### Article II.—THIRD CONTRIBUTION TO THE SNAKE CREEK FAUNA

**By W. D. Matthew**

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This article is based upon the results of the American Museum Expeditions of 1918, 1921 and 1922 in charge of Albert Thomson. Large additions to the collection from these quarries were made by these expeditions, and studies of the stratigraphy and faunas of the different quarries and pockets showed that three distinct faunal zones were present, each now represented by large collections. The writer spent a part of the summer of 1922 with the party at the Snake Creek quarries and revised and extended the stratigraphic observations of previous years.

STRATIGRAPHY OF THE SNAKE CREEK QUARRIES

The relations between the "Snake Creek," and "Sheep Creek" beds had not been clearly understood. The former appeared when first examined to be a distinct and later formation overlying the eroded surfaces of the latter. A more careful study of the quarry cuts and faunas makes it necessary to modify this conclusion to some extent, the two representing different facies of the same formation or sequence of strata, in part contemporaneous, rather than two distinct formations. The Snake Creek beds are channel-fillings throughout (except near the top), and they fill and overlie eroded channels in the Sheep Creek beds,
which are rather a fine-grained uniform backwater or floodplain formation. But the stratigraphic and faunal evidence jointly show that the floodplain beds are contemporary with at least the two older horizons (Miocene) of the channel beds. The third faunal horizon of the channel-beds has no recognized floodplain correlative; and the capping of the whole formation is certainly in part, and presumably as a whole, a dune-sand of Pliocene age.

The exposures of the Snake Creek and Sheep Creek lie at the heads of a number of "draws," which drain down into Dry Spotted Tail Creek, thence into the North Platte River. The locality is some twenty miles south of Agate and about the same distance north of Mitchell. These gullies are on the south margin of the sand-hill strip that separates the Niobrara from the North Platte drainage, on the south side of a series of small rounded hills that extend in a S. E.-N. W. direction for three miles or more. These small hills are typical sand-hill contour, but appear to be of Pliocene age, whereas the sand-hills surrounding them are regarded as Pleistocene or sub-recent in their contouring and in the occasional fossils found in them.

The working hypothesis adopted is that the Snake Creek beds are channel and floodplain deposits of the North Platte river at a time when the valley was at a considerably higher level than now. The Oligocene and Miocene formations of this region were deposited as broad sheets or, more exactly, as wide, thin, flat lenses of floodplain deposits, broadly overlapping but not constituting a continuous column in any one locality, the area of floodplain deposition being shifted to and fro as the streams changed their courses, and the deposition varying in rate, reduced to a minimum or wholly discontinued for considerable intervals. These extended floodplain deposits were traversed by channel-beds of coarser and cleaner sand, mud-balls and small pebbles. At certain points, probably due directly or indirectly to the existence of persistent pools or springs that served as waterholes for the animals, fossil bones and teeth are abundant but nearly always dissociated, much broken and often waterworn. They are much scarcer in the backwater or floodplain deposits but frequently associated, often articulated and more or less complete skeletons, although in many cases considerably damaged by subaerial weathering before burial.

The backwater deposits indicate continuance of sedimentation in this area until toward the end of the Miocene. The *Hipparion* and *Pliohippus* fauna, of Pliocene age, is found in channel-fillings cut down to perhaps fifteen or twenty feet below the highest adjacent exposures of the Miocene floodplain strata. At one or two points the channel evi-
dently undercut an overhanging bank of the Miocene formation, which has tumbled down in large blocks, the interspaces between which are filled up with coarse sand, pebbles and fossil teeth and bones. Overlying these unmistakable channel-beds are uniform fine, clear sands of eolian type, showing eolian cross-bedding very distinctly at one point, and capped by sod. Traces of old sod surfaces whose position and slope is wholly unrelated to the present topographic detail, were uncovered by some of the excavations in this uppermost member of the Mio-Pliocene sequence. As is usual beneath any persistent sod surface that overlies an unconsolidated formation, the uppermost foot or two of sand has been compacted and consolidated by the mineral residuum from ground water rising to the surface and evaporating. This residuum, forming a calcareous cement, aids greatly in stiffening the sod and helps it to resist erosion. It is evident in some of the old sod-lines noticed above. Corresponding conditions in a much more clayey formation have been pointed out by Sinclair as the probable significance of the "nodule layer" in the Oreodon beds of the South Dakota Brule and of similar concretionary layers elsewhere.

The series of little draws in which the quarries are situated were named by our party for convenient reference, beginning at the west end where the Mitchell-Agate road crosses the fence between the Ashbrook and Kilpatrick ranches: West draw, Aphelops draw, Merychippus draw, West Pliohippus draw, East Pliohippus draw, Stonehouse draw, West and East Sinclair draw, Olcott hill. The last two localities are in the Ashbrook ranch, the others in the Kilpatrick ranch. We are indebted to the courtesy of the Kilpatrick Brothers of Beatrice, Nebraska, for free permission to collect upon their land, especially in 1918, 1922 and 1923; and to Mr. Harry Ashbrook for permission to collect in the seasons of 1916 and 1921.

The occurrence of the fossiliferous beds in the different draws is shown diagrammatically in Fig. 1. The earlier collecting in 1908 was mainly picking up of surface material, a couple of small pockets in Sinclair draw being opened up. In 1914 the principal collecting locality of the Princeton party (loc. 1000C) was in this draw; and most of the material secured by the American Museum expedition of 1916 also came from a branch of Sinclair draw. In 1918 Mr. Thomson's principal collecting was from quarries in Aphelops draw. The type skeleton of Pliohippus leidyanus was obtained by H. J. Cook from East Pliohippus draw. In 1921 the American Museum party opened three quarries, two (Quarries A and B) in a branch of Sinclair draw, the third (Quarry C) on Olcott hill, the locality where Mr. Cook found the type of Hesperopithecus.
Fig. 1. Snake Creek quarries, Sioux Co., Nebraska.

Scale approximately four-fifths inch to the mile. The contours are from the U. S. Geol. Survey map and are far from accurate. The dotted squares are section lines. The star at Olcott Hill shows the quarry from which the Hesperopithecus tooth was obtained by Harold J. Cook.

