reduction of the large lunate internal cusp and the full development of a well-marked postero-internal cusp, or hypocone, on the first and second molars. This condition is seen in, and is characteristic of, *Homacodon.* The third step consisted in the disappearance of the true hypocone and the gradual usurpation of its place and function by the posterior intermediate in the crown of the second true molar, a condition seen in *Bunomeryx.* As a fourth step in this development one can readily imagine this process extended to the first true molar, when it would be complete.

This hypothesis may be objected to on the ground that *Bunomeryx* cannot stand as the direct ancestor of any of the Selenodonts at present known, on account of its reduced premolar dentition in the lower jaw, but if we are to regard the type of superior molar exhibited by either *Homacodon, Dichobune* or *Helohyus* as the one which preceded, and from which was derived the tetraselenodont or four-crescented crown, then this hypothesis must be accepted as true.

The only case so far known wherein the true hypocone has been preserved and has become crescentic, is in *Cœnotherium* and *Plesiomeryx,* and here we have three well-developed crescents upon the posterior moiety of the crown, of which the inner one represents the hypocone and the middle one the posterior intermediate. It is possible that the cusps of the two anterior superior molars of *Xiphodon* are to be interpreted in the same way, and that the posterior inner crescent is composed solely of the posterior intermediate, the true hypocone having come to occupy a more anterior and median position. In this case the anterior internal crescent would be made up of protocone and the anterior intermediate. Future discovery will no doubt reveal considerable variety in the formation of the internal crescents in the various

phyla of the Selenodonts, but it appears to me certain that the hypothesis herein advanced is the correct one for the formation of the tetraselenodont superior molars of the Cameloids, Pecora, Tragulines, and probably the Oreodonts and Anthracotheres.

Parameryx (Leptotragulus) proavus *S. & O.*

This genus was first described by Marsh[1] and later by Scott and Osborn,[2] who considered that it to belongs to the Traguline division of the order. Later Scott gave a fuller account of it[3] and placed it in the Tylopoda[4] immediately ancestral to *Poëbrotherium* of the White River Oligocene. The materials in the Museum Collection do not add very materially to the knowledge of this form ; however, there are some important points to be made out from it. There are four specimens which I refer to this species, the most important of which are a fragmentary skeleton containing a fairly good hind foot, together with the posterior part of the last lower molar (No. 2509). The other specimens pertain exclusively to the lower jaw (Nos. 1803, 1805 and 1808).

In the lower jaw there is one diagnostic character by means of which the last lower molar can be recognized, and that is the presence of an extra cusp upon the inner border of the heel near its point of junction with the postero-internal cusp. It is by means of this character alone that I associate the fragmentary skeleton with this species. The lower molars are of the typical selenodont pattern, and the cusps more elongated than in any of the cotemporary Selenodonts.

The inferior premolars are three in number, the fourth being provided with a well-developed internal cusp and heel. The second and third are simple and without accessory tubercles. In advance of the second premolar there is a considerable diastema, in front of which is the large procumbent alveolus for the canine. The incisors are not preserved, and this region of the jaw is so much broken as not to reveal their alveoli.

[1] 'Introduction and Succession of Vertebrate Life in America,' 1877.

[2] 'Preliminary Report on the Vertebrate Fossils of the Uinta Formation,' Proc. Am. Philos. Soc., 1877, pp. 255, 264.

[3] 'Mammalia of the Uinta Formation,' Trans. Am. Philos. Soc., N. S., Vol. XVI, Part iii, Aug. 20, 1896, pp. 479–486.

[4] Marsh had, however, clearly recognized the affinities of this genus with the Tylopoda ten years previously, since we find in the address above quoted the following statement : "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*.

Of the bones of the hind foot, the entire tarsus is preserved with the exception of the cuneiform. These parts of the skeleton present a most striking resemblance to those of *Poëbrotherium* in all the details of their structure, the only difference discoverable being that of size. The third metatarsal is present but unfortunately a small part of the shaft is missing so as not to exhibit its full length; there is enough, however, to indicate that it was unusually long and slender, much flattened upon the surface which it offered to the second metatarsal, and that the form of the shaft, moreover, had that peculiar squarish outline upon cross section, a feature so highly characteristic of the Oligocene Cameloids. Another distinctive cameloid feature is seen in the increased size of the medullary cavity. The lateral or fifth metapodial was reduced to a mere splint, as is indicated by the much-reduced facet upon the cuboid; this facet is relatively as small as it is in the cuboid of *Poëbrotherium*. The phalanges have about the same proportions and shape as the corresponding bones of the White River species.

That *Parameryx* (*Leptotragulus*) was a member of the Tylopoda, as has already been pointed out by Marsh and Scott, there can be very little doubt, but at the same time the evidence is equally conclusive that it does not stand in direct ancestral line with the succeeding Poëbrotheres. The evidence against such a conclusion is to be found in the fact that *Parameryx* (*Leptotragalus*) has only three premolars in the lower jaw, an enlarged caniniform canine and relatively short, thick inferior premolars, the last of which, or fourth, has a considerable development of the internal cusp. It may therefore be looked upon as a precociously specialized side branch which died out at the close of the Eocene and left no modified descendants.

Protylopus petersoni,[1] gen. et spec. nov.

This genus and species is primarily founded upon the anterior portion of a skull from which the left ramus is missing. The specimen is broken obliquely in such a manner as to show upon the right side all of the facial portion, including the orbit and the

[1] This species is named in honor of Mr. O. A. Peterson, whose explorations of the Uinta Beds have been attended with such marked success.

anterior root of the zygomatic arch, while upon the left side the greater part of the orbit is missing. Fortunately the skull contains the dentition nearly complete. In association with it were found the greater part of an ulna and radius of the same individual. A second specimen which I refer to this genus and species includes a large part of both hind legs, together with a large number of vertebræ, ribs and other parts of the skeleton. A

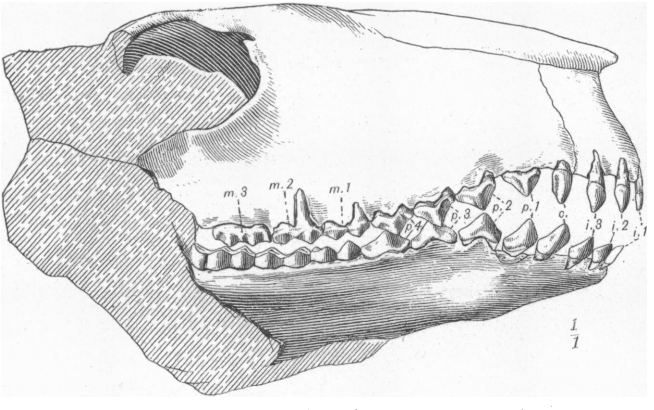


Fig. 3. Side view of skull of *Protylopus petersoni*.

third specimen contains hind limbs and vertebræ, while a fourth includes the greater part of a hind foot.

The more important generic characters may be stated as follows :

Molars tetraselenodont without intermediate cusps. Teeth of the typical number, forty-four, arranged in a continuous series. Canines of both upper and lower jaws small and incisiform, the first inferior premolar not caniniform. The first three superior premolars elongated from before backwards, secant and without accessory cusps, the fourth with single external and internal crescentic cusps. The inferior premolars elongated and cutting, the fourth without internal cusps. Hind feet provided with but two functional digits, the outer ones, second and fifth, reduced to mere vestiges. Lumbar vertebral formula 7. Ulna and radius, at least in old individuals, coössified in the middle part of their shafts but free at their proximal ends.

The skull is crushed laterally so as not to reveal the exact form of the face, but it can be safely stated that the muzzle had

moderate length, with slightly overhanging nasals, much as in *Poëbrotherium wilsoni.* The premaxillæ are relatively broad and extend upwards and backwards to articulate with the nasals. The orbit is not enclosed by bone posteriorly, but exhibits a marked tendency towards that peculiar roofing so highly characteristic of *Poëbrotherium* and the later Tylopoda. In advance of this bony shelf is seen a faint though distinct indication of the supraorbital notch, so constant a feature of the cameloid skull. The lower jaws may be described as long and slender, with a considerably elongated symphysis.

The superior incisors are relatively small, of a more or less conical form, and directed downwards. The premaxillæ were apparently not in contact in the median line. The superior canine is but little larger than the outer incisor, of a more or less hook-shaped appearance, and provided with a distinct sulcus upon the outer portion of the crown as in *Poëbrotherium wilsoni.* The first premolar follows after a very short interval and, like the second, is a simple two-rooted cutting tooth. The third premolar has a faint internal cingular ledge, while the fourth, as already mentioned, is provided with single external and internal crescents. The molars are much worn, and do not show clearly whether or not intermediate tubercles were present, but I think it may be safely assumed, from the general appearance of the crown, that they were absent. In the second and third molars, between the internal crescents, is to be seen a small styliform cingular cusp which is entirely absent, so far as I can determine, in *Poëbrotherium.*

In the lower jaw the incisors are of a more spatulate form and more procumbent in position. As in the upper jaw, the canine is slightly larger than the outer incisor, but of a very marked incisiform pattern. After a very short interval or diastema, is placed the first premolar, a two-rooted tooth whose crown closely resembles that of the canine, the two teeth being about equal in size. The second and third premolars have elongated secant crowns like the Tragulines.

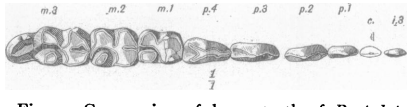


Fig. 4. Crown view of lower teeth of *Protylopus petersoni.*

The fourth has a well-marked heel and anterior basal cusp, but there is apparently no internal cusp present. The molars are so much worn that their structure is not very apparent. There can be very little doubt however that they had the usual structure. In the heel of the last molar a prominent accessory cusp is seen upon the border of the inner side near the point where it joins the lower posterior internal cusp. In *Poëbrotherium* this cusp is clearly present, but it has fused with the postero-internal, producing a prominent angle at this portion of the crown. In perfectly unworn teeth of *Poëbrotherium wilsoni*, it can be readily demonstrated to be an independent cuspule.

