# MEMOIRS

## OF THE

# American Museum of Natural History.

VOLUME I, PART VII.

Fossil Mammals of the Tertiary of Northeastern
Colorado.

By W. D. MATTHEW.

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# FOSSIL MAMMALS OF THE TERTIARY OF NORTHEASTERN COLORADO.

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VII.—FOSSIL MAMMALS OF THE TERTIARY OF NORTH-
EASTERN COLORADO.

AMERICAN MUSEUM COLLECTION OF 1898.

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## I.—INTRODUCTORY.

During the summer of 1898 the Department of Vertebrate Palæontology
under the direction of Professor Henry F. Osborn, Curator, sent out two expedi-
tions into the fossil beds of the Western States. One of these, in charge of the
writer, had for its object the collection of fossil mammals from the Neocene beds
of the Great Plains, and succeeded in northeastern Colorado in making a large
and interesting collection from the White River and Loup Fork formations of
that region. Besides the writer, the party consisted of Mr. Barnum Brown, Mr.
H. T. Martin, and Thos. Maxwell, teamster. I take great pleasure in calling
attention to the number of important specimens discovered by Mr. Martin, and
the exceptional skill with which, under guidance of Mr. Brown, the most fragile
specimens were taken up, and forwarded to the Museum without suffering the
slightest damage. The stratigraphic observations were made chiefly by myself;
they are unfortunately limited to the part explored early in the season, as I was

obliged to leave the party early in the summer. Mr. Brown, however, kept careful records of the occurrence and level of the specimens later discovered, as far as it was possible to identify the horizons with those distinguished at first.

The study of the collection has been carried on intermittently, hindered in part by the necessary delay in preparing the specimens ; some results have already been published in the American Museum 'Bulletin.'[1] In the present memoir the more complete description of the Horses and Rhinoceroses is reserved for special studies on those groups by Prof. Osborn and Mr. Gidley, now in progress.

## II.—STRATIGRAPHY.

### CHARACTERS OF THE TERTIARY IN N. E. COLORADO.

The White River formation, " Miocene " of most writers, Lower Miocene of Cope, Oligocene of the more recent American work, is the oldest Tertiary of this region. It consists of a series of fine chalky beds of about 300 feet thickness, pinkish white to buff-colored, very uniform in composition, underlying the level plains and well exposed in an irregular line of cliffs and badlands on the northern side of the broad open valley of the Platte.

Over the White River beds, and separated from them by an erosion-unconformity not always well distinguishable, lie the coarse gravels and half-consolidated sand and mud-beds of the Loup Fork, the heavy gravels filling erosion valleys in the older beds, the finer beds bringing up the level to the top of the plains. No rock projects above the level surface of the plains, which in this region is scantily covered by a thin gravelly layer, indicating apparently a very slow superficial erosion.

### Horsetail Creek Beds.

The lower part of the White River formation, the Titanotherium beds, Horizon A of Hayden and Leidy, consists of hard white or grayish white clays with considerable horizontal cleavage and containing some layers of sandstone, apparently of limited extent. The fauna is a scanty one, the recorded species limited to a few genera as follows :

? *Cænopus* sp. indet.
*Titanotherium* (*Symborodon*) *acer, altirostris, bucco, torvum, trigonoceras, helocerus, hypoceras.*
*Elotherium* ? *mortoni,* ? *crassum, ramosum* (upper sandstone layer).
*Poëbrotherium* sp. indesc.
? Oreodont indet.
? *Mesohippus* sp. indet.

The apparent scantiness of this fauna may be in part a matter of preservation rather than occurrence, for our party found great numbers of scattered bones and several badly preserved skulls, so fragmentary as not to repay collecting. The skeletons seem to have become much more broken up, and are not nearly so well preserved as in the upper beds. Remains of Rhinoceroses, Oreodonts, and Horses, too fragmentary for identification, were found by our party.

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[1] Matthew, '99 ; Wortman and Matthew, '99.

*Cedar Creek and Martin Cañon Beds.*

Above the Titanotherium assise lie the Oreodon and Leptauchenia beds, Horizons B and C of Hayden and Leidy, fine, light-colored, pinkish or buff clays, much softer than those of Hor. A, and becoming progressively softer towards the top of the formation. No horizontal cleavage or fine lamination is discernible in these beds, but from a distance the horizontal color-bands are sometimes marked and very uniform. They do not, however, present any wide variation in color. The fauna is large and varied. The upper part of the formation is separated on account of the difference in fauna, but no stratigraphic demarcation can be made out, the beds becoming gradually finer and softer as we ascend, but retaining all their characters to the top. The following list shows the faunal distinctions :

| OREODON ASSISE. | LEPTAUCHENIA ASSISE. |
|---|---|
| *Leptochœrus lemurinus.* | |
| "      *spectabilis.* | |
| ? *Didelphys* (*Peratherium*) sp. div. | *Proscalops miocænus.* |
| * *Mesodectes caniculus.* | |
| * *Geolabis rhynchæus.* | |
| * *Domnina crassigenis.* | |
| *Ischyromys typus.* | |
| * *Sciurus relictus.* | |
| "      cf. *vortmani.* | |
| * *Heliscomys vetus.* | |
| * *Gymnoptychus minutus.* | |
| "      *trilophus.* | |
| *Eumys elegans.* | |
| *Palæolagus haydeni.* | *Palæolagus haydeni.* |
| "      *intermedius.* | "      *intermedius.* |
| "      *turgidus.* | |
| *Hyænodon cruentus.* | |
| "      *horridus.* | |
| "      *crucians.* | |
| * *Daphænus vetus.* | |
| "      *hartshornianus.* | |
| *Cynodictis gregarius.* | *Phlaocyon leucosteus.* |
| "      *lippincottianus.* | *Cynodictis temnodon.* |
| * *Bunælurus lagophagus.* | |
| *Dinictis squalidens.* | |
| *Hoplophoneus oreodontis.* | |
| "      sp. | |
| *Mesohippus bairdi.* | *Anchippus,* cf. *texanus.* |
| *Hyracodon nebrascensis.* | *Hyracodon* sp. |
| "      *arcidens.* | |
| *Cænopus mitis.* | |
| "      *occidentalis.* | |
| *Elotherium* ? *crassum* | |
| "      ? *ramosum.* | *Leptauchenia decora.* |

* Cope collection only ; horizon uncertain ; placed here provisionally, as there is no evidence that any of Cope's collections came from the Leptauchenia level.

Oreodon culbertsoni.
"    gracilis.
Poëbrotherium wilsoni.
"        labiatum.
Hypertragulus calcaratus.
Leptomeryx evansi.
Hypisodus minimus.
* Stibarus obtusilobus.

Eporeodon major.
Merycochœrus proprius.
Protomeryx halli.
"        cedrensis.

Leptomeryx sp.

Sandstone layers occur in the western part of the exposure, of limited extent, and probably, as elsewhere in the White River, unconformable to the clays, filling little erosion valleys cut by streams during the progress of the formation. In the part of the formation observed by the writer there were no sandstone layers. Three good skulls of *Cænopus* and some other remains were found in these sandstones.

## Pawnee Creek Beds.

(See Fig. 17, p. 398.)

Where the White River is not eroded, the top is some fifty feet below the surface of the plains, and conformably overlain by fine muddy sand semi-consolidated, with sometimes one or more layers of coarse shingle. At other points the White River beds were deeply eroded before the deposition of the Loup Fork formation, and the valleys are filled up chiefly with coarse shingle beds, which contain rolled fragments of various mammals, the following being recognizable :

? Canis, cf. temerarius.
Carnivora indet.
Anchippus, cf. texanus. .
Protohippus sp.
? Blastomeryx sp.

Hipparion sp.
? Moropus sp.[1]
Merycochœrus sp.
Merychyus sp.

The soft muddy brown sandstone contains numerous hard calcareous gray concretionary masses usually a foot or two in diameter. This appears to correspond in lithographic characters to Div. D of Hayden, and to the Arickaree formation of Darton in Nebraska, and contains the following species :

Mylagaulus monodon.
Mustela ogygia.
? Anchitherium sp.
Anchippus texanus.
Protohippus ? perditus.
"    ? sejunctus.
Hipparion sp.
Aphelops profectus.
Merycochœrus proprius.

Merycochœrus rusticus.
Merychyus elegans.
"        medius.
Protolabis montanus.
"        angustidens.
Procamelus fissidens.
"        robustus.
"        altus.
Blastomeryx gemmifer.

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* Cope Collection only ; horizon uncertain ; placed here provisionally, as there is no evidence that any of Cope's collections came from the Leptauchenia level.

[1] Characteristic chalicothere bones, but apparently distinct from any of the European genera. If *Moropus* is edentate this animal must be renamed.

Above this, separated by a shingle layer (not always present), are beds of clearer and coarser sand extending to the surface of the plains, sometimes hardly consolidated, at others hard, coarse, crossbedded gray sandstones. They may correspond to Horizon E of Hayden and to the Ogallalla formation of Darton, but they are not well displayed in the region I have seen, and the separation from Hor. D appears to be very inconstant. The difference in fauna is equally unsatisfactory, and the separation will not here be maintained. As far as determinable the species occurring are :

*Canis* cf. *temerarius*.
Felid indet.
? *Tetrabelodon* sp. indet.
*Anchippus* sp.
*Protohippus* sp.
*Hipparion* sp.

*Pliohippus mirabilis*.
*Merycochœrus* sp.
*Merychyus* sp.
*Procamelus* sp.
*Blastomeryx* sp.

A number of species described by Prof. Cope appear from their matrix to have come from this horizon :

*Tomarctus brevirostris*.
*Pseudælurus intrepidus*.
*Tetrabelodon brevidens*.

*Aphelops megalodus*.
*Protolabis heterodontus*.

It appeared probable that the heavy beds of coarse gravel filling erosion valleys are connected with these upper beds rather than with the finer concretionary sandstones and are continuous with the shingle bed overlying the latter rather than the one underneath it. The *Moropus* and other species should therefore also be added to this list.

The divisions as found in this part of Colorado correspond most nearly with those determined by Mr. Darton in western Nebraska in 1897. The Titanotherium beds are the same in character and position ; the Oreodon and Leptauchenia correspond with his Brulé clays though how accurately it is impossible to say in the absence of lists of the Brulé fauna. The Gering formation I did not recognize ; the Arickaree "fine sand with pipy concretions" and the Ogallalla "impure calcareous grit, or sand cemented with carbonate of lime," often with beds of conglomerate at its base, correspond fairly well with the Loup Fork beds of Cedar Creek. The upper division of the Loup Fork at Cedar Creek, while of the same character as the "Mortar Beds" of Kansas, is considerably older as judged by the fauna, than those of the Republican River Valley, and somewhat older than the typical Loup Fork of central Nebraska.

## CONDITIONS OF DEPOSITION.

It was supposed by all the earlier geologists that the Western Tertiary and Quaternary mammal beds were deposited in vast fresh-water lakes formed by the upheaval of mountain chains across pre-existent drainage basins, and destroyed

by deepening of the outlet cañon and drying up of the climate. This very attractive theory seems to have been based in the first place on the supposed analogy with the great Quaternary extension of some of the salt-lakes of the Great Basin, and secondly on the general lake-like horizontality of the uneroded sediments of the Tertiary basins. It reached its culmination in its application to the extended and scattered Tertiary deposits of the Great Plains, which were supposed to have been deposited in a vast lake of extent equal to several Western States or to the whole of Europe excluding Russia. Within the last few years much exception has been taken to the universal application of this theory. Messrs. Gilbert, Haworth and Williston, Davis, and others have regarded the beds in which their special studies were made as being fluviatile rather than lacustrine, and the writer in a brief note in the 'American Naturalist' ('99-2), summarized some reasons for regarding a great part of the White River formation as being a subaërial (æolian) deposit, of similar origin to the prairie loess of western Kansas and elsewhere.

The origin of these badlands is fully discussed, with especial regard to the Eocene basins, by Profs. Davis,[1] Chamberlin, and Smith.[2] Most of the reasons, pro and con, given by these gentlemen apply also to the Tertiary of the Plains, although there are features of importance peculiar to the latter deposits. For example:—the predominance of fine white chalky clays in the middle and lower beds, and subordination of sandstones or laminated clays; the great extent and scattered character of the beds; the absence of a definite mountain-bounded basin; and especially the strictly terrestrial character of the fauna of the *clays* (a point to be discussed later).

In view of the important bearing that the origin of the sediments must of necessity have on the discussion of the character and relationships of the fauna found in them, it will be advisable to re-state this evidence against the lacustrine origin of the Tertiary of the Plains and that for the æolian origin of a great part of the White River formation.

### A.—Stratigraphic Evidence.

1. If the sediments were deposited in a single great lake as was assumed by King and others, the lake must have been sea-like in size and its action on its boundaries would have been comparable to that of a sea. Hence during the long period of its existence it should have cut heavy terraces all around its shores. This is not the case. There are no terraces as far as I am aware.

2. The lake must have been caused by deformation of the earth's surface. Such deformation must have been so sudden as greatly to exceed the rate at which erosion was working to restore the old state of affairs. For a slow secular rise of the eastern border of the Plains would result in the aggradation of the valleys but not in the formation of extensive lakes unless the combined process of cutting down the outlet and filling in the deposition area were so far outstripped

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[1] Proc. Amer. Acad. Arts and Sci., 1900, Vol. XXXV, p. 345.  [2] Jour. Geol., 1900.

by the rise of the mountain barrier that the flood-plain slope was reduced to less than zero.[1]   There is at present no basin nor indication of a basin on the Great Plains.   The thin and scattered Tertiary beds lie on a surface sloping gently and uniformly toward the east, and they become gradually thinner and finer with a continually smaller proportion of the coarser sediments as they are farther from the mountains, the Loup Fork beds concealing the eastern margin of the White River, and the Pleistocene loess the Loup Fork.   Where the beds approach the Rocky Mountains and swing around the base of the Black Hills, they are much thicker with a large proportion of coarse sediment.   But no such thickening is observed or indicated to the eastward or southward, and in these directions there is no trace of a mountain barrier, outlet cañon, terraced margins, or anything of the kind.   On the other hand the conditions are exactly what we should expect to find in sediments partly river deposited, partly carried or rearranged by the wind, brought down from the mountain areas to the west and north and spread in irregular sheets over the plains, becoming thinner, finer, and more interrupted to the east and south, and finally disappearing entirely (the Loup Fork directly overlies the Cretaceous at points in Kansas and Nebraska where the contact is visible).

3. The method in which the coarse beds are intercalated among the fine clays compels us to believe at least in a frequent interruption of lacustrine conditions.   These beds are very often of limited extent and lens-shaped in section, unconformable to the clays beneath them, showing marked cross-bedding and other swift current characters.   Such beds are found far from the western borders of the White River areas, although less commonly as we get farther from the mountains.   They could not be deposited far from the borders of a lake— the clays could not be deposited near the margin.   If lake deposits these indicate frequent, spasmodic, and extensive changes in the level of the lake.   If river deposits they indicate simply the change of course of a stream meandering over its flood-plain.

4. In a lake the marginal sediments must of necessity be of vastly greater thickness than the fine uniform sediments of the central parts.   The central sediments, being softer, thinner, and lower lying, would be first attacked by the renewed erosion after the draining or filling of the lake, and would be the first to disappear.   In the Great Plains Tertiary, on the contrary, we find the fine White River clays in greatest bulk and lying at a high level above the surrounding plains, while the coarse sediments are either absent or intercalated with or overlying the finer beds.   In some of the minor outlying basins, as in the Laramie Plains, Wyoming, the characteristic relations of the White River clays are most clearly shown, confined within a small area.   Here there is a mountain barrier to the east and south, and broken, irregular country to the north and west in which

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[1] Otherwise the sediments will form a flood-plain above the barrier, broader and longer as it continues to rise, the coarser sediments being deposited at its upper end, the finer sediments towards the lower end, but transgressing over the surface of the coarser beds as the plain increases in length and width.

directions the drainage runs.   The chief White River area is a high, isolated, flat-topped mesa, several hundred feet above the Upper Cretaceous mesa of the plains, and lying near its northern margin.   The sides of the mesa are eroded into steep badlands, which show that it is composed almost entirely of fine clays, a few sandstone lenses only, and these resting on eroded surfaces and gullies in the clays beneath, and less clearly separated from the more or less conformable overlying clays.   Nowhere is there any trace of the marginal sediments, which if the clays were deposited in an Oligocene lake should by proportion have been thousands of feet thick.   No cause can be assigned in the topography sufficient for the removal of such marginal beds, while the central ones still remain, and it seems impossible to believe that they ever existed.

5. The contact between the Tertiary and the older formations I had the opportunity of observing at Alcova on the North Platte.   Here, forming as usual the highest mesa level, it transgresses the upturned edges of the various formations from the Palæozoic granite to the Cretaceous.   At the contact with the older rock at every point observed, the latter is broken up into angular blocks, becoming smaller and more rounded, with a larger proportion of fine material derived from the disintegration of the older rock, finally with an increasing admixture of the White River clay until it merges into the upper formation, here composed of typical unlaminated clays.   There is no waterworn conglomerate at the base, and there are no coarse beds of the upper formation underlying the fine ones.   Now an advancing lake margin could hardly fail to do some sorting on the weathered rock surface ; here it is clear that there was none.   Should this sort of contact be a usual one it would also tell strongly, though not conclusively, against the stream origin of the clays, for the areas of heavy deposition (the ones most likely to escape subsequent erosion) would be those near the streams, and would certainly very often be begun by the change of the river course to the area in question, resulting at first in rapid deposition of coarse material.   Back-water deposits from a stream should, however, give a similar contact to that observed.   It certainly accords exactly with what one would expect to find if the clays are of terrestrial origin.   The contact of the Titanotherium beds with the older formations has been observed in various places, and is certainly not a soil-weathering contact, a conglomerate usually marking the base, and other evidences of aqueous action appearing.   But the Titanotherium beds are laminated clays, intimately associated with the sandstones and mud-pebble beds that occur with them, and precisely similar to some of the lenses of sandstone and laminated clays that lie on the eroded surfaces and gullies of the unlaminated clays.

6. The lamination of the clays has an important bearing on their origin.   All fine sediments slowly deposited from water are laminated, the reason being that the friction of even very slight motion in the water above prevents permanency in the position of the particles of sediment until they are so arranged that they will suffer least disturbance from it.   With air deposited sediments this friction is so slight as to be negligible, and accordingly such particles lie in the position in which

they fall, and there is no general rearrangement of them to a horizontal surface, and consequently no cleavage in the resulting rock. Rapidly deposited water sediments have often not time for rearrangement and are then also devoid of cleavage. Now this lack of cleavage is a characteristic feature of the Oreodon and Leptauchenia beds. Abyssal ocean deposits, such as the chalk, are often perfectly massive, but cleavage would hardly be lacking in sediments which, if the lake theory be true, were deposited in such shallow water that the fluctuations of the lake level caused frequent alternations with marginal or fluviatile sandstones. There is no lack of cleavage in the Niobrara chalks, closely similar in composition, and from the waste of which the White River clays were, no doubt, derived ; nor in the Green River shales, which *were* deposited in a great fresh-water lake, as is shown by their abundant fossil fish. Loess beds on the other hand, are notably distinguished by their unlaminated character.

There is indeed a well marked horizontal *banding* in the White River clays, and this has been taken by some writers as proof of their lacustrine origin, in consequence apparently of its being described as absent in the familiar text-book example of loess, that described by Von Richthoven in China. But the absence of banding cannot mean anything beyond a uniformity of climate ; seasonal or periodical changes of wind would produce changes in the source of supply of the deposits ; changes of climate would produce annual or periodic interruptions in the supply, and different chemical conditions from the temporarily greater relative amount of plant matter in the beds ; and either of these changes might well be, and probably would be, recorded in the consolidated beds by changes in color indicative of the changes in composition. The banding can hardly be considered a serious objection to the loess origin of the clays—there are others which I should consider much more important.

The chief of these is the question of the source of supply. Three sources present themselves, viz.— desert areas to the west and south (the prevalent winds in the dry season — summer and autumn — are now westerly and southwesterly, and we may fairly suppose that the same was then the case) ; erosion of various buttes and mesas chiefly of Niobrara chalk ; sorting and erosion of the flood-plain sediments of the rivers. Of these sources, the first seems too distant, the second and third inadequate for the hundreds of feet of clays we see. One should, however, remember the wide area over which the White River clays are found, and the comparatively small proportion of the surface which they now cover, except in a few localities where the source of supply from river erosion was obviously unusually great. I think too that the importance of river flood-plains as a source of supply is likely to be underestimated. The areas are limited it is true, but the supply of sediment is unlimited and the conditions for sorting and removal by the wind are exceptionally favorable, if we take as example the modern rivers of the Plains. It should be remembered that while rivers bring large amounts they also take away large amounts, whereas whatever wind-borne sediment is caught in prairie grasses is not likely to escape again.

## B.—Palæontological Evidence.

Much more convincing than the stratigraphic arguments are those derived from the fauna. Dr. Smith, reviewing only the stratigraphic points of my paper in the 'American Naturalist,' considers that the lacustrine origin is at least an open question but that the æolian origin of the clays cannot be considered as demonstrated. It is by no means intended to assert here the æolian origin of these Tertiary clays in all localities, although some additional evidence has been given above for their terrestrial, or at least non-lacustrine origin in other regions than Colorado. But the nature of the organic remains, where such have been found, seem to definitely negative the idea of any vast lake, and to favor less the theory of a series of lagoons and swamps than that of a broad, open, and comparatively dry plain, with shallow, probably wooded, rivers meandering over parts of it, and deposits partly or chiefly brought by rivers, but in large part re-distributed over the higher sodded grass-land by the agency of the wind. This would mean an approximation to the present conditions of climate, though probably not so dry as that of the region now is. And this condition of affairs is what we have reason to expect from modern conditions in the same region, and from what we know of the general evolution of this part of the continent. The burden of proof that climatic and geologic conditions were so widely different from those of modern times as to sustain a huge inland sea of fresh-water in the now arid Plains, lies not with the opponent but with the exponent of the lake theory.

The palæontological evidence is as follows :

1. The fauna of the White River *clays* is a strictly terrestrial fauna. It has not hitherto been distinguished from the fauna of the associated *sandstones*, but the two are in fact very different, as will be shown later on. There are no aquatic invertebrates, no fish, no aquatic reptiles or mammals in the clays. Land tortoises are the most abundant fossils, lizards and snakes also occur, and land mammals are in great numbers and variety, while aquatic mammals are absent.[1] Now it is true that land animals are found in *estuarine* or *delta* deposits, where their remains are swept down by floods along with a much greater proportion of remains of plants and of the aquatic inhabitants of the delta region. Types of such deposits are found in the European Tertiary beds, a fine example being afforded by the Eocene strata of the Paris Basin, which are obviously shore deposits, alternately brackish and fresh, layers of sand, mud, lignite, clay, etc., following one after another, crowded with shells and other invertebrates belonging to the indigenous fauna, and with the mammals a mere accidental addition, playing only a subordinate part, rare and generally fragmentary.[2] But *land* animals must

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[1] *Leptauchenia* is found in the uppermost clays and has been considered on insufficient evidence to be aquatic. The character of the teeth favors its being a grass eater.

[2] This does not include the " gyps lacustre," which contains a land fauna and flora but no aquatic forms. The finely preserved and historic specimens of fossil mammals from the Paris Eocene are all from the " gyps," a formation in some respects resembling the White River " clays," and perhaps of somewhat similar origin.

always be an extreme rarity in an *open-sea* or *open-lake* sediment. For every animal that is drowned and swept down by floods, thousands die on land, and for every river-brought carcass that by some chance floats out to the open sea thousands must be stranded and buried in the delta or flood-plain of the river. I cannot recall any open-sea deposit in which land animals form an appreciable proportion of the fossils. And to claim as an open-lake sediment a deposit where they form the *whole* of the fauna demands impossible conditions.

2. Furthermore, there are some peculiarities in the preservation of the fossils that accord with their terrestrial inhumation rather than with their burial in lake sediment. Skeletons more or less complete are frequent, although often lacking a head, a jaw, the end of the tail, the fore-limbs or the lower part of the hind-limbs, and often with the upper ribs bitten off so as to expose the interior of the body cavity; some of the bones, very frequently, removed only a short distance. These indicate that the carcass was devoured by carnivora in the place where it was subsequently buried, and that the trunk suffered no change in position, while the outlying parts were dragged off and either carried away or merely displaced in stripping the bones. This is well illustrated in our incomplete *Dinictis* skeleton (Fig. 14). At other times all the bones are displaced although very few may be missing — this is especially the case with the larger skeletons. Separate limbs and bones are also often found; these are often checked (whether from exposure to the sun or not, can hardly be determined) and sometimes show marks of teeth.[1] Parts of bones, especially vertebræ, are often eaten away in a manner that suggests the work of insects (cf. *Dermestes*). The skeleton of *Phlaocyon* suffered considerably in this way. Hollows in the bones (such as the cellular hollows in the skull of *Merycochœrus*, the tympanic bullæ of *Phlaocyon*), are still *empty*, never having been filled by mud or crushed in. This indicates that the specimen was not buried in oozy mud, which would have flowed in, nor in harder mud, which under the water-pressure would have crushed in what it could not fill. It indicates that the matrix, while fine and soft, was firm enough to resist crushing from the pressure above and probably not subject to the weakening effects of a large admixture of water. I doubt very much whether the upper part of the White River beds of Colorado has ever been under any great pressure or for any long period below the water level. It retains a singular amount of pulverulent character in some layers and, although other layers are much harder, and almost flinty, the whole rock is very porous, not like the solid clays of

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[1] In this connection an occurrence of bones in the Loup Fork beds deserves mention. It consisted of a number of separated limbs and limb-bones of at least three individuals of two species of Camel and two individuals of Horse, piled one on top of another as though they had been the bone pile of some carnivorous animal, and most of them showing marks of teeth. It is perhaps permissible to imagine that the animal had his lair in thickets by the river bank, and that a fortunate chance preserved the remains of his bone heap for us. Possibly the curious fact that limbs and skulls of camels and horses are frequently found in the Loup Fork sandstones, while complete skeletons of either have not yet been discovered, may be explained on this theory, that the Loup Fork sands were mainly deposited in the wooded river flood-plains, and the camels and horses were inhabitants of open country. The carnivores or carrion eaters of the thickets (*e. g.*, *Ælurodon* and *Amphicyon*) might well find the carcasses of such large animals too heavy to carry away and content themselves with carrying off the more manageable head and neck or limbs.

the South Dakota White River, which are overlain by so much greater thickness of aqueous sediment.

All these conditions are precisely those of the skeletons found to-day on the surface of the plains. The long exposure to the atmosphere, the much longer exposure to oxidation by alternate wetting and drying before they are permanently beneath the water level, cleans and bleaches the bones[1] and destroys all vegetable matter. Carrion feeders lay open the body-cavity and devour the entrails, and bite off and carry away easily removable parts, often dissociating the greater part of the skeleton, while the remainder, if long enough exposed, falls apart of itself. Insects eat out certain parts, especially haunting the under side of the trunk and nibbling out parts of the more cartilaginous bones on the under side. The large block of *Merycochœri* (Fig. 20) strongly suggests the appearance of the bleached skeletons of a group of antelopes or sheep caught by a blizzard or victims of some like accident. That a combination of circumstances might arise by which a similar appearance would be produced in the remains of animals carried out to sea is possible, but, as observed above, such occurrences must be excessively rare.

The fact that the fauna is a land fauna appears to me sufficient in itself to disprove the theory that the beds were deposited in the bottom of a great lake. Land animals in such beds might be found as a rare accident, but only so; and the accident is so rare that we can hardly parallel it from any other formation. The absence of a water fauna is as significant as the presence of a land fauna, for we cannot say in this case that the conditions were unfavorable for preservation. But I shall show later that the fauna of the clays is not only a land fauna, but by contrast with the fauna of the sandstones is distinctively an *upland fauna*, such as should be characteristic of open, grassy plains as opposed to forest-clad regions. If the clays were deposited in a broad lake and the organic remains in them brought down by streams and floated out, why should the streams have selected, for floating out, all the animals that did *not* live near their banks, and carefully have omitted to include those that did! I am unable to conceive of any possible, much less any probable, conditions that would bring about such a result. On the other hand, if the clays are mainly æolian and the sandstones fluviatile, the presence of an exclusively upland or open-plains fauna in the one and of the forest fauna (along with some aquatic types) in the other, is exactly what we should expect, just as naturally as we should expect to find a marine fauna in marine deposits like the Niobrara, a swamp fauna in the swamp deposits of the Carboniferous or Triassic coal beds or the Como beds of the Jurassic or the Laramie Cretaceous, and a fresh-water fauna in the marl beds of the little glacial lakes of the East.

The alternative theories to that of lake origin for the White River clays seem to be either that they are flood-plain sediments formed in the back-water lagoons, or that they are æolian loess formed on grass-covered prairies. That a part

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[1] Notwithstanding the perfection of the skeletons no trace of the soft portions of these animals is found.

of the clays (the laminated variety), and all of the sandstones, are flood-plain deposits is probable, both from stratigraphic and faunal reasons. That a large part of the clays (the unlaminated variety) is somewhat more probably of terrestrial origin I have endeavored to show above. Even for these clays the flood-plain theory of origin appears to be a not improbable alternate, but it does not seem that the hypothesis of a vast lake can be reconciled with the facts, especially the peculiarities of the fauna, stated above, in accounting for the origin either of the sands or of the clays.

The existence in the region just east and southeast of the White River area of a more recent sediment resembling the clays in many important characters, both in stratigraphy and fossils, and due apparently to an æolian sedimentation commenced early in the Pleistocene and still continuing, is another argument for the theory here upheld of the origin of the older formation, and it enables us to see more clearly the precise method of the sedimentation. While there is much discussion as to the mode of origin of the loess in the Mississippi Valley, the loess of the Plains, in the western parts of Kansas and Nebraska, is generally, I believe, considered as strictly terrestrial. The sediments brought down by the various rivers from the mountains are deposited largely in the vast semi-desert tract of eastern Wyoming, Colorado, and New Mexico. Here the prevalent westerly winds sift and sort them, rolling the sands but a short distance and leaving them as residual deposits, while all the finer material is carried much farther and caught by the grassy surface of the prairies to the east, finally merging perhaps into true flood-plain or lacustrine mud in the valley of the Mississippi. The denser the grass the more dust it sifts out and holds, hence the tendency to fill all lagoons and hollows, and bring the prairie surface to one uniform level. At the borders of such an area the sedimentation goes on until the slope of the border becomes too steep for grass to grow on it ; it is then rather rapidly undermined and cut into by the wind. Hence the tendency in erosion to attack the edges and cut them up into rapidly eroding badlands, while the level grass-covered top is well protected, and an isolated, flat-topped mesa is formed. The fossils found in the loess are the fauna of the Plains, and are preserved in the same way as those of the White River, except that they are incompletely or not at all infiltrated with mineral matter, and are less broken up by subsequent earth movements than those of the older formation. I have collected specimens of *Equus* bones almost entirely filled with mineral matter from near the bottom of the loess, and specimens of *Bison* not at all mineralized from near the top in the same region (near Smoky Hill River, Kansas), half a mile apart, the apparent vertical thickness being about 100 feet at this point, and the loess showing some horizontal bands not well marked and one layer with marked change in character near the top, in which were various fresh-water and some land shells,—*Helix* sp. div., *Succinea*, *Planorbis* and *Limnæa*. Mr. Hatcher has recently published[1] a note in which he records similar

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[1] Science, 1900, vol. xii, p. 718.

conditions indicating alternation of temporary lagoon with dry land deposits occurring in the White River beds of Wyoming.

<div align="center">POSTSCRIPT.</div>

While this article is passing through the press, a most valuable paper has appeared on the geology of the John Day Basin, by Dr. J. C. Meriram, embodying the stratigraphic results of his recent explorations in that region, and giving for the first time an adequate idea of its geology. Dr. Merriam's descriptions show many points of resemblance between the White River and John Day terranes, both in physical characters and in the fauna. The origin of the material is different, it being chiefly composed of volcanic ash, but like the White River clays it is uniformly fine-grained, with well-marked bedding ( ?banding or parting rather than cleavage), very regular over large areas, no layers of coarse sands or gravels interposed, and the fauna limited, like that of the White River clays, to terrestrial forms. The condition in which specimens are found is the same in either terrane. Land mollusca, land-tortoises, and numerous land mammals form the fauna, beavers being the only aquatic types; some petrified wood constitutes the flora, fish remains are not found in the series, plant remains and fresh-water shells are found only in the sands and gravels at the top of the terrane.