In 1922-3 some collecting was done in the Aphelops and Pliohippus draws, but the principal collection made is from a channel-bed in Stonehouse draw containing the Merychippus primus fauna.

The principal collecting localities for the different faunal zones and phases are as follows:

<table>
<thead>
<tr>
<th>Channel-Bed Phase</th>
<th>Floodplain Phase</th>
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</thead>
<tbody>
<tr>
<td><strong>Hipparion affine zone</strong></td>
<td>Olcott hill*</td>
</tr>
<tr>
<td><strong>Merychippus paniensis zone</strong></td>
<td>Sinclai draw*</td>
</tr>
<tr>
<td><strong>Merychippus primus zone</strong></td>
<td>Stonehouse draw*</td>
</tr>
</tbody>
</table>

The four starred localities are the most important.
<table>
<thead>
<tr>
<th>Primates</th>
<th>Carnivora</th>
<th>Lower Snake Creek M. primus Zone</th>
<th>Upper Snake Creek M. primus Zone</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hesperopithecus haroldcookii</em></td>
<td><em>Hyænomysus direptor</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Æturodon sexus</em></td>
<td><em>Tomarctus brevirostris</em></td>
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<td>&quot; lori</td>
<td>&quot; temerarius</td>
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<tr>
<td>&quot; opalus</td>
<td>&quot; mortifer</td>
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<tr>
<td>&quot; sp.</td>
<td>&quot; haydeni</td>
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<tr>
<td><em>Amphicyon idoneus</em></td>
<td><em>Tomarctus haydeni</em></td>
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<td>&quot; frendens</td>
<td>&quot; confertus</td>
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<tr>
<td>&quot; sinapius</td>
<td>&quot; opalus</td>
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<tr>
<td>&quot; gigas</td>
<td>&quot; mortifer</td>
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<tr>
<td><em>Pliocyon medius</em></td>
<td><em>Hyænomysus haydeni</em></td>
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<tr>
<td>&quot; ? sp.</td>
<td>&quot; haydeni</td>
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<tr>
<td><em>Probassariscus antiquus</em></td>
<td><em>Hyænomysus haydeni</em></td>
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<tr>
<td><em>Leptocyon vafer</em></td>
<td><em>Tomarctus haydeni</em></td>
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<tr>
<td><em>Euoplocyon praedator</em></td>
<td><em>Hyænomysus haydeni</em></td>
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<td><em>Leptarcus primus</em></td>
<td><em>Tomarctus haydeni</em></td>
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<tr>
<td><em>Brachypsalis matutinus</em></td>
<td><em>Tomarctus haydeni</em></td>
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<tr>
<td>&quot; modicus</td>
<td>&quot; temerarius</td>
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<td>&quot; obliquidens</td>
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<tr>
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<td>&quot; mortifer</td>
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<td><em>Mionictis incertus</em></td>
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<td>&quot; haydeni</td>
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<td><em>Tomarctus haydeni</em></td>
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<td><em>Heterofelis callidors</em></td>
<td><em>Tomarctus haydeni</em></td>
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</table>

**List of Vertebrate Fauna from the Snake Creek and Sheep Creek**

- *Hesperopithecus haroldcookii*: upper molar tooth
- *Hyænomysus direptor*: 2 lower jaws; upper teeth
- *Æturodon sexus*: upper and lower jaws, etc.
- *Tomarctus brevirostris*: 3 skulls, many jaws, etc.
- *Tomarctus haydeni*: jaws and teeth
- *Tomarctus confertus*: skull, several jaws
- *Tomarctus opalus*: upper and lower jaws, skull
- *Tomarctus mortifer*: jaw fragments, teeth
- *Amphicyon idoneus*: upper jaw, skull, etc.
- *Amphicyon frendens*: upper and lower jaws, teeth, etc.
- *Amphicyon sinapius*: skull, jaws, etc.
- *Amphicyon gigas*: part of lower jaw, teeth
- *Pliocyon medius*: skull, jaws, etc.
- *Pliocyon haydeni*: jaw fragments, teeth
- *Probassariscus antiquus*: part of lower jaw
- *Hyænomysus haydeni*: teeth
- *Leptocyon vafer*: lower jaws
- *Euoplocyon praedator*: lower jaw
- *Leptarcus primus*: skull, jaws
- *Brachypsalis matutinus*: upper and lower jaws
- *Brachypsalis modicus*: lower jaw
- *Brachypsalis obliquidens*: lower jaw, upper jaw
- *Brachypsalis pristinus*: jaws, teeth, etc.
LIST OF VERTEBRATE FAUNA FROM THE SNAKE CREEK AND SHEEP CREEK—Continued

<table>
<thead>
<tr>
<th>Glires</th>
<th>Sheep Creek Zone</th>
<th>Lower Snake Creek Zone</th>
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<td><em>Mylagaulus novellus</em></td>
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<td>&quot; paniensis</td>
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jaws and teeth
skulls, adult and young; jaws
skull, jaws, and teeth
palate, jaws, teeth
upper and lower jaws
lower jaws, teeth
jaw
" jaws
" jaw
" jaws
teeth
lower jaw
" jaw
molar; phalanges
jaws, fragmentary skeleton
upper and lower jaws, etc.
skull, skeleton bones
jaws, foot bones
" teeth, skeleton bones
" " and bones
parts of jaws, teeth, etc.
upper and lower jaws, teeth
lower jaw, teeth
upper and lower jaws, teeth
skulls, many jaws, etc.
LIST OF VERTEBRATE FAUNA FROM THE SNAKE CREEK AND SHEEP CREEK—Continued