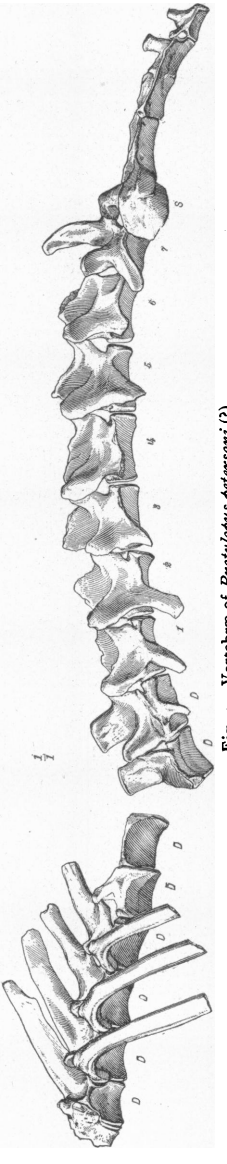


Fig. 5. Vertebræ of *Protylopus petersoni* (?).

Of the vertebræ, unfortunately, no cervicals are known, consequently it is impossible to say whether they exhibit the peculiar features of the more typical Camelidæ or not. The dorsals are well represented in specimen No. 2564, the whole series being present, with the exception of the first three or four, together with all the lumbars locked in position. 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. The lumbars are seven in number, the constant formula for the Tylopoda; they resemble closely the corresponding bones of *Poëbrotherium* and the later Cameloids. The sacrum is composed of only four vertebræ, but it is highly probable that another one or two was added from the caudal region as age advanced, just as in *Poëbrotherium* and the modern Llamas. The three anterior vertebræ of the sacrum have very reduced neural spines, while in the fourth the spine is well developed. The ribs do not display any characters of especial importance.

The pelvis is in a very fragmentary condition, but it may be stated that the ilium is well expanded, and, so far as one can judge, the whole bone would correspond closely with that of *Poëbrotherium.* The femur is present in its entire length with both ends in a good state of preservation, although the shaft is somewhat crushed. The proximal end has practically the same relations and arrangement of the different parts as that of *Poëbrotherium* and other members of the group. The distal end thus early gives slight though conclusive evidence of the peculiar and characteristic appearances which this part of the bone assumes in the later Camelidæ. This is especially seen in the great extension of the condyles backwards behind the median line of the shaft as well as the forward projection of the borders of the rotular groove, which serve to increase the antero-posterior diameter of this part of the bone. Although not clearly indicated on account of crushing, yet there seem to be distinct traces of the beginning of that peculiar depression at the proximal end of the rotular groove so highly characteristic of the later Tylopoda. In a like manner the patella has begun to assume the distinctively cameloid form by the great elongation of its lower border into a long, pointed process.

The tibia, which about equals the femur in length, shows a great resemblance to that of *Poëbrotherium.* The cnemial crest is unusually well developed, and extends quite one-third of the way down the shaft. The fibula is much reduced, and although the specimen does not show whether or not the shaft was complete, the probabilities are that it consisted of a distal portion

only. That part of the shaft which is preserved is very slender and closely applied to the shaft of the tibia. In the hind foot the tarsal bones have nearly the same relations as in *Poëbrotherium*. The tuber of the calcaneum is somewhat shorter proportionately than in the White River genus, but otherwise both the calcaneum and astragalus are strikingly alike in the two genera. The cuboid of *Protylopus* is slightly narrower in proportion to its height than the corresponding bone in *Poëbrotherium*, and the navicular is provided with a much better developed posterior hook. As in *Poëbrotherium*, there are two cuneiforms present, the inner of which is a vestigial nodule of bone only.

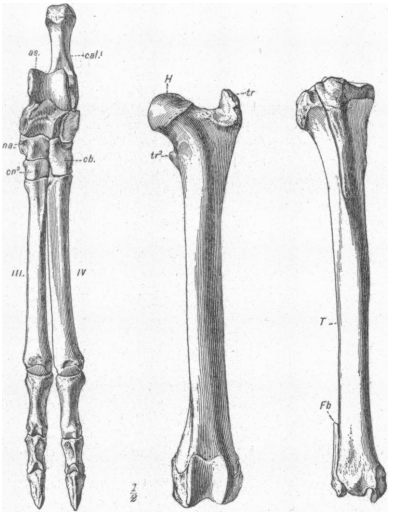


Fig. 6. Left hind foot, femur, tibia and fibula of *Protolypus petersoni* (?). *cal.*, calcaneum; *as.*, astragalus; *cb.*, cuboid; *na.*, navicular; *cu*³., external cuneiform; *h.*, head of femur; *tr.*, greater trochanter; *tr*²., lesser trochanter; *t.*, tibia; *fb.*, fibula.

There are but two functional metapodials, the third and fourth, the second and fifth being reduced to mere vestiges. Upon one side the vestige of the second metapodial is preserved in place, and it is seen to articulate by a peculiar ledge-like facet upon the principal cuneiform. Upon its posterior surface is a distinct facet by which it articulates with the small cuneiform. The remnant of the fifth is not preserved, but the facet by which it articulates with the cuboid is very small, and there can be no doubt that it was as much reduced as the second.

The functional metapodials are relatively much shorter than in *Poëbrotherium*, and of a considerably more primitive form. They are well flattened upon their opposed surfaces in the upper half of the extent of their shafts. Below this the inner surfaces of the two bones are well rounded. Unlike the metapodials of *Poëbrotherium*, they lack that characteristic four-sided appear-

ance of the later Camels, but on the contrary, are more or less triangular upon cross section, especially in the proximal half of their shafts. The metapodials as well as the long bones show their cameloid affinities in the unusually large size of the medullary cavities. The phalanges exhibit comparatively few differences from those of *Poëbrotherium*, the unguals being flattened upon their opposed surfaces. The fore foot is entirely unknown, but it is highly probable that it will be found to possess four complete functional toes.

It may transpire that the association of this skeleton with the above-described skull is incorrect, and that these bones belong to separate and distinct species; however, they agree so well in the matter of proportionate sizes of the different parts, and both are so distinctly cameloid, that I am persuaded to believe that they refer to one and the same species. It may be noted here, however, that in one of the specimens referred to above (No. 2067), there is evidence that at least one of the lateral metapodials of the hind foot was complete though very slender, and should probably be referred to another species on this account. The bones are, moreover, somewhat more slender and delicate than the one here described. At all events, whatever form of skull belongs with these skeletal parts it is nevertheless certain that the skull of *Protylopus*, above described, is just such a type as is required to satisfy all the necessary conditions in order to occupy a position in direct ancestral relation with *Poëbrotherium*. The true Tylopod phylum is therefore traceable directly to it. Beyond this, there is at present no satisfactory evidence to establish, with any degree of certainty, the identity of the true Camel pedigree.

Poëbrotherium *Leidy.*

With a consideration of this genus we pass from the Eocene to the Oligocene representatives of the group. It was established by Leidy as early as 1847 upon an imperfect skull presented to the Philadelphia Academy by Mr. Alexander Culbertson of Chambersburg, Pa., who was at the time engaged in the western fur trade. It was among the first of the mammalian fossils from the remarkable Bad Lands of the Cheyenne River

region, whose treasures were destined in later years to play such an important part in the development of American palæontology. Leidy at first[1] regarded the skull as pertaining to a genus nearly allied to the Musk Deer, but later[2] pointed out its true position among the Camelidæ.

The generic differences between *Poëbrotherium* and *Protylopus* are not great, and indeed it would appear at first sight that they are insignificant. It is more than probable, however, as stated

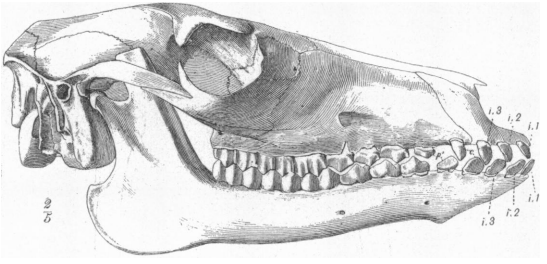


Fig. 7. Side view of skull of *Poëbrotherium wilsoni*.

above, that *Protylopus* will be found to have four complete and functional digits in the fore limb. So far as our knowledge extends at the present, the chief distinctions are as follows: In *Poëbrotherium* the molars are much more selenoid and the crowns more lengthened than in *Protylopus;* the third superior incisor is larger than the superior canine; the ulna and radius are firmly coössified, even before the epiphyses of the bones are joined to the shaft and the shaft of the fibula has completely disappeared.

Poëbrotherium wilsoni *Leidy.*

This species, although very abundant in the White River Beds of the Cheyenne River region, has not been very fully described. All of the specimens in the Museum collection have been found in the Lower Oreodon level, and it is doubtful if the vertical range of the species extends much above this point. It differs very markedly from its successor, *P. labiatum*, in the practical

[1] 'Ancient Fauna of Nebraska,' Dec., 1852, p. 19.
[2] 'Extinct Mammalian Fauna of Dakota and Nebraska,' 1869, p. 141.

absence of diastemata in the lower jaw. The canines of this series are, moreover, broad and incisiform, being separated from the first premolars by very short diastemata. In the same manner the second premolars follow after a very short interval. In

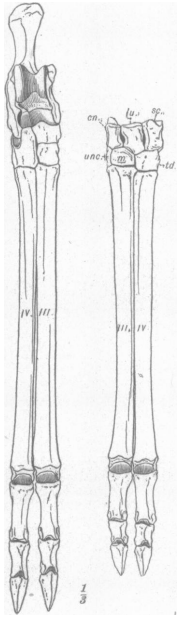


Fig. 8.