Dr. Merriam finds himself unable, after a careful consideration, to retain the lacustrine theory of the origin of these beds and suggests that "showers of ash, with tuff deposits, on a plain, occupied perhaps in part by shallow lakes, like the so-called lake-beds of the prairie region of the central plains, might form accumulations similar to those in a large part of the series. . . . Future investigations may show that some of the very thin bedded portions of the ash deposits were laid down in water, and that the less distinctly stratified beds are largely aeolian."

This conclusion is practically identical, except as to the source of the material, with that maintained in the present memoir for the White River clays, and further confirms the probability of this theory of the origin of such formations.

## III.—ANALYSIS AND DISCUSSION OF THE FAUNÆ.

### A.—THE TWO FACIES OF THE WHITE RIVER FAUNÆ.

In reviewing the White River fauna as a whole, and determining the occurrence of the species on the basis of the large collections made by the American Museum Expeditions of 1892, 1894, and 1898, and those made by Prof. Cope in 1873 and 1879, it became clear that two distinct facies were presented by the fauna of each horizon, the characteristic fauna of the clays being widely different from that of the sandstones. Certain of the species of the clays are occasionally found in the sandstones, and vice versa. But the species characteristic of each differ in a highly significant manner.

The divisions of the beds are as follows :

| | COLORADO. | | S. DAKOTA. | |
|---|---|---|---|---|
| | Unlaminated clays | Sandstones and laminated clays | Unlaminated clays | Sandstones and laminated clays |
| Hor. C | (Merycochœrus horizon) Leptauchenia clays | | Leptauchenia clays | Protoceras sandstones |
| Hor. B | Oreodon clays | A few lenses of sandstone | Upper Oreodon clays Lower Oreodon clays | Metamynodon sandstones |
| Hor. A | | Titanotherium Beds | | Titanotherium Beds |

The Titanotherium Beds are chiefly sandstones and laminated clays, although I have seen some in Colorado that may be of the unlaminated variety. The described fauna is limited, consisting of :

| | |
|---|---|
| *Titanotherium* (many species) | S. Dakota and Colorado |
| *Leptaceratherium* | " |
| *Cænopus* sp. div. | "   and Colorado |
| *Trigonias osborni* | "   and Wyoming |
| *Elotherium* sp. div. | "   and Colorado |
| *Poëbrotherium* sp. | Colorado (one specimen) |
| *Oreodon* sp. | S. Dakota (rare) |
| *Anthracotherium* | "   (one specimen) |
| *Daphænus* | "   and Nebraska |

The characteristic forms are the *Titanotheres* and early forms of *Cænopus* and the smaller *Elotheres ;* these indicate apparently relationship to the sandstone facies of the fauna of the Oreodon Beds.

The abundant and varied fauna of Horizon B enables us to distingush clearly two facies. The following list is based on specimens in the American Museum collections in which a record had been kept of the occurrence whether in sandstone or clay, or in which sufficient matrix remained with the specimen to safely determine its character. The number of specimens whose occurrence was thus determinable is indicated in parentheses after each species.

| OREODON CLAYS. | METAMYNODON SANDSTONES. |
|---|---|
| *Ischyromys* (20 specimens) | |
| *Sciurus* (3) | |
| *Gymnoptychus* (several) | |
| *Eumys* (very many) * | |
| *Palæolagus* (very many) | |
| *Hyænodon* (14) * | |
| *Cynodictis gregarius*, etc. (many) * | *Cynodictis* * (scarce) |
| *Daphænus* (4) | *Daphænus* (5) * |
| *Hoplophoneus* (8) * | *Hoplophoneus occidentalis* (2) * |
| *Dinictis* (10) | |
| *Ictops* (10) | *Metamynodon* (20) |
| *Mesohippus bairdi* (30) * | *Cænopus* (28) * |
| *Hyracodon* (20) * | *Leptaceratherium* (2) * |
| *Colodon* (3) | *Protapirus simplex* (2) |
| *Leptochœrus* (4) | *Agriochœrus antiquus* (4) * |
| *Oreodon* (50) * | *Elotherium* (7) * |
| *Poëbrotherium* (30) | |
| *Leptomeryx* (30) * | ? *Perchœrus* |
| *Hypertragulus* (30) * | *Hyopotamus americanus* (6) |
| *Hypisodus* (20) | *Anthracotherium curtum* (1) |
| (* Also found in the sandstones.) | (* Also found in the clays.) |

In Horizon C, the Leptauchenia clays and Protoceras sandstones present a corresponding facies to the above, but in this horizon the sandstones have yielded a somewhat larger fauna.

| LEPTAUCHENIA CLAYS. | PROTOCERAS SANDSTONES. |
|---|---|
| *Palæolagus* (several) | *Steneofiber* (4) |
| *Cynodictis temnodon* (6) * | |
| *Phlaocyon* (1) | |
| *Dinictis bombifrons* (2) | *Eusmilus* (2) |
| *Proscalops* (1) | |
| *Anchippus* (1) | *Mesohippus intermedius* (20) |
| *Hyracodon* (5) | *Cænopus* (21) |
| *Merycochœrus* (5) | *Protapirus* (3) |
| *Eporeodon* (20) | *Agriochœrus* (2) |
| *Leptauchenia* (25) | *Perchœrus* (4) |
| *Protomeryx* (2) | *Elotherium* (3) |
| *Leptomeryx* (5) | *Anthracotherium karense* (1) |
| | *Hyopotamus brachyrhynchus* (23) |
| (* Also found in the sandstones.) | *Protoceras* (23) |

The Oreodon clays occur interbedded with the Metamynodon sandstones, as do also the Leptauchenia clays with the Protoceras sandstones. Furthermore, many of the characteristic species of the sandstones are found occasionally in the clays of the same horizon, and vice versa; while very few species pass up from one horizon to another, in either clays or sandstones. Certain genera or groups are characteristic of the sandstones of both levels, as well as of the Titanotherium Beds, but represented in each by different species. Certain other genera or groups are characteristic of both levels of clay, likewise with different species in each level. The only explanation apparent is that the clay and sandstone fossils represent two coëxistent faunæ of different local habitat. Combining the three sandstone faunæ and the two clay faunæ we find the following to be the characteristic types :

| CLAY FAUNA. | | SANDSTONE FAUNA. |
|---|---|---|
| | *Rodentia.* | |
| Ischyromys | | |
| Sigmodontinæ | | Castoridæ |
| Sciuridæ | | |
| Leporidæ | | |
| | *Carnivora.* | |
| Hyænodon | | |
| Dinictis | | |
| Hoplophoneus | | Hoplophoneus |
| Cynodictis | | Eusmilus |
| Daphænus | | Daphænus |
| Phlaocyon | | |
| | *Insectivora.* | |
| Talpidæ | | |
| Leptictidæ | | |

*Perissodactyla.*

Mesohippus bairdi

Anchippus

Hyracodontidæ

Colodon

Mesohippus intermedius

Tapiridæ

Rhinocerotidæ

Amynodontidæ

*Artiodactyla*

Leptochœridæ

Oreodontinæ

Camelidæ

Hypertragulidæ

Suidæ

Elotheriidæ

Anthracotheriidæ

Agriochœrinæ

Protoceras

The analogy of the clay fauna is with that of the modern plains, of the sandstone fauna with that of the modern forests (with some aquatic forms). In the clays we have hares, squirrels (cf. *Tamias*), vesper-mice, and Ischyromyids (cf. *Cynomys*) as the characteristic rodents ; in the sandstones we have beavers. Among the carnivora we find both Sabre-Teeth and Dogs in both clays and sandstones, but those of the sandstones are mostly larger, more heavily proportioned and powerful. The Hyænodonts seem nearly limited to the clays. If the modern differentiation of Dogs and Cats had existed in the Oligocene we might expect to find Canidæ especially characteristic of a plains and Felidæ of a forest fauna. But a glance at the restorations of *Dinictis* and *Cynodictis* accompanying this paper shows that the present specialization of the Dogs for swift running had hardly commenced in the Oligocene, and that of the two species figured the *Dinictis* was the better fitted for speed.

Coming to the Perissodactyls we have much more striking differences. The Titanotheres, True Rhinoceroses, Aquatic Rhinoceroses, and Tapirs characterize the sandstone fauna ; the light-limbed Hyracodonts and the still slenderer Colodons and Horses, all with cropping incisors, comparatively hypsodont molars, and a strong tendency to reduction of the lateral digits, are equally characteristic of the clays. One species of horse (*Mesohippus intermedius*) indeed is characteristic of the upper sandstones, but while it is larger and more heavily proportioned, it is unprogressive in teeth and actually retrogressive in feet, compared with its supposed ancestor of the lower clays. And contemporaneous with it we find in the clays a much more advanced horse (*Anchippus*) of smaller size.

Among the Artiodactyls the distinctions are similar. The Pigs, Elotheres, and Anthracotheres are characteristic of the sandstones, the Oreodonts and Camels of the clays. The Hypertragulids are all from the clays except *Protoceras*, which is much larger and heavier, with very brachydont teeth and unusually primitive feet. Agriochœres, which differ from Oreodonts in the very brachydont teeth, disappearance of the cropping incisors, and development of digging claws on the feet, are found more commonly in the sandstones, while all the true Oreodonts are rare in the sandstones though very abundant in the clays.

Aside from the mere analogy with modern types there are some important points of functional differentiation to be observed in these two faunæ. The species from the clays are comparatively small, slender-limbed, with much more advanced reduction in the lateral toes, and the ungulates have cropping incisors and comparatively hypsodont molars. Those from the sandstones are larger, more heavily proportioned, with retarded reduction in the lateral toes, and hardly any of the ungulates have cropping teeth, while all are very brachydont. These would seem to be adaptations, in the one case to swift running over a hard and level surface and living on hard and innutritious grasses, in the other to the more abundant and softer food of the forest, its softer and more irregular surface, and the greater capability of fighting necessary where running is a less advantageous resource. Modern animals with cropping incisors and long grinders (e. g., horses, cattle, and antelopes) are pre-eminently grass-feeders, inhabitants of the open plains. The forest deer have comparatively brachydont teeth, and the pigs, forest-dwellers par excellence, are the most unprogressive in teeth and feet and the best armed for defense, of all the Artiodactyla, unless it be the aquatic Hippopotami. Similar differences are seen in living Perissodactyls if we contrast the Horses with the Rhinoceroses and Tapirs.

The above evidence seems to make it reasonably certain that the clays and sandstones contain respectively a plains and a forest fauna, the latter including some aquatic types. And the occurrence of two such faunæ in these circumstances exactly accords with the theory of terrestrial and flood-plain origin of these beds as set forth in the previous section of this paper, while it seems utterly inexplicable on the theory of their lacustrine origin.

B.—CORRELATION OF THE HORIZONS.

1. White River.

The equivalence of the Titanotherium Beds and Oreodon Clays with the corresponding horizons in South Dakota scarcely needs discussion, as the faunæ are largely identical. The equivalence of the Leptauchenia assise with the Protoceras sandstones is more difficult to show, as the two have almost nothing in common. The Leptauchenia clays of South Dakota, in the localities examined by Wortman ('93, p. 102), overlie the Protoceras sandstones; but others have found them interbedded and almost certainly contemporaneous. The uppermost levels of the South Dakota clays, which no doubt are considerably above the sandstones, are said to be barren; and in Colorado we found fossils scarce in Horizon C, but, when discovered, of much interest. They appear to indicate that these comparatively barren upper clays are considerably later than any of the more richly fossiliferous beds, and that the building up of the White River formation was continued into the Uppermost Oligocene or Lower Miocene. For in the

top levels we found genera and even species hardly separable from those which occur in the Loup Fork formation above, in company with the known Loup Fork fauna, viz.:

*Merycochærus proprius,*
*Anchippus texanus,*
*Blastomeryx,*

and others that indicate much more modernization than is apparent in the typical White River, *e. g.,*

*Phlaocyon leucosteus.*

These were certainly in the lower terrane (see Fig. 17), and at a level not much lower we found such typical White River forms as

| | |
|---|---|
| *Leptauchenia decora,* | *Eporeodon,* |
| *Hyracodon,* | *Leptomeryx.* |

The Leptauchenia clays, therefore, would seem to be approximately Upper Oligocene, but probably lapping over in places into the Miocene.

## 2. *Loup Fork.*

The Loup Fork of northeastern Colorado is distinguished from that of Kansas and Nebraska by the survival of a number of primitive types and the absence of certain of the more advanced types. These more primitive features are :

1. The large and highly specialized *Teleoceras* (*T. fossiger, malacorhinus, superciliosus, crassus, jemezanus,* etc.) of the Republican River, Santa Fé, and (probably) Niobrara Basins has not been found in Colorado. Its place is taken by the smaller and less specialized *Aphelops* (*A. megalodus, A. profectus*) and a still more primitive rhinoceros allied to *Cænopus.*

2. Along with the more advanced horses, *Protohippus, Pliohippus,* and *Hipparion,* occurs in equal abundance the primitive brachydont horse, *Anchippus* (*Desmatippus*), which is found also in the lower beds.

3. The *Merycochæri* form an important part of the fauna. These should, I think, be considered as rather primitive types in view of (a) their occurrence in the White River formation as well as in the Loup Fork ; (b) their rarity in the later Loup Fork, disappearance thereafter, and (c) the probability that they represent characteristic types of the unknown Lower and Middle Miocene faunæ of the West, the outgrowth of the indigenous White River fauna, before the irruption of the foreign elements which become prominent in the Loup Fork.

4. Along with the more specialized *Procamelus* we find a large proportion of remarkably primitive camels, much more antique in character than had been anticipated by any writer on the subject.

The above characters appear to place the Pawnee Creek Loup Fork in a position distinctly lower than that of the Niobrara, Santa Fé, and especially the

Republican River Basin. It seems most nearly equivalent to the upper beds of Smith Creek, Montana (Deep River sub-stage), as may be judged by the following comparison of the faunæ :

| SMITH CREEK. | PAWNEE CREEK. |
|---|---|
| " *Canis* " *anceps.* | " *Canis* " ? *temerarius.* |
| | *Mustela ogygia.* |
| | *Pseudælurus.* |
| *Mylagaulus* (" *Mesogaulus* "). | *Mylagaulus.* |
| *Tetrabelodon* ? *brevidens.* | *Tetrabelodon brevidens.* |
| *Anchitherium.* | |
| *Anchippus* (*Desmatippus*) | *Anchippus.* |
| *Protohippus sejunctus.* | *Protohippus sejunctus,* etc. |
| *Hipparion isonesum.* | *Hipparion isonesum,* etc. |
| | *Pliohippus.* |
| | *Cænopus.* |
| *Aphelops.* | *Aphelops.* |
| | *Moropus.* |
| | *Protolabis.* |
| *Procamelus* ? *robustus.* | *Procamelus* ? *robustus,* etc. |
| *Blastomeryx borealis.* | *Blastomeryx* sp. |
| " *antilopinus.* | |
| *Promerycochœrus.* | *Merycochœrus.* |
| | *Merychyus.* |
| *Cyclopidius.* | |

This list on the whole appears to indicate a fairly near equivalence. There are more primitive Oreodonts in the Smith Creek beds, more primitive camels in the Pawnee Creek. The horses are nearly the same, and in both localities we find the more primitive rhinoceroses. The slight remains of mastodons are, as far as known, the same, but, like the carnivora and rodents, have at present no correlation value.

## IV.—SYSTEMATIC DESCRIPTIONS.

### ORDER PRIMATES.

The entire absence of Primates from the White River formation constitutes a marked distinction from the Eocene, and again accords with the view that the Oligocene and later beds of the Plains were deposited in a comparatively open country, unfavorable to the existence of arboreal types. There are two or three White River types which have been or might be referred to the Primates, and a word in regard to these is necessary.

*Nanohyus* was described by Leidy as a small Artiodactyl, but might be considered a Primate. Examination of the type and only specimen, a part of the lower jaw preserved in the Museum of the Academy of Sciences at Philadelphia, shows that it is identical with *Ictops* or *Leptictis*—two genera which are not distinguishable on characters of the lower jaw. It is, therefore, an Insectivore.

The Leptictidæ seem to be most nearly allied in structure to the Erinaceidæ of Europe.

*Leptochœrus* of Leidy was referred to the Artiodactyla, and its reference has been more recently confirmed by Marsh's description of Artiodactyl limbs and feet associated with the skull. The correctness of this association is questioned by Wortman, who has seen the specimen, and the position of the genus is in that case very doubtful, but it certainly is not at all allied to any of the Eocene Primates, unless a distant relationship exists with the Primate or Condylarth *Mioclænus turgidus*. Whatever *Leptochœrus* may prove to be, it is certainly a very rare form. It is further discussed in this paper under the Artiodactyla. *Menotherium* Cope and *Laopithecus* Marsh are based on species of *Leptochœrus*.

## Order INSECTIVORA.

### Family TALPIDÆ.

### Proscalops miocænus, gen. et spec. nov.

*Generic Characters.*—Premolars not less than three above and two below, all except the fourth very small and one-rooted. $P^{\underline{4}}$ with strong crescentic deuterocone and rudimentary trittocone. Molars short-crowned, trigonal in outline, with crescentic paracone, metacone, and protocone, and very rudimentary hypocone on $m^{1-2}$.

Skull exceptionally short and broad at the back.

*Specific Characters.*—Last upper and lower molar greatly reduced. $P^{2}$ minute, $p^{3}$ slightly larger, $p^{4}$ with rather strong crescentic deuterocone and very faint trittocone. Protoconid greater than metaconid on all the molars, paraconid internal.

Founded on a skull and jaws (No. 8949*a*) from the Leptauchenia Beds. The end of the muzzle is lacking. This is the first Mole recorded from the American Tertiary. The shortness of the skull and width of the occipital region separate it from any of the modern genera. *Scalops* most nearly approaches it in form of skull (though not so extreme), but has quadrate molars, and all the teeth much higher crowned. *Scapanus* and *Talpa* retain the trigonal molars, but differ in the details of their dentition and are



Fig. 1. *Proscalops miocænus.* Side view of skull × $\frac{3}{1}$. Type specimen, No. 8949*a*, White River formation (Leptauchenia Beds), Colorado. Two lower premolars are restored from the left ramus; the muzzle is outlined conjecturally.

much longer in the cranial region. *Condylura* has a very much longer skull, premolars two-rooted and spaced, occipital foramen narrowed transversely, and other considerable differences. The remaining genera of the Talpidæ differ in the dentition, although the critical parts, the front teeth, are unfortunately not present for comparison in our specimen. From all of them it is most easily distinguished by the short, wide head with very small cranial cavity.

In a number of characters this skull suggests an approximation to the shrews ;. the shortness of the cranium, the slender angular process and large triangular coronoid process, the reduction of the premolars and last molar. Whether this suggestion would be confirmed by the skeleton characters it is not now possible to say ; if so, the position of the genus would be near *Urotrichus* or *Uropsilus*, genera somewhat intermediate between the two families.

It is interesting to observe that the only known shrew from the White River, *Protosorex crassus* Scott (1894-1.), shows approximations to the Talpidæ in the less reduced dentition. The approximations are not so great as to raise any question
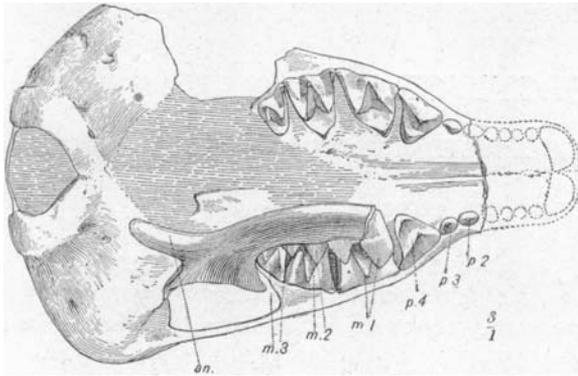


Fig. 2.  *Proscalops miocænus.*  Palatal view of skull, No. 8949*a*, the right ramus removed to show upper dentition.

as to the position of *Proscalops* and *Protosorex* in the Talpidæ and Soricidæ respectively, and indicate that these two Insectivore families differentiated much earlier than the Oligocene. But the *generic* differentiation of the Talpidæ may perhaps have occurred as late as the Oligocene, for *Proscalops*, as far as known, retains all the primitive characters, some of which appear in one modern genus, some in another. The reduced last molar I consider a primitive character; the lengthened skull a secondary one, developed to accommodate the larger brain.

MEASUREMENTS [1] OF SKULL OF *P. miocænus.*

Type, No. 8949*a.*

*Skull.*

| | | |
|---|---|---|
| p$^2$ m$^2$........9.5 | Transverse diam. m$^2$.........2.6 | Maximum width of skull behind arches........... 15.4 |
| m$^{1-2}$.........6.1 | Width palate at m$^{1-2}$.........9.4 | Length of part of skull preserved (p$^2$ to condyles).... 20. |
| m$^2$...........1.1 | p$^{2-2}$..........3.9 | "    " skull behind glenoid fossa (to condyles).... 5.1 |

*Jaw.*

| | | |
|---|---|---|
| p$_3$ m$_3$ .......9.1 | m$_{1-3}$.........6.7 | m$_3$ (longitudinal)................................. 1.4 |
| Depth of jaw below m$_1$............................1.8 | | |

## ORDER RODENTIA.

### FAMILY LEPORIDÆ.

### Palæolagus *Leidy.*

This very abundant White River Hare was reported by Cope as occurring also in the John Day Beds. An examination of the John Day specimens in the Cope Collection, referred by Prof. Cope to *Palæolagus*, shows, however, that they all have the three-lobed p$_3$ of *Lepus*, although, as in *L. ennisianus*, the anterior lobe is not clearly distinguished. I believe they represent a small variety of this

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[1] All measurements are in millimetres.

very abundant species. *Palæolagus* then is limited to the White River clays. It is not recorded from the Protoceras Beds but in Colorado is found in Horizon C (Leptauchenia Beds). I have not observed any constant differences between the specimens from the different levels. Three species are distinguishable, two well separated, the third doubtfully valid. These are :

*P. haydeni* Leidy, the most abundant.

*P. turgidus* Cope, a much larger species with shorter skull and stockier limbs.

*P. intermedius* Matthew, of intermediate size, with skull considerably shorter than in *P. haydeni*, cranium rounder. Considerably smaller than *P. turgidus*, with more slender jaws and longer diastema. Fragments of limb bones indicate a skeleton of the size and proportions of *P. turgidus*, of which species it may prove to be a variety. Six specimens are referred here, No. 8722, a skull, being the type.

*Palæolagus triplex* Cope I believe to be a young individual of *P. turgidus*. It is represented only by the type jaw.

### Family MYLAGAULIDÆ.

The anterior part of a skull with lower jaw, pelvis and some other fragments of *Mylagaulus monodon* were found by our party, and makes it possible to determine its relationship to other Rodentia. The characters amply confirm Prof. Cope's separation of it as the type of a distinct family. Its place is among the Sciuromorpha, but without close relationship to the other Sciuromorph families, the nearest being the Sciuridæ.

As in the Sciuridæ, there is a strong postorbital process, and the nasals are broad at the anterior ends, narrowing uniformly towards the posterior ends. The muzzle is constricted posteriorly and the zygomata spring almost at right angles from the skull. The antorbital foramen is close to the zygomata, as in *Meniscomys*, instead of considerably anterior to it as in most modern rodents. This character is presumably associated with shortening of the grinding series.

The family distinctions from the Sciuridæ are the great enlargement of the fourth premolar in the lower jaw and of a corresponding tooth in the upper one, with reduction and final disappearance of the teeth posterior to it, and the tendency to hypsodont teeth with closed enamel lakes.

### Mylagaulus monodon *Cope*.

Synonym, *Mesogaulus ballensis* Riggs.

The type of *Mylagaulus* is *M. sesquipedalis* Cope ('78, p. 384) based on an isolated upper tooth. Subsequently a lower jaw and an isolated lower tooth of a somewhat smaller species were described as *M. monodon* Cope, ('81, p. 374) and the genus was given family rank. In this jaw the posterior teeth had fallen out,

although their alveoli still remain. Nothing more of the group was known until 1898 when our party found in Colorado the specimen here figured. In 1899 Mr. E. S. Riggs ('99, p. 181) described a lower jaw from the Deep River beds near White Sulphur Springs, Montana, which he named *Mesogaulus ballensis*, distinguishing the genus from *Mylagaulus* by two characters: (1) first molar elongate anteroposteriorly with enamel slightly inflected externally; (2) the third molar rather stronger than the second, and rotund in outline. The first character given is equally shown by the lower tooth of *Mylagaulus*[1]; the second could not be determined in any of the three described *Mylagaulus* specimens and is in any case insufficient for generic separation. The absence in the *Mylagaulus monodon* specimen of the two molars retained in *Mesogaulus ballensis* might seem a good basis for separation. But the dropping out of these vestigial molars is so much a matter of individual variation, age, or accident of preservation, that it should be used with extreme caution even for specific separations, and only after comparison of a sufficiently large series of specimens has shown that it occurs at a very
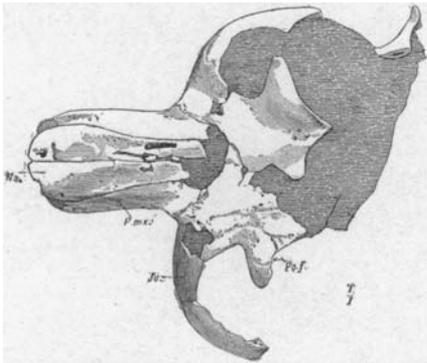


Fig. 3. *Mylagaulus monodon.* Front of skull, top view, natural size. No. 9043. Loup Fork Formation, Protolabis Beds, Colorado.
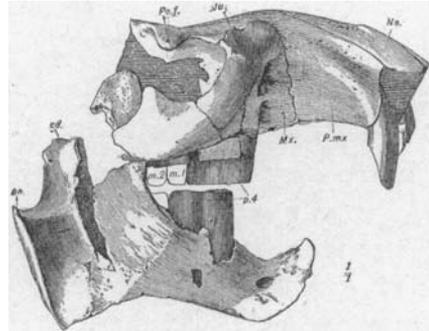


Fig. 4. *Mylagaulus monodon*, No. 9043. Front of skull and lower jaw, side view, natural size.

considerably earlier age in one animal than in another, and always at that age. Mr. Riggs's specimen, like the one found by our party, is a younger individual than the type of *M. monodon*, and still retains two molar teeth which later would fall out.

The specimen (No. 9043) discovered by our party in 1898 agrees very well with *Mylagaulus monodon* but it has two vestigial molars still in place in both upper and lower jaws. The large lower grinder bears the notch described by Mr. Riggs, and present also in *M. monodon;* the corresponding upper tooth is a little wider and has no notch. The angle of the jaw appears to have been of peculiar form, the point of the angle rising to the level of the grinders, and the inferior margin running thence downward and slightly forward, a form widely different from that of the Sciuridæ, suggesting the corresponding part in *Castor* but the angle projecting more upward and much less backward.

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[1] Mr. Riggs appears to have mistaken the upper tooth of *M. sesquipedalis* for a lower one, and not to have made comparison with the two specimens of *M. monodon* (all three are figured in the 'American Naturalist' for 1883, though with an error in the names, the type of *M. sesquipedalis* being called *M. monodon*, and the second specimen of *M. monodon* called *M. sesquipedalis*).

The upper incisors are nearly vertical, the enamel band nearly flat. The pattern of the upper molars might be interpreted as derived from two chief ridges, the larger one reinforced by a cingular ridge on each side. The lower teeth might be similarly interpreted. But any interpretation is purely conjectural without having (1) a series of young *Mylagauli*, and (2) some ancestral relatives. The latter Mr. Riggs would supply in Professor Cope's *Meniscomys hippodus ;* but the skull of *M. hippodus* does not especially favor that theory, as the postorbital processes are lack-
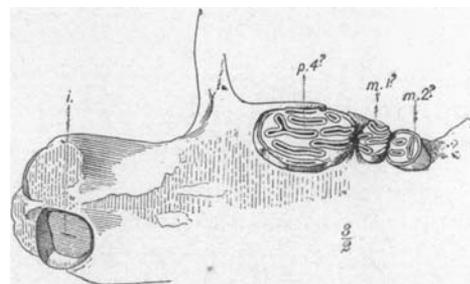


Fig. 5. *Mylagaulus monodon*, No. 9043. Upper dentition. crown view, × ⅓.

ing, and in this important character it is further away from *Mylagaulus* than are any of the Sciuridæ proper. The form of the posterior part of the jaw is quite different (primitive and *Paramys*-like). The muzzle is not expanded anteriorly as in *Mylagaulus ;* on the other hand, the nearness of the preorbital foramen to the zygomatic arch brings it somewhat nearer than the other Sciuridæ. The fourth premolar is enlarged in *M. hippodus*, though very brachydont, as an upper grinder is in *Mylagaulus*, but it is not yet shown that the teeth are homologous, and I can perceive no resemblance in pattern beyond what could be obtained by comparison of any other Sciurid. Altogether it seems better to consider *Mylagaulus* related to the Sciuridæ but not especially to any known member of the family.

The sacrum of *Mylagaulus* is highly specialized, consolidated even more than in *Castor*, and much more than in any Sciurid which I have been able to
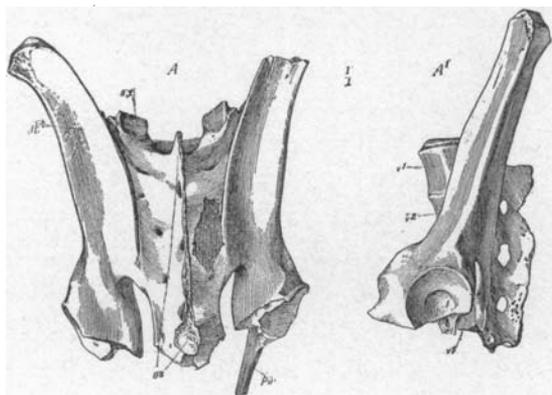


Fig. 6. *Mylagaulus monodon*, No. 9043. Sacrum and part of pelvis, natural size; *A*, from above; *A*¹, side view.

compare. It consists of four vertebræ. The neural spines are fused to a single thin plate pierced by three foramina. The transverse processes are also fused together into a plate and the zygapophyses apparently fused to each other and to the transverse processes, as a buttressing plate on their upper side. The anterior zygapophysis of the first and the posterior one of the last sacral have functional facets. The pelvis is attached to the first three sacrals ; the transverse plate at the fourth sacral has not the great width seen in the beaver, hence presumably the tail was not broad and flat. The ilium is much stronger and stouter than in the squirrel. The scaphoid and lunar are united.

## ORDER CREODONTA.

### Hyænodon cruentus *Leidy*

A skull, jaws, cervical and four dorsal vertebræ, fore limbs and feet (No. 8775), are very perfectly preserved, and include a perfect manus, nearly all in position.

The contrast between size of skull and size of body remarked by Professor Scott ('95) is very noticeable in this specimen.   Other specimens in the collection show much less contrast.    I suspect that the variation is chiefly a matter of sex, the males and old individuals having exceptionally large heads.   The carpus confirms the restoration by Professor Scott; the metacarpus is perhaps a little longer but not otherwise different from his description.   The ungual phalanges were in three instances preserved in position and were sharply flexed upward on the median phalanges, which nevertheless are not retracted on the metapodials as in the cats.

## ORDER CARNIVORA.

### FAMILY CANIDÆ.

### Cynodictis *Brav. & Pom.*

Two species of this genus appear in the collections, with a tolerably constant difference in size and robustness.   These were described by Cope as *Canis gregarius* and *C. lippincottianus;* of the latter he had but one jaw fragment and was uncertain as to the validity of the species.   *C. lippincottianus* appears to be the same as the previously described *Amphicyon gracilis* Leidy.   The latter specific name is, however, preoccupied.   Both *C. gregarius* and *C. lippincottianus* occur in the Colorado and South Dakota Oreodon Beds and have been considered identical by most writers.   Our series indicates that they are probably valid species.   The distinctions between them are of interest as they appear to be the beginning of a cleavage afterwards increased to subgeneric value, the *C. gregarius* pointing towards the group of South American foxes which Dr. Wortman and the writer have distinguished under the name *Nothocyon;* while *C. lippincottianus* leads probably into some of the more carnivorous wolves or foxes.