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<th>Artiodactyla</th>
<th>Sheep Creek</th>
<th>Lower Snake Creek</th>
<th>Upper Snake Creek</th>
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<td>Merychippus sejunctus</td>
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<td>&quot; eohipparion</td>
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<td>Hipparion affine</td>
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<td>&quot; major</td>
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<td>Miolabis tenuis</td>
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<td>&quot; angustidens</td>
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<td>Alticamelus priscus</td>
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<td>Megatylopus gigas</td>
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<tr>
<td>?Pocamelus cf. gracilis</td>
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<tr>
<td>Blastomeryx medius</td>
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<tr>
<td>&quot; elegans</td>
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<td>&quot; wellsi</td>
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- Palates, jaws, etc.
- Jaws, teeth, etc.
- Skeleton, skull, jaws, etc.
- Jaws, teeth, bones
- Teeth, foot bones
- Jaws, teeth, etc.
- Fragmentary upper jaw parts, skull, jaws, etc.
- Jaws, teeth, etc.
- Jaw fragments
- Jaws, etc.
- Palate, jaws, etc.
- Upper and lower jaws
- Skull, jaws, etc.
- Lower jaws, skull, etc.
- Upper and lower jaws, etc.
- Lower jaws, etc.
- Skull, jaws, etc.
- Skull, jaws, etc.
- Skeleton, jaws, etc.
- Jaws, etc.
- Skull, jaws, etc.
- Parts of jaws, teeth, etc.
- Upper and lower jaws, etc.
- Parts of jaws, etc.
LIST OF VERTEBRATE FAUNA FROM THE SNAKE CREEK AND SHEEP CREEK—Continued

<table>
<thead>
<tr>
<th>Species/Genus</th>
<th>Sheep Creek</th>
<th>Merycodus primus Zone</th>
<th>Lower Snake Creek</th>
<th>M. poniemani Zone</th>
<th>Upper Snake Creek</th>
<th>Hesperotherium affinis Zone</th>
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<td>Dyseomeryx riparius</td>
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<td>&quot; sp.</td>
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<td>&quot; altidens</td>
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<td>Drepanomeryx falciformis</td>
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<td>Buteo typhoicus</td>
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<tr>
<td>Ortalis phengites</td>
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<td>Crocodilia</td>
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<td>Alligator thomsoni</td>
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<td>Chelonia</td>
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<tr>
<td>Testudo cf. orthoppygia</td>
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<td>Plicagnostus matthewi</td>
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<td>Pisces</td>
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<tr>
<td>Silurid, large, indet.</td>
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<td>Pisces div. indet.</td>
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DISTINCTIONS BETWEEN THE FAUNAL ZONES

When this fauna was discovered in 1908 it was supposed to represent a single faunal horizon. The fauna when studied was necessarily referred to the Lower Pliocene, on account of the presence of a series of typically Pliocene mammals, but a large part of the collection consisted of Middle
or Upper Miocene species whose presence in this fauna was explained as a survival.

Dr. J. C. Merriam, in connection with his correlation work upon the later Tertiary faunas of the Pacific coast, found that in that region the Miocene and Pliocene faunas were clearly separate in time, and that no such survival occurred of characteristic Miocene genera into the Pliocene. He suggested that the apparent association at Snake Creek might be due to the confusion of two distinct faunal horizons. A reexamination of our material suggested that this explanation might be tenable, since there appeared to be certain differences in the preservation of the material referable to the older and younger faunal stages, the latter tending to be more water-worn, more broken up, harder and more heavily silicified and of a brownish-black color as compared with the prevalent blue-black tinge seen in the older faunal elements.

Merriam’s suggestion was provisionally accepted but no field observations were made to verify it until 1918. Mr. Thomson’s observations and collecting during that season placed the matter beyond question. Further observations were made by Thomson in 1921–1923 and by the writer in 1922.

As is shown in the preceding list, the Miocene faunae are quite distinct from the Pliocene faunae. A few species appear to pass through unchanged but these exceptions may be due in some cases to the accident of redeposit, in some others to our imperfect knowledge of the species in one or both horizons. The uppermost, or fourth fauna, is by no means clearly distinguished.

The most important distinction is in the Equidae, these being by a wide margin the most abundant fossils in each horizon. *Merychippus* is the principal genus of the two older faunae. *Parahippus* and *Hypohippus* are scarce. In the third fauna *Hipparion* and *Pliohippus* are abundant, *Protoprhippus* rather scarce and *Hypohippus* rare. The fourth fauna is doubtfully characterized by predominance of large, progressive *Pliohippus*, *Peraceras* and *Megatylopus*. A few jaw fragments and teeth of *Merychippus* have been found with the collections from the *Hipparion* zone quarries, but these may be due to redeposit or, in certain instances, to error in field records. *Parahippus* is not found. The distinction in adult teeth between progressive species of *Merychippus* and primitive species of the three later genera is not so sure and easy as one might suppose from the statements made by various writers, but the milk premolars are more clearly distinguishable, those of *Merychippus* much broader and lower-crowned and imperfectly cemented, while in the
three Pliocene genera they are higher-crowned, narrower and heavily cemented at a much earlier ontogenetic stage. Out of some thousands of jaws and teeth of the milk dentition all that I have seen in the older beds are unmistakably *Merychippus*,\(^1\) while that type is entirely absent in the later fauna and all the teeth are of the later type.\(^2\)

The camels are not so clearly distinct, but in the older faunæ we find the smaller types of giraffe-camel (*Alticamelus*) abundant and with them a smaller number of *Miolabis* (brachydont camels, mostly split-foot). In the later faunæ we find species of giraffe-camel, mostly of larger size, and with them the gigantic *Megatylopus*.

Third in point of abundance is *Merycodus*, very common in the lower levels and mostly referable to *M. necatus*. The genus is much scarcer in the upper fauna and is represented chiefly by larger species, some of which may prove when better known to belong to distinct genera more nearly related to *Antilocapra*.

The Carnivora, especially the Canidæ, show well-marked distinctions. The typical Canidæ in the lower levels belong mostly to *Tomarctus*, and *Elurodon* is absent. In the upper level *Elurodon* is the common form and *Tomarctus* is doubtfully represented by fragmentary material. Amphicyonine dogs are represented by *Amphicyon* and *Pliocyon* in the lower levels; in the upper the material is too fragmentary for certain allocation but the species appear to be distinct.

The rhinoceroses of the three faunæ are probably distinct but their comparative scarcity and lack of complete skulls makes the references somewhat provisional. A large *Aphelops* comparable to *A. malacorhinus* is represented by a perfect skull from the upper beds; a small and primitive *Teleoceras* found in the lower Snake Creek is referred to *T. medicornutus*. A fine *Peraceras* skull of unrecorded level is provisionally placed in the later fauna. The majority of the teeth and jaw fragments from the lower Snake Creek belong to a large *Aphelops* provisionally identified with *A. crassus* of Leidy, and the small, typical *A. megalodus* is not recognized except in the Sheep Creek quarries (Hor. A).