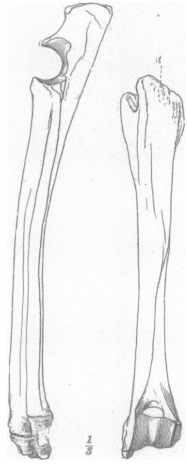


Fig. 9.

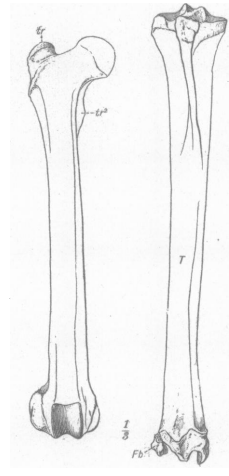


Fig. 10.

Fig. 8. Fore and hind foot of *Poëbrotherium wilsoni.*
Fig. 9. Ulna and radius and humerus of *Poëbrotherium wilsoni.*
Fig. 10. Femur and tibia of *Poëbrotherium wilsoni.*

P. labiatum, on the other hand, the lower canines and outer incisors are almost in contact, the canines are subcaniniform in shape, and there is a short diastema in front of, and a long diastema behind, the first inferior premolar. The bones of the limbs and other parts of the skeleton are, as far as can be determined, very much alike in the two species. As in *P. labiatum*, there is a considerable range in size in the various specimens referred to this species.

Poëbrotherium labiatum *Cope.*

The type of this species consists of the larger part of a skeleton of a single individual from the White River Beds of northeastern Colorado (No. 6520). Associated with this specimen are two almost complete lower jaws from the same locality (Nos. 6517, 6518) showing the characteristic diastemata of *P. labiatum*, but considerably smaller. These specimens were erroneously referred by Cope to *P. wilsoni*. I have not been able to correlate with certainty the level from which these specimens were taken, with that in which similar remains in the Cheyenne River region occur, but judging from Cope's unpublished sketch of the section of the bed, there can be little doubt that it corresponds closely with the upper part of the Oreodon horizon. This surmise is strengthened by the fact that there is one specimen in the collection (No. 638), from the extreme upper part of the Oreodon Bed, which agrees in every way with the type of *P. labiatum*, except that it is a little larger. Another specimen from the Cheyenne River Bad Lands includes a lower jaw and a good part of the skeleton. The lower jaw exhibits the characteristic diastemata of *P. labiatum*, but is much smaller than the type, and of the same size as the two jaws mentioned above. Unfortunately the exact level of this specimen is not known, but it has every appearance of having come from the upper part of the Oreodon stratum.

Whether or not these smaller specimens are to be referred to a species distinct from *P. labiatum* is a matter which requires a greater amount of material than we at present possess in order to decide correctly. So far as one can determine at present, the only distinction between the two is one of size, and this is not great. I have thought best to regard them as belonging to the same species until other differences are shown to exist. Taken as a whole, *P. labiatum*, as exemplified by the larger individuals, was considerably larger than *P. wilsoni*, and in the possession of diastemata in the lower jaw, as well as the more caniniform shape of the lower canines, makes a distinctive approach to the species from the John Day Beds. In this connection it is proper to observe that no remains of Camels are known from the Protoceras level of the White River Beds. When such are found they

will probably establish a complete transition between *P. labiatum* and the John Day species.

Gomphotherium *Cope.*

It is especially to Cope that we are indebted for the discovery of Camels in the John Day Beds. The first remains secured by him from this horizon were referred to *Poëbrotherium*, but later he established the genus *Gomphotherium*[1] for their reception,

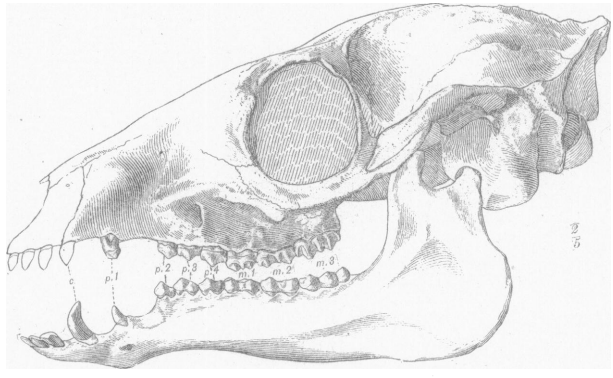


Fig. 11. Side view of skull of *Gomphotherium sternbergi.*

which he distinguished from *Poëbrotherium* by the more simplified character of the crown, and the one-rooted condition of the first superior premolar. As this distinction was founded largely upon error, I am now able to give the more important and true characters which serve to separate the two genera in a satisfactory manner.

In *Poëbrotherium* the inferior canine is either in contact with the outer incisor, or is separated from it by a very short diastema, and the form of the canine is either like that of an incisor or very imperfectly caniniform. In *Gomphotherium*, on the other hand, the inferior canine is either separated from the outer incisor by a very distinct diastema or the diastema is absent, and the shape of the canine is strongly pointed and recurved, as

[1] 'The Phylogeny of the Camelidæ,' Amer. Nat., 1886, p. 618.

in many of the later Camelidæ. In *Poëbrotherium* again, the orbit is not inclosed by bone posteriorly, whereas in *Gomphotherium* the posterior boundary of the orbit is complete. Another important distinction is seen in the character of the articular facets of the third and fourth metapodials of the fore foot. In *Poëbrotherium* these bones give evidence of having been more widely separated in the living animal, and capable of considerable independent movement, the facets being relatively large and the opposed surfaces comparatively smooth. In *Gomphotherium* these facets are much reduced, the metapodials closely applied to each other and their contiguous surfaces much roughened, clearly foreshadowing the coössification of these elements into a cannon bone.

Gomphotherium sternbergi *Cope.*

The type of this species consists of the greater part of the skeleton of a single individual in good preservation from the lower beds of the John Day Valley, Oregon. Other specimens from the same horizon include more or less perfect foot-bones, fragments of jaws, and other parts of the skeleton. The form of the skull presents a striking resemblance to that of the modern Camels in its general make up. The nasal bones are, however, proportionately longer, the bony roof of the orbits not so broad, and the muzzle apparently more laterally constricted in front of the infraorbital foramen. As compared with *Poëbrotherium* and the Llama the face is less bent down on the basicranial axis, in this respect resembling more the skull of the Camel. The vertical depth of the face immediately in front of the orbit is relatively greater than in *Poëbrotherium*, and the opening of the posterior nares has a more forward position.

A very interesting transition from the relatively low, much-swollen otic bullæ of *Poëbrotherium*, to the high, little-swollen condition of these parts in the living species, is observable. The otic bullæ of all the Camels are highly characteristic ; they consist of an inner, longitudinally-directed swollen part, together with an outer vertical buttress, which joins the inner part at an angle, and at the upper limit of which is placed the external

auditory meatus. Immediately behind the point of junction of these two parts is seen the deep recess where the hyoid arch is articulated to the skull. In *Poëbrotherium* the inner portion of the bulla is much the larger, and the recess for the tympanohyal is inconsiderable. In *Gomphotherium* the two parts are about equal in size, and the tympanohyal recess much more pronounced. In the living genera, *Camelus* and *Auchenia*, the inner

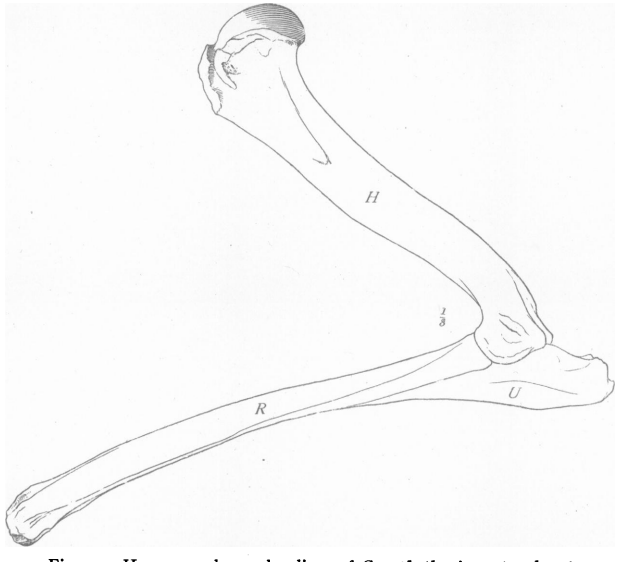


Fig. 12. Humerus, ulna and radiaus of *Gomphotherium sternbergi.*

part of the bulla is much reduced and the tympanohyal recess is converted into a deep circular pit surrounded by bone.

In the skeleton of the limbs the lower end of the femur is peculiar in the unusual size and development of the areas of attachment of the outer and inner heads of the gastrocnemius. This same peculiarity is seen in the femora of old individuals of both *Poëbrotherium labiatum* and *Procamelus occidentalis*, although to a somewhat less extent, and is doubtless a result of age. The head of the humerus shows the first distinctive change leading to the development of the double bicipital groove, a feature so char-

acteristic of the later Camelidæ. In no individual in the collection is there evidence, even in those of the most advanced age, of any traces of bony union of the metapodials. In size *G. sternbergi* exceeded *P. labiatum* by at least one-third.

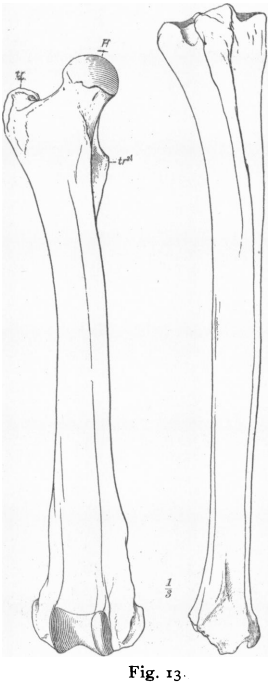


Fig. 13.

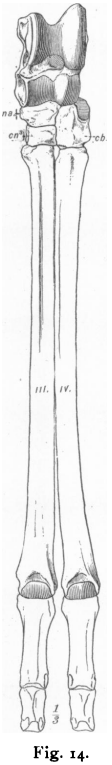


Fig. 14.