Of *C. gregarius* our party obtained a skeleton which has been partly described in a previous article (Wortman and Matthew, '99, p. 122).

### Cynodictis gregarius (*Cope*).

#### Plate I.

The limbs, part of the backbone and ribs were found in position ; the rest of the bones were displaced ; the fore feet, two dorsals and several ribs, and part

of the tail were missing. A thorough comparison of the various parts of the skeleton with the corresponding parts of a modern genet showed such close functional resemblance that a skeleton and photographs of this animal were largely used as a guide for pose in restoring the *Cynodictis* skeleton. At the same time Mr. Horsfall, the draughtsman, kept a careful watch for all discrepancies in structure not observed in the preliminary studies, and the proper interpretation of these discrepancies was discussed with Mr. Chas. R. Knight and the writer. The restoration, thus criticised from three points of view, and based on adequate material, may therefore claim to be tolerably accurate.

The entirely viverrine character of the skeleton, very different from that of the dogs, is striking. Were it not for the intermediate skeletal characters of the John Day *C. geismarianus*, and the less known Miocene Canidæ, it would be difficult to believe that *Cynodictis* is really ancestral to the Canidæ, or anything more than a civet with abnormally primitive dentition. As it is, the gap is a distressingly wide one, and is emphasized by the characters of the European *Cynodictides*, which, judging from what I have seen of them, are in dentition more like the Viverridæ than the American species, and are equally like them in skeleton characters.

Yet this viverrine resemblance of *Cynodictis*, when analyzed, is not in progressive characters ; while the wide distinctions separating it from *Canis* are, in every case, progressive characters, in the latter contrasting with the primitive characters of the ancestral form. The retention by *Cynodictis* of the third lower molar, already lost by the Lower Eocene *Viverravus*, is the chief technical ground for the separation from the Viverrid phylum.

The detailed description of the skeleton of *Cynodictis* has been fully given by Professor Scott from a number of incomplete skeletons of *C. gregarius* and *C. lippincottianus* in the Princeton Museum.

## FAMILY PROCYONIDÆ.

### Phlaocyon leucosteus *Matthew*.

This unique and beautifully preserved skeleton has already been described by Wortman and the writer ('99, p. 131). It was found in one corner of the large block of *Merycochœrus* skeletons (Fig. 21) and removed for separate mounting not yet completed. I give here figures of the skull and feet, with a brief summary of the characters as follows :

Raccoons with the dentition of *Cynodictis* and of the modern Canidæ, but with skull and jaws more as in *Procyon* ; teeth short and thick with low rounded cusps and a postero-internal cusp on the upper carnassial. Skeleton of intermediate character between those of *Cynodictis* and *Procyon*. Limbs proportionately longer, and feet more tetradactyl than in *Procyon*, claws ? partly retractile.
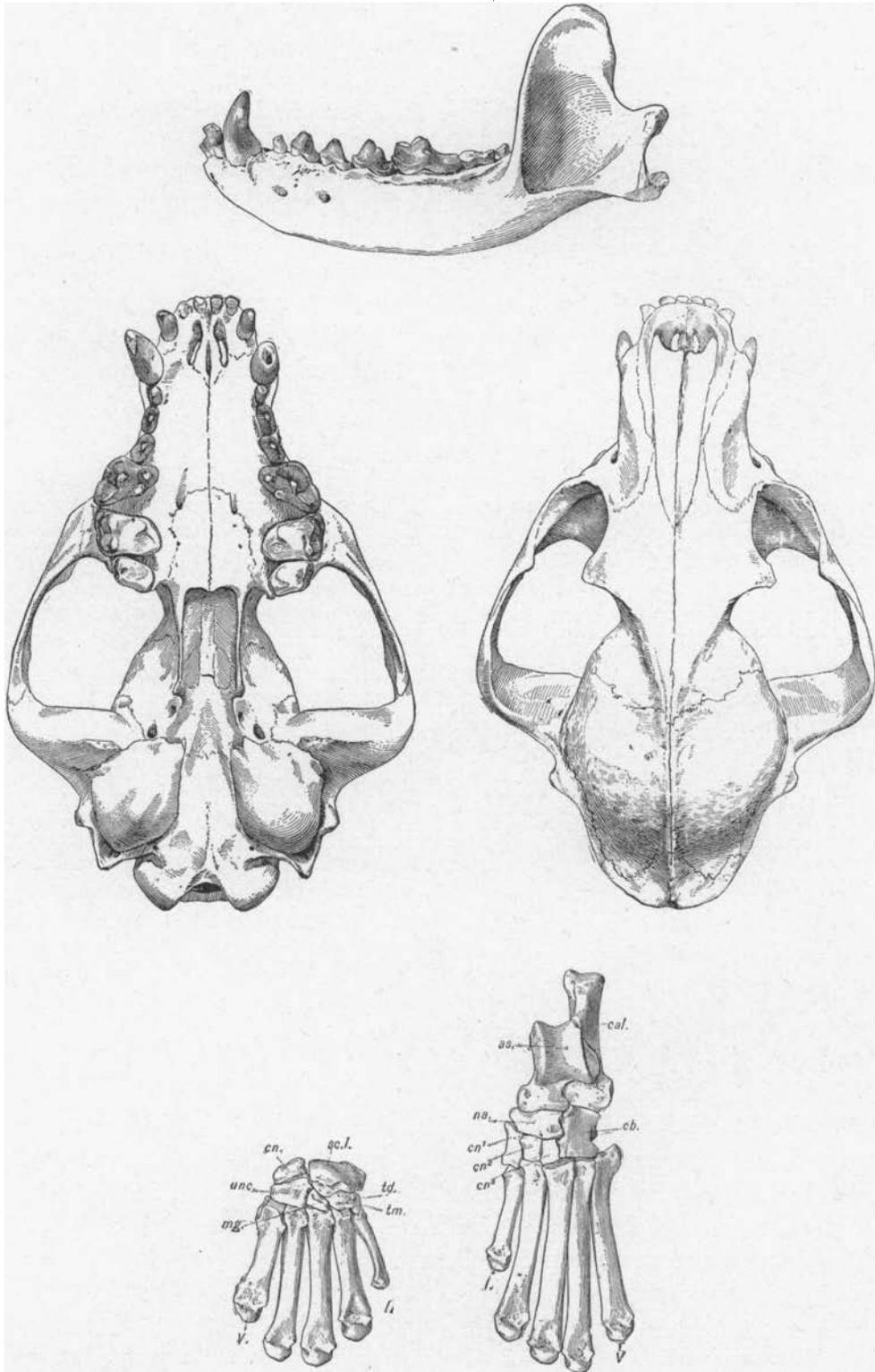
Fig. 7. *Phlaocyon leucosteus.* Type specimen No. 8768, natural size. White River Formation, Leptauchenia Beds, Colorado (locality shown in Fig. 17). Top and palatal views of skull; side view of lower jaw; fore and hind feet.

## FAMILY MUSTELIDÆ.

### Mustela ogygia, sp. nov.

*Mustela* sp. MATTHEW, 'Fresh Water Tertiary of the West,' Bull. Am. Mus. Nat. Hist., 1899, 68.

Type and only known specimen 'a well-preserved skull and jaws, No. 9042, from Horizon E of the Upper Miocene of Colorado.

In size equal to *M. americana*, but with broader and somewhat shorter muzzle, and much smaller brain-case. Dentition I $\frac{3}{2\text{-}3}$, C$\frac{1}{1}$, P$\frac{3\text{-}4}{3}$, M$\frac{1}{2}$. Upper incisors (Fig. 9) nearly as in *M. americana*. Canine somewhat stouter, the root a little straighter, the tip of the crown slightly more recurved. First premolar minute and one-rooted on one side, absent on the other. Second and third premolars shorter and higher than in *M. americana*, approaching *Putorius*. Carnassial with somewhat smaller internal cusp, and somewhat broader heel, tubercular with rather smaller metacone and internal cingulum not flared out. In the lower jaw there are either two or three incisors; the canine is like that of *M. americana*; the first premolar appears to be absent on both



Fig. 8. *Mustela ogygia.* Side view of skull and jaws, natural size, Type specimen, No. 9042. Loup Fork Formation, Protolabis Beds. Colorado.

sides of the jaw, the second, third, and fourth are shorter than in *M. americana*, the cingulum less developed in front, the posterior accessory cusp very rudimentary. The carnassial has a shorter and smaller heel and a strong, well-separated metaconid. The tubercular molar was minute, vestigial.

COMPARATIVE MEASUREMENTS.

|  | *M. ogygia.* | *M. americana.* |
|---|---|---|
| Width of muzzle at canines | 16 | 13 |
| Width of brain-case | 25 | 35 |
| Length of skull, occipital crest to premaxillæ | 71 | 76 |
| "       " upper dentition | 28 | 31.5 |
| "       "       " premolars 1 to 3 | 10 | 12.5 |
| Width of internal shelf of m$^1$ | 3 | 4.5 |

*Mustela parviloba* Cope is a much larger animal, about the size of a cat, as indicated by the fragments of jaws by which it is known. *Mustela nambiana* Cope, of the New Mexican Loup Fork, has a much shorter jaw and was afterwards referred by Professor Cope to *Putorius*, where it more probably belongs.
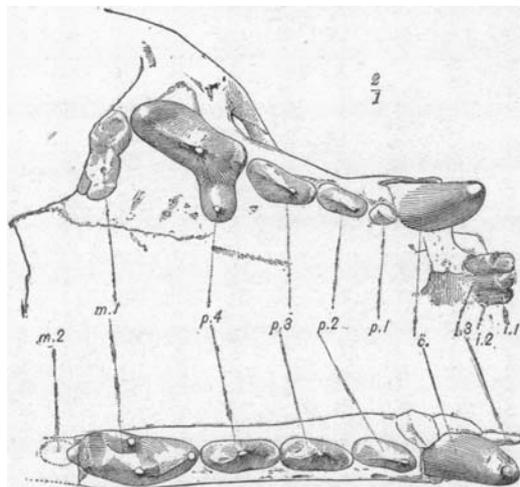


Fig. 9. *Mustela ogygia*, No. 9042. Upper and lower dentition, crown view, × $\frac{2}{1}$. The first upper premolar is absent on the left side (see Fig. 8).

The skull is very similar in its lines to that of *M. americana*, the only noticeable differences being those due to the much smaller brain capacity and shorter, wider muzzle. There is a low sagittal crest, almost disappearing anteriorly; the postorbital constriction is further behind the postorbital process. The zygomatic arch is somewhat heavier. The coronoid process of the lower jaw is higher and considerably broader, the tip projecting more backward.

The jaw is somewhat shorter, hardly any deeper in front, condyles heavier.

The distinctions from *M. americana* are either primitive characters or approximations to *Putorius*. In *Proputorius* of Filhol the lower premolars are practically one less in number, the second being represented by a single minute alveolus, while in our species this tooth is two-rooted and of good size; the upper dentition of Dr. Filhol's genus is unknown. In *Mustela* p$\frac{1}{4}$ is always minute and often absent; it our species it is present on one side, absent on the other side of the upper jaw, and absent on both sides of the lower jaw. In premolar reduction then, *M. ogygia* comes within the limits of *Mustela*. The strongly developed metaconid on the carnassial is not quite equalled by any modern marten, but is seen in *Proputorius*. I assume, however, that *Proputorius* had the skull lines of *Putorius* as well as a dentition typically ancestral to that genus, whereas *M. ogygia* has more nearly those of *Mustela*.

## FAMILY FELIDÆ.

### SUBFAMILY MACHÆRODONTINÆ.

The presence in the same White River beds of two genera, *Dinictis* and *Hoplophoneus*, which have been assumed to represent two well separated stages in the evolution of Sabre-tooth Tigers, and the identical range of the two, is a singular fact. It seems complicated by the presence in the John Day Beds, later than the White River, when the sum-total of their fauna is considered, of more ancient types, if the assumption be correct, of Sabre-teeth than any known from the White River, and of none more advanced. No adequate explanation of this occurrence of species is evident at present, because we know practically nothing of the origin of the group. With a single doubtful exception they are absent from the Eocene, and appear suddenly in the lower Oligocene of Europe and America, forms as specialized in dentition as almost any of their descendants, being associated with and followed by the more primitive types. *Eusmilus* of the Phosphorites and *Hoplophoneus* of the Oreodon Beds are as highly specialized in dentition and in most of their skull characters as the Pliocene *Machærodus*. The evolution of the family, if they rose from Viverroid Creodonts, must date far back in the Eocene, and is almost or quite unrepresented by known species. The apparent stages in evolution known to us are either really survivals of primitive types, or they may represent an actual retrogression, a progress of part of the Machærodont stock towards the true cats, correlated with the increasing abundance of the long-necked ruminants which probably, then as now, formed the chief prey of the larger felines of modern type. The especial prey of the Machærodonts, as I shall attempt to show, was more probably the short-necked, thick-skinned Rhinoceroses, Elotheres, Oreodonts, and similar animals. The Pliocene *Pseudælurus quadridentatus* appears to me more comprehensible as a retrogression than as an actual unimproved survival of its Lower Oligocene congener, *P. edvardsi*, which itself, existing side by side with the highly specialized *Eusmilus*, must have been a survival from a much older type.

The complete knowledge of the *Dinictis* and *Hoplophoneus* skeletons shows, however, that the former is by no means a primitive survival, but had its own peculiar adaptations, and was on the whole fully as specialized as *Hoplophoneus*, but fitted to a somewhat different life. It may be that a more complete knowledge of the remaining genera will equally show that the supposed unspecialized types are equally advanced in the sum of their characters.

## THE USE OF THE MACHÆRODONT CANINE.

The habits of Sabre-tooth Tigers and the cause of the development of their peculiar upper canines have been the subject of widely varied opinions, which have given rise to some singular statements. The long tusks of *Smilodon* have even been quoted as the cause of the extinction of the genus, on the theory that the animal could not open his mouth wide enough to admit food, because the tusks barred the entrance. This idea is perhaps drawn from a false analogy with cases of hypertrophy of rodent incisors, the radical difference between an individual accident and a racial character being ignored. For in view of the constant check that natural selection places on the development of any peculiarity that would even so far *inconvenience* the individual as to hinder it in obtaining food, it is impossible to believe that any innate tendency to evolution—if such exists—could so far overcome the repressive influence of selection as to produce finally a race that would be self-extinguishing.
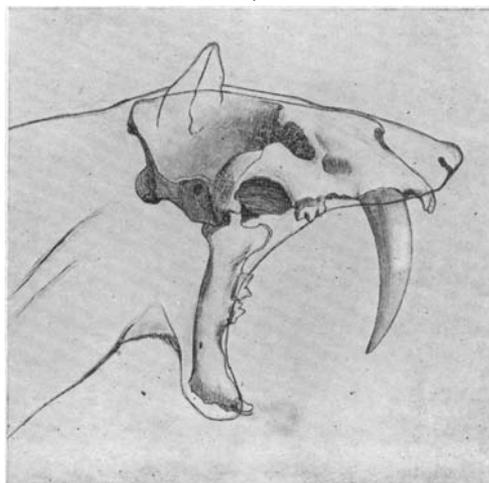


Fig. 10. Sketch for a restoration of the Head of a Sabre-tooth Tiger, *Smilodon necator*. By Charles Knight. Based on the perfect skeleton in the Cope Pampean Collection. About one tenth natural size. Republished from American Museum Journal, January, 1900.

Another curious conception is that the tusks were used indeed as stabbing weapons, but used with the mouth closed. This method of attack could not be used of course among the earlier Sabre-teeth, but only with such long-tusked genera as *Smilodon*, and if it were true it would involve, after a long adaptation to striking with the mouth wide open, a sudden change in habit in the latest type to keeping the mouth tight shut while striking. By such a change the efficient length of the weapon would be diminished by about one half; the closed mouth would be a very serious disadvantage to a blood-drinking animal, and natural selection would again exert a heavy repressive effect against the lengthening of the canines to such an extent that they must be used this way.

The suggestion has also been made that the tusks were useful in climbing trees ! for which of course their slender serrate edges and brittle material would have totally unfitted them. Still another suggestion, based apparently on a fancied

analogy with the teeth of the walrus, gives the group an aquatic habitat, a theory not very easy to absolutely disprove, but I think quite impossible to prove, or even favor by evidence.   The supposed walrus analogy is hardly to be considered —the use of the walrus tusk is now well known, and while its incidental use for fighting is probably considerable, it would hardly be the most effective weapon for capturing an agile prey in the water, and we have good reasons for thinking it very improbable that our earlier Machærodonts were aquatic, and no grounds for supposing that the later ones were.

But there are other striking characters in the evolution of the skull in this race, correlated with the development of the upper canines ; and these show that the above explanations of supposed difficulties are quite unnecessary, as the difficulties do not exist ; they at the same time give a definite evidence of the adaptation of the canine to a particular method of attack.

The first is the great increase in size of the mastoid process and its shifting from a position close to the occipital condyle, forward and outward nearly one fourth the total length of the skull, to a position close to the postglenoid process. This gives a great increase, both in power and leverage, to the muscles (chiefly the sterno-cleido-mastoid) drawing the head downward and forward towards the body. It enabled the animal to strike downward with its tusks with enormous power. The whole form of the back of the skull is subordinated to this change, which is strictly correlated with the evolution of the upper canines, the modern Felidæ standing at one end of the series, *Smilodon* at the other, and *Archælurus, Nimravus*, *Dinictis, Hoplophoneus*, and *Machærodus* intermediate in the order named.   Its great importance shows that the chief use of the canine was in stabbing, striking downward with great force.

Another equally striking character is the degeneration of the lower jaw.   The high backward curving *coronoid process* of the primitive carnivora, which is considerably emphasized in the cats, is reduced in the later Machærodonts to a short, low, vertical process, losing two thirds of its height relative to the length of the jaw, and the greater part of the space for muscular attachments.   At the same time the *angle* of the jaw is greatly reduced, and projects more outwardly than in any other carnivores, while the condyle becomes looser and more extended.   All these changes enable the jaw to be opened very much wider, without unduly stretching the temporal or masseter muscles, without the angle of the jaw interfering with the zygoma, and without the condylar borders limiting the motion.   Presumably the ligaments were adjusted to these changes, and if so there appears to be no reason why the Sabre-tooth should not open his mouth far wider than is possible for the cat, laying back the chin against the neck without inconvenience. Along with this change there is a decrease in power of the muscles closing the jaw, due probably to lack of use of the lower canines (used against the upper ones by other carnivores, but useless in this way to the Sabre-tooth) ; the premolars (used chiefly in bone-crushing by modern carnivora) almost disappear, and the shearing carnassials (used in flesh-cutting) alone remain.

Is it not the simplest explanation of the above peculiarities of the Sabre-teeth, that their prey consisted of large, short-necked animals, probably thick-skinned, and in consequence, instead of breaking or biting through the neck as do modern large Felidæ (which prey chiefly upon the slender-necked ruminants, etc.), their most advantageous method of attack was to inflict stabbing and ripping cuts at points where an artery could be reached, using their short, broad and powerful forefeet as fulcrums, and, probably, bleeding the animal to death? This would explain the thin, dagger-pointed canines, their backward curve, sharp, serrate edges, especially posteriorly. It would explain the form of the skull, so different in *Smilodon* from any modern Felidæ, the degeneration of the jaw, the exceptionally powerful forelimbs and short, wide forefeet. The abundance of Sabre-teeth and scarcity of true cats during most of the Tertiary is correlated with the abundance of short-necked and probably thick-skinned Perissodactyls, etc., and scarcity of the slender-necked and thin-skinned Ruminants during most of that time. The early appearance of true cats in Europe and their great rarity in America throughout the Tertiary may be correlated with the earlier appearance and greater abundance of the higher Ruminants in the Old World. And finally we may perhaps correlate the extreme type of Sabre-tooth *Smilodon*, the largest and best armed but among the slowest runners of the race, with the existence of the thick-skinned, slow-moving Ground-Sloths of the American continent.

The development of a large protective flange on the lower jaw in the older stages of the Sabre-tooth evolution, and its complete disappearance in the latest stage, is explicable on the ground that the canines finally became so long that an adequate protective flange would have interfered with the wide gaping of the mouth, the points of the flange striking the neck and preventing further opening of the jaw. Beyond this stage any further development of the canine would involve strengthening as well as lengthening it, and the flange, being now a hindrance instead of a help, would disappear slowly. Beyond the extreme reached in *Smilodon* it probably was not advantageous to go, that length, even, being probably correlated with exceptionally large and thick-skinned prey, for we find during the Oligocene, Miocene, and Pliocene of Europe and America but little advance in relative length of the canines.

As we shall now proceed to show, the shorter canines of *Dinictis* were correlated with greater speed, and indicate in all probability that the animal preyed on smaller, swifter-footed herbivores than did the more powerful and slower *Hoplophoneus*, with its much longer canines and more advanced dentition and skull.

## Dinictis *Leidy.*

Five species of this genus have been described from the White River but, as is usual among the Felidæ, the specific limits are difficult to draw. The species were published as follows:

1. *Dinictis felina* Leidy, '54, p. 127; '69, pl. v, figs. 1-4. Type, a skull and jaws in the Hall Collection, Amer. Mus. No. 455.

2. *Daptophilus squalidens* Cope, '73, p. 2 ; '84, pl. lxviia.    Type, part of a lower jaw, young, with $p_{\overline{3}}-m_{\overline{1}}$, and upper milk canine.    Am. Mus. No. 5335.
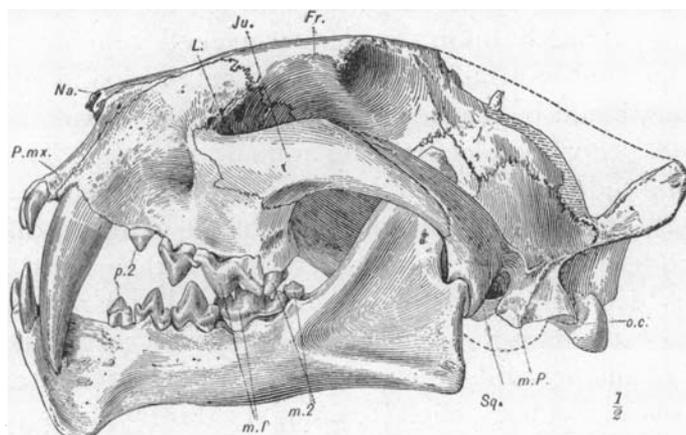


Fig. 11.  *Dinictis squalidens.*  Side view of skull and jaws, × ⅓, No. 8777.  White River Formation, Oreodon Beds, Colorado.

3. *Dinictis fortis* Adams, '95, p. 574.    Type, front of skull and jaws and parts of skeleton.    Princeton Museum No. 11085.

4. *Dinictis bombifrons* Adams, '95, p. 577.    Type, a nearly complete skull and jaws. Princeton Museum No. 10502.

5. *Dinictis paucidens* Riggs, '96, p. 237.    Type, a skull and jaws and large part of skeleton in Kansas University Museum.

The type skull of *D. felina* is fairly well preserved, but the arches, crests and ends of canines are broken off.    It came from the Lower Oreodon Beds of the badlands of White River, South Dakota.    Other skulls from the same region in the museums at Princeton, Philadelphia, Washington, and New York agree rather nearly with it.

*Daptophilus squalidens* was described by Prof. Cope in 1873 from the milk dentition of a *Dinictis* from Cedar Creek, northeastern Colorado.    He afterwards recognized that the premolars were temporary and transferred the species to *Dinictis*, separating it from *D. felina* by distinctions which were obtained not from the type but from another specimen, an adult lower jaw ramus.    These were : (1) smaller size ; (2) one-rooted $p_{\overline{2}}$ ; (3) $i_{\overline{1}}$ probably absent.    Of these three characters the first is a correct statement as regards the associated jaw, No. 5336, but the carnassial of the immature type, the only part that can be properly compared with the adult type of *D. felina*, is of exactly the same length as in Leidy's species and ten per cent. larger than in No. 5336.    The second character cannot be determined in the type, but is correct as regards No. 5336.    The third is not determinable on the type, and probably erroneous as regards No. 5336.    The root of the median incisor in *Dinictis* is short, and the narrowing of the anterior surface of the ramus toward the flange gives less space for the roots than for the crowns of the incisors, and causes the lower part of the root of the second to lie behind that of the third.    When the crowns only are broken off, as in Leidy's type, there appear three incisor roots in a row ; when a little of the edge of the alveolus is broken off, the roots alternate, the second being behind the first and third ; a little more of the edge broken off (as in Cope's specimen, and in the type of *D. paucidens*, according to Dr. Riggs's statement), and there is no indication of $i_{\overline{1}}$, while $i_{\overline{2}}$ is directly behind $i_{\overline{3}}$.    Dr. Adams has ('96, p. 430) referred a young skull, Pr. Mus. No. 11379, to this species, on size and other unstated characters ;

but in view of the above considerations its reference requires revision, for if it is identified with *D. squalidens* it must be with No. 5336, not with the type, and if it be distinct from *D. felina* it is also distinct from the type of *D. squalidens*, and co-specific with No. 5336 only.

Our material shows that there are two species, at least, concerned, one slenderer, lighter-muzzled, with narrower skull and more compressed teeth, chiefly represented by specimens from Colorado. Some individuals are as large as the type of *D. felina*, others smaller and shorter-jawed. For these slenderer individuals I retain Prof. Cope's name, as the chances are in my opinion about three to one that his type specimen really belongs with them. If the supposed single root of $p_{\overline{2}}$ observed on the associated specimen No. 5336 be specifically valid, there is also a smaller unnamed species represented by No. 5336, and I presume by No. 11379. But in all *Dinictides* $p_{\overline{2}}$ has two closely approximate roots, connate sometimes below, sometimes above the alveolar border, and the alveolus is sometimes single and deeply constricted, sometimes double nearly to the border. The difference between two roots and one root is therefore really very small. No. 5339, from Colorado, has the precise dimensions and proportions of No. 5336, but $p_{\overline{2}}$ is two-rooted. For these reasons it seems that the larger and smaller Colorado specimens do not present distinctions important or constant enough to be of specific value. But from the skeleton to be described we can derive good characters to distinguish the Colorado species from *D. felina*.

*Dinictis fortis* Adams was distinguished from *D. felina* by larger size, more robust dentition and skeleton, absence of anterior basal cusp on $p_{\overline{3}}$, etc. If my reference to this type of Am. Mus. No. 1393, upper and lower jaws and part of skeleton, be correct, the distinctions are sufficiently constant. On the other hand, if Dr. Adams's later reference of his *D. bombifrons* type and of Am. Mus. No. 1400 to *D. fortis* be correct, I cannot see that any characters except size are left, for *D. bombifrons* is a long, rather narrow skull with moderately wide muzzle, while No. 1400 is an exceptionally broad, heavy muzzled skull, and both have the dentition like that of *D. felina* and unlike that of *D. fortis*, as far as comparison is practicable. It would be preferable to consider No. 1400 as an exceptionally large and heavy *D. felina*, and *D. bombifrons* as a distinct species.

*Dinictis bombifrons* Adams was described in the same article as *D. fortis*, and afterwards identified by him with *D. fortis*. The skull is long and large, the dentition like that of *D. felina*. Two skulls in our collection, one associated with most of the skeleton, both from the Leptauchenia clays, correspond very well with the figures, description, and measurements given by Dr. Adams. These have the dentition of about same dimensions as in *D. felina*, but the premolars are smaller and less trenchant, posterior cusp of $p^{\underline{3}}$ larger, anterior cusp of $p_{\overline{2}}$ smaller, internal cusp of $p^{\underline{4}}$ somewhat smaller. *D. fortis*, as represented by No. 1393, has much larger molar teeth, more trenchant than in *D. bombifrons* but hardly as much so as in *D. felina*, flanges of mandible almost obsolete, lower tubercular and heel of carnassial more reduced, anterior cusp of $p_{\overline{2}}$ almost gone, inner cusp of

upper carnassial nearly obsolete, and limb bones shorter but one third greater in transverse diameters.

*Dinictis paucidens* Riggs was based on a skull and part of a skeleton from Wyoming. It was distinguished by the absence from the lower jaw of the median incisor and tubercular molar, the slender base, concave external border and prominent antero-internal cusp of $p^{\underline{4}}$, and absence of postero-internal cusp on $m_{\overline{1}}$, and by the slender limbs. The absence of $i_{\overline{1}}$ is a doubtful character, as noted above ; the other characters seem to be valid, and the place of this species appears to be rather with the Colorado *D. squalidens* than with either *felina, fortis*, or *bombifrons*. The technical resemblance to the John Day *Pogonodons* in the absence of $m_{\overline{2}}$ and of the metaconid of $m_{\overline{1}}$ is not supported either by the proportions of the skull or the forms of the teeth ; it seems more likely that *D. paucidens* is an outgrowth from *D. squalidens*.

The John Day species, *Dinictis cyclops*, and *D. (Pogonodon) platycopis* and *brachyops* are easily distinguishable, both from the White River species and from each other. *D. cyclops* has an extremely short head, very wide frontal region and small muzzle, and the internal cusp of $p^{\underline{4}}$ is very prominent. *D. platycopis* and *D. brachyops* are much larger, dentition not unlike that of *D. felina* in many respects, but no metaconid on $m_{\overline{1}}$, and $m_{\overline{2}}$ absent. The skulls of both are long, muzzles heavy. A close comparison of these three species is not necessary here.

## Dinictis squalidens *Cope.*

No. 8777 is of necessity somewhat arbitrarily identified with *D. squalidens*, but represents a species distinct from *D. felina*, preferably placed here because :
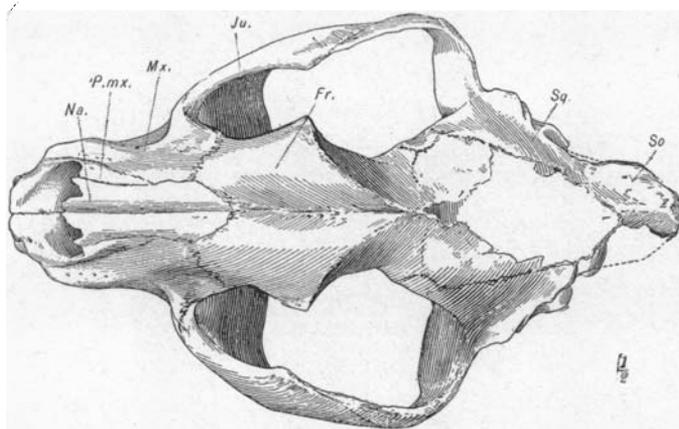


Fig. 12. *Dinictis squalidens*, No. 8777. Skull from above, × ½.

1. The type of *D. squalidens* agrees equally well with this specimen and with *D. felina.*

2. Cope's secondary type of *squalidens* does not agree with this specimen in length of diastema, reduction of premolar two, and size of carnassial ; but neither does it agree with the type in size of carnassial, the only character in which comparison can be made.

3. The broader distinctions separating No. 8777 from *D. felina* are those which very generally characterize the Colorado White River fauna as opposed to that from South Dakota. The identity in locality of the type and No. 8777 gives therefore some reason to suppose that the two individuals were of identical habitat, hence the probabilities are in favor of the type of *D. squalidens* being co-specific with No. 8777 rather than with another species.

No. 8777 consists of a finely preserved skull and jaws, the top of the brain-case eaten away but the rest of the skull perfect, the back-bone, hind limbs, and the greater part of the ribs all in position. It was found in Horizon B, in the Cedar Creek beds of northeastern Colorado.

Another specimen referable to this species, from South Dakota, No. 1396, consists of a broken skull and vertebræ with well-preserved fore and hind limbs. In skull characters it is intermediate between *D. squalidens* (No. 8777) and *D. felina* (type) ; the skeleton agrees accurately with the former. In the accompanying restoration (Plate II) the fore legs and hind feet are supplied from No. 1396 ; the rest of the skeleton is drawn from No. 8777. The drawing is by Mr. Horsfall, the position and arrangement of the bones being determined by Mr. Charles Knight and the writer, from comparative study of photographs and originals of modern Felidæ, assisted by the skilful osteological preparations of Mr. Chubb ; such changes being made as the different construction of the *Dinictis* bones appeared to involve.