*Palæomeryx* is characteristic of the Lower Snake Creek, *Dyseomeryx* and *Blastomeryx* are found in all levels, but the species appear to be distinct. The horizon of *Cranioceras* and *Neotragoceras* is not definitely recorded, but the former is from the Miocene and the latter from the Pliocene, so far as one can judge from the preservation of the specimens. *Megalonyx* is definitely from the Pliocene.

\(^{1}\)Setting aside those of *Parahippus* and *Hypohippus*.

\(^{2}\)It is difficult to distinguish milk teeth of *Hipparion*, *Pliohippus* and *Protohippus* from each other by any characters that will apply to all the species referred to each genus.
The occurrence of these scarce forms, like that of the primitive-toothed *Talpa* in the lower and the progressive-toothed *Scalops* in the upper level, and of various other rarities in the collection, conforms well enough with expectation, but can hardly be cited as evidence for the distinctness of the two.

**CORRELATION OF THE FAUNAS**

*Merychippus primus Zone*

This zone is on record as the lower part of the Sheep Creek beds, containing *Merychippus* "isonesus" *primus* (now regarded as a distinct species). A channel-bed facies of the formation is well exposed in a small "draw" which is designated as "Stonehouse draw" and was worked by the Museum party in 1922–3. The collection obtained is as large as has been secured from the *paniensis* zone, and clearly earlier, although not so sharply distinct as are the *M. paniensis* and *H. affine* zones. The correlation seems to be with the earliest phases of the *Merychippus* zone, older than the Mascall, possibly equivalent to the rather scanty and fragmentary fauna described by Merriam from Phillips Ranch in the Mojave region.

*Merychippus paniensis Zone*

It will be observed that all the species which Leidy recorded from Bijou Hills are found in the Pawnee Creek and Snake Creek, except for *Hippodon speciosus*, which was based upon an indeterminate type. The metatypes of *H. (Merychippus) speciosus* are upper teeth which may quite well be the same as *M. paniensis* of the Pawnee Creek and Snake Creek, but it is not certain whether or not they are true topotypes. *Merycodus necatus* of Bijou Hills is represented in the Pawnee Creek by *M. osborni* (? = *M. necatus*), in the Snake Creek by *M. necatus* and a doubtful subspecies, *M. n. sabulonis*; *Leptarctus primus*, based on an upper p4 from Bijou Hills, is represented by skulls and jaws from both Pawnee Creek and Snake Creek described in this paper.

The correlation with Pawnee Creek is based on the following species:

**PAWNEE CREEK**

*Tomarctus brevirostris*

"temerarius"

*Euoplocyon* sp.

*Amphicyon sinapius*

*Leptarctus primus*

*Plionictis ogygia*

"parviloba"

**LOWER SNAKE CREEK**

*Tomarctus brevirostris*

"temerarius"

*Euoplocyon* praderi

*Amphicyon sinapius*

*Leptarctus primus*

*Plionictis glare*

"? parviloba"
This is a remarkably close correspondence for two formations of different physical type situated about a hundred miles apart. It amounts to a practical identity of fauna, making allowances for merely nominal species and for the accidents of preservation among rare or little-known forms, excepting as follows:

(1.) The camels correspond only in part. Nothing corresponding to the gigantic *Alticamelus giraffinus* has been found at Snake Creek.

(2.) The oreodonts (*Agriochceridae*) appear to be different generically, *Metoreodon* and *Pronomotherium* taking the place of *Merychys* and *Merychoerus*.

(3.) No proboscideans have been recorded from the lower levels of Snake Creek. They are very rare in the Pawnee Creek beds, so this may not have much significance.

These distinctions, such as they are, cannot be interpreted as indicating any difference in age. The absence of *A. giraffinus* from the Snake Creek would point one way, while the scarcity of the smaller and more primitive camels would point the other way; *Metoreodon* of the Snake Creek might be regarded as a descendant of *Merychys* of Pawnee Creek. *Pronomotherium* of the Snake Creek is certainly not derived from *Merychoerus* of Pawnee Creek, nor is it on the whole any more specialized. It appears to be derived from some species of Lower Miocene *Ticholeptus*. The differences between the two faunæ are probably only facies, due to some environmental difference, geographic range, or the selective action of different conditions of sedimentation.

**Hipparion affine Zone**

The principal upper Snake Creek fauna is clearly distinct and of Pliocene age, comparable with that of the Republican River beds. There are some forms in it suggesting a later stage, but they are rare and im-
perfectly known, and their evidence is not weighty. The correspondence, however, is by no means so close as that between Pawnee Creek and lower Snake Creek. There are few species in common. *Teleoceras fossiger*, so abundant in Republican River, is not positively recorded from the Snake Creek. The Equidae correspond fairly well as to genera, but not as to species. *Ælurodon* is the characteristic canid in both faunas.

**Pliohippus leidyanus Zone**

This doubtfully distinct zone has not been well differentiated and is still only tentatively separated, as it was in Osborn's Equidae memoir. A few specimens, mostly *Pliohippus*, have been found in the eolian 'dune-sands that appear to be the final member of the Mio-Pliocene sequence at the Snake Creek fossil quarries. Among them are the type skeleton of *P. leidyanus*, a skull of the same species, a number of *Pliohippus* teeth, and, if the writer's memory does not play him false, two jaws, one of *Protohippus*, the other of *Hipparion*, found in 1908. Also several rhinoceros jaws and bones of very large size but mostly indeterminate, a skull of *Megatylopus gigas*, and perhaps some other specimens, are probably from this horizon. Fossils are so scarce in it, however, that its distinctness has not been verified.

**INSECTIVORA**

**TALPIDÆ**

**Scalops cf. aquaticus**

A humerus, A. M. N. H. No. 17577, *Hipparion affine* zone, complete except that part of the head is broken off, agrees with the average of half a dozen specimens of the existing *S. aquaticus*.