Fig. 13. Femur, tibia and fibula of *Gomphotherium sternbergi.*
Fig. 14. Hind foot of *Gomphotherium sternbergi.*

Gompotherium cameloides, sp. nov.

This species is represented in the collection by an almost complete mandibular ramus from the uppermost levels of the John Day deposits (No. 8179). To this same species I also refer an upper dentition (No. 7915), an almost complete fore limb (No. 7912), as well as several other fragments. The chief distinctions

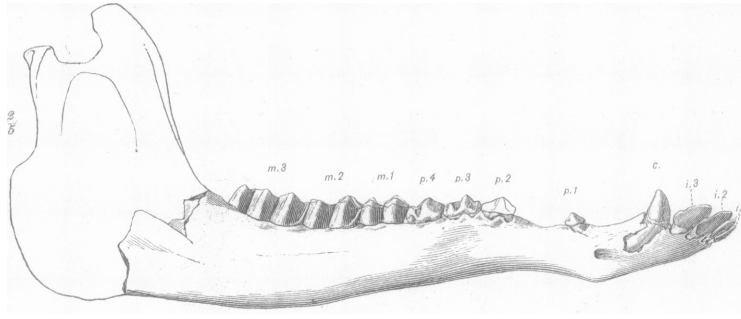


Fig. 15. Lower jaw of *Gomphotherium cameloides.*

between this species and the older *G. sternbergi* are seen in the increased size and the absence of a diastema between the lower canine and the outer incisor in *G. cameloides.* The comparative measurements display these differences in size at a glance ; they are as follows :

	G. sternbergi.	*G. cameloides.*
	MM.	MM.
Length of sup. ms. and three posterior pms...	60	83
" " inf. ms. and three posterior pms...	65	97
" " entire inferior dentition.	110	170
" " anterior metapodials.....	180	228

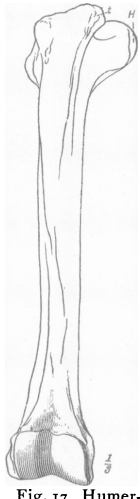


Fig. 17. Humerus of *Gomphotherium cameloides.*

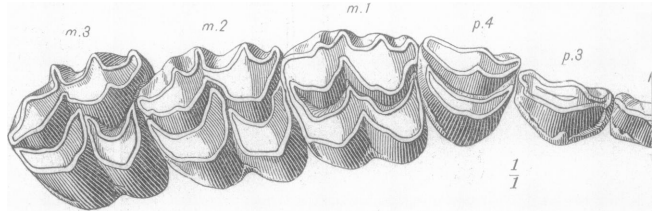


Fig. 16. Upper teeth of *Gomphotherium cameloides.*

It will therefore be seen that *G. cameloides* shows the same increase in size over *G. sternbergi* as *G. sternbergi* does over *Poëbrotherium labiatum.* Of the bones of the anterior limb, no differences are observable between them and the corresponding parts of *G. sternbergi*, except in the matter of size already noted above.

The exact stratigraphical position of this species is several hundred feet above that of *G. sternbergi*, and there can be no doubt whatever that *G. cameloides* is not only the direct lineal descendant of the older species, but is, at the same time, the progenitor of the succeeding Loup Fork species. This conclusion is somewhat at variance with the view expressed by Scott,[1] in which he says : " The Camels of the John Day formation do not present any important modifications of the dentition ; in some of them the first upper premolar has but a single fang, and others are decidedly reduced in size ; the former Cope has erected into a separate genus, *Gomphotherium*. It seems probable that these forms are not in the direct line of the cameline descent." A careful examination of Cope's type of *Gomphotherium sternbergi*, the only species, by the way, with the exception of the one above named, which has so far been described from these beds, reveals the fact that the first superior premolar, instead of being a single-rooted tooth, is *strongly two-rooted ;* and that the succeeding premolars exhibit a most interesting and instructive transitional stage between *Poëbrotherium* and *Protolabis*, not only as regards their form but their degree of reduction as well. I have been unable, after the most exhaustive study, to find any evidence whatever tending to show that

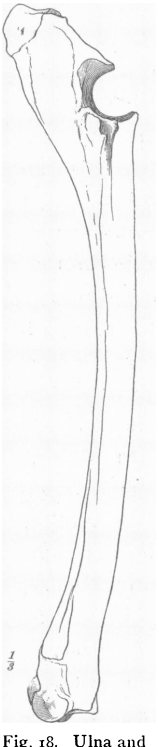


Fig. 18. Ulna and radius of *Gomphotherium cameloides.*

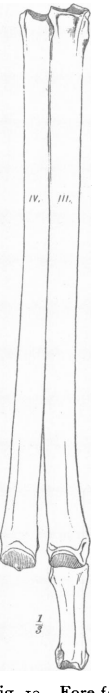


Fig. 19. Fore foot of *Gomphotherium cameloides.*

[1] ' The Osteology of Poëbrotherium,' 1891, p. 49.

these John Day species are not in the direct line of the tylopodean ancestry.[1]

Protolabis *Cope.*

The next step in the line of cameline ancestry is furnished by the genus *Protolabis*, originally established upon the greater portion of both premaxillæ and maxillæ, together with the front of the lower jaw upon one side. This specimen was found near Pawnee Buttes, Colorado, and is from the typical Loup Fork horizon.[2] Another specimen was found by the writer in the so-called Loup Fork Beds of the upper John Day Valley of central Oregon, which was described by Cope as a new species of the same genus. It consists of the anterior portion of the cranium bearing the complete upper dentition in good preservation.

As regards the type specimen upon which the genus was originally founded, it is necessary to remark that the only distinction between it and *Procamelus robustus* is to be found in the possession of alveoli for the first and second incisors above, which would indicate a complete superior incisor dentition. In *Procamelus*, of the adult stage at least, these incisors are wanting. A careful examination of the specimen shows that the part of the premaxilla in front of the third incisor, upon the right side, is much shorter than that upon the left side, and instead of two alveoli there are in reality three, which would make altogether four incisors in the premaxilla upon this side. The corresponding part of the premaxilla upon the opposite side is much longer, and contains the two alveoli for the first and second incisors. In every other detail the specimen agrees perfectly with *Procamelus robustus*. Indeed, Cope has pointed out that these first and second incisors of this series, in all the species of *Procamelus*, were

[1] In this connection it is proper to call attention to the fact that there are important faunal differences between the upper and lower beds of the John Day deposits. These distinctions are so marked as to entitle them to be regarded as separate and distinct divisions of the North American Miocene Besides the species of cameloids above described, this upper division contains two species of *Merycochœrus* among the Oreodonts. *Mesohippus præstans* among the Horses, and *Elotherium humerosum* of the Elotheres, which have not been found thus far in the lower division of the beds. There can be little doubt that other important faunal distinctions will be discovered when careful collections are made with this particular object in view. For the lower series the name Diceratherium Beds may be retained, but for the upper series I herewith propose the name Merycochœrus Beds.

[2] Proc. Philad. Acad., 1876, p. 145.

retained in the jaw for a longer or shorter period, and in some instances until the animal was almost if not quite adult. In view of these facts I am disposed to interpret this specimen as a case of abnormal retention of the incisors of the rather abundant species *P. robustus*. If this conclusion is correct, then the species *Protolabis heterodontus* becomes a synonym of *Procamelus robustus*. The second species regarded as belonging to this genus from the Nebraska Loup Fork, *Protolabis prehensilis* Cope, was founded upon the anterior portion of a lower jaw without teeth, and as there is no indication whatever what the upper dentition was like, the reference at most is mere guesswork. In fact, I doubt very much if it even is specifically distinct from *Procamelus robustus*.

With the elimination of these forms from the Nebraska Loup Fork, we have left the single species *Protolabis transmontanus*, represented by the Oregon specimen above referred to. In this specimen we have a genuine case of normal retention of the superior incisors, a fact which separates it at once from *Procamelus*, but the distinctions between it and its predecessor, *Gomphotherium*, are less clear. Cope assumed that it differed from this latter genus, in the coössification of the metapodials into a cannon bone, but of this there are no specimens at present known to demonstrate the truth or falsity of such an assumption. It is true that Camel remains have been found in the Deep River Beds of Smith's Valley, Montana, which deposits have been generally looked upon as older than the Loup Fork of both Oregon and Nebraska. These fossils have been uniformly referred to the genus *Protolabis* by Cope and Scott, but it does not appear, from any materials with which I am acquainted, whether these remains have been correctly determined or not. Neither skulls, jaws, nor even teeth, are known from this horizon which would enable one to say definitely whether the dentition was that of *Protolabis* or *Procamelus*. The metapodials of both fore and hind feet are united into a cannon bone, and the size almost, if not quite, equals that of *Procamelus robustus*, a circumstance which would seem to indicate that if they belong to the genus *Protolabis* they must represent a different and later species, since *Protolabis transmontanus* is much smaller, scarcely exceeding *Gomphotherium*

cameloides in size. The only valid distinction between *P. transmontanus* and *G. cameloides* is seen in the marked reduction of the second superior premolar in the former, and as this is in the direct line of modification leading to the Loup Fork *Procamelus*, I have thought best to regard it as of generic rank, especially until the question of the coössification of the metapodials is definitely settled.

Protolabis transmontanus *Cope.*

This species was somewhat smaller than the modern Llama, and so far as one can judge from the imperfect remains, exhibits very similar proportions in its general form. The crowns of the molars are notably shorter and have a more quadrate outline than those of either the modern genus or *Procamelus*. This, however, may be due in a measure to wear. The superior canine is smaller than the third incisor; the first premolar is two-rooted, and the second is much reduced in size, as in *Procamelus*. The first and second incisors are of goodly size, implanted by strong roots and with obliquely-directed, more or less spatula-shaped crowns. The nasals are relatively longer than in the Llama, and the muzzle is moderately compressed laterally.