The anatomy of *Dinictis felina* has been so thoroughly described by Prof. Scott, that it is necessary only to point out the distinctive characters of *D. squalidens* and to supply a few omissions in his material. The comparisons are with Leidy's type of *D. felina*.



Fig. 13. *Dinictis squalidens*, No. 8777. Palatal view of skull, × ½.

*Dentition.*—The premolars are more compressed and one tenth smaller. The tubercular molar of the lower jaw is elongate-oval, longer than the round-oval one of *D. felina*. The diastema and flange of the lower jaw are longer. The canines and incisors are smaller and slenderer. Inner cusp of $p^4$ stronger and more separate ; $m^1$ is more compressed anteroposteriorly.

COMPARATIVE MEASUREMENTS OF TEETH.

|  | D. squalidens No. 8777. | D. felina No. 455, Type. |
| --- | --- | --- |
| Length of upper dentition | 75 | 77 |
| Length of six upper molars | 21 | 24 |
| Anteroposterior diameter of canine | 13 | 14 |
| Vertical length of canine | 39 | |
| Anteroposterior space of upper premolars | 39 | 42 |
| Upper carnassial, anteroposterior | 20 | 20 |
| "       "       transverse | 11 | 12 |
| "   tubercular, anteroposterior | 14 | 14 |
| "       "       transverse | 4 | 5 |
| Length of lower dentition | 78 | 79 |
| "       "   diastema | 16 | 12 |
| "       "   premolars | 29 | 33 |
| "       "   carnassial | 19 | 19 |

*Skull.*—The muzzle is smaller than in *D. felina*, the anterior nares being smaller, canines nearer together, and palate narrower in consequence. The orbits are a little closer together, the postorbital constriction narrower. The brain-case appears to be smaller and the zygomatic arches (judging from other specimens than the type of *D. felina*) somewhat narrower in No. 8777. The flange of the mandible is deeper, the coronoid process is shorter and more triangular than in the type species.

COMPARATIVE MEASUREMENTS OF SKULLS.

|  | *D. squalidens* No. 8777. | *D. felina* No. 455, *Type.* |
|---|---|---|
| Length of skull (incisors to condyles) | 152 | 157 |
| Width across zygomata | 117 |  |
| "    of muzzle | 39 | 49 |
| "    between orbits | 38 | 46 |
| "    of postorbital constriction | 32 | 35 |
| Length of lower jaw (incisors to condyles) | 124 | 125 |
| Depth of flange below incisive border | 35 | 35 |
| Height of coronoid process from condyle | 30 | 32 |

*Skeleton.*—This species appears to be the slenderest of the *Dinictides* in the proportions of the limbs. Except for the greater slenderness and smaller size,
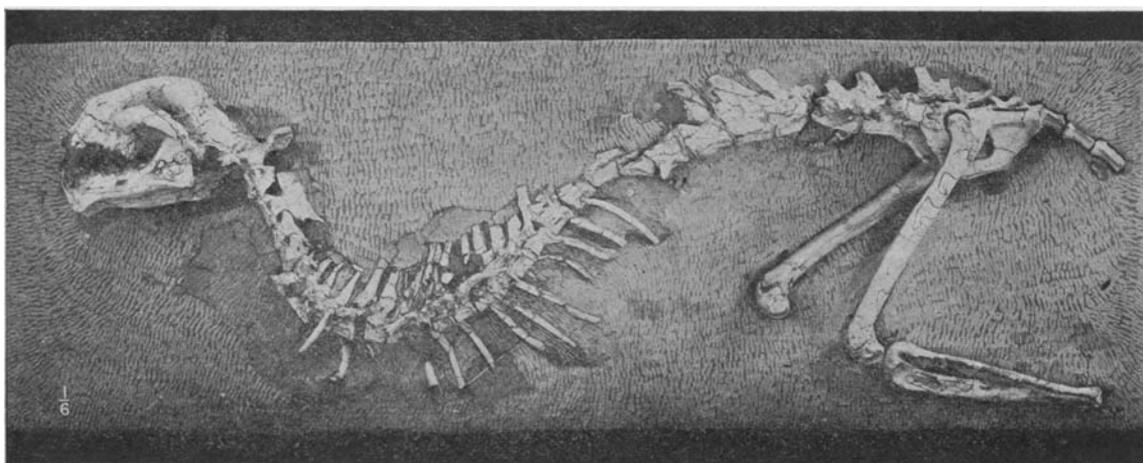


Fig. 14. *Dinictis squalidens*, No. 8777. Skull and greater part of skeleton, as found in the rock. One sixth natural size.

the characters appear to be mostly those of *D. felina*. A comparison with the mounted skeleton of *Hoplophoneus robustus* (Am. Mus. No. 1406) brings out some marked contrasts, partly of generic value.

The *Hoplophoneus* is on the whole a larger animal. The length from the tip of the nose to the root of the tail is about one seventeenth greater. The tail is much heavier, and may have been longer. The legs are about a fifteenth shorter than in the *Dinictis*.

The *Dinictis* cervicals are much smaller and shorter, their spines and processes smaller and slenderer throughout. The dorsals are shorter, smaller, and

with much lighter spines ; the ribs are shorter and lighter ; the lumbars, on the other hand, are fully as large and heavy as in the *Hoplophoneus*, and the sacrum is a little longer.   The upper joints are of about the same length in the two, but the lower leg bones are one sixteenth and the feet one seventh longer in the *Dinictis ;* but all the limb bones are from one sixth to one fourth less in diameter, and with shafts of much more uniform diameter throughout their lengths.   In the slender species of *Hoplophoneus*, although the bones are light, the joints are comparatively heavy and the shaft decreases in diameter to the middle.

The carpus of *Dinictis* has not been adequately known. It is somewhat more modernized than that of *Hoplophoneus*, the pisiform lying more externally to the unciform and the ulna to the pisiform.   The unciform-scapholunar contact is larger, the magnum correspondingly reduced in height.   The whole carpus is much narrower and higher.   The metacarpals



Fig. 15.   *Dinictis squali-dens,* No. 8777.   Fore foot, anterior view, X ⅓.

are longer and less spreading, the phalanges longer and narrower, the single ungual preserved is small and without hood.   The tarsus is also higher and narrower than that of *Hoplophoneus*, and the metatarsals nearly a third longer but considerably smaller in diameter.

COMPARATIVE MEASUREMENTS OF SKELETONS.

|  | Dinictis squalidens. | | Hoplophoneus robustus. |
|---|---|---|---|
|  | No. 8777 | No. 1396 | No. 1406 |
| Length, incisors to root of tail | 867 |  | 917 |
| "      skull | 152 |  | 196 |
| Width     " | 117 |  | 121 |
| Length of seven cervicals | 141 |  | 177 |
| Axis, anteroposterior length of spine | 50 |  | 70 |
| Sixth cervical, antero-posterior length of transverse process | 25 |  | 30 |
| Length of thirteen dorsals | 253 |  | 287 |
| First dorsal, length of centrum | 16 |  | 20 |
| "      "      width  "      " | 16 |  | 23 |
| "      "      height to top of spine | 70 |  | 78 |
| Tenth  "      "      "      " | 47 |  | 59 |
| Length of seven lumbars | 217 |  | 217 |
| Third lumbar, length of centrum | 32 |  | 28 |
| "      "      height to top of spine | 61 |  | 55 |
| Length of sacrum | 74 |  | 70 |
| First caudal, breadth across transverse processes | 38 |  | 58 |
| Length of hind limb and foot | 525 |  | 495 |
| "      " femur | 205 |  | 205 |
| Diameter of proximal end of femur | 40 |  | 49 |
| "      distal      "      " | 36 |  | 43 |
| Length of tibia | 177 |  | 165 |
| Tarsus, width (cuboid and navicular) |  | 26 | 32 |
| Metatarsal II, length |  | 51 | 39 |
| "      diameter of shaft |  | 6 | 7 |
| Length of humerus |  | 171 | 173 |
| "      radius |  | 141 | 135 |

The difference between the proportions of *Dinictis squalidens* and *Hoplophoneus robustus* is nearly paralleled by that between the cheetah and the leopard.

*D. squalidens* had nearly the proportions of a cheetah, somewhat smaller, but with larger head. It was distinguished by the same short, weak neck, small dorsals and light barrel, large and heavy lumbars, light tail, long, slim legs and feet, and imperfectly retractile claws, the ungual phalanges without hoods. I think we may fairly infer a parallelism in habits as in construction, and explain the apparent conservatism in the *Dinictis* dentition by the assumption that its prey consisted in greater part of the smaller, speedier animals of the plains, which it must run down by superior speed or endurance, while the *Hoplophoneus* preyed more on the larger, slower animals of plains or forest, whose destruction required a more powerful animal with more effective weapons of attack.

## Hoplophoneus *Cope.*

A badly preserved skull, No. 8779, agrees well in form and measurements with Leidy's type of *H. primævus* and the specimen described and figured by



Adams ('96, p. 426). There is no trace of $p^2$ although the teeth are but moderately worn, hence if the reference to *H. primævus* of No. 8779 be correct, the presence of $p^2$ cannot be used to distinguish the species from *H. robustus*. The skull has the short, high-rounded *Dinictis*-like outline of the *H. primævus* skull, considerably shorter and rounder than in *H. robustus* (*H. primævus* O. & W., not of Leidy), with shorter and smaller canine and longer $p^4$ than in *robustus*.

A well-preserved lower jaw, No. 8773, corresponds closely to *H. robustus*, agreeing well with three specimens from South Dakota now in the American Museum, one of which was described by Osborn and Wortman under the name of *H. primævus* ('94, p. 228) but which
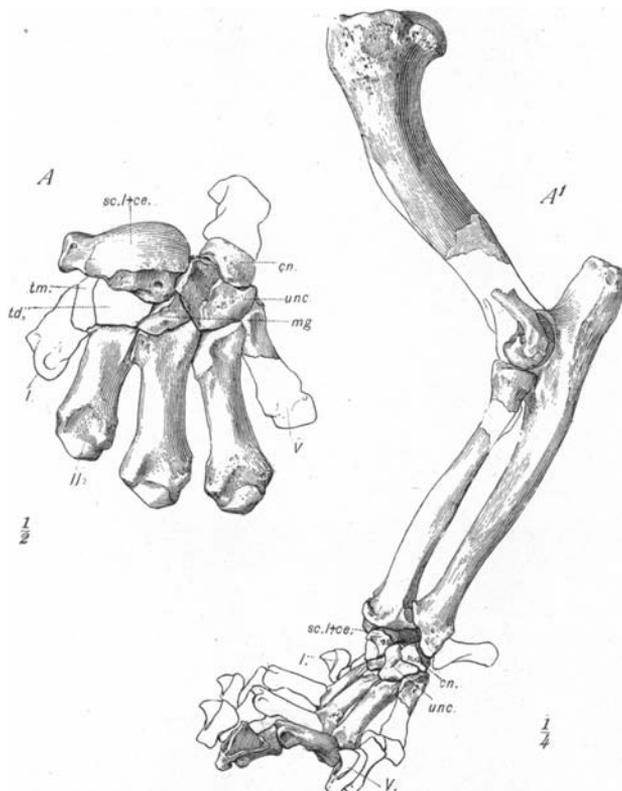
Fig. 16. *Hoplophoneus occidentalis*, No. 1401, Oreodon Beds, S. Dakota. *A*, fore foot, X ½; *A'*, external view of fore limb, X ¼. Figured here for comparison with *Dinictis*.

was afterwards separated by Adams from that species ('96, p. 49).

## ORDER ARTIODACTYLA.

### FAMILY OREODONTIDÆ.

Material for the study of this group is more complete and abundant than for any other fossil mammals, but several of the genera have remained imperfectly known. Of these the most remarkable one is *Merycochœrus*, as represented by the typical species *M. proprius* and *M. rusticus* Leidy, which prove to be quite distinct from the John Day species afterwards referred to it, and to present, among other peculiarities, the character, unique among ruminants, of a well-developed proboscis of some kind, analogous to those of the tapir and elephant. Of this remarkable genus our party obtained two complete adult skulls and three young ones, all parts of the skeleton of several individuals, and various fragmentary specimens, all of the typical species, and a skull, several jaws, an incomplete skeleton, and other specimens of the very distinct species *M. rusticus*. We were fortunate also in obtaining sufficient skeleton material of *Merychyus elegans* Leidy, to enable us to show very considerable differences from the better-known *M. arenarum* Cope. Good skeleton material of the more typical Oreodons of the Leptauchenia horizon shows that they belong to the genus *Eporeodon*, although not easily referred to any of the described species.

The new material herein described makes it possible to arrange the genera more satisfactorily than hitherto. They may be analyzed as follows:

A. Primitive types, more than four crescents on molars....................PROTOREODONTINÆ.
B. Toes clawed, p⁴ molariform, very brachydont...........................AGRIOCHŒRINÆ.
C. Toes hoofed, p⁴ simple, becoming hypsodont.............................OREODONTINÆ.
    I.    Five toes on manus..............................................................*Oreodon*.
    II.   Four toes on manus
        a.  Skull elongate
            Premaxillæ separate...............................*Eporeodon, Mesoreodon*.
            Premaxillæ united.........................................*Promerycochœrus*.
        b.  Skull shortened
            Premaxillæ united, nasals unreduced...............................*Merychyus*.
            Premaxillæ and maxillæ united, nasals reduced.................*Merycochœrus*.
        c.  Skull flattened
            Premaxillæ separate, reduced, facial vacuities present..*Leptauchenia, Cyclopidius*.

*Oreodon* is typically ancestral to all the following genera; that is to say, it represents a stage through or close to which the ancestors of all the others have passed.[1] It is easily separable by the presence of a pollex, the short-crowned teeth, and undeveloped tympanic bulla. The following table shows the most important distinctive characters of the remaining genera, excepting *Mesoreodon* and *Cyclopidius*, which do not rank with the others in distinctness, and perhaps are hardly more than subgenera.

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[1] Whether it was directly ancestral is in some cases very doubtful, and only the discovery of a complete fauna of Upper Eocene age in the Plains region can be expected to decide such a question. As already indicated, the probable climatic difference between the known Eocene lake areas and the region of the Plains makes it improbable that the characteristic animals of these Eocene basins were the same as those prevalent at the same time in the drier regions to the eastward.

| Eporeodon. | Promerycochœrus. | Merycochœrus. | Merychyus. | Leptauchenia. |
|---|---|---|---|---|
| Premaxillæ separate. | Premaxillæ united at tips. | Premaxillæ entirely coössified with each other and with the maxillæ. | Premaxillæ united at tips. | Premaxillæ separate, reduced. |
| Nasals normal. | Nasals normal or somewhat elongated. | Nasals much reduced. | Nasals narrow and somewhat reduced. | |
| No facial vacuities. | No facial vacuities. | No facial vacuities. | Small prelachrymal vacuity. | Large prelachrymal and prefrontal vacuities. |
| Zygomatic arches moderate. | Zygomatic arches very wide and heavy. | Zygomatic arches very wide and deep. | Zygomatic arches slight. | Zygomatic arches deep. |
| Skull somewhat elongated. | Skull more elongated. | Skull shortened. | Skull shortened. | Skull shortened and flattened. |
| Occiput high and narrow, crests prominent. | Occiput high and narrow, crests more prominent and overhanging. | Occiput broader, less overhanging, crests buried in cellular bony tissue. | Occiput narrow, crests not prominent nor overhanging. | Occiput low and broad, crests rather prominent. |
| Mastoid process not expanded. | Mastoid process somewhat expanded into a laterally projecting plate. | Mastoid process enormously enlarged into two broad flat plates projecting laterally. | Mastoid process somewhat expanded. | Mastoid process somewhat expanded. |
| Brachydont. | Brachydont. | Hypsodont. | Hypsodont. | Very hypsodont. |
| Molars more uniform in size. | Molars more uniform in size. | Last molar much the largest. | Molars more uniform in size. | Molars more uniform in size. |
| Premolars spaced, unreduced. | Premolars spaced, unreduced. | Premolars crowded, unreduced. | Premolars crowded, unreduced. | Premolars crowded, reduced. |
| Muzzle square. | Muzzle square. | Muzzle square. | Muzzle rounded. | Muzzle rounded. |
| Legs and feet moderately short. | Legs and feet very short. | Legs and feet very short. | Legs and feet long and slender. | |
| Ungues intermediate. | Ungues short and wide. | Ungues short and wide. | Ungues long and pointed. | |

## Eporeodon *major*, var. *cedrensis*, var. nov.

A number of skulls and incomplete skeletons from Horizon C are referable to this genus, and may be placed provisionally as a dwarf variety of *E. major* Leidy, distinguished also by a somewhat shorter skull from our examples of *E. major* from South Dakota. It stands a little nearer to *Oreodon culbertsoni* and to *Merychyus* than does the typical *E. major*, and is considerably nearer to them than is the John Day species *E. occidentalis*, which approaches *Promerycochœrus* of the same region.

The skulls of the new variety, which may be called *cedrensis*, do not exceed in size the average specimens of *O. culbertsoni* from South Dakota. The teeth, in vertical length, proportion of premolars to molars, individual form of premolars, especially of their external crescents, and the presence of a small postero-external lobe on m³, differ from *Oreodon* and agree with *Eporeodon major*. Four skulls show that the bulla is inflated, and one skeleton that the thumb was absent on either manus. From the typical *E. major*, as represented by about a dozen skulls from the Leptauchenia Beds of the Big Bad Lands, South Dakota, it differs in the smaller teeth and much smaller and shorter skull, the more convex frontal region, general absence of the lachrymal pit, smaller projection of the occipital and sagittal crests, smaller and slenderer skeleton. From *E. occidentalis*, as represented by some twenty cleaned skulls and three or four incomplete skeletons from the John Day region in the Cope Collection, it differs in the same characters but to a greater degree. The skeleton is decidedly smaller and slenderer than that of *E. occidentalis*, the neck considerably shorter (it is shorter than that of *Oreodon*) ; the ends of the cervical centra are flattened-oval, whereas in the John Day species

they are round. The scapula has a weaker metacromial process, but in other respects accords well with Prof. Scott's figure of the *Mesoreodon* scapula ; I am unable, however, to see any important distinction from the specimens of *Oreodon culbertsoni* in our collection. The carpals are not nearly as high as in *Mesoreodon*, and there is no facet between the trapezoid and mc III ; the trapezium is larger than in *Mesoreodon* and overlaps the side of mc II. The unguals are unlike those of *M. chelonyx*, but resemble rather closely those of *M. intermedius*.

This variety shows less tendency toward the long and flat-topped *Promery-cochœrus* type of skull, and more toward the *Merychyus* and *Merycochœrus* type, short and round-topped. A similiar varietal differentiation is observable in the more *Promerycochœrus*-like *E. occidentalis*, but in the John Day species the long, flat-topped type of skull runs to excess, while in Colorado we have the short, round-topped one prevalent. Extremes of the two types (*Promerycochœrus* in Oregon, *Merycochœrus* and *Merychyus* on the Plains) characterize later horizons in the two regions, and may provisionally be considered as products of adaptation to the different climatic conditions of the Eastern and Western slopes. The Western slope was probably then, as now, a region of more abundant rainfall, which the small elevation of the Coast and Sierra ranges would allow to extend much further inland in Tertiary time than now ; reasons are given on a previous page of this paper for assuming a Neocene climate on the Plains not greatly dissimilar to the present one.

## Merycochœrus *Leidy*.

*Historical.*—*Merycochœrus proprius* was described by Leidy in 1858, from upper and lower jaws, found in dull reddish grit beds, Horizon D of Hayden, near Fort Laramie, Wyoming, and in 1873 he added the species *M. rusticus* from the Loup Fork of the Sweetwater River, Wyoming. Bettany, in 1876, referred to the genus the new species *M. leidyi* and *M. temporalis*, based on incomplete skulls from the John Day beds of Oregon, and extended and somewhat altered Prof. Leidy's original generic definitions. Cope, in 1884, referred *Oreodon superbus* Leidy to *Merycochœrus*, and described several new species, *M. chelydra* and *M. macrostegus*, from the John Day, and *M. montanus* from the Deep River of Montana, the last three based on nearly complete skulls. Scott in 1890 added *M. cænopus* from the Loup Fork of Nebraska, and in 1894 described the skeleton of *M. montanus*. The characters of the genus have been taken from these later referred species, chiefly from the John Day beds. In 1898 the American Museum party found a number of fine specimens of each of Leidy's species, and examination of these made it clear that the true *Merycochœrus* was quite a different animal from the species later referred to it. Additional material was found in Montana in 1899, by Mr. Douglas, and described by him in recent articles. The species he describes are allied to *M. proprius*, but show apparently a higher degree of specialization.

The following analysis illustrates the most important distinctions :

*Merycochœrus* Leidy. Type, *M. proprius*. Referred species, *M. rusticus* Leidy (subgenus

*Brachycrus*), *M. laticeps* Douglas (typical group), *M. madisonius*, *M. elrodi*, *M. compressidens* Douglas (position undetermined).

*Promerycochœrus* Douglas.[1] Type, *P. superbus* (Leidy). Referred species *P. chelydra, P. macrostegus, P. obliquidens* (Cope), *P. leidyi, P. temporalis* (Bettany).

### DISTINCTIVE CHARACTERS.

| *Eporeodon.* | *Promerycochœrus.* | *Merycochœrus.* |
|---|---|---|
| Premolar series not reduced in length. | Premolar series not reduced in length (Douglas). | Premolar series reduced in length. |
| Molars of subequal size, the last a little larger. | Molars of subequal size, the last a little larger. | Molars rapidly increasing in size from first to third. |
| Skull somewhat elongate. | Skull elongate. | Skull shortened. |
| Occiput narrow, overhanging. | Occiput narrow, produced backwards. | Occiput broader and more vertical. |
| Mastoid plates small. | Mastoid plates moderate in size. | Mastoid plates widely expanded. |
| Zygomatic process of squamosal moderately wide, not thickened externally, nor produced posteriorly. | Zygomatic process of squamosal very wide, with a thickened rounded margin ending bluntly at posterior edge. | Zygomatic process of squamosal very wide, its margin expanded to a flat, sharp-edged plane surface facing outward and upward, and produced backward into a long process. |
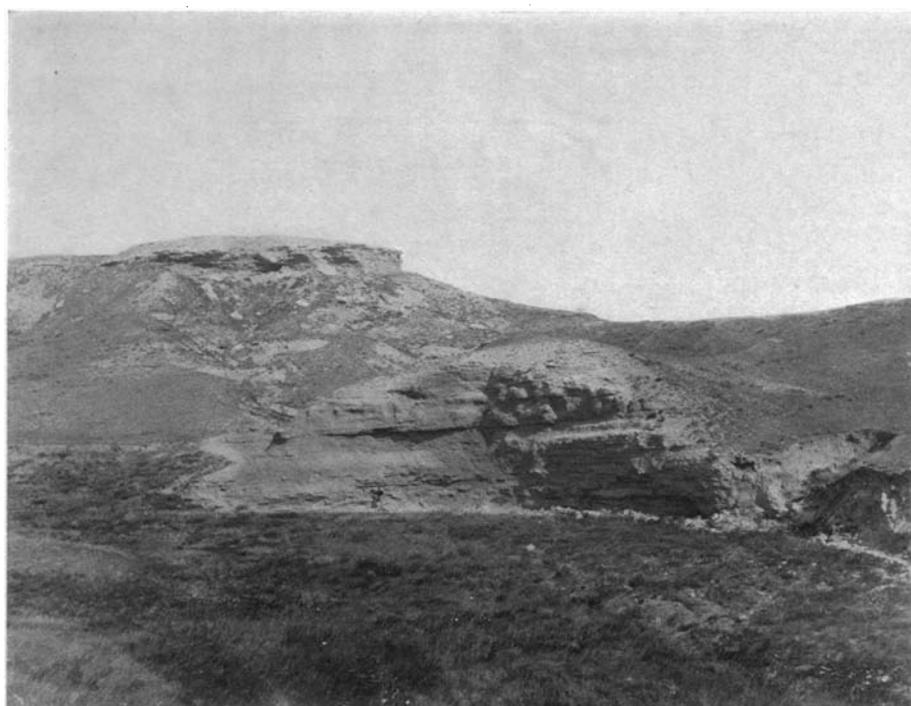


Fig. 17. White River and Loup Fork strata, Martin Cañon, Cedar Creek, Colorado. Locality of *Merycochœrus* and *Phlaocyon* skeletons. (see Figs. 7, 18, 20, 23–26). The hind limb of the *Merycochœrus* was found three feet above the base of the cliff at the point where Mr. Martin stands in the photograph; the remainder of the specimen a little further to the left, on the same level. The White River clays extend up to the conglomerate at the base of the Loup Fork, which appears as a projecting ledge about half-way up the cliff. The Loup Fork beds continue above to the prairie level.

[1] Mr. Douglas uses this name only " provisionally " (Am. Jour. Sci. 1901, Vol. XI, p. 82) in order to avoid anticipating my previously written but until now unpublished work on the subject. While appreciating his courtesy in the matter, I think it will avoid possible confusion to use his name, as it was published with a valid definition.

Fig. 18. *Merycochærus proprius*. Skull, side view, x ⅖. No. 8968. White River Formation, Leptauchenia Beds, Colorado.



Fig. 19. *Promerycochærus macrostegus*. Skull and jaws, side view, x ⅖. Type specimen No. 7444. John Day Formation, Promerycochærus Beds, Oregon. Figured here for comparison with *Merycochærus*.

The special characters of the *Merycochœrus* skull indicate that the animal had a large proboscis of some kind, of a character quite unparalleled among Ruminants, and not very closely paralleled by the Elephant or Tapir.   The evidence is :

1.—Great reduction of the nasals, extending the flexible part of the snout.   Development of rugosities and ridges for strong muscular attachments immediately in front of the orbits ; these give rise to the muscles controlling the motions of the upper lip and the flexible parts of the nose.

2.—Complete coössification of the premaxillæ with each other and with the maxillæ into a solid mass of bone, pierced by a single anterior palatine foramen.  This gives the solid fulcrum necessary to wield a heavy proboscis.

3.—Great broadening of the occipital wings and of the mastoid process of the squamosal, giving power and leverage to the muscles controlling the motion of the skull on the vertebral column.   This increased power is obviously necessary in order to control the correspondingly increased length and size of the snout.

4.—Extensive development of cellular bony tissue in front of the broad occiput, serving to brace the flanges of the transverse crests and the great plate-like mastoid processes, without unduly weighting the skull.

5.—Extreme shortening of the neck, the head proper being no longer obliged to reach the ground, and the shorter neck giving more advantageous leverage for the skull on the body.

Of these characters, Nos. 1, 2, and to some extent 3 and 5, are seen in the Tapir.   All are seen in the Proboscidea, and, aside from the teeth, are the chief points of difference from other Ungulates.   In the modern Elephants they are carried much further than in *Merycochœrus*, but if we compare *Merycochœrus* with the Loup Fork Mastodons we find a remarkable resemblance in most of the skull characters.   The teeth are very different, the Oreodont retaining unchanged the square muzzle, cropping incisors, and pig-like canines of the family ; and its broad, heavy zygoma is a contrast to the weak and slender one of the Proboscideans.   The Tapir has not gone so far in skull changes as has *Merycochœrus*— he has nearly as much increase in power but less increase in flexibility of the snout, and the increase in control of the skull by the neck muscles has been comparatively small.

The peculiar way in which the tips of the nasals are bent upward in the most highly differentiated species of the genus, *M. laticeps*, suggests that the direction or form of the proboscis was very different from that in the Tapir, a hypothesis strengthened by the retention and evident usefulness of the cropping incisors and vertical canines, which would apparently be of little use to an animal with a proboscis like the Tapir.   Whatever the form or proportions of this organ, it can hardly be denied that the above evidence is sufficient to reasonably prove its existence.

It is interesting to observe that Dr. Leidy, in 1873, suggested from the characters of the fragmentary specimens at his command that *Merycochœrus* possessed a "short proboscis like that of the Tapir"—a prophetic suggestion now verified by our complete material.   I had not noticed his suggestion until finally revising this manuscript.

Two species of *Merycochœrus*, so widely distinct that it is doubtful whether they should be retained in the same genus, occur in the Loup Fork formation

(Horizons D and E) of Colorado. One of these I identify with *M. proprius* Leidy; the other, provisionally, with *M. rusticus* Leidy. Each species is represented by several specimens, including the skull, jaws, and various parts of the skeleton. In addition I am obliged to refer to *M. proprius* an exceptionally fine specimen from near the top of the White River formation (Horizon C).

The two species have in common the generic characters of *Merycochœrus* given in the diagnosis above. Their distinctive characters are :

*M. proprius.*—Larger size, cranial region very short, occiput high and broad, mastoid plates very wide, arches heavier, forehead less convex, no sagittal crest, the temporal crests sweeping back to the occiput without joining. Limb bones longer, feet shorter, more tetradactyl, metapodials more compactly bound together, ungues broader and shorter.

*M. rusticus.*—Smaller size, cranial region longer, occipital region lower, mastoid plates (?) moderately wide, arches lighter, frontal region strongly convex in both directions, temporal crests uniting immediately behind postorbital constriction to form a distinct sagittal crest. Limb-bones shorter, feet longer and more spreading but lateral toes more reduced, ungues narrower and longer.

## Merycochœrus proprius *Leidy.*

To this species I refer

No. 9052. Complete skull with some fragments of skeleton.
Nos. 9051, 9053. Upper jaws.
Nos. 9055, 9057, 9058, 9062. Parts of lower jaws.
No. 9064. Teeth, parts of jaw and fore limb, vertebræ, etc.

All these are from Horizons D and E, similar beds to those in which the type specimen was found.

The White River specimen, No. 8948 (photographed in Fig. 20), presents many minor points of difference, but none that can be considered on the evidence at hand as due to more than individual or sexual variation. It consists of the skulls, jaws, and all parts of the skeletons of one adult and four young individuals found together. With them was found the nearly complete skeleton of the primitive raccoon, *Phlaocyon leucosteus,* and a tooth of *Anchippus.* The bones are beautifully preserved, creamy white in a fine pinkish buff clay matrix, and so perfect in surface as to appear like those of a well prepared recent skeleton. ·

The horizon of No. 8948 must be given as in the White River *formation,* but its age is probably Lower Miocene. The specimen was found in the fine pinkish buff clays of the older formation, near the bottom of a somewhat overhanging cliff (Fig. 17) fifteen feet below the conglomerate which immediately overlies the clays. The way in which the bones lay scattered through one level, and the undisturbed condition of the beds about and above them, preclude any possibility of the specimen being other than contemporaneous with the enclosing stratum. At this locality, however, the surface of the White River is very high up, representing the latest deposits of the formation, most nearly approximating the Loup Fork in age. The fauna of the Loup Fork of this region also has a more ancient facies than the better known Loup Fork faunas of Nebraska and Kansas, and indicates that the beds are as old as the Deep River beds of

Fig. 20. *Merycochœrus proprius*, No. 8968. Block of matrix containing skulls and skeletons of one adult and four young individuals. The *Phlaocyon* skeleton was found lying in the lower left-hand corner of this block, but was removed to be mounted separately.

Montana, if not older. Their age is then perhaps rather Middle than Upper Miocene, and the break between the White River and Loup Fork formations would not be so great as in most other localities. Hence the occurrence of two or three identical species in both is less surprising.