It is altogether probable that this Lower Pliocene species would prove distinct from the modern form if one had a skull or even a good lower jaw for comparison. The humerus, however, is completely "modernized," quite distinct from "*Talpa* platybrachys" Douglass of the Flint Creek Miocene of Montana¹ (which may possibly be *Talpa* but probably is not).

*Scalops* sp. occurs in the Lower Pleistocene (typical "Loup Fork") of Nebraska.² It is not distinguishable from *S. aquaticus* in the lower jaw, the only part at hand for comparison.

¹Douglass, Earl. 1904. 'New Vertebrates from the Montana Tertiary.' Ann. Carn. Mus., II, p. 171, Fig. 13.
**Talpa incerta**, new species

**Type.**—A. M. N. H. No. 18891, a lower jaw with the last molar and alveolus of $m_3$.

**Horizon and Locality.**—Merychippus paniensis zone; Quarry B of 1921.

**Characters.**—Posterior portion of the jaw, so far as preserved, agrees with *Talpa*. The form and position of the coronoid appear to have been the same, although the major part of the process is broken off. The dental foramen agrees in size and position and in the form and curvature of the parts adjoining it. The angle is broken off. The depth and thickness of the jaw beneath the molars corresponds with *Talpa*. The size and general form of the last molar accords, so far as one may judge from the rather heavily worn tooth, except for the talonid, which is broader and lacks the deep external notch between trigonid and heel that is found in *Talpa* and various related genera. The alveoli of $m_2$ indicate a tooth of about the same size as in *Talpa*; the jaw is broken off in front of this point.

The reference of this jaw to *Talpa* is provisional. It certainly is not a shrew, as it has nothing of the deep coronoid pocket characteristic of the shrews. The position of the mental foramen and relations of adjacent parts are like the moles and unlike any bats that I have examined, nor does the molar agree as nearly with any of the latter as it does with *Talpa*. Nevertheless, it is likely that a better knowledge of the species would distinguish it generically from *Talpa*; but it is not advisable to base a new genus on the notch in the heel of $m_3$. *Scalops* and *Scapanus* have much higher-crowned molars; in *Proscapanus* and *Proscalops* they are also higher.

Comparison with "*Talpa*" *platybrachys* Douglass is impossible as that species is known only from a humerus.

**RODENTIA**

Rodents are not especially common in the Snake Creek quarries, but a considerable variety of diverse types is represented, chiefly by fragmentary specimens. *Mylagaulus* and *Dipoides* are the most abundant. The following is the list:

- *Sciurus* represents the family Sciuridae.
- *Dipoides* and
- *Amblycastor*, different sections of the Castoridae
- *Poamys* and *Muridae*
- *Thomomys* and *Geomyidae*
- *Peridomys* and *Heteromyidae*
- *Mylagaulus* and *Mylagaulidae*
- *Lepus* (*Hypolagus*) and *Leporidae*

It is to be observed that in spite of the relative scarcity of material the diversity of type represented—seven families—is greater than the
six families of the John Day, the five families of the White River, the three of the Uinta, two of the Bridger, one of the Wasatch. The progressive increase in diversity is not due to absolute or relative abundance of specimens in the collections compared, for rodents are quite as common, absolutely and relatively, in the Wasatch or Bridger as in the later Tertiary formations compared. It is not due to more diverse environment or wider geographic range, for the comparison is made between faunas each from a limited area and representing a single facies. It is explicable only by a progressive diversity of type in the order itself. The Wasatch rodents are all of one family and not of half a dozen or more presumably because there was only one family of rodents in the Lower Eocene. If this were true only of North America, we might suppose it possible that these diverse types existed elsewhere but had not yet reached this continent. But the same conditions prevailed in Europe at the corresponding epochs; so far as the record shows, they prevailed elsewhere; and from these data one must conclude that these diverse types had not come into existence in the Lower Eocene, that the number and divergence of the rodents increased progressively from a single family in the Wasatch to a dozen in the Pleistocene, and that most of the existing families were already established by the end of the Oligocene, but that their divergent specialization increased down to the present day. As this conclusion will be disputed by some zoologists and paleontologists, I think it well to point out the facts upon which it is based. I cannot see any other reasonable conclusion from these facts.

**MYLAGAULIDÆ**

A skull, a considerable number of palates, upper and lower jaws, many isolated teeth (mostly the enlarged premolar) and a few doubtfully referred limb bones represent this family in the lower Snake Creek. In the upper beds it is rare, known only from a few teeth.

The genera of Mylagaulidae remain in considerable doubt and confusion. *Mylagaulus* was described by Cope from an upper p4 of a small species, *M. sesquipedalis*, which is the type, and a lower p4 of a somewhat larger species, *M. monodon*, both from the Republican River beds. Gidley's *Epigaulus hatcheri* is based on a skull and skeleton from the same formation, and is probably identical with *M. monodon*. In the Pawnee Creek beds of Colorado two skulls have been found, a smaller, hornless form described as *M. levis*, and a larger, horned skull described

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1 There are some slight differences in pattern of p4, probably due to age.
as *Ceratogaulus rhinocerus*. It may well be doubted whether *M. sesquipedalis* is really congeneric with the hornless *M. levis*; and it is open to question whether *Epigaulus* should be regarded as a distinct genus from *Ceratogaulus*, although undoubtedly a distinct species. The age variations in the tooth patterns are very wide, but the age variations in the skull are not known. It is possible that the horned and hornless

types are sex variations. It is quite true that no other rodents display such wide sexual differences, but no other rodents bear horns, and horned mammals frequently do display similar sex variations. A fourth genus has been described, *Mesogaulus*, based upon a lower jaw from the Deep River, which, if correctly described, differs from any other specimens that I have seen in a heavy external investment of cement. Pend-
ing evidence to clear up these problems, I retain the described genera provisionally.

The molars in the Mylagaulidæ are progressively deciduous, $m_1$ dropping out shortly after the large premolar breaks through the jaw, $m_2$ and $m_3$ at later stages of wear. The alveolus of $m_1$ is early reduced and disappears as the premolar pushes its way upward; the alveolus of $m_2$ is similarly eliminated and that of $m_3$ is reduced and finally disappears before the premolar is wholly worn down. Mr. Douglass has interpreted the $m_1$ as $dp_4$ and the $p_4$ as $p_3$, but this interpretation is certainly erroneous.