Procamelus *Leidy.*

In the widespread Loup Fork deposits of the plains region remains of Camels are very numerous; next to the Horses, they are perhaps the most abundant fossils to be found in these beds. A number of genera and species of these Camels have been described, but, as has too frequently happened in the history of the science in this country, unfortunately, misplaced zeal in the finding and describing of new forms has been allowed to run riot, and much of this work is apparently characterized by an utter lack of the most ordinary display of judgment and discrimination. No less than four or five genera have been proposed, of which not more than two are entitled to recognition. Of these *Procamelus* is the more abundant, and is represented by three well-marked and easily-distinguished species. The most distinctive features of the genus are the possession of a full complement

of premolars in both jaws, the loss of the first and second pairs of incisors in the upper jaw in the adult stage, and the at least partial coössification of the metapodials of both fore and hind feet into cannon bones.

Procamelus robustus *Leidy.*

I place as synonyms of the above those proposed by Cope, *Protolabis heterodontus* and *Protolabis prehensilis.* The type specimen, as figured by Leidy, consists of a lower jaw bearing all the premolars and molars with the exception of the second, together with the second and third molars of the upper jaw. The jaw is broken just in advance of the first premolar so as not to show the characters of the incisors, canine and chin. In Cope's type of *P. heterodontus* the lower jaw is preserved as far back as the root of the last premolar, and this is associated with the almost complete superior dentition. The type of *P. prehensilis* is represented by the front of both rami of the lower jaw, associated with a last lower molar. A careful comparison of these specimens reveals a remarkable agreement in all details, and I do not think there can be any question of their belonging to one and the same species. The only difference worthy of note is seen in the jaw fragment which constitutes the type of *P. prehensilis ;* in this specimen the chin is not so abrupt nor deep, and the lower border of the symphysis is more nearly in line with the long axis of the jaw. The size is practically the same in all. I distinguish the species by the following characters : Size, large ; lower molars with much greater transverse diameter than in other species ; symphysis not coössified ; chin abrupt and deep. In one specimen only is the upper incisor dentition known, and in this the first and second incisors are retained. It may transpire that this is not an abnormal case as expressed above, but that it is a further character of the species. No other parts of the skeleton are known with certainty.

Procamelus occidentalis *Leidy.*

This species is by far the most abundant of the Camels in the Loup Fork Beds. I regard the name proposed by Leidy, *Homo-*

camelus caninus, as synonymous with the above, together with *Procamelus angustidens* given by Cope to various remains. It is somewhat smaller than *P. robustus*, and is altogether intermediate in size between this latter species and *P. gracilis*. It can be readily distinguished from *P. robustus* by the coössification of the two rami of the lower jaw at the mandibular symphysis, and especially by the narrow lower molars. The first and second incisors disappear early in life and no traces of their alveoli are seen in the adult skull. A large part of the skeleton is known, and this is surprisingly like the modern genera. The two main metapodials are firmly united into a cannon bone, and the vestigial representatives of the two lateral metapodials are coössified with them. No ungual phalanges, however, are known, and it is a matter of uncertainty whether they were relatively high and compressed like the early Camels, or whether they were broad and depressed like those of the living *camelus*. It is probable that when found they will show the intermediate conditions between these two extremes. Most of the skeleton has been described and figured by Cope,[1] and need not be repeated here.

Procamelus gracilis *Leidy*.

The species, described by Cope under the name of *P. fissidens*, agrees in every particular, so far as the measurements are concerned, with the above, and I therefore regard them as synonymous. *P. gracilis* is the smallest species of the genus, and its remains are not uncommon in the Loup Fork Beds of Colorado and Nebraska. It about equals the modern Llama in size, and is considerably smaller than *P. occidentalis*. Of the materials in the collection referable to this species, there are three lower jaws. One of these has the posterior part of the symphysis preserved, and this agrees with *P. robustus* and differs from *P. occidentalis* in the lack of coössification of the rami, although the well-worn teeth indicate an old animal. The lower molars are of the narrow type, in this respect agreeing with *P. occidentalis* rather than *P. robustus*. In two of the specimens the second premolar is well developed and two-rooted, but in the third specimen this tooth is much reduced and single-rooted, thus indicating a ten-

[1] Surv. W. 100th M., p. 329.

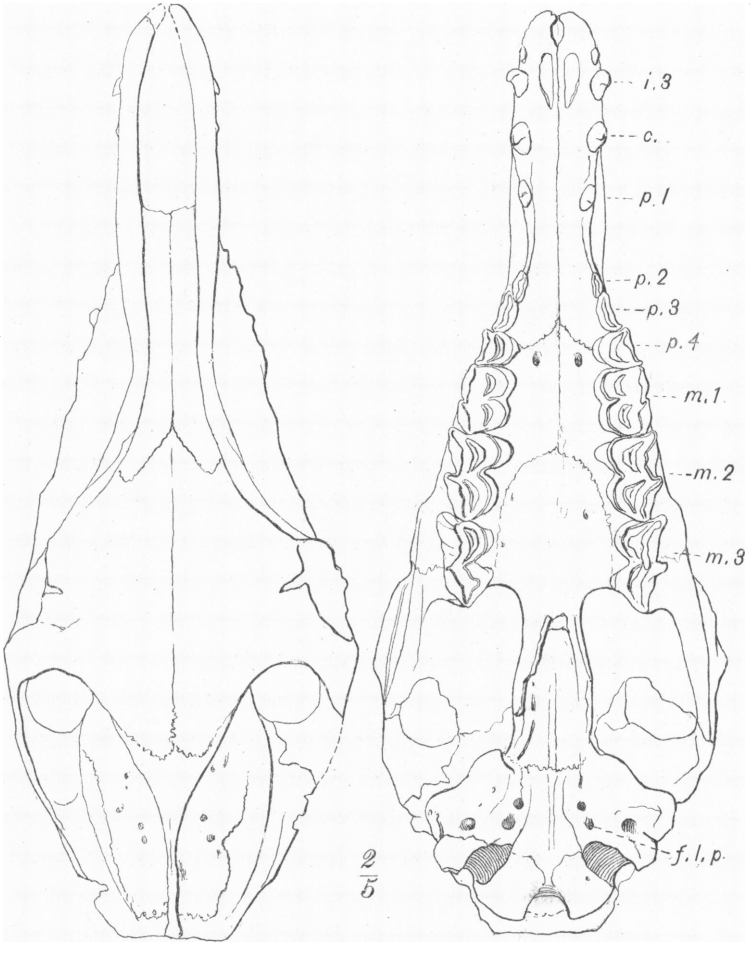


Fig. 20. Top and under view of skull of *Procamelus gracilis*, after Cope.

dency to disappear. This, it may be said, constitutes a decided advance in the direction of the next genus, *Pliauchenia*, in which this tooth is permanently absent. I give herewith some comparative measurements of the three known species in order that the differences in size may be more readily understood :

	P. robustus.	*P. occidentalis.*	*P. gracilis.*
	MM.	MM.	MM.
Length of last three pms. and ms.....	152	126	111
		133	
		126	
		135	
Length of last three pms. and first two ms.....	106	90	77
		85	76
		88	76
		92	

Two incomplete metapodials in the collection, which are of suitable size for those of this species, show lack of bony union, notwithstanding the fact that the epiphyses are completely joined to the shaft. It is not certain, but there is evidence, that these metapodials belong to the fore foot, in which event it will not be surprising to find in more complete and perfect specimens that these bones are not coössified in this species, except in old individuals. In the hind foot the metapodials are completely united, as is shown by several specimens. In one specimen, which corresponds in size with *P. occidentalis*, the proximal part of the cannon bone shows lack of bony union for a distance of nearly two inches down the shaft.

Pliauchenia *Cope.*

The only character so far known in which this genus differs from *Procamelus* is found in the absence of the second lower premolar, and as this constitutes an important step in the dental evolution of the Camels, the species displaying it are entitled to rank as a separate and distinct genus. The exact stratigraphic position of the group is not known, owing to the imperfect collecting that has been done in the Loup Fork Beds. It is generally stated that *Pliauchenia* was contemporaneous with *Procamelus* in the Loup Fork, and comes from the same horizon, but of this one cannot be certain. It must be remembered that this deposit is several hundred feet in thickness in places, and it would not be a matter for surprise if it is found, upon more careful investigation, that *Procamelus* comes from the lower levels and *Pliauchenia* from the upper strata of the same bed.

Three species have been described by Cope, of which two are from the Loup Fork of New Mexico and one from the later

Blanco Beds of Texas. One of these species, *P. vulcanorum*, was founded upon a superior maxillary bone with most of the teeth in place, but as the diagnosis of the genus rests exclusively upon the number of premolars in the lower jaw, I do not see how this species can be admitted until the lower dentition is determined. It is therefore discarded.

Pliauchenia humphresiana *Cope.*

The type of this species consists of the anterior portion of two lower jaws from the Loup Fork of New Mexico. A second specimen which I refer to this species is from the Loup Fork Beds of Long Island, Phillips County, Kansas, collected by the Museum party during their explorations there. The specimen consists of the greater part of a lower jaw broken just in advance of the first premolar and bearing all the molars and premolars with the exception of the first and third. In size the specimen about equals the smaller individuals of *Procamelus occidentalis*, which it otherwise closely resembles in the structure of the teeth. The molars are of the narrow and elongated type, and the premolars have the same structure as that seen in the various species of *Procamelus*.

Pliauchenia minima, sp. nov.

The smallest species of Cameloid yet known from the Loup Fork deposits is represented in the collection by the greater part of a lower jaw, from Decatur County, Kansas, which I provisionally refer to the above genus. The specimen is broken posterior to the symphysis and does not display the incisors, canine nor first premolar, if indeed this latter tooth were present. The diastema in front of the third premolar is unusually long and the ramus in this region remarkably slender; more so, in fact, than in any known species of the Camelidæ. The third and fourth premolars are present but considerably reduced in size. The molars are of the usual pattern. Some fragmentary remains of a hind foot from this same region are probably to be referred to this species. The phalanges and distal ends of the metapodials are extremely cameloid, but unusually slender and delicate. The

metapodials are firmly coössified. The size of the species is about equal to that of *Poëbrotherium labiatum* of the White River. The reference of this species to *Pliauchenia* is of course only provisional, and until the entire dentition is known the reference is uncertain. If it should transpire that the first premolar is absent it could not be placed in *Pliauchenia*, but would occupy a position between this genus and *Auchenia*.