The descriptions and measurements following are based in the first place upon
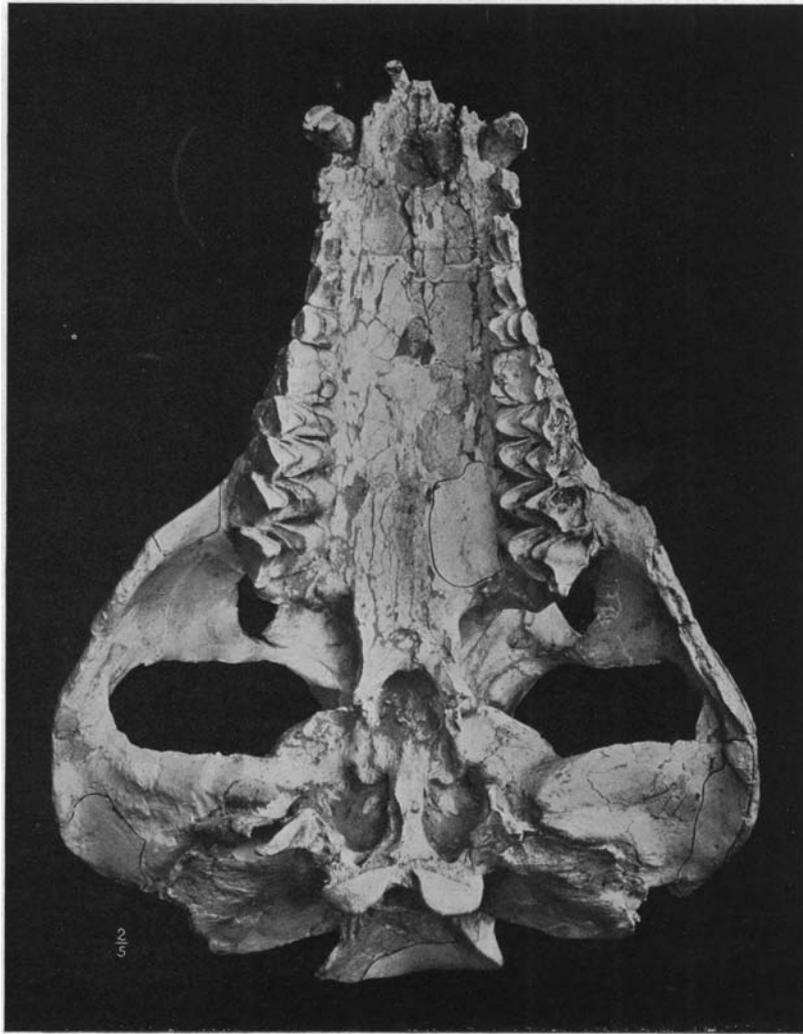


Fig. 21. *Merycochœrus proprius.* Palatal view of skull, x ⅖. No. 9052. Loup Fork Formation, Protolabis Beds, Colorado.

the Loup Fork specimens, but largely supplemented from the White River one.

*Teeth and Jaws.*—The upper teeth form a continuous row except for slight diastemata behind canine and first premolar. The incisors are rather small, short-crowned, much less spatulate than in *Promerycochœrus.* The canine is moderately large and directed more forward than in *P. superbus.* The first premolar is simple with internal cingulum, set somewhat obliquely in the jaw, and spaced in front and behind, one third of its length. The remaining teeth are more hypsodont than in *Promerycochœrus,* the fourth premolar is more quadrate, a small postero-internal

cusp being present.   The molars increase rapidly in size, the length of $m^3$ being about equal to the sum of $m^1 + m^2$.   The metastyle on $m^3$ is strong and the posterior half of this tooth is twisted inward, so as to bring the metastyle in line
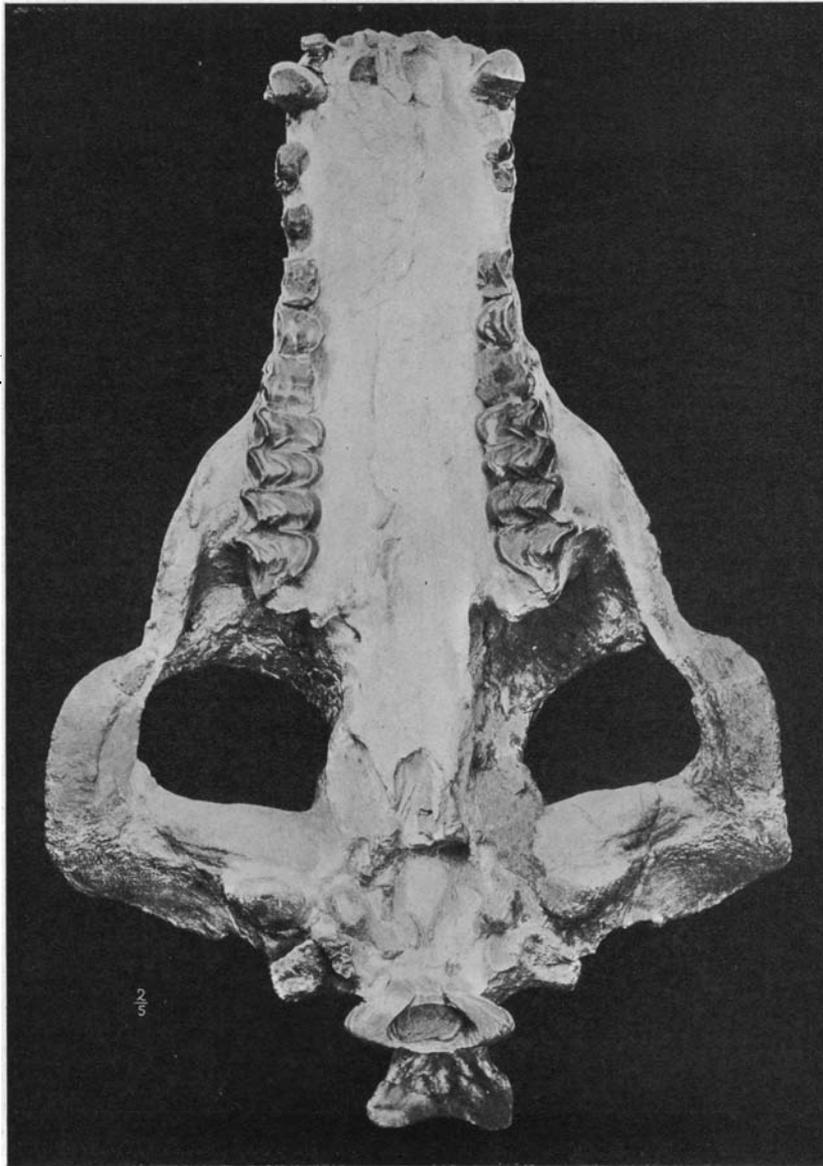


Fig. 22.  *Promerycochœrus macrostegus*, No. 7444.   Palatal view of skull, x ⅖.

with the middle of the row of teeth in front of it.   The palate is much wider posteriorly than in *Promerycochœrus*, in which the outer lines of the teeth from c – $m^3$ are nearly parallel.

The lower teeth differ correspondingly from those of *Promerycochœrus*, the premolars being shorter, the second one set obliquely in the jaw, the molars more hypsodont and increasing rapidly in size from the first to the third.   The coronoid

process has the form of that of *Promerycochœrus*, but is more reduced than in any other Oreodont. The coronoid of *Merychyus* most nearly approaches it in size, but is directed more upwards at its base, then strongly recurved, while the
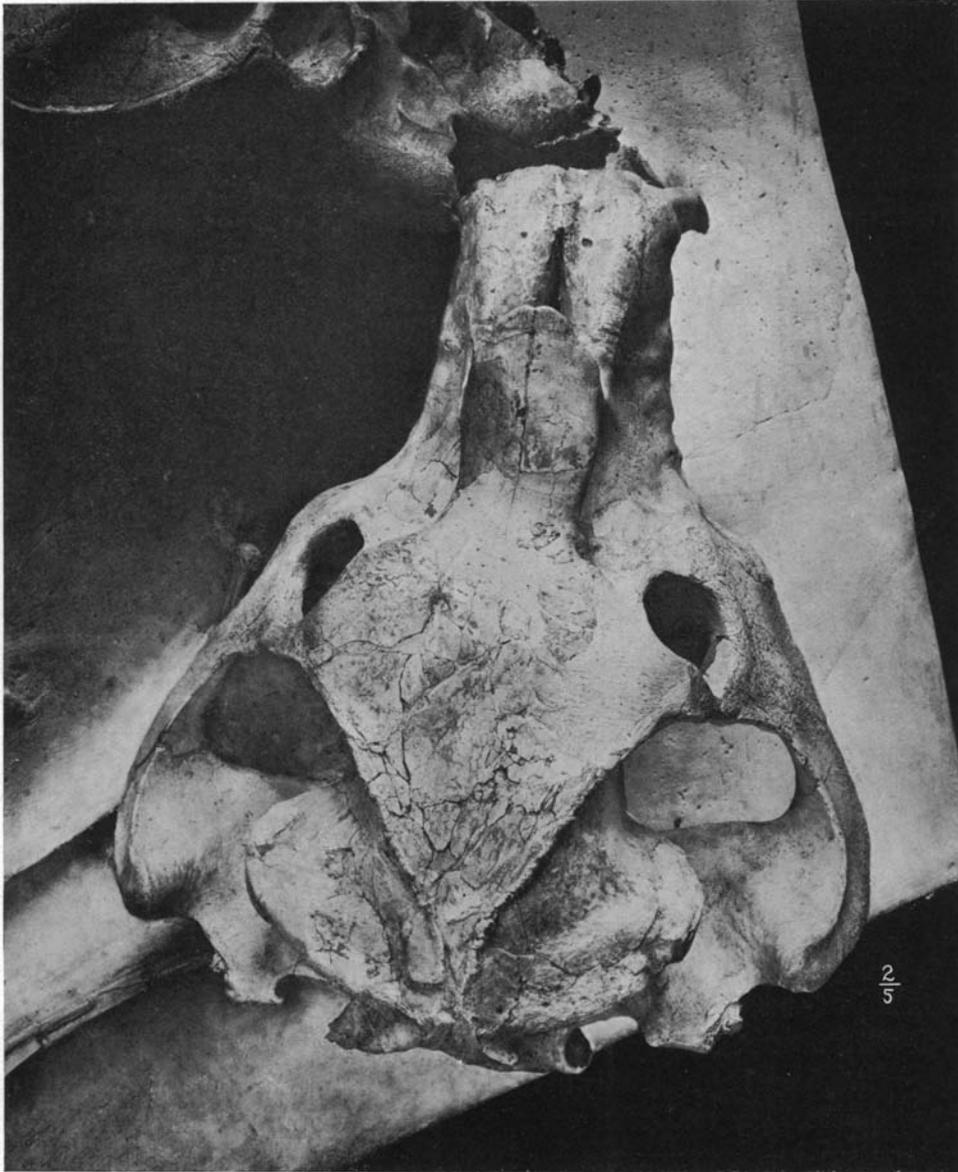


Fig. 23. *Merycochœrus proprius*, No. 8968. Top view of skull, x ⅖.

*Merycochœrus* coronoid is straighter and directed more backward from the base; also in *Merycochœrus* and *Promerycochœrus* there is a strong supporting buttress from the inside upper edge of the jaw, reaching more than half-way up on the process.

*Skull.*—Width about the same as in *Promerycochœrus* but molar region of palate much longer and wider and cranial region much shorter. Nasals much reduced, projecting only a little beyond $m^1$; premaxillæ firmly coössified with each

other and with the maxillæ, obliterating the sutures and forming a solid upper jaw bone with a flat antero-superior surface, and divided posteriorly by a fissure which commences about opposite the front of $p^2$ and broadens uniformly backward to the ascending processes of the maxillæ, above $m^1$. These processes are about twice as wide as long, the free anterior edge rising upward, then forward to a blunt point, and then backward in a small notch where it joins the free edge of the nasals. The whole posterior part of the maxilla, including the lachrymal, is excavated, the borders of the depression with more or less pronounced rugosities. The muscles whose origin is at these rugosities are those controlling the motions of the nose and upper lips, as follows: *levator labii superioris* and *orbicularis*



Fig. 24. *Merycochœrus proprius*, No. 8968. Posterior view of skull, x ⅖.

*palpebrarum* in front of orbit, and *levator labii superioris alæque nasi*, at junction of frontals with maxillæ.

The *frontals* are considerably inflated, their upper surface moderately convex, both antero-posteriorly and transversely. The zygomatic arches are nearly one half deeper than in *Promerycochœrus superbus*, and differ from all the species of *Promerycochœrus* in the uniform continuous upward and outward slope of their external surfaces. The squamosal process extends forward to opposite the posterior end of $m^3$, wedged in between two posterior branches of the jugal; posteriorly this process continues, with a flat surface, facing upward and outward, nearly an inch wide, with parallel sharp edges, curving backwards and upwards and ending in a long flat process pointing backwards, upwards, and inwards, about opposite the condyle. The depth of the arch under the orbit is about two inches. From the post-orbital bar the two temporal ridges sweep backward and upward, not joining until

they reach the occiput. From the posterior part of the nasals the top of the skull rises in an irregularly convex curve until it reaches the occiput. The orbits are situated much higher above the jaws than in *Promerycochœrus*, but at the same distance below the top of the skull. The occiput is higher than in *Promerycochœrus*, projects less backward, and is about twice as broad. The broad, wing-like mastoid plates project laterally in nearly the same plane to a width nearly equal to three fifths the length of the skull; at their lower inner corners they merge into the paroccipital processes, which are rather stout, directed downward and outward. The external auditory meatus emerges at the widest point of the mastoid plate, between it and the zygoma ; the lower border of the plate lies against the post-glenoid process and projects beyond it externally. The condyles are smaller, the basisphenoid much shorter and narrower than in *P. superbus ;* the bullæ were large, but have been broken away in one skull and are not exposed in the others, so that they cannot be described. The frontals, parietals, and squamosals are thickened by a heavy layer of cellular bony tissue which fills in the space between the temporal ridges and in front of the occipital crest and the mastoid plates and is especially thick along the anterosuperior border of the squamosals, where it forms a prominent ridge.

MEASUREMENTS OF SKULL.

| | No. 9052. | No. 8948. Adult and three young. | | | |
|---|---|---|---|---|---|
| Length of skull, incisors to condyles | 286 | 283 | 247 | 242 | 239 |
| Extreme width across zygomata | 244 | 250 | 160 | .. | 168 |
| Height of occiput | e.118 | 125 | 185 | 191 | .. |
| Width of mastoid plates | 160 | 176 | 106 | 103 | 108 |
| Depth of zygoma beneath orbit | 55 | 53 | 30 | 32 | 36 |
| Width of palate at third molar | 120 | 120 | .. | .. | .. |
| Length of dentition, $i^1$ to $m^2$ | 185 | 188 | 141[1] | 142[1] | .. |
| " premolars | 61 | 65 | 65 | 64 | .. |
| " true molars | 88 | 93 | .. | .. | .. |
| " $m^1$ | 20 | 20 | 28 | 24 | .. |
| " $m^2$ | 47 | 47 | .. | .. | .. |
| Distance from condyles to posterior nares | 82 | .. | .. | .. | .. |
| Width of occipital crest | 68 | 83 | 50 | 47 | 47 |
| Length from occiput to tips of nasals | 232 | e.233 | 185 | 181 | 181 |
| " " " " post. border of orbit | 130 | 129 | 99 | 106 | 104 |
| Distance between orbits | 80 | 89 | 69 | 69 | 70 |
| Width at postorbital constriction | 60 | 83 | 58 | 68 | 61 |
| Width at external surface of brain-case | 115 | 144 | 81 | 85 | 94 |

MEASUREMENTS OF LOWER JAW.

| | No. 8948 (three young). | | | No. 9058. | No. 9062. | No. 9064. |
|---|---|---|---|---|---|---|
| Length of lower jaw | 210 | 207 | 200 | .. | .. | .. |
| " dentition | 130 | 136 | 123 | .. | e. 190 | .. |
| " premolars | 61 | 63 | 62 | .. | 70 | .. |
| " molars | .. | .. | .. | 10 | .. | .. |
| " first molar | 21 | 22 | 23 | 22 | .. | .. |
| " third " | .. | .. | .. | 52 | .. | .. |
| Depth of jaw at second " | 43 | 42 | 50 | .. | .. | .. |
| " " " " coronoid process | 107 | 104 | 107 | .. | .. | 134 |

[1] $i^1$ to $m^2$.

SKELETON.— The skeleton resembles most nearly that of *Promerycochœrus montanus* described by Scott ('94, p. 151) but exaggerates the peculiarities of that species. The Loup Fork specimens do not illustrate very much of the skeleton, and in the White River specimen, unfortunately, nearly all the skeleton bones, except for one complete hind limb, belong to the young individuals and give an imperfect idea of the extreme peculiarities of the adult.

*Vertebræ.*—The cervicals have very short centra ; the seventh is about one fifth shorter and wider than that of the pig, with much larger zygapophysial facets. There is no foramen for the vertebral artery. Two anterior dorsals have rather large centra and stout triangular spines of unknown length. Judging from the characters of the young individual, the dorsal spines were stout and rather long, the lumbars much reduced in length, their centra averaging only about one third more than the dorsal centra. The caudals are not known.

MEASUREMENTS.

| | No. 9064. | No. 8948. | |
| --- | --- | --- | --- |
| | | Adult. | Young. |
| Atlas, antero-posterior diameter | .. | 35 | .. |
| "　transverse diameter | .. | 96 | .. |
| Seventh cervical, length of centrum without epiphyses | 15 | .. | 15 |
| 　　　　width　　"　　anteriorly | 23 | .. | .. |
| 　　　　width across zygapophyses | 50 | .. | 34 |
| 　　　　height to top of neural canal | 38 | .. | .. |
| 　　　　"　　"　　spine | .. | .. | 46 |
| Fifth or sixth dorsal, length of centrum | 23 | .. | .. |
| Sixth or seventh dorsal, length of centrum | 27 | .. | 20 |
| 　　　　　　width | 25 | .. | .. |
| 　　　　　　height to top of spine | .. | .. | 135 |
| Length of centrum of a lumbar vertebra | 36 | .. | 29 |
| Height to top of spine of a lumbar vertebra | .. | .. | 39 |
| Length of centrum of another lumbar | .. | .. | 30 |
| Height to top of spine of another lumbar | .. | .. | 41 |
| Length of centrum of first sacral vertebra | .. | 41 | 23 |
| Width　　"　　"　　"　　" | .. | 139 | 104 |
| Longest complete rib preserved | .. | 260 | 210 |

*Fore Limb.*—The humerus is known from the young individual, only fragments of the adult (No. 9064) being preserved. It is short and stout, agreeing well with Professor Scott's description of the humerus in *P. montanus*, not as short or massive as in *M. rusticus*. The ulna and radius are moderately short, the shaft of the ulna larger than that of the radius, not greatly recurved. The scaphoid has a narrow facet for the trapezoid and one about twice as wide for the magnum. The fourth and fifth metacarpals are very short and stout, the latter over one fifth shorter but of the same proportionate weight of shaft. The fore legs and feet of the younger individuals are shown on the block in undisturbed position, and illustrate the actual appearance of this foot more correctly than could be done by reconstruction. The foot is small and the short metapodials are very closely bound together, while the stubby toes spread somewhat like those of an elephant.

The radius and ulna have not attained their full length, so that the young were comparatively short-legged. The phalanges are shortened and the terminal ones reduced and flattened to a greater degree than in any other Oreodont.

MEASUREMENTS.

| | No. 9064. | No. 8948 (young). | | |
|---|---|---|---|---|
| Height of scapula............................................. | .. | 140 | 146 | 125 |
| Length of humerus (without epiphyses)......................... | .. | 146 | 148 | 142 |
| Length of ulna (with epiphyses) .............................. | e. 215 | 170 | .. | .. |
| Width of shaft of ulna........................................ | 22 | 20 | .. | .. |
| Length of radius (the young individuals without epiphyses) ....... | e. 150 | 102 | 103 | 97 |
| Length of fore foot..... ..................................... | .. | 120 | 134 | 115 |
| Height of carpus.............................................. | .. | 36 | .. | .. |
| Width     "        ........................................... | .. | 40 | 42 | .. |
| "        scaphoid ........................................... | 18 | 18 | .. | .. |
| Width of metapodium at proximal end .......................... | .. | 42 | 45 | 36 |
| Length   metacarpal   II..................................... | .. | 46 | 49 | .. |
| "        "        III..................................... | .. | 61 | 60 | 60 |
| "        "        IV...................................... | 63 | 48 | .. | 52 |
| "        "        V..... .................................. | 50 | 43 | .. | 44 |
| "        1st phalanx......................................... | .. | 17 | 17 | 20 |
| "        2d      "        .................................. | 9 | 10 | 10 | 11 |
| "        ungual phalanx..................................... | 13 | 11 | 10 | 11 |

*Hind Limb.*—A complete hind limb and foot of the White River specimen is preserved, and agrees exactly with the fragments of hind limbs and feet of Loup Fork specimens. The iliac part of the pelvis is short and wide, but its border is not preserved, so that the exact shape is unknown. The femur is long in proportion to the tibia and foot, giving the limb a curious resemblance to many Eocene mammalia; the shaft is straight, oval in section, the distal end rather wide but not as deep anteroposteriorly as in most Oreodonts. The trochlea is short, broad, low, and shallow, the condyles wide apart and not very prominent. The tibia is rather short, straight-shafted, the cnemial crest prominent and extending nearly half-way down on the bone; the external end more quadrate than is usual among Oreodonts, from the thickening of the external side; the internal malleolus long, and exceptionally broad anteroposteriorly. The fibula is slender, the proximal end rudimentary with no facet for the tibia, the distal end enlarged suddenly anteroposteriorly to about the same width as the internal malleolus ; the shaft has in its middle third a prominent crest projecting antero-internally towards the tibia, and is otherwise of oval section, the lesser diameter transverse. The astragalus is like that of *Promerycochœrus*, shorter and more oblique than in any other Oreodont. The foot is very much like that of *P. montanus*, but one seventh smaller, the lateral toes a little less reduced, the second cuneiform united to the third with a less noticeable step on the distal facet, the internal cuneiform narrower and its facet for metatarsal II less distal and more external. The toes are proportionately shorter, and the ungual phalanges reduced to small, almost nodular bones of semicircular outline, flattened and rugose without any trace of the medial ridge seen in other artiodactyls (except the camel).
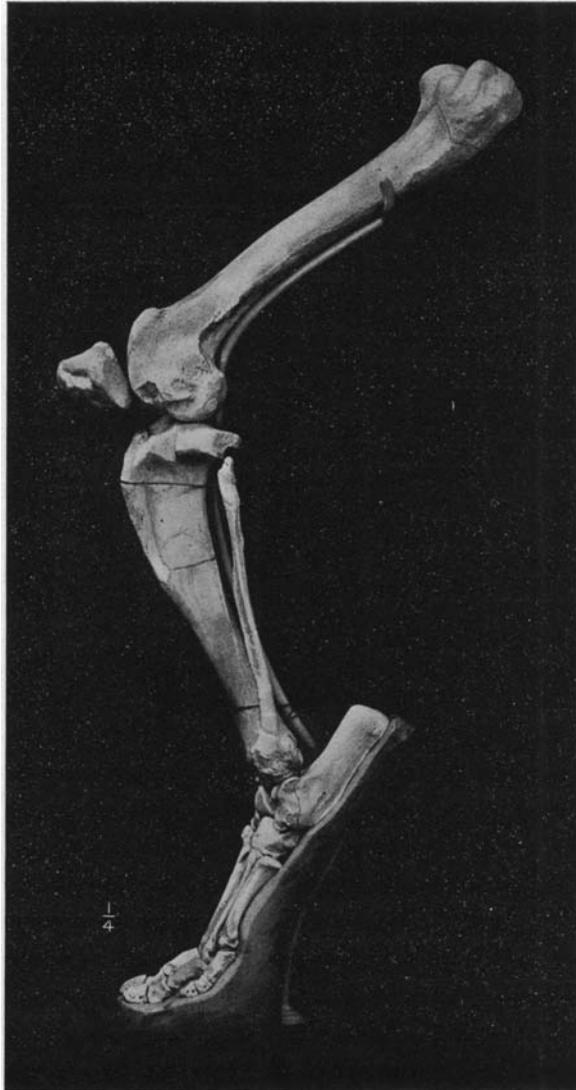
Fig. 25. *Merycochœrus proprius*, No. 8968. Hind limb, external view, x ¼.

Fig. 26. *Merycochœrus proprius*, No. 8968. Hind limb, front view, x ¼.

*Female and Young* (Fig. 21).—The skull No. 9052 I suppose to be that of an adult female, the large skull of No. 8948 an adult male, and the smaller ones are those of young individuals of the same species.

The main distinctions between male and female skulls would seem to be the shorter and wider muzzle, larger canines, broader skull, heavier arches, heavier layer of cellular tissue over the frontal and cranial regions in the male.

In the young skulls the proportions and outward appearance are very different from the adult, so that when the block was sent in from the field no suspicion was entertained that they would prove to be the same species. The teeth, however, are identical, all the generic characters are the same, and the differences from the adult skull when analyzed are what ought to be seen in young

individuals of the same species. They also possess such of the distinctive specific characters of *M. proprius* as could be determined in an immature animal.

MEASUREMENTS OF HIND LIMB.

| | No. 9052. | No. 8948. | | |
|---|---|---|---|---|
| | | Adult. | Young. | |
| Length of femur (young individuals without epiphyses)........... | .. | 250 | 162 164 | 157 |
| Width of shaft.......................................... | .. | 27 | 22 21 | 22 |
| "    distal end.......................................... | .. | 59 | 46 .. | .. |
| Depth   "   ..................................................... | .. | 59 | .. .. | .. |
| Length of tibia (young individuals without epiphyses)............. | .. | 195 | 124 132 | 120 |
| Width of head.......................................... | .. | 60 | .. .. | .. |
| "      shaft ...................................... | .. | 23 | 19 19 | 19 |
| Anteroposterior diameter of distal end......................... | .. | 28 | .. .. | .. |
| Transverse      "      "      "   .......................... | .. | 40 | .. .. | .. |
| Width of internal malleolus (anteropost.).......... ............. | .. | 22 | .. .. | .. |
| Length of fibula ............................................ | .. | 171 | .. .. | .. |
| Transverse diameter of shaft (least diam. near distal end)......... | .. | 5 | .. .. | .. |
| Anteroposterior diameter of distal end. ........................ | .. | 24 | .. .. | .. |
| Length of foot (astragalus to ungues)........................... | .. | 168 | .. .. | .. |
| Width of tarsus............................................ | .. | 46 | .. .. | .. |
| Length of astragalus......................................... | 36 | 40 | .. .. | .. |
| Width of   "   ......................................... | 28 | 31 | .. .. | .. |
| Length of metatarsal II.......................................... | .. | 55 | .. .. | .. |
| "      "      III.......... ........................... | .. | 66 | .. .. | .. |
| "      "      IV......................................... | .. | 68 | .. .. | .. |
| "      "      V......................................... | .. | 54 | .. .. | .. |
| "    1st phalanx............................................ | .. | 25 | .. .. | .. |
| "    2d   "   ........................................ | .. | 15 | .. .. | .. |
| "    ungual phalanx .................. .................... | .. | 16 | .. .. | .. |
| Width of   "      "   ................................... | .. | 13 | .. .. | .. |

In the outlines of the skull the young resemble other Oreodonts much more than does the adult. The shortness of the cranial region is marked, as in the adult, and the maxillo-premaxillary coössification is complete and the nasals much reduced. But the occiput is not nearly so high nor so wide, the mastoid plates are quite moderately developed, the zygomatic arches not nearly so wide nor so deep, and the cellular bony tissue layer on the frontal and cranial region is quite moderate in amount, so that the back of the skull is not exceptionally high, and the temporal crests unite to form a short sagittal crest before reaching the occiput.

The anterior milk teeth have been recently lost, a few still remaining in one of the jaws; the milk premolars, except the first, are still retained; the permanent incisors have not yet cut the bone, the first permanent upper premolar is fully out, while the upper and lower canines are just appearing. The first upper and lower molars are moderately worn, the second have hardly come to the level of the grinding surfaces, and there is no indication of the third. The order of the appearance of the teeth is then $m\frac{1}{1}$, $p\frac{1}{1}$, $m\frac{2}{2}$, $c\frac{1}{1}$, $p\frac{}{\overline{1}}$, $i\frac{1-3}{1-3}$, $c\frac{}{\overline{1}}$, $p\frac{2-4}{2-4}$.

The limb bones are, as already noted, proportionately shorter in the young individuals than in the adult.

The measurements of the young individuals are given with those of the adult.

## Merycochœrus rusticus Leidy.

*Merycochœrus rusticus* Leidy, Extinct Vert. Fauna of the Western Terrs., Report U. S. G. S. Terrs., 1873, p. 199, pll. vii and xx.

Type, pieces of upper jaws ; of doubtful association, parts of lower jaws, astragalus, part of scapula, distal end of tibia, etc., all from supposed Loup Fork beds of Sweetwater River, Wyoming.

I refer provisionally to this species a number of well-preserved specimens from Horizon E. They differ somewhat from the type specimen, as figured, in the form of the external crescents of the upper molars, and more widely from the skeleton fragments referred by Prof. Leidy to the species, so that if the latter really belong to it, the Colorado specimens represent a distinct undescribed form. Further collections made in the Sweetwater locality are needed to settle this question. The specimens from Colorado are

No. 9050. Incomplete skull and jaws with the greater part of skeleton, not yet entirely extracted from the matrix.

No. 9056. Pair of lower jaws, complete.

No. 9115*a*. Pair of lower jaws, one incomplete ; three upper molars.

No. 9049. Fore leg and foot and various fragments of skeleton.

These four are certainly conspecific ; they are true *Merycochœri* in general characters, but present some striking differences from *M. proprius* in form of skull and proportions of limbs and feet. It seems hardly advisable to create another genus on these distinctions, as the *Merycochœri* were evidently an abundant and rapidly differentiating race during the Miocene, and in skull characters the adult of the smaller species is quite near to the young of *M. proprius*. The teeth are very close to those of the type species, and the skeleton, while showing various specializations different from those of *M. proprius*, is yet more like it than to any of the *Promerycochœri*.

*Teeth.*—Upper premolars unknown ; upper molars, in Nos. 9050 and 9115*a*, about as hypsodont as in *Merycochœrus proprius*, but more symmetrically quadrate, the inner crescents, especially of $m^3$, of equal size and their branches equally developed. Outer walls of external crescents uniformly concave, whereas there is in *M. proprius* (as also in Leidy's figures of the type of *M. rusticus*) a faint median ridge on each crescent-wall.[1]

## MEASUREMENTS.

|  | No. 9050. | No. 9115*a*. |
|---|---|---|
| $M^1$ to $m^3$ | 68 | |
| $M^1$ | 14 | |
| $M^2$ | 21 | 24 |
| $M^3$ | 34 | 34 |
| " transverse | 27 | 24 |
| $M^2$ " | 24 | 22 |

[1] This is in part an age character, hence unreliable for specific distinction.

The lower teeth may be described best from the young individual, No. 9115a (Fig. 28), in which the permanent teeth are present but not greatly worn. Lower incisors like those of *M. proprius*, with triangular-oval crowns, rather small and crowded, anteroposterior diameter greater than transverse diameter. A median ridge and basal cingulum on posterior face. Canine transversely oval, incisiform, with median internal ridge and basal internal cingulum. First premolar caniniform, rather small for the genus, of oval section with oblique axis; $p_{\overline{2}}$ set obliquely, more than twice as long as wide, protoconid median, external, a strong median internal ridge, and strong internal cingulum. $P_{\overline{3}}$ obovate, pointed in front, blunter behind, main cusp external, with strong ridges directed posteriorly, internally, and anteriorly, and two minor ridges redividing the two sections of the inner face. $P_{\overline{4}}$ submolariform, with broad, square, bicrescentic heel divided by a deep external indentation from the anterior part of the tooth, which is like the corresponding part of $p_{\overline{3}}$, but broader. Molars rapidly increasing in size from before backward; the valleys between the external and internal crescents have already disappeared by wear, except on the heel of $m_{\overline{3}}$. The internal walls are nearly flat, but still show some trace of the internal ridge on each crescent which in a younger tooth would be more prominent.

The chin is abruptly concave, the inferior border of the mandible gently convex beneath the teeth, then gently concave back to the angle. The angle is a large uniform sweeping curve; the coronoid process is greatly reduced, as in all Oreodonts.

The jaw of the older individual, No. 9056, is more perfect, both sides being entire. It is instructive as showing the changes produced by age in the apparent form of the teeth, proportions of the jaw, etc.