In the Lower Snake Creek beds two species are represented, apparently *M. levis* and *C. rhinocerus*. In the upper beds there are also two species more doubtfully identified as *M. sesquipedalis* and *E. monodon*. It may be that these represent two parallel phyla, one hornless, the other horned. More primitive species, *M. vetus* and *M. novellus*, are found in the Sheep Creek beds.

Fig. 3. *Mylagaulus levis*; superior view of skull, same as Fig. 2.
Mylagaulus levis Matthew


The type is an incomplete skull and pelvis from the Pawnee Creek beds of Colorado.

The best Snake Creek specimens referred to it are No. 17256, a skull, finely preserved, but lacking the nasal bones, part of the basi-cranial region and the right zygomatic arch, and No. 18896, a palate of a very old individual, with p^4 worn down almost to the roots, m^2 worn down to the posterior root, and the open alveolus of m^3.

The skull is rather young, with the sutures distinct. P^4 has but recently come into use and has not yet attained full size; it has not yet wholly obliterated the alveoli of m^1, of which the posterior outlines are still recognizable. M^2 is represented only by a circular alveolus on each side. M^3 is still retained on both sides, a small short tooth which has evidently but just begun to wear, but is apparently destined to fall out early. It is subconical, the point of the cone removed by wear, to a surface of pattern as in the figure, the diameters, especially the antero-posterior one, increasing toward the base of the crown. The palate between the tooth rows is of constant width and extends a little behind m^4; the outer alveolar borders converge rapidly. The skull resembles that of Haplodontia more than that of any other rodent, but is more exaggerated in its peculiar proportions. The width across the zygomata is slightly greater than the total length of the skull; and the width of the occipital crest is only slightly less than the entire length of the skull. This excessive occipital width is attained through an extreme lateral expansion of the occipital and lambdoidal crests into a wide plate. On the posterior face of this plate the excioccipitals occupy the inner third, and external to them lies a very wide mastoid plate, continuous with the tympanic bulla and with the petrosal, but separated by a suture from the overlapping excioccipital plate. On its external and superior border this mastoid plate overlaps in turn and is suturally separated from a wide flange forming the lateral extension of the occipital crest. I cannot be certain of the composition of this flange. The post-tympanic portion of the squamosal is plastered on to the front of it, separated by a suture along the margin; the rest of the flange may be a lateral expansion of the supraoccipital, as the more mediad portion certainly is; but there appears to be an obliterated suture marking the lateral limit of the supraoccipital, and the portion of the flange beyond it may be the parietal, which among the hystricomorph rodents certainly does send out a postero-lateral projection that is intercalated between the post-
Fig. 4. *Mylagaulus lxvis*; posterior, anterior and left side views of skull shown in Fig. 2.
tympanic portion of the squamosal and the lateral wing of the supraoccipital, and projects a little further laterally along the transverse occipital crest than does the supraoccipital. The condition in *Myla-gaulus* may be a specialization based upon such relations as may be seen among hystricomorph rodents.

The tympanic bulla is moderately expanded, hollow, and has a long bony meatus; its proportions throughout are much like those of *Haplo-

dontia*. The alisphenoid is plastered against the anterior face of the bulla, but does not extend far over it. The sutures of the sphenoidal group and of the squamosal are mostly obliterated. The sutures separating the parietals from each other and from the frontals are mostly obliterated but apparently the parietals extend far enough forward to share in the postorbital process, extending out on its postero-inferior surface almost to the tip of the process. The postorbital crests on the parietals are quite near together, converging backward from the postorbital processes
to the anterior end of a small raised triangle of bone that is probably the interparietal, then diverging sharply and curving outward to join the occipital crest. The supposed interparietal is separated from the postorbital crests by a sharp deep furrow, and by a smaller one from the median portion of the occipital crest.

The postorbital process is quite prominent, flat and blunt-ended. A somewhat similar projection at the anterior margin of the frontal projects laterally, making the antero-superior border of the orbit; and between these two equally prominent processes lies the orbital notch. The lacrimal? the maxilla, the premaxilla and the nasal bones abut successively against the anterior border of the frontal, almost in a transverse row, except that the premaxilla extends somewhat farther back than the others. The width of the premaxilla at this suture is about twice that of the nasal, and about equal to the conjoined maxilla-? lacrymal sutural line.

The zygomatic arch is very thick and heavy. Its width is comparable with that in some fossorial rodents; the postorbital process of the jugal is strong; the masseteric scar is limited to the inferior face of the arch and does not quite reach its inner base; it is separated from the anterior surface by a sharp angulation. The infraorbital foramen is small, circular, surrounded by a larger depressed area, characteristically like the Sciuravus-Ischyromyoid group from which Mylagaulus, Aplodontia and a few other rodents have retained this primitive condition.1

DENTITION.—A lower jaw obtained in 1921 gives the long desired evidence of the milk dentition in this group. It is clear that the Mylagaulus paniensis, Mesogaulus ballensis and other peculiar types of dentition that were considered by Matthew as possibly the milk teeth of Mylagaulus, are not so but are permanent dentitions of different species, very likely pertaining to different genera. The milk premolar is a short-crowned Allomyx-like tooth, totally unlike its permanent successor. Were it not for the presence of that successor, preformed beneath the milk

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1 Miller and Gidley, in their recent revision of the super-generic groups of rodents, have distributed this primitive group into a number of more specialized stocks which, at first glance, appear in their classification to be rather widely diverse in structure. A re-examination shows, however, that there is no such wide diversity of structure among the Eocene rodents as their classification would appear to indicate, as (1) the Eocene and Oligocene genera assigned to the specialized groups lack the specialized structures distinctive of these groups and have to be cited as exceptions in the diagnoses; (2) the broad distinction made, into fundamentally tricuspid and tetracuspid types, appears to the present writer wholly imaginary in some instances, clearly erroneous in a few, and a gratuitous and unnecessary distinction in all cases. In instance of this may be cited the wide separation made between Mylagaulidae and Almomysidae, the only cited justification being that the primary pattern of the teeth is tetragonal in the one, trigonal in the other, family. In point of fact, the surface pattern of the unworn teeth is almost identical in Allomyx and Mylagaulus. For these reasons and others not specified here, it seems inadvisable to accept the very elaborate and complex scheme of revision proposed by Miller and Gidley and the old arrangement is retained provisionally, although undoubtedly capable of much improvement.
tooth, and of the three molars behind, unmistakably those of *Mylagaulus*, although only $m_3$ is worn, the lower jaw in question would not have been referred to this family.