Pliauchenia spatula *Cope.*

This species is founded upon an unusually complete lower jaw from the Blanco beds of Texas. According to Cope it is one of the largest Camels yet found, and considerably exceeds the modern Dromedary in size. A comparison of the measurements of the three known species will exhibit the striking difference in size ; they are as follows:

	P. spatula.	*P. humphresiana.*	*P. minima.*
	MM.	MM.	MM.
Length of last two pms. and ms....	188	110	70

Camelops *Leidy.*[1]

Camel remains in the Pleistocene, Equus Beds, are very numerous ; they have been found in nearly every State and Territory west of the Mississippi River, and are, in places, exceedingly abundant. Unfortunately, however, in most instances the fossils are so fragmentary that it is impossible to determine the genus or species to which any given specimen is to be referred. This fact has been taken advantage of, it appears to me, to inordinately multiply the genera and species, upon no better ground, frequently, than mere guesswork. These remains have been grouped at different times in no less than five distinct genera and ten species. The first of these genera, *Camelops*, was proposed by Leidy (Proc. Acad. Nat. Sci. Phila., 1854, p. 172), upon the fragment of an upper jaw of a large Camel from the gravel drifts of Kansas. The second genus, *Megalomeryx*, was also proposed by Leidy (Proc. Acad. Nat. Sci. Phila., 1858, p. 24), for the reception of some large teeth supposed to belong to an extinct Camel, from the Pleistocene of Nebraska. In 1872

[1] Proc. Acad. Nat. Sci. Phila., 1854. p. 172.

Dr. Leidy again described some large Camel remains from California, which he referred to the living genus *Auchenia*.[1] Following this Cope[2] described two new genera, *Holomeniscus* and *Eschatius*, which he based upon fragmentary materials from Oregon, Mexico and elsewhere. He distinguished these genera from *Pliauchenia*, *Auchenia* and *Camelus* by the possession of a single superior premolar, the fourth, and separated *Eschatius* from *Holomeniscus* by the extreme reduction of this tooth to a simple cone. The evidence upon which a knowledge of the superior premolar dentition of these forms rests is furnished, so far at least as I have been able to learn, by (1) a fragment of an upper jaw of *H. vitikerianus*, containing the first and second molars, together with the roots and alveoli of the premolar or premolars immediately in advance, as well as a portion of the free border of the jaw; (2) a much damaged fragment of a superior maxilla of *H. hesternus*, in which no knowledge of the premolar dentition is possible, since neither the teeth nor their alveoli are preserved; and (3) a portion of a superior maxilla of *Eschatius conidens* without teeth but having nearly all the alveoli preserved.

It appears from a careful examination of this material that the number of superior premolars in all these Pleistocene cameloids, with the exception of *Eschatius conidens*, is uncertain. In the only specimen in which it can be possibly made out, there are undoubted traces of an alveolus for a third premolar. If there were two premolars above, then the dental formula is the same as in the living genus *Auchenia*, and is indistinguishable from it, so far, at least, as the number of teeth is concerned. The third superior premolar is very small in *Auchenia*, and it will not be surprising to find, when a larger number of suitable specimens of these North American Pleistocene species are known, that in some cases a vestige of this tooth remained in the jaw for a longer or shorter time during the life of the animal; at least this seems to be the rule in many cases wherein a tooth is about to disappear from the series.

I therefore reject the definition given by Cope, but retain the genus as distinct from *Auchenia*, upon an entirely different

[1] Report U. S. Geolog. Surv. Territories, 1873, p. 225.
[2] Proc. Amer. Philos. Soc., 1884, p. 16.

ground. In the lower molars of *Auchenia* there is a very prominent buttress, amounting almost to a lamina, developed at the outer extremity of the antero-external crescent, especially in the second and third molars. This structure is not present in the lower molars of any of the North American species which I have seen, although there are faint traces of it to be found in some of them.

As regards the generic name to be applied to these North American species, I revive the one originally given by Leidy, *Camelops*, notwithstanding the fact that no attempt was made by him to give a generic definition. The extreme reduction of the fourth premolar, together with the small size of the inferior canine, satisfactorily distinguishes *Eschatius*, which is undoubtedly a distinct genus and is here regarded as such.

In the description of the numerous remaining species which have been proposed, apparently very little latitude has been allowed for individual and sexual variations, and because of the very fragmentary condition of the material so far known any accurate understanding of their limits is quite impossible. On this account it is very difficult to determine what species are valid and entitled to recognition. Until a larger number of specimens in a less fragmentary state are obtained, I cannot distinguish more than two, or at the utmost three species, and these determinations rest solely upon size.

Camelops kansanus *Leidy.*

This species is by far the most abundant of all the North American Pleistocene Cameloids, and of the widest geographical distribution. I regard as synonymous of the above the following specific names: *Megalomeryx niobrarensis* Leidy,[1] *Auchenia hesterna* Leidy,[2] *Holomeniscus hesternus*[3] Cope, *Auchenia huerfanensis* Craigin,[4] and *Holomeniscus sulcatus* Cope.[5] Leidy's type of *Camelops kansanus* consists of a fragment of the anterior portion only of the upper jaw, bearing the root of the incisor and a portion of the alveolus of the canine, and does not reveal the

[1] Proc. Acad. Nat. Sci. Phila., 1858, p. 24.
[2] Rep. U. S. Geolog. Surv. Territories, 1873, p. 225.
[3] Proc. Amer. Philos. Soc., 1884, p. 16.
[4] Amer. Geologist, 1892, p. 257.
[5] Rep. Geol. Surv. Texas, 1893, p. 84.

number of premolars nor the character of the lower molars. It agrees so well in size and character, however, with the corresponding parts of other specimens from different localities in which the dentition can be accurately determined, that there can be very little doubt that they belong to one and the same species. The type of *Megalomeryx niobrarensis* consists of lower molars from the sand hill region of Nebraska; and since they do not present any characters which will serve to distinguish them from the corresponding teeth of *C. kansanus* they may be safely regarded as belonging to the same species. In the same way the teeth described by Leidy from California under the name of *Auchenia hesterna* present no differences, either in size or structure, that would lead one to consider them as belonging to a distinct species. *Auchenia huerfanensis* of Craigin comes apparently in the same category and does not differ, so far as can be made out from the description, from *C. kansanus.* Neither can one detect any characters in the type of *Holomeniscus sulcatus* of Cope from the Pleistocene of Texas that separate it from the above species. Cope described a sulcus upon the inner face of the lower molars, which he thought distinguishes this species. Upon careful comparison I find this sulcus is quite as well developed in many other specimens, the reference of which to *C. kansanus* there can be no reasonable doubt. I find it to be a character which not only varies with the state of wear of the tooth but is subject to a considerable degree of individual variation.

The dentition of the species thus considered is as follows: $I\frac{1}{3}$, $C\frac{1}{1}$, $Pm\frac{1-2}{1}$, $M\frac{3}{3}$. In size the majority of the specimens about equal the corresponding parts of the Dromedary, although some are notably more robust, while others are decidedly more slender. In fact, there appears to be a very great range, as far as size is concerned, in certain bones, especially those of the feet. The length does not seem to vary so much as the degree of robustness, and this probably is due to differences in sex and age. I give herewith the measurements of some of the principal limb bones of this species from the Pleistocene sand beds near Hay Springs, Nebraska, collected by the Museum expedition during last summer. These bones, it is proper to remark, pertain to many

individuals, and were found hopelessly mixed together. I also give measurements of the corresponding bones of the Dromedary for comparison :

	C. kansanus.	*Dromedary.*
	MM.	MM.
Length of posterior cannon bone	345	325
	360	
	365	
Length of anterior cannon bone	330	325
	370	
Length of ulna and radius	555	580
Length of humerus	375	420
Length of scapula	415	460
Length of phalanges, proximal row	98 to 124	102

A specimen from an anterior cannon bone from the Silver Lake locality in Oregon is considerably more robust than either the Dromedary or those of *C. kansanus* from Hay Springs; it measures 385 mm. There is yet another specimen in the collection consisting of a complete posterior cannon bone from the Pleistocene of Hitchcock County, Nebraska, which greatly exceeds in length that of any known Camel. It is notably more slender than the cannon bone of the Dromedary, has less distal spread of the metapodials, but is nearly double the length; its exact measurement is 555 mm. It is highly probable that this represents a distinct species, but I refrain from creating another specific name until we know more of the skeleton.

Camelops vitikerianus *Cope.*

A fragment of an upper jaw containing the first and second molars, together with the roots and alveoli of the two superior premolars, is the only specimen of this species so far known with certainty. A complete lower jaw was described by Cope from the Pleistocene of Texas under the name of *Holomeniscus macrocephalus*,[1] which I strongly suspect belongs to this species. It agrees, so far as one can judge, in size, but no exact comparison is possible, since the inferior condition of *C. vitikerianus* is unknown. Cope remarks in his description: "I observe here that it is not certain that the species now described is not an *Auchenia*, as the superior dentition is not known." The lower molars, as figured, are

[1] Rep. Geolog. Surv. Texas, 1893, p. 85.

certainly not those of any *Auchenia* with which I am familiar, since they entirely lack the antero-external buttress of this genus and agree with those of *Camelops*. I cannot see any reason whatever to regard this jaw as belonging to a species different from that represented by the upper molars above noticed. The size of the species is near that of the living *Auchenia*, and is hence much smaller than *C. kansanus*, the only character to my knowledge by which it can be distinguished.