The incisors have lost about half



Fig. 27. *Merycochœrus rusticus.* Lower jaws, external view, × ⅔. No. 9056. Loup Fork Formation, Protolabis Beds, Colorado.

their transverse width and are more nearly in a straight row, crowded, oval in cross-section, worn down below the enamel except in front. The canine has become subquadrate, is widest in a direction transverse to its former spatulate surface, and is worn as much as are the incisors. The caniniform premolar has gained one third in width and lost slightly in length; it is

quadrate in section, wider than long, and worn below the enamel except externally. $P_{\overline{2}}$, has gained in width and lost in length ; $p_{\overline{3}}$ has lost one fifth in length and $p_{\overline{4}}$ one sixth. The first molar has lost in length, the second is stationary, and the third has gained a little, as it was hardly out of the jaw in the younger specimen. All have, of course, gained greatly in width. The dentition as a whole has lost five per cent., partly in the premolar, partly in the incisive region. The position of the mental foramen has changed, bringing it nearer the front of the jaw, but as all the teeth have also moved forward during wear, and to a somewhat greater degree, its relative position is further back.

The jaw of the skeleton, No. 9050, is intermediate in wear between the two above described, and intermediate in all the above differences of form.

That these characters of the teeth are not of specific value is easily proved by measuring the teeth of the three specimens at points of corresponding wear, when their size and proportions are identical throughout, as far as it is possible to make the measurements. The validity of characters of this kind in specific diagnoses is discussed under the Camelidæ.

MEASUREMENTS.

| | No. 9115a | No. 9050 | No. 9056 |
|---|---|---|---|
| Total length of lower jaw................ | 227 | .. | 223 |
| Height at coronoid process................ | 113 | .. | 120 |
| Depth under $m_{\overline{2}}$................ | 40 | ? 46 | 48 |
| Width across caniniform premolars........ | 51 | .. | 55 |
| Width of six incisors.................... | 33 | .. | 26 |
| Anteroposterior space occupied by incisors and canines................ | 21 | .. | 25 |
| Anteroposterior space occupied by premolars...... | 53 | 49 | 50 |
| "　　　"　　　"　　" true molars. ... | 74 | 68 | 71 |
| Length of first molar................ | 15 | 14 | 14 |
| "　　" third "， ................ | 37 | 37 | 40 |
| Width　"　　"　　" in front................ | 16 | 17 | 17 |

Comparison of these specimens with the several species of small *Merycochœri* from Montana recently described by Mr. Douglas (*M. madisonius, M elrodi, M. compressidens*) confirms the reference to *M. rusticus* of the four Colorado specimens. Making the proper allowance for differences of age and other probably individual characters, the Montana species seem to be more specialized, the difference corresponding to the distinctions between *M. laticeps* and *M. proprius*, and. indicating the Montana bed as perhaps a later horizon.

The skull in No. 9050 shows important differences from that of *M. proprius*, but chiefly in the lack of specialization, causing it to resemble more nearly the young skulls of the type species. Compared with the adult *M. proprius* the cranial region is much longer, occiput not so high, mastoid plates apparently not so wide, sagittal crest lower, but not obliterated by cellular tissue, frontal region much more convex, both transversely and anteroposteriorly, zygomatic arches not

so wide or massive, temporal crests uniting to form a sagittal crest close behind the postorbital constriction and continuing to the occiput as a low but well-defined crest. The triangular process produced by union of the sagittal and occipital crests is very moderately developed, as in *Merychyus*. The face was shortened, and the nasals probably reduced, as in other species of the genus, but of the extent of the reduction the specimen is too imperfect to judge. The palate is prolonged backward less in proportion, and the distance from the posterior nares to the condyles is both relatively and absolutely greater than in the larger skull. The top of the skull between the orbits is much inflated with cellular tissue, the cranial region more moderately so ; the ridge along the anterosuperior border of the squamosal is not as prominent as in *M. proprius* or any of the *Promerycochœri*.

### MEASUREMENTS.

Estimated total length of skull............................................. 240
Length from first molar to occipital condyle............................ 172
    "    " posterior nares to " " ............................ 95
Height of skull at $m^2$.................................................. 83
Width of postorbital constriction....................................... 59
Height of skull at occiput............................................... 75
Width of palate at $m^2$, $(53 \times 2)$................................ 106

SKELETON.—The *stylohyal* is a long curved bar, flat and thin, expanded at both sides but especially at the proximal one. The shape corresponds with Professor Scott's description of the stylohyal bone of *Mesoreodon* except that in our species it is longer in proportion and more expanded at each end. Length, 78 ; diameter of distal end, 11 ; of shaft, 7 ; of proximal end (estimated), 16.

The *dorsal vertebræ* have longer spines, wider and heavier transverse processes, than in *Oreodon* or *Eporeodon*, standing intermediate as far as can be judged between these older genera and the *M. proprius*. The centra of four *lumbar vertebræ* in series are exposed on a block, and show that the lumbars were small and remarkably short in proportion, their length being actually less than in *O. culbertsoni*. This reduction of the lumbar region likewise characterizes *M. proprius*, but whether to the same extent I am unable to say. Four caudal vertebræ in series are exposed on the same block, and show that the tail was widely different from that of *Oreodon* or *Eporeodon* (in *Merycochœrus proprius* it is not known). The centra are small and rather short, the anterior zygapophyses quickly becoming rudimentary, the posterior ones uniting to form a small process projecting over the next succeeding vertebra, while the transverse processes dwindle to small pointed median lateral projections, and the proximal and distal lateral processes do not appear. This form of tail resembles most nearly that of the pig, and is quite unlike any ruminant tail. The vertebræ of the pig's tail diminish more rapidly, so that the tail of *M. rusticus* was either longer or more powerful, but the resemblance was much greater to the pig than to any of the earlier Oreodonts. The *ribs* are much stouter and apparently longer in proportion than

in *Oreodon culbertsoni* and *Eporeodon major cedrensis*, and as stout in proportion as in *M. proprius*. None are preserved complete, so that exact comparisons are not possible.

<div align="center">MEASUREMENTS.</div>

| | |
|---|---|
| Fifth dorsal vertebra, length of centrum............................... | 25 |
| " width across transverse processes..................... | 48 |
| " length of spine from anterior zygapophyses............ | 80 |
| Length of four lumbar centra........................................ | 120 |
| Length of four anterior caudals in series................................. | 80 |
| Width of the first of the series across transverse processes.................. | 35 |
| " " fourth " " " " .................. | 15 |
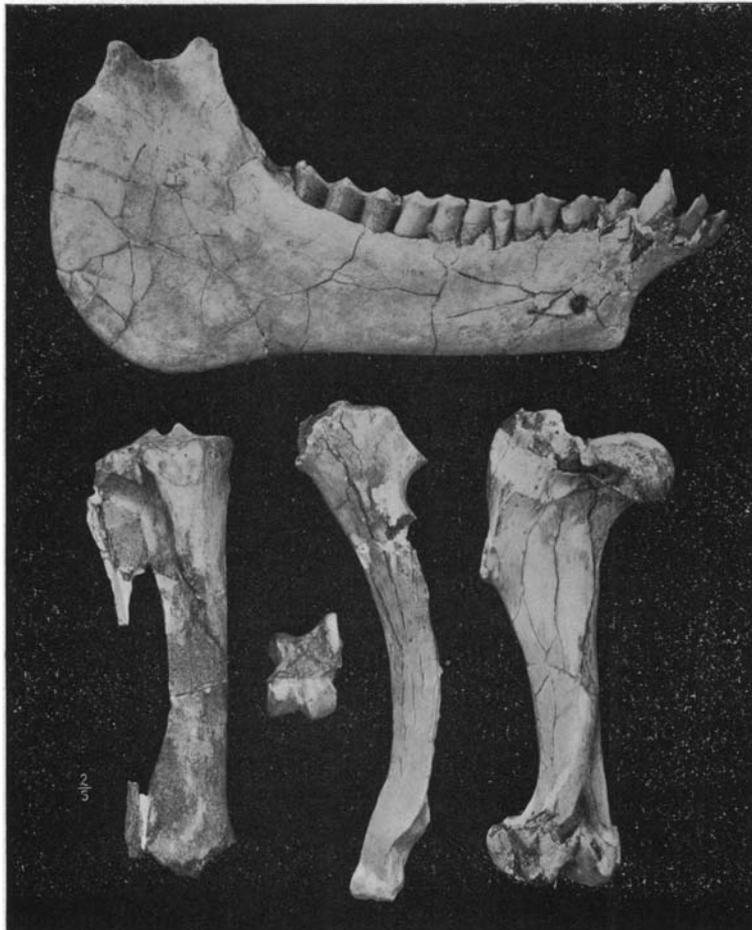


Fig. 28. *Merycochœrus rusticus.* Lower jaw of young individual, No. 9115a, external view; humerus, ulna, tibia and astragalus of a fragmentary skeleton, No. 9050. All two fifths natural size. Loup Fork Formation, Protolabis Beds, Colorado.

The fore limb cannot be accurately compared with the type species, as in *M. proprius* it is known chiefly from the young individuals in the large block (Fig. 20). It appears, however, that the limb bones of *M. rusticus* are shorter and the feet longer, the lateral toes being smaller and less compactly bound to the central ones than in the type species.

The *humerus*, compared with that of *Eporeodon occidentalis* (No. 6783), is about the same length but one half wider across the proximal end and one third stouter in the shaft; the greater tuberosity is larger than the head; the deltoid crest hardly extends as far down as in *Eporeodon*, but is higher and ends in a strong hooked process; the trochlea is broader, its external edge lower, the ectepicondylar crest much higher.

The *ulna* is in proportion shorter and stouter than in *Eporeodon*, with short and very heavy olecranon and very strongly curved shaft.

The *manus* is wide and short, the metacarpals considerably shorter than in *E. occidentalis* but stouter at their proximal and distal ends ; the lateral ones have about the same extent of reduction. The carpus is wider and considerably higher ; the condition of the trapezium cannot be determined. The phalanges are not nearly so short as in *M. proprius*, comparing more nearly with *Promerycochœrus superbus ;* the unguals are even less broadened than in that species.

MEASUREMENTS.

|  | No. 9050. | No. 9049. |
|---|---|---|
| Humerus, length | 153 | .. |
| " width of proximal end (antero-posterior) | 62 | .. |
| " " " shaft | 20 | .. |
| Ulna, length estimated | 175 | .. |
| " width of olecranon (anteroposterior) | 38 | .. |
| " " " shaft " | 18 | 16 |
| Radius, length | .. | 121 |
| " width of shaft | .. | 18 |
| Height of carpus | .. | 30 |
| Length of metacarpal II | 51 | 50 |
| " " III | .. | 61 |
| " " IV | .. | 59 |
| " " V | .. | 49 |
| " first phalanx of fourth digit | .. | 24 |
| " third " " " " | .. | 14 |

The hind limb differs from that of *M. proprius* in the shorter leg and longer foot, with metatarsals less closely bound together and the lateral ones more reduced, also probably in the longer phalanges and narrower unguals.

The *femur* is one sixth shorter in proportion than that of *M. proprius*, with heavier, more angulate shaft, the low ridge from the external epicondyle extending up to the shaft more than two thirds the length of the bone. Lesser trochanter less prominent but more massive and rugose.

The *tibia* is one tenth shorter in proportion, shaft less rounded, cnemial crest equally high but not extending so far down. Distal end much more flattened, rectangular in cross-section, twice as wide as deep, concave in front, a broad triangular surface for the fibula on external side and a broad, blunt malleolus on the internal, the trochlea shallow and wide and very limited anteroposteriorly.

The *metatarsals* are one fifth longer in proportion (their absolute length greater than in *M. proprius*), much slenderer in the shafts, the lateral pair more reduced ; the facet for the second cuneiform on mt II is very small, and that for the internal cuneiform nearly proximal, instead of lateral as in *M. proprius*.

MEASUREMENTS.

|  | No. 9050. | No. 9049. |
|---|---|---|
| Femur, length | 181 | .. |
| width of proximal end | 57 | .. |
| "    "    shaft | 23 | .. |
| Tibia, length | 151 | .. |
| "   width of proximal end | 49 | .. |
| "    "   internal malleolus | 14 | .. |
| Length of astragalus | 35 | 35 |
| Width of   " | 25 | 21 (crushed) |
| Length of metatarsal II | .. | 44 |
| "    "    III | 63† | .. |
| "    "    IV | 69 | .. |
| "    "    V | 50 | .. |
| "    phalanx first row | 27 | .. |
| "    "    second " | 16 | .. |

From the above characters it would appear that *Merycochœrus rusticus* was smaller than the pig, and rather nearly resembled this animal in its proportions, except that the feet were more tetradactyl and the trunk apparently shorter. It differed from its nearest relative, *M. proprius*, in the longer and lower skull, more bulbous frontal region, shorter limbs, and longer, more spreading, but less tetradactyl feet. In many respects it stands intermediate between *Merycochœrus proprius* and the other Oreodonts, approximating *Merychyus* in some characters and *Promerycochœrus* in others.

A more complete knowledge of the various species of *Merycochœrus* recently found in Montana may make it necessary to divide the genus as now constituted, making *M. proprius* the type of one group, and *M. rusticus*, as exemplified in the Colorado specimens, the type of the other.

## Merychyus *Leidy.*

This genus was constituted by Dr. Leidy in 1858 to embrace three species of Oreodonts from the Loup Fork of Nebraska, distinguished from *Oreodon* by the hypsodont teeth, and from *Merycochœrus* by the position of the infraorbital foramen. The subsequent reference to Leidy's genus *Merycochœrus* by Bettany and Cope of species now distinguished as *Promerycochœrus* seemed to show that the position of the infraorbital foramen was not a valid generic character. Mr. Bettany in consequence united *Merycochœrus* and *Merychyus*, and Prof. Cope, whose more complete material demonstrated the distinctness of the two, re-defined the genus *Merychyus*, basing it on the presence of a larmier (lachrymal vacuity),—a character not known in any of Leidy's species, but found in two species from the Deep River of Montana and Wyoming. As is shown on a preceding page, the posterior position of the infraorbital foramen in the true *Meryco-chœrus* is correlated with the reduction of the nasals and other important skull changes caused by the presence of a proboscis. It seems to be a valid distinction,

and in this case Dr. Leidy's original definition will hold good. The generic characters of chief importance will then be :

1. Nasals unreduced (infraorbital foramen above $p^3$ or anterior end of $p^4$) ; premaxillæ coössified.

2. Skull rather short with slender zygomata and moderate occipital crests.

3. Teeth hypsodont, muzzle more or less rounded, canines not large.

4. Facial vacuity at junction of maxillary, frontal, and lachrymal bones (not known in type species).

5. Limbs and feet slender, manus adaptively reduced.

The best known species is *M. arenarum* Cope, from the Loup Fork formation near Laramie Peak, Wyoming. Considerable parts of the skeleton of *M. elegans* Leidy have been described by Prof. Scott, but the skull of this species is not known. *M. zygomaticus* and *pariogonus* Cope, from Deep River, are known by incomplete skulls, and *M. medius* and *major* Leidy by fragments of jaws.

The specimens of *Merychyus* obtained by the Colorado Expedition are, with one exception, referable to *M. elegans*, and while adding little to our knowledge of the osteology of the genus, enable us to clearly differentiate this species from *M. arenarum*, its nearest ally. *M. pariogonus* is much more brachydont ; *M. zygomaticus* considerably larger ; *M. medius* is larger and more brachydont, while *M. major* is much the largest in the genus.

## Merychyus elegans *Leidy*.

Distinguished from *M. arenarum* by smaller size, more advanced hypsodonty, longer and slenderer limbs and feet.

The second and third upper premolars are not as wide and scarcely so long as in *M. arenarum* and the external wall of the third is slightly convex anteroposteriorly toward the base of the enamel, instead of uniformly concave as in *M. arenarum*. The fourth premolar has less transverse diameter. The outer walls of the outer crescents of $m^3$ are uniformly concave in some individuals and have a median ridge, variably prominent in others ; this character is also variable in *M. arenarum* and is probably not of specific value. The third and fourth lower premolars are narrower than in *M. arenarum* and the external notch between protoconid and heel is deeper on $p_4$ (more molariform).

MEASUREMENTS.

|  | No. 9045. ♀ | No. 9047. ♂ | No. 9048. |
| --- | --- | --- | --- |
| Length of lower jaw | 144 | 142 | ? 137 |
| "    " dentition | 94 | 92 | |
| "    " premolars | 33 | 34 | |
| "    " true molars | 49 | 46 | 50 |
| "    " $m_1$ | 11 | 10 | 11 |
| "    " $m_3$ | 22 | 23 | 25 |
| Depth of jaw under $m_3$ | 27 | 24 | |
| "    " at condyle | 72 | 68 | |

No. 9047 is a somewhat younger individual than No. 9045 ; the measurements, therefore, indicate less depth of jaw and apparent greater size of teeth ; the actual size of corresponding parts, however, is almost identical.

*Limb Bones.*—The slenderness of the limbs and feet has already been observed by Prof. Scott. The radius and ulna are more closely conjoined, the fibula more reduced, the carpus narrower and more rounded than in other Oreodonts, and the ungues are narrow and pointed. The trapezoid is a small, laterally compressed bone, suggesting the trapezium of *Oreodon* in its shape; it has a distal facet for mc II, and a smaller distal external facet for mc III. There seems to have been a small nodular trapezium, but its facets are indistinct if present. The metacarpals are rather closely compact, the lateral ones one fifth shorter and one fourth slenderer than the median pair. There was therefore no tendency to functional didactylism of the fore foot, in spite of its extreme (for an Oreodont) slenderness. The unguals are long, pointed, as high as they are wide, except toward the distal end.

The hind limb is similar to that of *M. arenarum*, but uniformly more slender. The tibia has a deep trochlea and rather small malleolus. The fibula is unusually small, laterally compressed, with a small calcaneal facet, and above this it is flattened to a thin-edged plate, closely united to the tibia, though not coössified. The shaft is reduced to a mere thread and is again united to the tibia for the second fifth of the distance up the shaft; whether it extended free from the tibia above this point our specimens do not show.

COMPARATIVE MEASUREMENTS.

| | *M. elegans.* | | | | *M. arenarum.* | |
|---|---|---|---|---|---|---|
| | No. 9045. | No.9046. | No.9047. | No.9048. | No.8145. | No.8142. |
| Length of radius | | 117 | 114 | | | 114 |
| Diameter of shaft of radius | 11 | 10 | 11 | | | 14 |
| Diameter of shaft of ulna | 9 | 8 | 8 | | | |
| Width of carpus | | 21 | | | | 24 |
| Height of carpus | | 20 | | | | 20 |
| Length of metacarpal II | | 45 | | | 47 | 56 |
| "        "    III | | 57 | 56 | | 60 | 53 |
| "        "    IV | | 55 | 55 | | 58 | 42 |
| "        "    V | | 45 | | | | |
| "    first    phalanx | | 18 | | | 21 | |
| "    second  " | | 9 | | | | |
| "    third    " | | 11 | | | | |
| Length of tibia | 144 | | | | | 133 |
| Width of distal end | 19 | | | | | 23 |
| Transverse diam. distal end of fibula | 5 | | | | | |
| Anteropost.  "    "    "    " | 9 | | | | | |
| Length of calcaneum | 46 | | | | 47 | |
| "    astragalus | 24 | | | | 25 | |
| Width of    " | 15 | | | | 16 | |
| Length of metatarsal III | | | | 66 | 67 | |
| Width of shaft of  "    " | | | | 7 | 8.5 | |

FAMILY CAMELIDÆ.

The evolution of the Camels is illustrated by a series of fossil remains more complete, perhaps, than can be shown in any other group of animals, except the Horses. The studies of Leidy, Cope, Scott and Wortman have successively

added link after link in the chain until it seems well-nigh complete as far as the Upper Eocene. Much remains to be done, however, in clearing up the exact relations of various species to the direct line of descent. It becomes more and more evident as data accumulate that there were side branches at every stage, some precocious in one character, some in another. At no time were these side branches more numerous than in the later Miocene, while the gap in the stratigraphic succession just below this period makes it difficult to disentangle them. And as most of the described species have been founded on exceedingly fragmentary types, the nomenclature is in great confusion. The White River offers no great difficulty, as the species are few in number and well known.

Our expedition was fortunate in obtaining a large number of specimens of Camelidæ, which seem to have been especially abundant in this region, both in the White River and Loup Fork Beds. Those from the upper beds show an extraordinary range in size, and variation in development hitherto unsuspected. They enable us to make valid distinctions between a number of species hitherto separated only on trifling differences of size and proportion — differences which Dr. Wortman in his recent article on the Camelidæ very properly refused to accept as valid specific distinctions. The identification of these fragmentary types with our more complete specimens is in some cases by no means certain ; but it is the result of minute and repeated comparison of all the available material, especial care being taken to eliminate differences due to age or individual variation.

This new material enables us to distinguish in the Loup Fork two divergent branches, neither of which seems to be in the line of descent leading to any existing Camelidæ, which may best be derived from intermediate species somewhat less known. The two extremes may conveniently be called

(1) *Giraffe-Camels*, distinguished by excessive elongation of neck and legs, precocious evolution of the feet (metapodials united, unguals reduced), and rather retarded evolution of the grinders (brachydont) and disappearance of the upper incisors.

(2) *Split-foot Camels*, distinguished by short neck and legs, primitive feet (separate metapodials, unguals unreduced), more hypsodont grinders, and retention of the upper incisors.

These divergences seem to indicate adaptation on the one hand towards tree-browsing, on the other towards grass-cropping habits. They suggest to some extent the less pronounced difference between camels and llamas, but are probably parallel adaptations only, for the divergence is already greater and different in its exact direction, so that both the modern genera must be derived from some of the intermediate types.

The known White River species show no indication of this divergence ; they seem to lead, however, into the larger, more brachydont camels of the John Day on the one hand, and into the smaller and more hypsodont species of the Leptauchenia Beds on the other. But until the intermediates are better known it would not be safe to connect them with the two series of the Loup Fork in any definite way.

## Poëbrotherium *Leidy.*

Two fine skulls and several less complete specimens of *P. labiatum* Cope were collected by our party from the Oreodon Beds, and a few fragmentary jaws of *P. wilsoni* from the same level. We were unable to substantiate the division of the two species observed by Dr. Wortman as from the Upper and Lower Oreodon Beds respectively. In the Titanotherium Beds, which have not hitherto yielded any Camel remains, Mr. Martin found the hind foot of a *Poëbrotherium* somewhat longer and about one fourth heavier than either of the known species. It is not very well preserved, and I refrain from naming the species in the expectation that better specimens will be obtained from the same horizon, and more definite characters determined. In either the Titanotherium or Protoceras Beds one may anticipate that camels, if found, will be large, heavy species, rather primitive in characters of feet and teeth.

## Protomeryx *Leidy.*

Syn., *Gomphotherium* Cope.

Lower teeth as in *Poëbrotherium* except that the canine is caniniform and the diastemata behind it greatly increased in length. Metapodials separate. Skull unknown in the type species, in associated species the orbit is complete behind ; other characters as in *Poëbrotherium*.

Wortman has observed that the distinctions on which Cope founded *Gomphotherium* are largely errors in observation, and has redefined the genus. As redefined, however, it does not seem separable from Leidy's *Protomeryx*, a genus which has been ignored in the mistaken belief that the specimen on which it was based came from the Loup Fork Beds and was identical
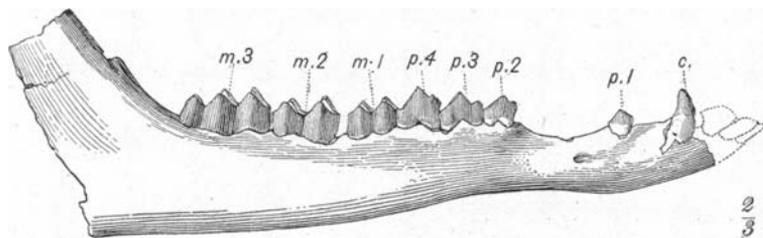


Fig. 29. *Protomeryx cedrensis.* Lower jaw, × ⅔, external view. Type specimen, No. 8969. White River Formation, Leptauchenia Beds, Colorado.

with *Procamelus*. He states, however, that the horizon is " D," a level certainly equivalent to the Leptauchenia and Protoceras Beds as far as the fauna goes. The appearance of the type specimen in the Philadelphia Academy Museum also indicates that it is from the lower beds, and it certainly is not identical with *Procamelus* or any of the Loup Fork camels, in which the second premolar is more reduced and the teeth in other ways more advanced.

## Protomeryx campester, n. sp.

The type species, *P. halli,* is larger than any *Poëbrotherium.* No. 8969 represents a smaller species, of the size of *Poëbrotherium labiatum,* with postcanine diastema equal to $p_{\overline{4}}$ in length, and the diastema behind $p_{\overline{1}}$ equal in length to $p_{\overline{2}}$, $p_{\overline{3}}$ and half of p--. Canine smaller and more recurved

than in the type species ; first premolar small, two-rooted, trenchant, second, third and fourth increasing successively a little in length and much more in width. Molars much as in *Poëbrotherium*, the heel of $m_{\bar{3}}$ more reduced. Distinguished from *Protomeryx* (*Gomphotherium*) *sternbergi* by the slenderer jaw with longer diastemata and higher-crowned, more compressed teeth ; from *Protomeryx* ? (*Gomphotherium*) *serus* Douglas by smaller size, different proportion of diastemata, etc.

COMPARATIVE MEASUREMENTS.

|  | Poëbrotherium. | Protomeryx. | | | |
|---|---|---|---|---|---|
|  | *P. labiatum*, No. 8953. | *P. halli*, type. | *campester*, type. | *sternbergi*, type. | *serus* |
| Dental series, c-$m_{\bar{3}}$ | 90 |  | 100 | 94 | .. |
| Diastema behind canine | 2 | 4 | 8 | 9 | 15 |
| Diastema behind first premolar. | 11 | 11 | 19 | 13 | 17 |
| Length of $p_{\bar{1}}$ | 5 | 8 | 4.5 | 4.5 | 6.5 |
| Length of $p_{\bar{2}}$ | 83 | 10 | 7 | 7.5 | 8 |
| Length of $p_{\overline{2-4}}$ | 27 | .. | 24 | 23 | 29 |
| Length of true molars | 40 | .. | 42 | 42 | .. |

# THE LOUP FORK CAMELS.

## HISTORICAL REVIEW.

Eighteen species have been described from the Loup Fork and Blanco formations of the United States, as follows :

*Procamelus occidentalis* Leidy, Proc. Phila. Acad. Sci. 1858, p. 23 ; *ib.* p. 29.
"         *robustus* Leidy, *ib.* p. 89.
"         *gracilis* Leidy, *ib.* p. 89.
"         *angustidens* Cope, Bull. U. S. G. S. Terrs. 1873 (1874), p. 20.
"         *heterodontus* Cope, *ib.* p. 20 ; *Protolabis heterodontus*, Cope, Proc. Acad. Nat. Sci. Phila. 1876, p. 144.
*Pliauchenia humphresiana* Cope, Proc. Acad. Nat. Sci. Phila. 1875, p. 258.
"         *vulcanorum* Cope, *ib.* p. 259.
*Procamelus fissidens* Cope, Proc. Acad. Nat. Sci. Phila 1876, p. 145.
*Protolabis transmontanus* Cope, Bull. U. S. G. S. Terrs. 1879, p. 67.
"         *prehensilis* Cope, Am. Nat.
*Procamelus leptognathus* Cope, Texas Survey Rep. 1892, p. 37.
*Pliauchenia spatula* Cope, *ib.* p. 70.
*Procamelus altus* Marsh, Am. Jour. Sci. 1892, Vol. XLVIII, p. 274.
*Pliauchenia minima* Wortman, Am. Mus. Bull. 1898, p. 127.
*Gomphotherium serus* Douglas, Neocene Lake Beds of Western Montana, 1899, p. 12.
*Protolabis montanus* Douglas, *ib.* p. 13.
*Procamelus madisonius* Douglas, *ib.* p. 15.
*Procamelus lacustris* Douglas, *ib.* p. 18.

1. *Procamelus.* Leidy proposed this genus on the lower premolar dentition of *P. occidentalis* from the Nebraska Loup Fork, and shortly afterwards referred to it parts of jaws and teeth of two other species from the same locality, distinguished only by size. Cope described, in 1874, a complete skull, fore limbs and parts of neck, etc., belonging to this genus, so that it is fairly well known.

2. *Pliauchenia* Cope was proposed for camels with the second premolar absent in the lower jaw. Type, *P. humphresiana*, from New Mexico, represented by a lower jaw in which a single-rooted vestigial stump may have been present, but no second inferior premolar *tooth* properly so called.

3. *Protolabis.* On discovery of the fine *Procamelus* "*occidentalis*" (later referred to *P. gracilis*) skull from New Mexico, Prof. Cope placed his Colorado species, *P. heterodontus*, in a new genus, distinguished from *Procamelus* by the retention of all the superior incisors. He afterwards added to this genus the species *P. prehensilis* and *P. transmontanus*.

4. Dr. Wortman in 1898 pointed out the small size and abnormal number of the incisors of *Protolabis heterodontus* and considered that both it and *P. prehensilis* were probably identical with *Procamelus robustus* Leidy. He retained the name *Protolabis* for *P. transmontanus*.

5. The present writer in 1899 redefined, in a foot-note, the genera of camels on the new material then accessible, making use, for the definitions, of the foot-characters, previously unknown, but erroneously identifying with *Protolabis heterodontus* a species of *Procamelus* hereafter to be described. It appeared necessary in consequence of this identification to separate from any named genus the Loup Fork camels with separate metapodials, and for these the name *Miolabis* (suggested on grounds of nomenclature rules in a letter by Dr. O. P. Hay) was used. Dr. Hay shortly afterwards published a note in which this generic name was proposed in correction of Dr. Wortman's transference of *Protolabis* from the type species to *P. transmontanus.*

### DISTINCTIVE CHARACTERS.

The characters which can be used in distinguishing the species and genera of camels are :

1. *Dental Formula.* The stages in the reduction of the dentition form an excellent basis for generic distinction if applied with proper limitations. As during the gradual loss of a tooth in a race, it will be lost by the individual at progressively earlier time of life, and the alveolus will remain for some time after the tooth has dropped out, caution is necessary to distinguish the genera only on differences in dental formula of mature individuals. A persistent alveolus, or a minute crownless stump, can hardly be regarded as enough of a tooth for a generic distinction from a species in which no trace of the tooth remains.

2. *Proportion of the molars one to another.* This character has been used by Prof. Cope, and seems a tolerably valid one, although the relative lengths of the molars vary somewhat with age.

3. *Size of molars and premolars.* This is the chief character used hitherto in distinguishing the species, and is an extremely unreliable one in the Camelidæ, because it varies with age and degree of wear of the long-crowned molars. The width of the molars at the alveolar border doubles during the growth of the individual, while the length decreases one third, because the *base of the crown is*

*shorter as well as wider than the upper part*, and the teeth are pushed forward in the jaw as they grow upward. Hence a young individual, both in appearance and measurements, seems to belong to a larger species with narrower molars, and premolars proportionately smaller. Length and width in the premolars changes in the same direction as the molars, but much less.

4. *The tendency of the first premolar to become caniniform* is an important character phylogenetically but not very constant specifically among the Loup Fork camels.

5. *The depth of the jaw* varies much with age and in different individuals and is of little value as a specific distinction.

6. *The characters of the feet* were unknown or disregarded in the original descriptions of all the species except the last two. They furnish the most marked and probably the most constant distinctions ; but as the genera and species were separated on dental distinctions the feet can be used only to confirm or check the rather hazy characters of the teeth.

7. *The shape of the angle of the lower jaw* is a point of phylogenetic importance and fairly constant. In *Poëbrotherium,* and especially in the modern camels, it is prolonged upward into a strong hook or projecting process below the condyle. In the llama and vicuña the hook is vestigial.

8. *The contact of nasals and premaxillæ* is an important character, although not often observable. In the South American Camelidæ the premaxilla is extended backward for about half an inch between nasal and maxilla ; in the camel the nasal and premaxilla are entirely separated by the maxilla. This reduction of the premaxilla in the camels may be connected with the earlier disappearance of the anterior incisors.

9. *Length of diastemata*, and of muzzle.

10. *Hypsodonty* is an important character and a rather constant one, but usually difficult to measure.

11. *Union of metapodials.*—This is the most important distinction among the Loup Fork camels.