![Mylagaulus vetus; top view of skull No. 18903.](image)

**Fig. 6. Mylagaulus vetus; top view of skull No. 18903.**

*Mylagaulus vetus*, new species

**Type.**—No. 18905, a lower jaw with $p_4$, $m_3$ and alveolus of $m_3$.

**Paratypes.**—18903, 18904, skulls with milk dentition and permanent teeth beneath; 18906, 18907, lower jaws.

**Characters.**—The species from the Sheep Creek A beds is intermediate in size between *M. levis* and *M. paniensis* of the Snake Creek A beds, but the molars are relatively larger and more persistent, the premolars less elongate-oval.

The most interesting feature in the rodent material collected in 1922 was the proof that *Mylagaulodon* Sinclair is the milk dentition of *Myla-
Fig. 7. *Mylagaulus vetus*; part of skull No. 18904, palatal view with milk dentition, twice natural size. Dp\textsuperscript{1-4} and m\textsuperscript{1-2} are preserved. From the same quarry as No. 18903.

Fig. 8. *Mylagaulus vetus*; lower jaw; young individual with dp\textsubscript{4}-m\textsubscript{1}, the permanent premolar preformed in the jaw. No. 18902, Sheep Creek beds, *M. primus* zone, inner and outer views of jaw, three halves natural size; and crown view of teeth, three times natural size.
Mylagaulus. Two skulls of this species show the milk dentition, dp₄ in place and well worn, m₁ moderately worn, m₂ and p₃ emerging but not yet in wear, m₃ and p₄ preformed in the jaw.

The characteristic resemblance in form of the milk premolar to Meniscomys, together with the marked approach in pattern of the unworn p₄ and molars of Mylagaulus to Meniscomys and the Aplodontiidae generally, affords strong support to the view advanced by E. S. Riggs in 1899 that the Mylagaulidae are a specialized offshoot from the Meniscomys-Allomys group of the John Day. The tenor of the evidence appears, on the other hand, to be quite adverse to the wide separation between Allomyidae and Mylagaulidae indicated by Miller and Gidley. Nevertheless, as the published revision of these authors is based upon a more thorough study of the most complete series of existing and extinct rodents that has been brought together, their conclusions are highly authoritative, although unfortunately they have not yet been able to publish the evidence upon which they rest.

**Mylagaulus novellus**, new species

**Type.**—No. 18911, lower jaw, dp₄, p₃-m₂ and alveolus of m₂ r.

**Horizon and Locality.**—Middle Miocene, Lower Sheep Creek beds (Hor. A), Stonehouse draw, Exped. 1922.

**Characters.**—Size the least in the genus, premolar small in proportion, conical rather than cylindrical in middle portion. The anteroposterior diameter of the premolar about 4.8 mm. as against 8.5 in *M. paniensis*, 8.5-9 in *M. vetus* and *levis*, 12 in *M. monodon*.

The type and only specimen is of minute size and immature, the premolar preformed in the jaw, while the milk molar was in place as found but has been removed to clear up the surface of p₄. The crown of this tooth shows the usual structure of four oblique cross-crests, the second interrupted towards the inner half of its course, bending sharply forward to join the first, but restored at the inner margin as an isolated pillar, all four crests connected by sub-median commissures. This pattern is progressively changed so that in the lower half of the crown it has become a series of narrow transverse lakes.

**Sciurus cf. aberti**

A well-preserved lower jaw, A. M. N. H. No. 17578, from Quarry No. 1, Upper Snake Creek beds is not distinguishable from the jaw of the modern *S. aberti*, but is almost equally like any other of the large western black squirrels. It is a little too large, too deep-jawed and heavy-toothed for the common eastern gray squirrel.
Peridiomys\textsuperscript{1} rusticus, new genus and species

Type.—No. 18894, lower jaw with incisor, p\textsubscript{4}-m\textsubscript{2} and alveolus of m\textsubscript{8}, from M. paniensis zone, Quarry B., 1921.

Characters.—Molars very short-crowned, with simple cross-crests without commissures, buttresses or irregularities of line, or any noticeable forward pitch. Size and proportions of jaw much as in Heteromys; construction of molar teeth nearer to Perognathus.

![Fig. 9. Peridiomys rusticus; type, lower jaw with incisor and p\textsubscript{4}-m\textsubscript{2} preserved. No. 18894, Snake Creek beds, M. paniensis zone. Inner and outer views of jaw, enlarged two-and-a-half times; and crown view of teeth, enlarged to five diameters.](image)

This pocket-mouse appears to be most nearly related to Perognathus, but it can hardly be included within the modern genus. The cross-crests of the molars are very simple and smooth, as in Heteromys, but much shorter-crowned and lacking the commissures of that genus. The crests of Perognathus are somewhat higher, irregular, and pitch forward in a marked degree; the species are all of smaller size with more slender jaws.

\textsuperscript{1}Derivation: \textit{πηδακων}, dim. fr. \textit{πης}, a pocket; \textit{μου}, mouse.
Poamys rivicola, new genus and species

**Type.**—No. 18892, a lower jaw with \( m_2 \) and alveoli of \( m_1 \) and \( m_3 \); from *M. paniensis* zone, Quarry B, 1921.

**Characters.**—Teeth brachyodont, crown nearly as short as in *Peromyscus*, but the pattern of the tooth fundamentally that of the meadow-mice, with two sharp angulate external pillars and rounded internal pillars, connected by transverse crests and with a commissure between the crests toward the inner end.

![Figure 10](image-url)

Fig. 10. *Poamys rivicola*; type, lower jaw with incisor and \( m_2 \) preserved, No. 18892, Snake Creek beds, *M. paniensis* zone. Inner and outer views of jaw enlarged two-and-a-half times; and crown view of teeth, enlarged to five diameters.