Camelus americanus, sp. nov.

From the Pleistocene Beds of the Hay Springs locality were obtained by the Museum expedition last year several specimens of a Cameloid apparently different from anything hitherto described from this country. One specimen consists of the greater part of

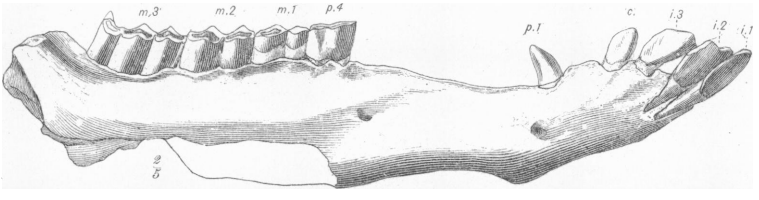


Fig. 21. Lower jaw of *Camelus americanus*, side view.

both rami of the mandibles of a fully adult individual, in excellent state of preservation, but broken in such a manner as to display but little of the jaw posterior to the last molar. The second specimen consists also of a mandibular ramus, but the individual was young, in which the milk molars had not yet been shed.

The inferior dental formula of the adult specimen is as follows: $I\frac{3}{3}$, $C\frac{1}{1}$, $Pm\frac{2}{2}$, $M\frac{3}{3}$. This it will be noticed is the dentition of the genus *Camelus*, from which I cannot distinguish it generically at present. If this is a true Camelus, as I suspect, it is the first time that it has been found in the western hemisphere.

The incisors display the usual spatulate cameloid pattern, and are very procumbent in position. Almost immediately behind the third incisor follows a rather weak incisiform canine. At the posterior termination of a comparatively short diastema is placed

the first premolar, a moderately well developed tooth, with a compressed, internally grooved, pointed, recurved crown, very similar to the lower canine of *Auchenia*. After a relatively long interval follows the fourth premolar, which with the molars makes a continuous series. The fourth premolar is relatively more robust than that of the Llama or Dromedary, and gives evidence by this fact of a less reduced condition. Its form is the same as in these two genera. The molars display the same structure as those of the later Cameloids in general, except the second and especially the third show the first indication of the external buttress so characteristic of *Auchenia*. The two rami are firmly coössified at the symphysis. I distinguish the species from *Camelus dromedarius* by the relatively small incisiform canine, as well as by the less reduced fourth premolar and much smaller size. A comparison of the measurements of this species with *C. dromedarius* and *A. lama* are herewith given :

	A. lama. MM.	*C. americanus.* MM.	*C. dromedarius.* MM.
Length from incisive border to end of last molar	165	205	265
Length of molars and fourth premolar	80	92	132
Length from incisive border to fourth premolar	85	114	233

Eschatius conidens *Cope.*

The last of the American Cameloids to be considered is this species which, so far as we are now aware, was the most specialized of the Camelidæ. As already noted, the characters which

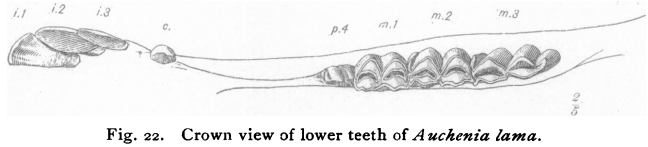


Fig. 22. Crown view of lower teeth of *Auchenia lama.*

distinguish this group from all others is found in the extreme reduction of the fourth superior premolar to a simple cone, as originally pointed out by Cope ; this is associated with a marked reduction in size of the lower canine. The specimens from which

the genus and species is known are, unfortunately, very fragmentary, so that it is impossible to say much concerning it. It was first found at the Silver Lake locality in southeastern Oregon, but subsequently Cope identified remains referable to it from certain localities in Mexico, showing that it was most widely distributed. Two species have been described by Cope, *E. conidens* and *E. longirostris*, but it is very doubtful indeed whether the material at

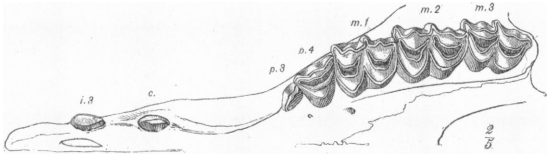


Fig. 23. Crown view of upper teeth of *Auchenia lama*.

present known warrants the recognition of more than a single species. There are some trifling differences in the length of the diastema of the lower jaw, it is true, but this is probably due to individual variation. The size of the species about equals that of the Dromedary.

The Evolution of the Camelidæ.

We come next to consider the evolution of the Camelidæ, and although the principal facts of their development have been quite fully set forth in the foregoing pages, yet it seems proper to summarize them here. The earliest forms in which one can detect true tylopodean peculiarities, as already pointed out, are found in the upper Eocene or Uinta stage ; at the same time it is quite certain that the phylum was detached from the main stem of the Artiodactyla at a much earlier date. Both Cope and Scott have expressed the opinion that the ancestry of the group is traceable directly to the Wasatch genus *Pantolestes*, and Scott believes that the connection is established by the Bridger genus *Homacodon*. Whether or not these opinions will bear the test of future discovery time alone will reveal. At present I am of the opinion that the osteology of these genera is too imperfectly

known to speak with any degree of confidence as to its correctness.

The principal changes of structure in the evolution of the group relate largely to the limbs and skull, although, as is well known, the cervical vertebræ are highly characteristic in the whole family. Unfortunately the cervicals are entirely unknown in the earliest representative, *Protylopus*, but in the succeeding genus, *Poëbrotherium*, they had already assumed the typical cameloid peculiarities. If one is permitted to judge by analogy, it is more than likely that *Protylopus* possessed the peculiar cameloid cervicals, and it seems highly probable that one of the crucial tests of tylopodean affinity, in any genus older than this, will be found in the incipient changes leading to this modification.

The changes in the limbs consisted mainly in (1) their gradual elongation, (2) coössification of certain bones, (3) modification of the patella and loss of the greater part of the tibia, and (4) the subtraction of digits, the change in the character of the feet and modification of the phalanges, together with the coössification of the podial elements into a cannon bone. In this connection should also be mentioned the development of a double bicipital groove upon the humerus and the modification of the carpal and tarsal elements.

The question of the elongation of the limbs is closely associated with the general increase in size, in which there is as complete a gradation, from the little *Protylopus*, scarcely larger than a good-sized Jack Rabbit, to the more modern species, larger than the Dromedary, as the most hypercritical opponent of the Evolution Theory could possibly demand. In the matter of the coössification of certain bones, the ulna and radius were the first to be affected by this process. As we have already seen, it had taken place in *Protylopus* in *a very old individual*, and then only in the middle of the shaft, leaving the proximal ends entirely ununited. In *Poëbrotherium* the complete coössification of these elements was accomplished in young individuals before the milk dentition had been completely shed, and before the epiphyses had united to the shafts of the long bones, as is demonstrated by many specimens in the Museum collection. In all the later types these bones are firmly united.

The patella of the later Camels is peculiar in that it is narrow and of great vertical depth. The first evidence of this modification is seen in the development of a long pointed process upon the inferior border of the bone in *Protylopus;* this is continued in *Poëbrotherium* and *Gomphotherium*, until in *Procamelus* the modern condition is reached. The shaft of the fibula in all the modern types has completely disappeared, and the bone is represented by a distal nodular element which lies under the end of the tibia. In *Protylopus* a considerable part of the shaft of the bone was present, but it was probably not complete. In *Poëbrotherium* the shaft is reduced to a very short bony spicule, and the distal part is partially pushed under the end of the tibia; in *Gomphotherium* the shaft has completely disappeared, and in *Procamelus* the modern arrangement is attained.

In the matter of the loss of digits I cannot speak with any very great degree of confidence, especially as regards the older types. Our materials fail to reveal the number of toes in the fore feet of *Protylopus*, but there is very little doubt that there were four. In one specimen which I have referred to this genus, the lateral toes of the hind feet are reduced to mere nodular splints, while in another specimen in the collection there is evidence that the lateral toes of the hind feet were complete but very slender. In *Poëbrotherium* the lateral toes are reduced to vestiges in both fore and hind feet, while in the later forms even these vestiges disappear.

The modifications in the character of the feet refer to what may be properly termed a retrograde change, if we regard the subject from the standpoint of the podial evolution of the Ungulates generally. *Protylopus*, as well as *Poëbrotherium* and *Gomphotherium*, had apparently a fully developed unguligrade gait. The ungual phalanges are relatively high, keeled upon their dorsal surfaces, and more or less flattened upon their opposed sides. The distal ends of the proximal phalanges do not have their articular surfaces extended upon the dorsal side, while the distal phalanges of the second row have this surface well extended upon the dorsal portion of the bone. This arrangement is highly characteristic of all the higher Artiodactyla, and is the strongest possible evidence that can be adduced from the skeleton of the unguligrade gait.

In *Procamelus*, on the other hand, the distal ends of the proximal phalanges, as well as those of the second row, have the articular surfaces reaching well back upon the dorsal aspect, just as in the modern Camel and Llama, and this we know to be accompanied by the digitigrade gait and the peculiar cushioned foot. There is likewise a marked change in the character of the ungual phalanges, which are much reduced and flattened vertically especially in *Camelus*.

The conclusion is obvious, therefore, that this peculiar tylopod character is secondary, and was developed from the unguligrade condition. Just what led to it is impossible to say. Zittell's explanation that it resulted as a consequence of the coössification of the metapodials can hardly be the correct one, since the same thing occurred in all of the Pecora in which the unguligrade gait was retained.