12. *Elongation of feet, limbs, and neck* is another important and the most obvious character.

13. *Relative proportions of fore and hind limbs.*—With more complete material it will be possible to use this character more, but it is known in only two or three species, although showing singularly wide variation in these.

### ANALYSIS OF THE GENERA AND SPECIES.

The following analysis and descriptions are based on material much more extensive and complete than has hitherto been known, but cannot yet be considered as final. The association of skull and limbs in the Loup Fork species is exceptional, and since, as above observed, they have been defined on the unsatisfactory dental characters, the position of several in this scheme is only conjectural. Changes in these species will in some cases affect the

nomenclature, but the generic divisions made here are more permanent. Characters in the definitions of genera and species derived from other than the type (species or specimen as the case may be) are placed in brackets :

### A. Procamelus *Leidy*.

First and second upper incisors absent. Premolars unreduced in number. [Metapodials united. Neck of moderate length.] Angle of jaw hooked as in modern camel. Molars of comparatively uniform size.

1.—$P_{\overline{2-4}} = 36$; $m_{\overline{1-3}} = 85$. Angle moderately hooked. [Limbs and feet of moderate size and elongation, the hind limb exceeding the fore limb in length and robustness.]....*P. occidentalis*.

2.—$P_{\overline{2-4}} = 31$. [$M_{1-3} = 80$; fore limb and foot small and slender, proportions probably as in the last species.]........................................................................*P. gracilis*.

3.—$P_{\overline{2-4}} = 50$; $m_{1-3} = 111$. [Limbs and feet long and slender, hind foot slenderer than fore foot.]........................................................................*P. robustus*.

4.—$P_{\overline{2-4}} = 38$; $m_{1-3} = 73$. Size of *P. gracilis*, but premolars, especially $p_{2}$, less reduced. Angle of jaw moderately hooked [feet small and slender, forefoot more robust]........*P. fissidens*.

### B. Pliauchenia COPE.

Second premolar absent. [Other characters not known, but probably as in *Procamelus*.]
1.—Small, short diastema, $p_{2}$ vestigial..............................*P. humphresiana*.
2.—Large, long diastema, $p_{2}$ absent..............................*P. spatula*.
3.—Smallest, long diastema, $p_{2}$ and probably $p_{1}$ absent..............................*P. minima*.

The last species suggests in several respects *Protolabis montanus*, but is smaller and seems to have united metapodials. It is very imperfectly known.

### C. Alticamelus, new genus.

First and second upper incisors absent. Premolars unreduced in number. Metapodials united. Neck and legs greatly elongated. Angle of jaw hooked. Molars of comparatively uniform size.

1.—$P_{\overline{2-4}} = 47$; $m_{\overline{1-3}} = 102$. Hind limb and neck about as long as those of the giraffe; fore limb unknown..............................*A. altus*.

### D. Protolabis *Cope*.

First and second upper incisors retained (except in the higher beds). Second premolar retained (first lost in one species). [Metapodials separate. Limbs and feet short and disproportionately small.]

1.—First and second incisors reduced in size. First upper and lower premolar incipiently caniniform. Molars rapidly increasing in size from before backward. [Metapodials short and stout.]..............................*P. heterodontus*.

2.—First premolar not caniniform [incisors present, reduced, in one referred specimen, but absent in a doubtfully referred specimen from a later horizon. Metapodials short, stout, cervicals short]..............................*P. angustidens*.

3.—Smaller, muzzle much elongated, teeth more hypsodont, $p_{1}$ absent, $p_{2}$ vestigial ; incisors unreduced ; molars more uniform in size. [Metapodials small, slender. No hook on angle of jaw. Cervicals short]..............................*P. montanus*.

4.—Brachydont teeth, incisors and premolars unreduced, molars uniform in size, feet unknown (perhaps = *Protomeryx*)..............................*P. transmontanus*.

DISTRIBUTION OF THE SPECIES.

| | LOWER LOUP FORK. | | | UPPER LOUP FORK. | | | BLANCO. |
|---|---|---|---|---|---|---|---|
| | Oregon. | Deep R. | Colo. | N. Mex. | Nebr. | Kans. | Texas. |
| Pliauchenia spatula | | | | | | ? | X |
| "      humphresiana | | | | X | | ? | |
| "      minima | | | | | | X | |
| Procamelus occidentalis | | ? | ? | X | X | X | |
| "      gracilis | | | | X | X | X | |
| "      robustus | | ? | ? | | X | | |
| "      fissidens | | | X | | | | |
| Alticamelus altus | ? | | X | | | ? | ? |
| Protolabis heterodontus | | | X | | | | |
| "      angustidens | | | X | | | | |
| "      montanus | | | X | | | | |
| "      transmontanus | X | | | | | | |

## Procamelus *Leidy*.

The typical species is *P. occidentalis*, and to this or the closely allied *P. gracilis* belongs the fine skull, neck, and fore limbs from New Mexico described by Professor Cope. A specimen in the American Museum collection, from northwestern Nebraska, includes jaws, fore and hind limbs of two individuals, both probably *P. occidentalis*, and from these specimens the length of the neck vertebræ, size and proportions of the limbs can be determined. A number of larger limbs from Colorado of the same proportions as in these specimens, but mostly unaccompanied by skull material, may be provisionally referred to *P. robustus*, but will probably be found distinct from the Nebraska species when the skull is known.

There is in the American Museum collection a large and complete fore and hind limb from the Loup Fork, equalling the modern camel in size and exceeding it in robustness. This specimen may be a large *Pliauchenia* or it may be *Procamelus robustus*. But the Kansas Loup Fork is very late in age, most nearly allied to the Blanco, where, as far as is known, *Pliauchenia* takes the place of *Procamelus*, and where a large camel of the same proportions as the Kansas specimen is known to occur. Also, since the other three species of *Procamelus* are slender, it is more probable that *P. robustus* would likewise be slender. For these reasons I provisionally call the large Kansas species a *Pliauchenia*, and identify with *Procamelus robustus* the slender Colorado specimens proportioned much like *P. occidentalis* and *P. gracilis*, but of larger size.

## Procamelus robustus *Leidy*.

Some twelve or thirteen specimens consisting of fore and hind limbs, but only one with the jaw, and that an immature individual with milk dentition, are placed provisionally here.

The limbs are long and slender, giving a height hardly less than that of a modern camel, but much slighter proportions. The feet are not nearly so widely

spread as in the later camels and the ungues are small and triangular, reduced in size as compared with those of *Poëbrotherium* but not broad and flattened as in the more recent species. The trapezium is still present, although reduced to an oval nodular bone with a small trapezoid facet and no contact with scaphoid or metacarpus. The metatarsus has about the same length as the metacarpus but is much slenderer; the tibia is correspondingly slenderer in shaft than the radius.

MEASUREMENTS.

|  | No. 9116 | No. 9114 | No. 9117 | No. 9112 | No. 9112a |
|---|---|---|---|---|---|
| Lower jaw, length of three milk molars.............. | 54 | .. | .. | .. | .. |
| Lower jaw, length of two true molars.................. | 63 | .. | .. | .. | .. |
| Length of radius,........est. | 379 | 417 | 430 | 464 | 436 |
| Height of carpus........... | .. | .. | .. | 50 | .. |
| "  " ............ | .. | .. | .. | 56 | .. |
| Length of metacarpus....... | .. | 362 | 360 | 389 | 367 |
| " proximal phalanx.. | 90 | .. | 96 | 103 | .. |
| " middle " .. | .. | .. | 42 | .. | .. |
| " ungual " .. | .. | .. | 23 | .. | .. |
| Length of tibia..........est. | 410 | .. | .. | .. | .. |
| " metatarsus....... | .. | 355 | .. | .. | .. |

### Procamelus fissidens *Cope.*

This species has the premolars less reduced than in any others of the genus. The type specimen is a lower jaw. I refer provisionally to it part of a skull of an immature individual, No. 9120, with molars somewhat smaller than in *Protolabis montanus*, more brachydont, and with the medial ridge on the external walls of each crescent very faint. Here may also belong No.



Fig. 30. *Procamelus robustus.* Fore and hind legs of one individual, No. 9114, and fore limb of a somewhat larger individual, No. 9117. × ⅛. Loup Fork Formation, Protolabis Beds, of Colorado.

9106, a small fore and hind foot with metapodials united, slenderer than those of *P. montanus* but much longer. It is too long and slender for *Procamelus gracilis.* The metacarpus is a little stouter than the metatarsus, but somewhat shorter, as nearly as can be determined from the specimen, in which a little of the shaft is missing; it is somewhat too long and much too slender to belong to *P. gracilis* if that species be correctly represented by the skull and fore limbs described by Professor Cope.

MEASUREMENTS OF No. 9106.

Metacarpus, length (est.)........... ............. ..... ............. 241
    "     diameter of shaft..... ................................ ...... 20

Proximal phalanx of fore foot, length ..................... ........ .... 63
Metatarsus, length............................................ .... 233
"    diameter of shaft.............................. .... ......... 17
Proximal phalanx of hind foot, length.............................. 53

## Alticamelus, new genus.

The most remarkable find made by our party was the discovery by Mr. Martin of the head, neck, and hind limb of a camel which resembled the modern giraffe in its proportions and equalled it in size. The discovery of this specimen introduces to science one of the most interesting instances of convergence yet observed. The effect of extreme height, in order to enable the animal to feed upon the inaccessible foliage of high and thorny shrubs, is obtained in this species, as in the giraffe, by the elongation of the neck vertebræ and the legs. But the giraffe is derived from the early antelopes, and *Alticamelus* from early camels, and the difference of origin has caused the attainment of the desired result in a somewhat different manner.

In the antelopes the fore quarters are usually higher than the hind quarters, and especially so in the group most nearly allied to the giraffe. The femur and tibia are comparatively short, the metapodials comparatively long. The greater height of the fore quarters causes the anterior part of the back to slope upwards towards the neck and thus increases its height. The elongation of the anterior dorsals will increase the stature of the animals as well as will the elongation of the cervicals. Accordingly we find that in the giraffe the fore quarters are much higher, the elongation of the limbs is greatest in the metapodials, which are much longer than either femur or tibia, and the elongation of the cervicals is continued into the dorsal region.

In the camels, on the other hand, the fore quarters are not any higher than the hind quarters, the anterior cervicals are long while the posterior ones are quite short, and the tibia is unusually long while the metapodials are comparatively short. Correspondingly we find in *Alticamelus* that the anterior cervicals are enormously elongated, the posterior ones are but little increased in length, while the anterior dorsals are both short and small. The elongation of the last cervicals and anterior dorsals would have only increased the length of the body without altering the stature, because the fore legs are not longer than the hind legs and consequently the backbone does not slope upward towards the neck. Also the great elongation in the limbs of *Alticamelus* has been in the femur and tibia, while the metatarsus is shorter.

The Giraffe-Camel was not so bulky an animal as the giraffe, and scarcely equalled a moderate sized northern giraffe in height. The trunk was considerably smaller, if one may judge from the known remains. The hind limb was longer, and the neck equally long, but as we may assume the equality of fore and hind limbs, the stature was no higher, if as high.

The generic distinctions are in the elongated neck and legs seen in the typical species. The skull does not greatly differ from that of *Procamelus*.

## Alticamelus altus (*Marsh*).

PLATE XXXIX.

Professor Marsh in 1894 described and figured a camel calcaneum which agrees in size with that of the giraffe-camel (among others), and states that other portions of the skeleton show that it exceeded in size any other described from this country and that "the extremities were especially elongated." The horizon and locality of this specimen are the so-called Loup Fork beds of the John Day Basin, Oregon, equivalent in age to the Colorado Loup Fork, or perhaps older. Besides the giraffe-camel here described there are specimens in the American Museum collection of two or three other species of equal bulk, one of which, from a later horizon, has the extremities unusually long; but as the horizon of the Colorado specimen agrees with that of *Procamelus altus* we may place it with that species.

The specimen, No. 9109, consists of skull and jaws, all the cervical and the first two dorsal vertebræ, the left hind limb and right hind foot, found in Horizon E in Logan County, Colorado.

The *skull* is as long as that of the modern camel but about a fourth narrower; the proportions like those of *Procamelus* and *Protolabis*. The nasals are not preserved. The brain case is considerably smaller than that of the camel, the occipital crest narrower and less prominent, the condyles smaller. The region of the bullæ is in the same condition as in the modern species except that the paroccipital process is less firmly soldered to the bulla.

*Dentition.*—The first and second upper incisors are represented by small crownless stumps, perhaps remains of the milk dentition. The third incisor, canine, and first premolar are all large one-rooted caniniform teeth, separated by diastemata slightly exceeding their own diameters. A longer diastema separates $p^1$ from $p^2 - m^3$, which are of the usual *Procamelus* type but worn down to the roots in this old individual. The second premolar is unreduced.

The lower jaw is as long and as deep as in the living camel, but not nearly as massive. The teeth are smaller and are indistinguishable from those described by Leidy as *Procamelus robustus*. The lower incisors are not preserved; the canine was as large as in the camel, and is worn to a stump. The first premolar is apparently one-rooted, nearly as large as in the camel but considerably more compressed, separated from the canine by a diastema equal to its own antero-posterior diameter, from the second premolar by a diastema three times its own diameter. The second premolar is but little reduced; the molars increase but little in size. The hook below the condyle of the jaw is even more marked than in *Camelus*.

MEASUREMENTS OF SKULL AND DENTITION.

| | |
|---|---:|
| Length of skull | 433 |
| Length of lower jaw | 358 |
| Depth of lower jaw beneath second molar | 56 |
| Depth of lower jaw at coronoid process | 218 |

Upper dentition, c–m$^{\underline{2}}$....... ............................... ............ 200

Upper true molars (26+29+32 mm)................................... 87

Lower dentition c–m$_{\overline{3}}$...... ..............................................  236

Lower premolars p$_{\overline{2}}$–p$_{\overline{4}}$ (13+17+19 mm).............................. 49

Lower true molars (26+32+47 mm).. ................................ 105

*Neck.*—Six vertebræ (cervicals 2–7) are greatly elongated, probably more than in any other mammal, living or extinct. The atlas is not elongated, and at the seventh cervical the size and elongation rapidly decrease, the second dorsal being smaller than in the camel. The middle cervicals are longer than in the giraffe, although not so large. It is the six long vertebræ of *Poëbrotherium* that are further elongated in this species, instead of the eight long vertebræ of the antelopine ancestors of the giraffe.

COMPARATIVE MEASUREMENTS OF NECK.

*Lengths of Cervical and Dorsal Vertebræ.*

| | Giraffe-Camel. | Modern Camel. | | Nylghau. | Giraffe. | |
|---|---|---|---|---|---|---|
| Six vertebræ elongated. Average 24 centimetres. | 110 | 60 | Atlas | 80 | 200 | Eight vertebræ elongated. Average 215 millimetres. |
| | 250 | 190 | Axis | 100 | 230 | |
| | 300 | 200 | 3rd cervical | 90 | 260 | |
| | 290 | 190 | 4th " | 80 | 260 | |
| | 260 | 180 | 5th " | 80 | 260 | |
| | 210 | 150 | 6th " | 70 | 200 | |
| | 140 | 130 | 7th " | 60 | 180 | |
| | 90 | 90 | 1st dorsal | 50 | 130 | |
| | 75 | 70 | 2nd " | 40 | 90 | |
| | .. | 70 | 3rd " | 30 | 70 | |
| | .. | .. | 4th " | 30 | 70 | |

The fore limb is unknown in *Alticamelus*, but there is every reason to assume that, as in other Camelidæ, it was of the same length as the hind limb.

The *hind limb* is somewhat longer than in a northern giraffe, and notable for the extreme length of the tibia. The femur is scarcely stouter than in the modern camel, although much longer, moderately curved, the shaft of very uniform diameter. The tibia is greatly elongated, with straight uniform shaft, rather small head, and distal end little enlarged. The tarsus is that of *Procamelus*, and the metatarsus differs only in length, the spread of the distal ends being, as in that genus, much less than in more recent camels. The ungues are not known. The proportions of the three long bones form an interesting contrast with those seen in the giraffe.

COMPARATIVE MEASUREMENTS OF HIND LIMB.

| – | Giraffe-Camel. | Poëbrotherium. | Prodremotherium. | Giraffe. |
|---|---|---|---|---|
| Total length of hind limb............. | 2230 mm. | .. | .. | 2033 mm. |
| Of which the femur is................ | 25 % | 28 % | 28 % | 24 % |
| Of which the tibia is......:.......... | 33 % | 33 % | 30 % | 28 % |
| Of which the metatarsus is........... | 28 % | 22 % | 26 % | 34 % |

The above measurements show that in both the giraffe-camel as derived from primitive camels and the giraffe as derived from primitive antelopes, there has been a proportionately greater increase in length of the lower part of the limb compared with the femur — this is a change common to all evolving races of hoofed animals and the majority of clawed races. But the initial advantage in greater proportionate length of metatarsus in the antelope as compared with the camel (made practical by the greater consolidation of the tarsal and metatarsal elements) has been seized upon and emphasized in the giraffe. That it is an advantage seems to follow from the fact that while an equal height is obtained, there is less loss in speed, because the fleshy part of the leg is higher above the ground, its centre of gravity consequently nearer to the body, and the pendulum-swing which is involved in the running of an animal for any considerable distance is quicker than if the centre of gravity of the leg were further from the hip-socket.

The stature of *Alticamelus altus* when alive, as nearly as can be judged from the above data, was in the neighborhood of twelve feet. A northern giraffe reaches a height of thirteen feet, while the larger southern species may be sixteen and occasionally even seventeen feet in height.

## Protolabis *Cope.*

Proposed by Cope to include camels retaining the first and second upper incisors, but (as Professor Cope supposed) with united metapodials. Dr. Wortman, in 1898, identified the type species with Leidy's *Procamelus robustus*, and considered that the retention of the upper incisors was merely an abnormality in the type specimen. Comparison of all the available material, however, shows that there are distinctions of specific value between *P. heterodontus* and *Procamelus occidentalis* in the proportionate size of the true molars and of the premolars, and that *P. heterodontus* is extremely close to *Procamelus angustidens* in all the characters of its teeth. Other specimens obtained by our party show also that the retention of the incisors is a normal character, and that the foot, in both *P. heterodontus* and *P. angustidens*, is of small size, short and stout, with metapodials entirely separate. *Protolabis* is therefore a perfectly good genus, as against *Procamelus*, which, on equally good evidence, is known to have the metapodials, in three species at least, completely united, and the limbs and feet long and slender. From *Protomeryx* (= *Gomphotherium*) it is separated by the much more hypsodont teeth, and other minor modernizations. But *P. transmontanus*, which is placed provisionally in *Protolabis*, has much more brachydont teeth, and I know of no distinction from *Protomeryx* which can fairly be called of generic value. Wortman based a generic separation on the reduction of the second upper premolar in *P. transmontanus*, but intimates that he raises this character to generic rank simply because it indicates a stage in the evolution of the Camelidæ. Under the present circumstances it seems to the writer better to leave it

provisionally under *Protolabis*, as it comes from a horizon nearly equivalent to that of the other species of the genus.

The small species, *P. montanus*, is now described from a complete skull, jaws, four cervical vertebræ, and most of the fore and hind legs, certainly distinct specifically from any described species of *Procamelus*, and referable to *Protolabis* only as a distinct subgenus.

## Protolabis heterodontus *Cope.*

As the nomenclature now stands this is the type species of the genus; but should further material prove it impossible to maintain the distinction between it and the previously described *Procamelus angustidens*, it will become a synonym of that species, which then becomes the type of the genus. The only distinction in the type specimens is the position and character of the first premolar of the lower jaw, which in *P. heterodontus* is further forward and sub-caniniform. This involves a corresponding difference in the position of the first upper premolar, and on this distinction I refer to *P. heterodontus* and to *P. angustidens* another of three specimens obtained by our party. The third may belong to either.

No. 9103, which I place under *P. heterodontus*, is the front of a skull, with premaxillæ complete. The second incisor of the left side and the third of the right side remain in place, and alveoli of the others. The muzzle is extraordinarily long and slender, the canines not large, first premolars only a little caniniform, second and third not greatly reduced. It probably belongs to a female; the teeth are well worn, and the second incisor preserved appears to be a permanent tooth.

MEASUREMENTS OF No. 9103.

| | |
|---|---|
| Length of jaw from incisive border to $m^1$ inclusive | 170 |
| Length of second incisor, root and crown | 21 |
| Diameter of "      " | 5 |
| Diameter of third incisor | 6 |
| Diastema behind third incisor | 17 |
| Diameter of canine | 8 |
| Diastema behind canine | 19 |
| "        "        $p^1$ | 28 |
| Length $p^2$ | 12 |
| "      $p^3$ | 16 |
| "      $p^2 - p^4$ | 45 |
| Width of palate at third incisor (including the incisor) | 32 |
| "        " behind canines | 21 |
| "        " behind first premolar | 20 |

Another specimen referred arbitrarily to *P. heterodontus* might belong equally well to *P. angustidens*, as the first premolar is not preserved. The second, third, and fourth are present, and the three molars in a lower jaw which is in poor condition. The animal is an old one, for the teeth are greatly worn. Besides the jaw, four cervical vertebræ, the scapula, humerus, and metacarpus are preserved.

The lower premolars are unreduced, resembling those of *Procamelus fissidens* and *Protolabis angustidens*, the second and third considerably larger than those of *P.* "*angustidens*" skull and jaws from Kansas, or than any of the three species of *Procamelus* from Nebraska. The lower molars exhibit the rapid increase in size from first to third which has been pointed out as characteristic both of *P. heterodontus* and *P. angustidens*.

The axis is comparatively short and stout, and the other cervicals exhibit less elongation than in *Poëbrotherium*. The odontoid process is imperfectly spout-shaped, retaining in great part the peg-like form of the older Artiodactyls. The process is smaller, the lateral facets which form the under surface of the spout not continuous beneath but separated by a median notch. The third cervical is much larger than that of the llama, but nearly a third shorter in proportion. A posterior cervical is very short. The humerus is heavy in the shaft, and of moderate length ; compared with that of the llama it is estimated at one sixth longer and one half stouter in the shaft, but the distal trochlea of no greater width. The scapula is too broken to exhibit very much character, but appears to be short and wide, one fifth larger than in *Auchenia llama* and somewhat wider, glenoid facet and posterior fossa wider in proportion, spine shorter. The metacarpals are completely separate, shorter and proportionately stouter than in any of the camels in which these parts have been described, and singularly small in proportion to the estimated size of the skull.

## Protolabis angustidens *Cope.*

The distinctions between this species and *P. heterodontus* are very slight, and a considerable series of specimens would probably make it necessary to unite the two. The fine skull and jaws from Kansas referred by Cope to *P. angustidens* appear to be a later development of the Colorado form, in which the upper incisors have entirely disappeared in the adult, while in *P. angustidens* proper there were certainly milk incisors, and from its close relationship to *P. heterodontus* probably permanent ones as well. To this later variety or species may belong a fragmentary specimen from Nebraska (No. 8467), consisting of carpal and tarsal bones, and the distal parts of two metapodials showing that the metapodials were not united. They were referred to *Procamelus gracilis* by Wortman, but the size and proportions agree much better with *P. angustidens*.

To *P. angustidens* proper I refer No. 9100, foot bones and parts of upper and lower jaws of a young individual retaining the milk dentition. The measurements of the teeth, making due allowances for the differences in proportions of the teeth caused by difference in age of the individual, correspond with those of Prof. Cope's type specimen. The fore limbs are preserved, showing that the metacarpals were entirely separate, at this age at least. An individual (No. 9116) of *P. robustus*, shown by the teeth to be of the same age as No. 9100, has both metacarpals and metatarsals thoroughly coössified, the step between the two proximal metatarsal facets much reduced, the limb bones much larger in proportion. In No.

9100 the radius is moderately long, the coössified rudiment of the ulnar shaft is larger than in *Procamelus*. The metacarpus is longer and more slender than that of No. 9113, referred to *P. heterodontus;* the proximal end has a well-marked facet on the inferior surface for the trapezium. The proximal phalanges are shorter than in *Procamelus*, the second phalanges are higher and narrower, and the distal ones much longer, triangular in section, higher than wide, slightly curved laterally, much less rugose towards the laterally compressed pointed distal end.

The above characters, although the individual is young, and the diameter, and to some extent the length, of shafts of bones are still subject to change, indicate a camel with the metacarpals separate (except perhaps in old age), the proportions most like those of No. 9113 (*Protolabis? heterodontus*) but longer limbed, much more primitive in the feet than the *Procamelus* species, and most nearly approximating in dentition to *Protolabis angustidens*. If it belongs to this species, there is a good specific distinction from, and probable generic identity with, *P. heterodontus*, the generic distinctions of both from *Procamelus* and *Alticamelus* being clear.

MEASUREMENTS OF No. 9100.

| | | | | |
|---|---|---|---|---|
| Length of radius | 281 | diameter distal end | | 44 |
| "      3rd metacarpal | 284 | "      "      " | | 20 |
| "      4th      " | 281 | . | | |
| "      1st phalanx | 58 | | | |
| "      2nd      " | 27 | | | |
| "      3rd      " | 23 | width proximal end 12, height 14 | | |
| Third upper milk molar, diameter (anteropost.) | 20 | transverse... | 14 |
| Fourth   "     "     "     diameter     " | 20 | "     .. | 16 |
| First   "     true molar     "     " | 21 | | |
| Second   "     "     "     " | 29 | | |
| First lower     "     "     " | 24 | | |
| Second   "     "     "     " | 30 | | |

## Protolabis montanus *Douglas*.

A skull and jaws, cervical vertebræ, fore and hind legs, from the soft brown Loup Fork sandstones, are referred provisionally to this species in spite of some considerable discrepancies.[1]

*Subgeneric Characters.*—Molars long-crowned, subequal in size. First lower premolar absent, second vestigial.

*Specific Characters.*—Long diastemata behind third incisor, canine, and first (upper) premolar. Size about that of *P. transmontanus*.

The *skull* is one sixth longer anteriorly, somewhat shorter in the cranial region than that of *Auchenia llama;* premaxillæ projecting less beyond nasals, supra-orbital fissure less than half as deep, maxillæ much excavated in their upper

---

[1] Mr Douglas's type is an upper jaw in which the general characters are much the same, but the first premolar is less reduced, the molars are an eighth larger, according to the measurements given, although the specimen is of the same age, and are described as closely resembling those of *Protomeryx cameloides*, which is more brachydont than the specimen here described.

part, with apparently small vacuities on the postero-superior border and within the bone. Sagittal crest smaller than in llama, brain case about one fifth less in diameter. Occiput nearly a third narrower, the lateral flare of the occipital crest



Fig. 31. *Protolabis montanus.* Skull and jaws, side view, × ½. No. 9108. Loup Fork Formation, Protolabis Beds, Colorado.

being less than half as great. Premolar-molar series nearly one half longer. Anterior border of orbit opposite middle of m$\underline{3}$; in *Auchenia llama* it is anterior to m$\underline{2}$.

*Upper Dentition.*—Canine smaller, straighter, more slender than in the llama; third upper incisor straighter, first and second incisors large, spatulate, with strong internal ledge; p$\underline{1}$ quite small, with oval pointed crown, apparently one-rooted; p$\underline{2}$ two-rooted, small, compressed oval with imperfect internal ledge; p$\underline{3}$ much larger, strong internal ledge, ovate, apparently two-rooted; p$\underline{4}$ with well-developed internal crescent and three roots.

The *lower jaw* is longer than in the llama, the molar-premolar series considerably so. The canine is smaller, its section a less flattened oval. The post-canine diastema is about as long as in the llama. The second premolar is a minute stump, the third two-rooted, the crown a nearly simple oval, shorter and less compressed than in other Loup Fork camels. The fourth premolar is much larger than in *Auchenia*, about as in *Procamelus* but somewhat less compressed behind. The molars are rather long-crowned, and show no sign of the antero-external accessory style, a marked character of the llama. The hook at the angle of the jaw is rather more reduced than in the llama.

*Cervicals.*—The neck is much shorter and somewhat smaller than in the llama. The *atlas* has the alæ somewhat more prolonged posteriorly. The *axis*

is of the same width anteriorly but one fourth shorter.   The odontoid process is smaller, and the lateral facets are not continuous beneath it, but separated by a median notch, the condition being intermediate between the peg-shaped and spout-
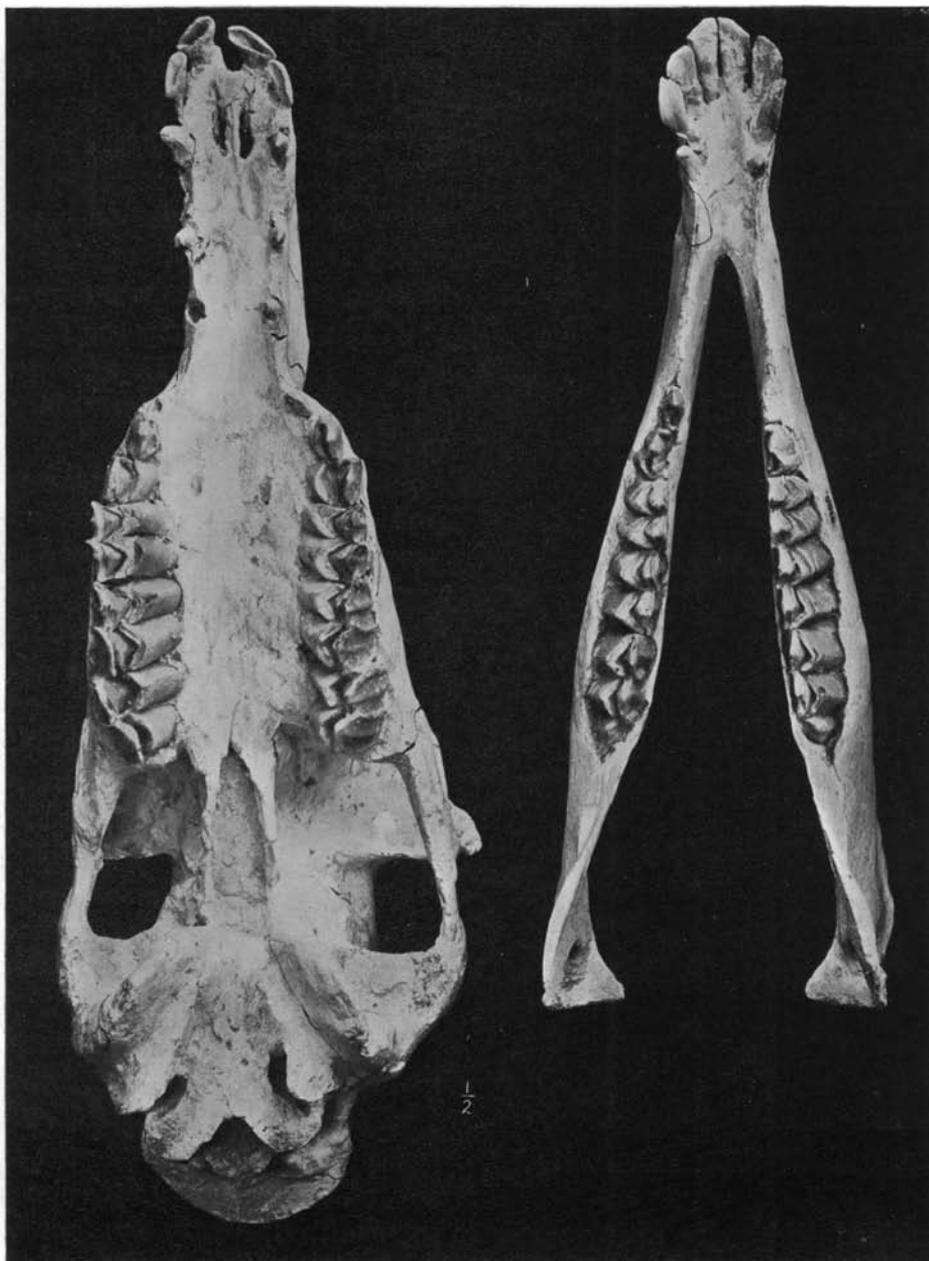


Fig. 32.   *Protolabis montanus*, No. 9108.   Skull and jaws, × ½.

shaped form, and somewhat more primitive than that of *P. heterodontus*.   The axial spine is as long as in the llama, higher and overhanging in front, less deeply bifid behind.   The zygapophyses and transverse processes are much smaller and scarcely project beyond the posterior end of the spine.   The inferior surface of

the centrum has a continuous median ridge instead of the small lateral ridges in the middle part of a llama axis. The *third and fourth cervicals* are about one-third shorter than the corresponding bones of the llama, zygapophyses shorter with more circular facets, hypapophyses continuous from end to end of the centra.