The coössification of the metapodials and the consequent formation of a cannon bone took place comparatively late in the history of the phylum, much later in fact than the union of the ulna and radius. In *Protylopus* and *Poëbrotherium* the metapodials were not only free but capable of considerable independent movement, as indicated by the facets. The opposed surfaces of these bones, moreover, are relatively smooth and less flattened than in the succeeding *Gomphotherium*. In this latter genus the bones are more closely applied to each other, the surfaces roughened, and the articular facets, by which they join one another, much reduced. The feet of *Protolabis* are wholly unknown. In one species of *Procamelus* (*P. gracilis*), there is evidence that the metapodials of the fore feet were not united until late in life, if at all, while those of the hind foot were fully coössified into a cannon bone. *Procamelus occidentalis* had the posterior metapodials fully united and those of the fore foot only partially coössified, being free at their proximal ends for some distance.

In the Pleistocene species the metapodials were fully united into a cannon bone early in life, and in the modern Camelidæ bony union of these elements takes place before birth, almost as soon in fact as bony tissue is thrown down in the shafts.

It will thus be seen that the coössification of the metapodials, as well as that of the ulna and radius, was a gradual process, and

is always found first in the old individuals; its further advance has consisted in reducing the time of its appearance to such an extent that it is now altogether intra uterine. I leave for a future paper the discussion of these important facts in their relation to the question of the transmission of acquired characters. I may state here, however, that they furnish very strong presumptive, if not conclusive, evidence of the transmission of a pathological change.

The modifications of the skull include some minor changes in the position of the orbit, its inclosure by a complete bony rim, a broadening of the frontal region and a shortening of the nasal bones. There have also occurred some modifications of the tympanic bullæ and a change in the position of the posterior nares. The most important of all the modifications connected with the skull, however, are found in the dentition, and here the changes are quite as profound as have occurred in any other group of mammals within the same length of time. In *Protylopus* the structure of the molars is, to a large extent, intermediate between the bunodont and selenodont pattern. This is especially seen in the lower molars, the internal cusps of which are rather more conical than crescentic; the outer cusps are not perfectly crescentic, and the crowns of all the molars are very short. The lower canines are small and incisiform, the inferior incisors are sub-erect, and there is evidence of the fact that these teeth had a more or less effective bite against the upper ones.

In *Poëbrotherium* the crowns of the molars are much more elongated and the crescents fully developed. The lower canine is yet incisiform in the older species, *P. wilsoni*, but has begun to assume the caniniform shape in the later *P. labiatum*. The lower incisors have a very procumbent position, but while yet opposing the superior incisors, the effectiveness of the bite is considerably diminished on this account. The only important change in the teeth of the John Day species is seen in the reduction in size of the first upper premolar and the assumption of the caniniform shape of the lower canine. The inferior dentition of *Protolabis* is not known, but an important change has taken place in the second superior premolar, in that it is much reduced in size.

If the specimen which I have referred to *Procamelus robustus* is normal, it offers the first evidence of the diminution in size,

leading to the final loss of the first and second pair of superior incisors. In *Procamelus occidentalis* these teeth have completely disappeared in the adult, but vestiges of them have been found in the young, a fact which was demonstrated by Cope.

Pliauchenia furnishes us with the next step in which the second premolar has disappeared from the lower jaw, leaving the first, third and fourth of this series. The superior premolar dentition of this genus has not yet been found, but it is highly probable that some of the species will show a loss of the corresponding tooth in the upper jaw. It is highly probable that at this stage, or the one preceding, three diverging lines took origin, of which one continued into *Auchenia*, another into *Camelus*, and a third into *Camelops* and *Eschatius*.

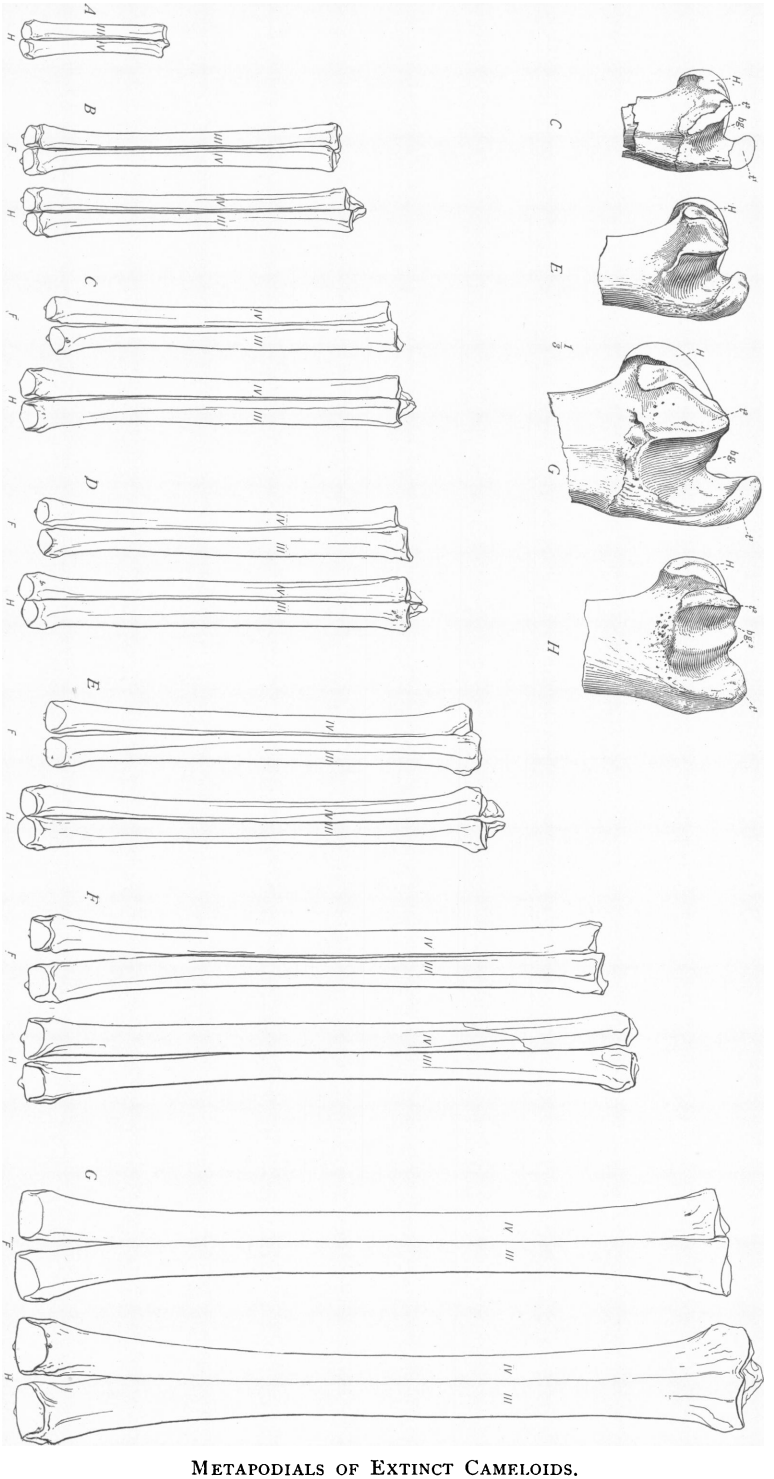
From *Pliauchenia* the transition is easy to *Camelus*, in which there are three premolars in the upper and two in the lower jaw. In *Auchenia* the premolars are still further reduced, there being two above and only one below. The first evidence of the peculiar buttress found in the lower molars of this genus is seen in *Procamelus gracilis*, and on this account I am of the opinion that this species is the ancestor of the Llamas. It is highly probable that the species migrated to South America at the close of the Miocene, and that the intermediate links between it and the living genus will be found in that country. *Camelops* could have easily been derived from *Pliauchenia spatula*, requiring the loss of only two premolars in the lower jaw and probably one above; in a like manner *Eschatius* follows *Camelops* and carries dental reduction to the extreme limit reached in the Camel group.

In this attempt to indicate the more exact specific evolution of the group one is necessarily handicapped by want of knowledge of the osteology of many species which are at present represented by fragmentary remains only. I doubt not that it will be materially altered when we come to have a more perfect understanding of these forms. I give herewith a table of distribution in time, of the Cameloids treated of in the foregoing pages.

Periods.	Formations.	Thickness.	Faunal Divisions.	Evolution of Species.
Recent.	Recent.			*Camelus.* *Auchenia.*
Pleistocene.	Equus.	150	Equus.	*Eschatius* *Camelus americanus.* *Camelops kansanus.* *Camelops vitikerianus.*
Pliocene.	Blanco.	100	Pliauchenia.	
			Hippidium.	*Pliauchenia spatula.*
Miocene.	Loup Fork.	400	Procamelus.	*Pliauchenia humphresiana.* *P. minima.* *Procamelis occidentalis.* *Procamelus robustus.* *P. gracilis.*
	Deep River.	200	Cyclopidius.	*Protolabis.*
		INTERVAL	OF MIGRATION.	
	John Day.	1000	Merycochœrus.	*Gomphotherium cameloides.*
			Diceratherium.	*Gomphotherium sternbergi.*
Oligocene.	White River.	800	Protoceras.	
			Oreodon.	*Poëbrotherium labiatum.*
			Titanotherium.	*Poebrotherium wilsoni.*
Eocene.	Uinta.	800	Diplacodon.	*Protylopus.* *Parameryx.*
			Telmatotherium.	
	Bridger.	2000	Uintatherium.	*? Homacodon.*
	Wind River.	800	Bathyopsis.	
	Wasatch.	2000	Coryphodon.	*? Pantolestes.*
	Torrejon.	300	Pantolambda.	
	Puerco.	500	Polymastodon.	

EXPLANATION OF PLATE XI.

A, hind metapodials of *Protylopus petersoni ; B*, fore and hind metapodials of *Poëbrotherium wilsoni ; C*, fore and hind metapodials and head of humerus of *Poëbrotherium labiatum ; D*, same species from higher level ; *E*, fore and hind metapodials and head of humerus of *Gomphotherium sternbergi ; F*, fore and hind metapodials of *Gomphotherium cameloides ; G*, fore and hind metapodials and head of humerus of *Procamelus occidentalis ; H*, head of humerus of *Auchenia lama.*



METAPODIALS OF EXTINCT CAMELOIDS.