The *humerus* has a larger and more projecting entepicondylar process than in the llama.

The *ulnoradius* is one sixth shorter than in *A. llama*, diameter of shaft the same in both, olecranon much slenderer, width of proximal facets one sixth less (distal facets unknown).

The *carpus* calls for no especial comment, except that a trapezium is indicated by a small facet on metacarpal III.

*Metacarpus.*—The two metacarpals are entirely separate, one fifth shorter than in *Auchenia* and proportionately smaller at the facets, but their combined width is nearly a fourth greater in the shafts. The *phalanges* show also proportionately heavy shafts and small facets. The unguals are like those of *P. angustidens*, sharper, higher, and more compressed than in *Auchenia*.

The *tibia* is smaller and shorter than in *Auchenia*, with somewhat smaller shaft and much smaller distal facet.

The hind foot is somewhat longer than the fore foot, but much slenderer. The *tarsus* is smaller and much narrower than in the llama; the *metatarsals* are separate, one fifth shorter, and their combined width one fifth greater in the shaft but nearly one fourth less at the proximal facets, than the corresponding parts in the llama. The distal facets are narrower than in the fore feet, the phalanges are slenderer but of the same length as in the fore feet.

Fig. 33.  *Protolabis montanus*, No. 9108.  Fore and hind legs, × ¼.

*P. montanus* is a well-marked species, which in certain respects is more advanced than any other Loup Fork camel (hypsodonty and reduction of premolars) ; in most others it is exceedingly primitive (retention of incisors, characters of feet

and neck), and shows one or two specializations of its own (lengthening of muzzle, disappearance of $p_{\overline{1}}$ before $p_{\overline{2}}$, etc.). It suggests the llamas in many ways but is lacking in the most characteristic mark of the genus, the anterior accessory cusp on the molars. No very direct connection can be admitted, although it seems probable that the llamas may stand nearer to *Protolabis* and the camels to *Procamelus*.

### COMPARATIVE MEASUREMENTS.

| | *Protolabis montanus.* | *Auchenia llama.* |
|---|---|---|
| *Skull and Jaws.* | | |
| Total length of skull, incisors (or premaxillæ) to condyles | 308 | 280 |
| Width of skull behind orbits | 104 | 142 |
| "   " occiput | 57 | 84 |
| "   " brain-case | 62 | 73 |
| Dentition, incisors to last molar | 200 | 172 |
| Length of molar-premolar series | 90 | 70 |
| "   " premolar series | 36 | 17 |
| Diastema behind $i^2$ | 16 | 17 |
| "   " $c^1$ | 13 | } 43 |
| "   " $p^1$ | 20 | |
| Length of lower jaw | 265 | 252 |
| "   " dentition | 200 | 179 |
| "   " premolar-molar series | 101 | 71 |
| "   " premolars | 25 | 12 |
| Post-canine diastema | 56 | 54 |
| *Vertebræ.* | | |
| Atlas, length (exclusive of alæ) | 53 | 55 |
| Axis, length (exclusive of odontoid process) | 73 | 97 |
| Approximate length of first four cervicals | 254 | 344 |
| *Fore Limb.* | | |
| Length of radius | 214 | 270 |
| Width of radial shaft | 22 | 29 |
| Height of carpus | 28 | 28 |
| Length of metacarpus | 163 | 213 |
| Width of metacarpus, shaft | 24 | 19 |
| "   "   " proximal end | 31 | 35 |
| Length proximal phalanx | 49 | 58 |
| "   second   " | 19 | 33 |
| Total length of fore foot | 274 | 351 |
| *Hind Limb.* | | |
| Length of metatarsus | 172 | 216 |
| Width "   " shaft | 21 | 17 |
| "   "   " proximal end | 25 | 32 |
| Length of proximal phalanx | 44 | 64 |
| Width "   "   " shaft | 11 | 10 |
| Length of second   " | 20 | 26 |
| "   " ungual   " | 15 | 19 |
| Width "   "   " | 9 | 13 |
| Height "   "   " | 12 | 15 |

## Family HYPERTRAGULIDÆ Cope.

*Leptomeryx* and *Hypertragulus* are abundant in Horizon B; no very complete specimens were found and no evidence of specific difference from the common species of the Oreodon clays of South Dakota. In Horizon C were found a considerable number of specimens of *Leptomeryx*, but none of *Hypertragulus;* the *Leptomeryx* appears to be a species distinct from that of the Oreodon Beds, but the specimens are not yet extracted from the matrix, and cannot be properly described. No trace of *Protoceras* was found in Horizon C.

### Hypisodus *Cope.*

Part of a skeleton (No. 8989) of this smallest of Artiodactyls was found in the Oreodon Beds. It includes upper and lower jaws, occiput, incomplete limb bones and the hind foot.

The *jaws* are already known. The *occiput* is much more modernized than in either *Hypertragulus* or *Leptomeryx*, somewhat less so than in *Tragulus*. It is high with slight occipital and sagittal crests, and a prominent bulge over the foramen magnum, giving increased space for the cerebellum. The tympanic bullæ are exceptionally large, and equalled only by the little *Madoqua* among the modern skulls that I have been able to examine. The bullæ meet anteriorly in the median line of the skull, covering up almost all of the basisphenoid. They are empty, not filled with cancellous tissue. The paroccipital processes are rather short, not projecting beyond the bullæ, and fused to them except near the tip.

The *limbs* are much more slender than those of *Tragulus*, but the joints are pro-
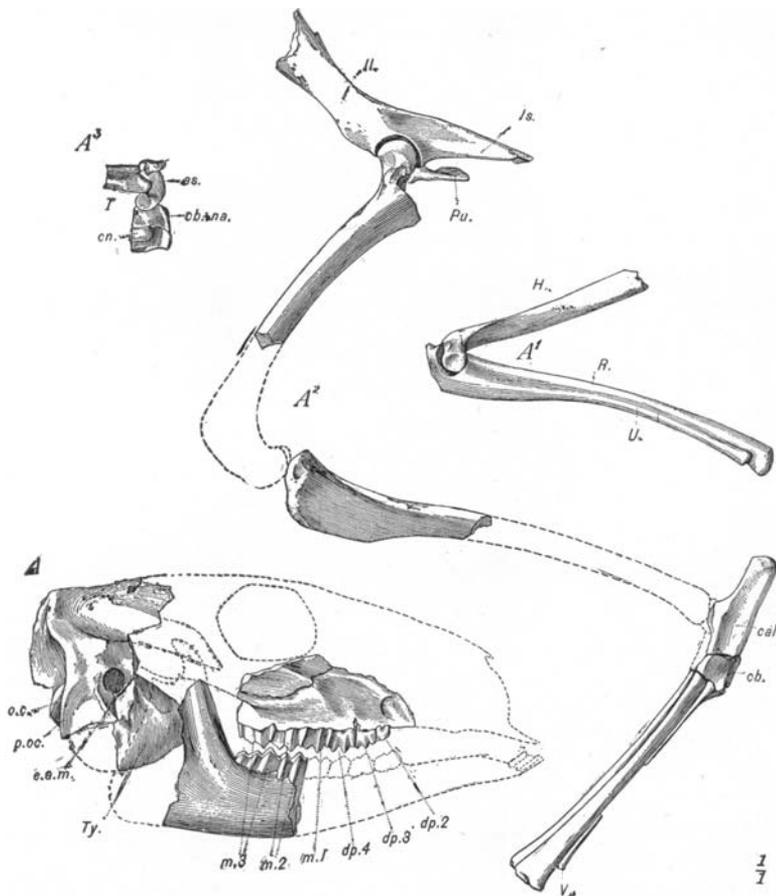


Fig. 34. *Hypisodus minimus.* Parts of skeleton, natural size, No. 8989. White River Formation, Oreodon Beds, Colorado. *A*, side view of part of skull and jaws; *A¹*, external view of humerus and ulnoradius; *A²*, external view of hind limb; *A³*, internal view of tarsus,

portionately large compared with the shafts. The *ulna* and *radius* are firmly coössified, although the individual is still young and retains the milk premolars. The *pelvis* is quite small and slender, the iliac and ischial portions little expanded. The anterior *sacral vertebra* has a strong median keel under the centrum and weak transverse processes. The *femur* has a slender shaft, and the lesser trochanter is higher up than in *Tragulus*. The distal end of the *fibula* was firmly coössified with the tibia ; whether the proximal end was present or not does not clearly appear from this specimen. The cuboid and navicular bones are coössified, the cuneiforms separate (except that the ento- and meso-cuneiform were presumably united to each other). The median metatarsals are distinct, but considerably appressed ; the lateral ones were complete, although the shaft is reduced to a thread. The foot is not over three fifths the length of that of *Tragulus*, while the limb bones were apparently one fourth shorter than in the modern genus.

The above characters place *Hypisodus* quite near to *Hypertragulus*, from which it differs chiefly in the more modernized occiput and long-crowned teeth. The tooth-pattern is the same, except for the flattening of the external wall of the metaselene (metacone crescent), a character probably associated with the lengthening of the crown. The fourth milk molar of *Hypisodus* has exactly the pattern of the permanent molars of *Hypertragulus*. The smaller genus is more modernized in teeth and skull, but less so in foot-structure, as the lateral metatarsals are still retained, while in *Hypertragulus* they have disappeared.

## POSITION OF THE HYPERTRAGULIDÆ.

Professor Scott has recently strongly advocated removing these genera (*Leptomeryx, Hypertragulus, Hypisodus, Protoceras* and several new Eocene genera) from the Tragulidæ, and placing them among the Tylopoda. His main reasons, as far as the present writer is able to appreciate them, are :

1. The great resemblance in skull and considerable resemblance in skeleton between *Poëbrotherium* and *Leptomeryx*.

2. The close approximation in the Uinta of genera considered ancestral respectively to *Poëbrotherium* and *Leptomeryx*.

It appears to the writer that the comparison of *Leptomeryx* with *Poëbrotherium* on the one hand and *Tragulus* on the other hardly gives a just view of the relationship to the two lines of descent, as the two Oligocene genera would be extremely likely to retain many primitive characters lost by all modern genera. The proper comparison would be with *Tragulus* and *Auchenia*, or with *Poëbrotherium* and a supposed Traguline from the Upper Eocene or Oligocene of Europe. When, in fact, we review the resemblances, undoubtedly very striking, between *Poëbrotherium* and *Leptomeryx*, we find that they are all in characters probably or certainly primitive. Professor Scott does not instance, nor can the present writer discover, a single certainly progressive character of the Camelidæ, in any of the Hypertragulids. On the other hand, they do possess the most important diagnostic character of the higher ruminant skeleton. In

the camels the consolidation of the metapodium is precocious, the consolidation of the podium is retarded.   In the Hypertragulids, as in the higher ruminants, the consolidation of the podium is precocious, that of the metapodium retarded. Unless they can be shown to possess progressive cameline characters of greater weight than this, it is difficult to see why they should be placed nearer to the Camelid than to the Tragulid line of descent.

As for the second reason, it will naturally be the case that all the Eocene Selenodonts, except the early aberrant branches, approximate rather closely.   But if we are to place the Hypertragulids in the Tylopoda, it is incumbent to show that the Upper Eocene ancestors of *Leptomeryx* are nearer to the contemporary camels than to the *contemporary* Tragulines,— a comparison not easy to make.

If the Tylopoda be considered as the central group which should include all the primitive types of Selenodont Artiodactyls, whether European or North American, making the group analogous to the Lophiodontidæ of Cope and Lydekker among the Perissodactyla, or to the Creodonta among the Carnivores, then the Hypertragulidæ should unquestionably be placed among them.   But if the two be opposed as specialized groups, Tylopoda on the one hand, Pecora on the other, it would seem that, whatever the geographic probabilities, the present morphologic evidence compels us to place the Hypertragulids near the Tragulidæ.   The hypothesis that all the early American Selenodonts were Tylopods is indeed an inherently probable one, but it seems to the writer that as yet no really valid evidence has been adduced to support it, and that there is some evidence against it.

FAMILY ANTILOCAPRIDÆ (?).

### ? Blastomeryx, sp.

Part of a skeleton found by our party is referred provisionally to this genus although it does not agree with the described species.   In the absence of any skull material the reference cannot be certain.   The specimen is not completely extracted from the matrix, and, as it does not add much to our knowledge of the genus, may be very briefly described.

The animal is smaller than *B. antilopinus*, but much larger than the limbs referred to *B. gemmifer* by Professor Scott ('90, p. 80).   The fore cannon-bone is proportionately smaller and slenderer than in either *B. gemmifer* or *B. antilopinus*.   The distal rudiments of the lateral digits are preserved in position. They are more reduced than in *B. gemmifer ;* the proximal end of the first phalanx has disappeared, and the distal end is a small laterally compressed rudiment with a nearly flat distal facet.   The second phalanx is a short rod of oval section, its depth greater than its width or length, with proximal facet slightly concave and distal facet slightly convex.   The ungual phalanx is quite recognizable as such, short, triangular, somewhat rugose along the external side and distal end.   I could find no trace of a metacarpal proximal to the rudiment

of the first phalanx. The ulna is reduced much as in *B. antilopinus ;* the shaft is continuous, very thin and flat, becoming quite small towards the distal end. At the back of the hind cannon-bone are two small facets close to the proximal end, presumably for a sesamoid, as the proximal rudiment of mt II appears to be fused to the cannon-bone ; a similar facet and bone appear in *Antilocapra.* The remaining bones call for no especial remark.

### MEASUREMENTS.

| | |
|---|---:|
| Width of ulnar shaft at middle, 10 ; thickness........................................ | 3 |
| Radius, length ..................................................................... | 170 |
| "      breadth of distal end......................................................... | 26 |
| Fore cannon bone, length........................................................... | 160 |
| "      "      "      breadth of distal end............................................ | 23 |
| Second digit, length of vestigial first phalanx, 10 ; breadth, 3 ; depth......... | 5 |
| "      "      "      " vestigial second phalanx, 4 ; breadth, 4 ; depth....... | 6 |
| "      "      "      " vestigial ungual phalanx, 7 ; breadth, 4 ; depth....... | 7 |
| Tibia, width of distal end.......................................................... | 25 |
| Astragalus, length, 29 ; width..................................................... | 20 |
| Hind cannon-bone, length........................................................... | 177 |
| "      "      "      width of proximal end........................................... | 20 |
| First phalanx of hind foot, length.................................................. | 33 |
| Second "      "      "      "      ............................................... | 22 |
| Ungual "      "      "      "      ............................................... | 22 |

## Family LEPTOCHŒRIDÆ Marsh.

### Leptochœrus *Leidy.*[1]

With this genus I identify *Menotherium*[2] Cope and *Laopithecus* Marsh, both represented by lower jaws only, and referred to the Primates. Prof. Marsh in 1894[3] described under the name of *Leptochœrus gracilis* a specimen with which were found artiodactyl limbs and feet. The teeth of *Leptochœrus* differ so widely from those of any other Artiodactyl in the simply tritubercular molars, that their association with the foot bones might be questioned. Marsh's description of the limbs and feet, however, forbids their reference to any other White River species in which these parts are known.[4] If they truly belong to *Leptochœrus*, Marsh's (undefined) family Leptochœridæ is warranted by the combination of Tragulid limbs and feet with simple bunodont tritubercular molars. An upper jaw from Colorado, No. 8701, Coll. 1898, is referred doubtfully to *L. gracilis.* The third premolar differs from Marsh's figure in showing a well-marked deuterocone, medial instead of posterior. The diastema between p$\underline{2}$ and p$\underline{3}$ is very slight, p$\underline{4}$ is ten per cent. larger, p$\underline{3}$ fifteen per cent.

[1] Proc. Acad. Nat. Sci. Phila., 1856, p. 88.

[2] Hayd. Sur., Bull. No. 1, Jan. 1874, p. 22.

[3] Am. Journ. Sci., XLVIII, p. 272.

[4] They differ from *Leptomeryx* in the " four usable digits" on the hind foot, from *Hypertragulus* in the separate ulna and radius, from other White River species in the coössified cuboid and navicular. A mixture of remains of *Hypertragulus, Leptomeryx,* and *Leptochœrus* is a possible solution.

larger, m$\underline{3}$ twenty per cent. smaller than the corresponding teeth in Prof. Marsh's specimen. The wear of the teeth prevents exact comparison of the cusps. A lower jaw, No. 8702, shows a similar reduction in size of the third molar, and the width of the teeth is much less, being intermediate between *L. gracilis* and *L.* (*Menotherium*) *lemurinus* of Cope. These characters may indicate a distinct species, but the limits of variation are not known in either *L. gracilis* or *L. lemurinus*, and there seems no advantage in distinguishing a new species.

## V.—SUMMARY.

The stratigraphy of the White River and Loup Fork formations is described, and their origin discussed. The Loup Fork is thought to be a flood-plain deposit, and the White River a mixture of flood-plain and sub-aërial deposits, on evidence of the stratigraphy and especially of the palæontology of the beds. The White River fauna is divisible into two distinct facies, according to the occurrence of the specimens in the unlaminated clays (æolian) or in the sandstones and laminated clays (river-deposits). The clay facies has the characters of a fauna of open plains; the sandstone facies has the characters of a forest and riverside fauna, including aquatic and amphibious types. The successive strata of sandstone and of clay show the parallel evolution of the two faunas; the characteristic species of the clays are found occasionally in the sandstones, and vice versa, proving contemporaneity. The age of the White River formation in Colorado is Oligocene, but the uppermost strata are probably Lower Miocene. The Loup Fork formation belongs to the Deep River sub-stage,. and is nearly equivalent to the typical Deep River beds of Smith Creek, Montana. The break between the White River and Loup Fork formations is not very wide.

There are no known Primates in the White River fauna. The first Mole found in the American Tertiary is described from a skull and jaws, and is generically distinct from any moles hitherto known, presenting several approximations toward the shrews. The characters of the rare rodent *Mylagaulus* are described from a skull, jaws, pelvis, etc., confirming Cope's separation of it as the type of a distinct family, which is shown to be related, although not closely, to the Sciuridæ. A complete skeleton of *Cynodictis* is the basis of a restoration of this very viverroid primitive dog. A well-preserved skull and jaws represent an undescribed species of Marten, approaching the ferrets, and showing various primitive characters. The species of *Dinictis* are revised, *D. squalidens* described, and the skeleton restored; the animal had the proportions and many characters. of the cheetah, contrasting with the leopard-like *Hoplophoneus*. The use of the sabre tooth of the Machærodonts is discussed and a theory propounded as to their habits.

Two distinct genera have been included under *Merycochœrus* Leidy, of which the typical form, hitherto little known, is described from complete skulls

and skeletons of two species, and shown to be an animal of very curious proportions, possessing a large proboscis of some kind.   New material of the Loup Fork camels shows that they possess extraordinarily varied characters and include, besides the intermediate type *Procamelus* with united metapodials and moderately long neck and legs, species which paralleled the giraffe in size and in length of neck and limb, and others which were comparatively short-necked and short-legged, with the metapodials entirely separate.

## POSTSCRIPT.

The manuscript of this paper, written more than a year and a half ago, was finally revised during the past winter.   While the article was in the printer's hands this summer, the writer had opportunity to see the White River and Loup Fork Tertiary beds at several localities on the Western Plains, spending two months in prospecting and collecting, chiefly in the Pawnee Creek Beds of Colorado.   The stratigraphic conclusions set forth in this memoir are confirmed by the subsequent work, as far as time could be given to this line of investigation.   The discovery of *Anchitherium*, *Blastomeryx borealis* (?), and *Cyclopidius* (?) in the Pawnee Creek Beds further indicates their equivalence to the typical Deep River of Montana.   No satisfactory division between horizons " D " and " E " of this upper formation could be maintained, but it is always distinct from the White River, lying usually on its eroded surface.

Several fragmentary specimens of Mylagaulidæ throw some light on the method of evolution of the large premolar in this singular group, showing that some at least of the enamel ridges of the tooth began as successive cingular ridges, the cingulum increasing greatly in height at certain points, and becoming covered with heavy deposits of cement; then another cingulum forming outside at the base, which in its turn rises to the level of the grinding surface.

Other interesting additions to the fauna are *Daphænus* and a small Mustelid allied to *Stenoplesictis* from the Upper Oreodon Beds (both are represented by complete skulls); *Eucastor* (?), *Tapiravus* (?), and a gigantic *Amphicyon* from the Loup Fork.   A large amount of fine material of Equidæ, Rhinocerotidæ, Camelidæ, etc., was obtained, but it is not yet extracted from the matrix, and will be described in future publications.

## ERRATA.

Page 362, line  1, for isolated   read semi-isolated.
 "   368,   "   5,  "  Meriram   "   Merriam.
 "   380,   "  32,  "  Plate I   "   Plate XXXVII.
 "   391,   "   9,  "  Plate II   "   Plate XXXVIII.

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PLATE XXXVII.
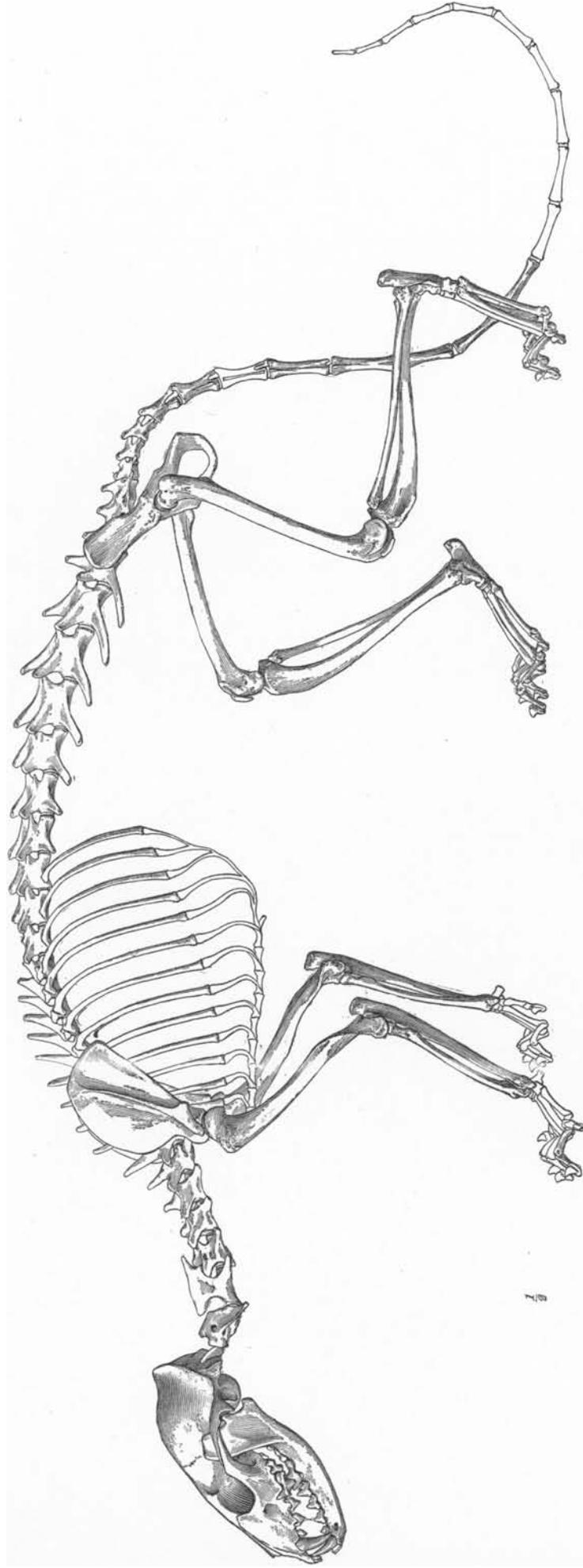
Plate XXXXVII.



CYNODICTIS GREGARIUS.

Restoration of skeleton.   One half natural size.   Based on a nearly complete skeleton, No. 8774, from the Oreodon Beds of Cedar Creek, Colorado.
The missing parts are restored in outline from other specimens.

PLATE XXXVIII.

Plate XXXXVIII.
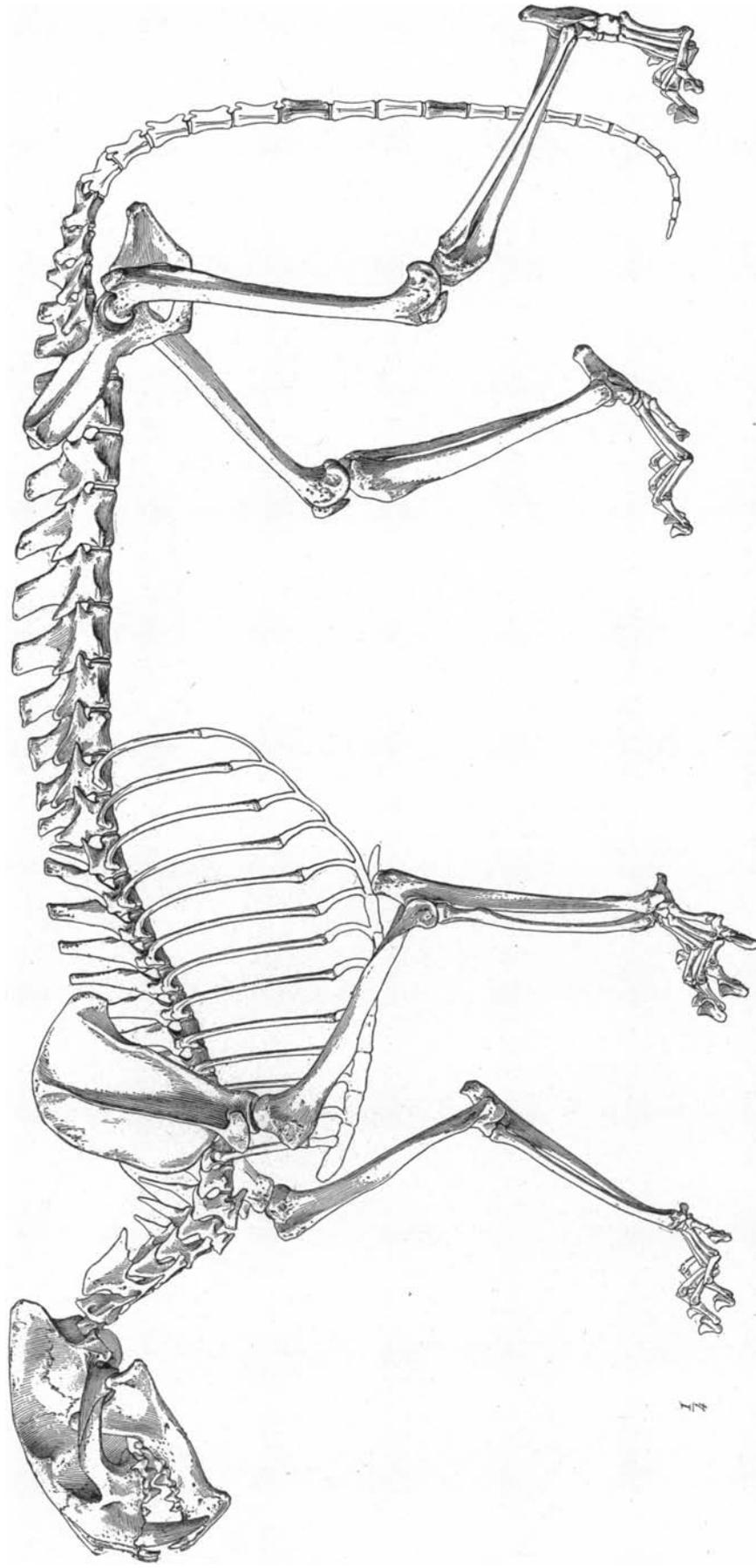


DINICTIS SQUALIDENS.

Restoration of skeleton. One fourth natural size. Based chiefly on skeleton No. 8777, from the Oreodon Beds of Cedar Creek, Colorado. The fore limbs and hind feet are supplied from No. 1396, from the Oreodon Beds of South Dakota.

PLATE XXXIX.
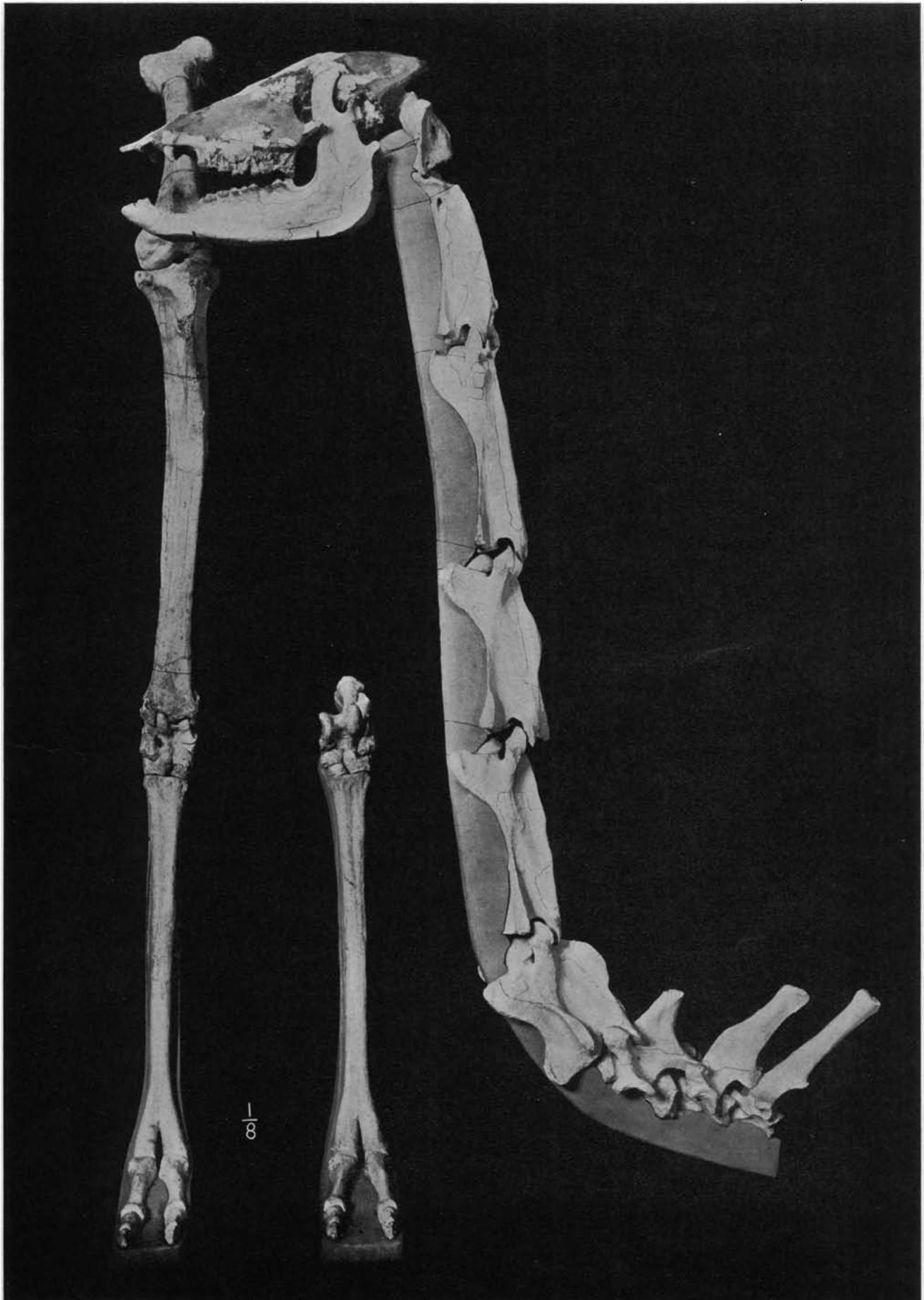
ALTICAMELUS ALTUS.

Skull, neck, left hind limb, and right hind foot of one individual, No. 9109.   One eighth natural size.
Loup Fork Formation, Protolabis Beds, Colorado.

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