I am unable to find any modern genus in which this species can be included. So far as the evidence goes, it appears to be a short-crowned type, structurally ancestral to the Microtinae. Whether it was even approximately ancestral in a genetic sense remains to be proven. It is of interest to note, however, that hypsodont Microtinae do not appear in the geological record until late in the Pliocene.

**Lepus (Hypolagus) vetus** Kellogg

This species is distinguished by a less development of the anterior column of \( p_3 \) than in the modern *campestris* and *virginianus*. It is intermediate between the *L. ennisiatus* of the John Day, *macrocephalus* and *primigenius* of the Rosebud, and the modern typical *Lepus*. Matthew in

1Derivation: *ros*, grass, by *epon*, a meadow; *mus*, mouse.
1907 distinguished these three species as a primitive group intermediate between *Paleolagus* and *Lepus* in dentition, pointing out that *L. macrocephalus* at least has the skeleton proportions of *L. campester*, not of such supposedly primitive survivals as *Sylvilagus*, *Caprolagus*, etc.

Doctor Dice in 1917 erected *L. ennisianus* into a separate genus, *Archaolagus*. He does not allude to the two Rosebud species but they would presumably fall into the same genus, which is separable by a number of generic characters of the skull from any of the existing rabbits. He also distinguishes *L. vetus* generically under the name of *Hypolagus*. This species is based upon a lower jaw from the Thousand Creek Pliocene of Nevada, and two lower jaws and an upper tooth from the Virgin Valley Miocene were referred to it by Miss Kellogg. I refer to it provisionally No. 18909, a lower jaw from the *paniensis* zone of the Snake Creek beds with $p_2$-$m_1$ preserved. No. 18910, two incomplete jaws from the *primus* zone (Hor. A) of the Sheep Creek beds, may be referred with still more doubt to *L. vetus*; neither of these has $p_2$ preserved. It is open to doubt, as Doctor Dice observes, whether the referred specimens belong to the same species as the type, and it does not appear to me that the intermediate character of $p_2$ between *L. ennisianus* and modern *Lepus* is in itself a sufficient basis for full generic distinction. A better knowledge of the later Miocene and Pliocene rabbits may prove that one or both are entitled to rank as generically distinct from the modern forms on one side, and the Upper Oligocene and Lower Miocene species of *Archaolagus* on the other, or that they are closely allied to the earlier or to the later group; but until we have adequate evidence as to their real position it seems better to rank *Hypolagus* as a provisional subgenus, and avoid giving it equal status with the well-distinguished genus *Archaolagus*.

**CARNIVORA**

Fossil remains of carnivora are not unusually abundant in the Snake Creek collections, but they represent a surprisingly large variety of genera and species, chiefly of Canidae and Mustelidae. The best specimens are from the lower beds, in which have been found skulls of *Tomarctus*, *Pliocyon*, *Amphicyon* and *Leptarctus*, which aid greatly in clearing up the affinities of these genera and the phylogeny of the two families.

The *Leptarctus* skull is not only of great interest on its own account, but it has enabled me to identify a skull and jaws found in 1901 in the Pawnee Creek beds, which, on account of the damaged teeth, I could
never identify before and had refrained from describing because of its very singular skull proportions, widely different from the normal carnivore type. It is now positively identifiable with the Snake Creek skull, and through that with Leidy's type of *L. primus*. The canid skulls have provided the evidence necessary to support a somewhat different view of the phylogeny from that generally accepted.

**Canidae**

**Tomarctus** Cope, 1873


Type: *T. brevirostris* of the Pawnee Creek beds, based upon a lower jaw fragment with ml, A. M. N. H. No. 8302.

The genotype is a young individual with the carnassial unworn and only partly emerged from the jaw. The specimen is broken off behind the carnassial and broken away obliquely in front of it, so that part of the premolar root-sockets can be distinguished, although nothing of the alveolar border. Cope interpreted these sockets as indicating a reduced number of premolars; but of this there is no real evidence. A similarly immature *Tephracyon* or *Canis* jaw, broken off in the same way, would show the same incomplete and unreliable indications of the premolar roots. The genus really rests upon the characters of the carnassial, which are very clearly shown in the unworn type. They are as follows:

1. Heel bicuspid, as in the typical dogs (*Tephracyon, Elurodon*, and the modern wolves, foxes, jackals, etc.

2. Trigonid relatively large, compressed, with small metaconid set partly back of the protoconid, as in *Tephracyon* and some modern Canidae.

*Tomarctus* is certainly excluded by the characters of the carnassial heel from the amphicyonine, cuonine, or other aberrant groups of Canidae, as well as from the genera of the Oligocene and Lower Miocene, all of which retain the primitive viverroid construction of ml. It is allied to *Elurodon*, but distinguished by the somewhat more compressed and elongate carnassial. It agrees exactly with *Tephracyon hippophagus*, is of the same geological age and part of an equivalent, closely related and largely identical fauna, not widely separated geographically from the Snake Creek quarries, which have yielded species unquestionably of the Mascall genus. There are no characters in the carnassial to distinguish it from *Canis* and related modern genera, but if *Tephracyon = Tomarctus*, there are good generic distinctions from any of the existing dogs.
I have long suspected this identity and have hesitated to adopt *Tomarctus* mainly because of the lack of topotypes, and the possibility that it might represent an allied but distinct genus. It has become increasingly evident, however, that the fauna of the Lower Snake Creek zone is very close to the Pawnee Creek fauna, and there is no longer any reasonable probability that the two genera are distinct. It is quite probable that the species are identical, but adequate proof of this is lacking, and they may yet prove to be distinct.

Whether or not generic distinctions may be found between *Tomarctus* and *Tephrocyon rurestris* of the Mascall may be left open for the present,
Fig. 12. Tomarctus brevirostris; skull, No. 18242, Snake Creek beds, M. paniensis zone. Side view, three-fifths natural size.

as it calls for a careful comparison of the typical skull of T. rurestris with the skulls herein described, which may be regarded as neotypes and approximate topotypes of Tomarctus.

Affinities of Tomarctus.—Merriam has expressed the opinion that Tephrocyon is in a broad way ancestral both to Eulurodon and to Canis. The affinities of the species here considered as typical of Tomarctus would bear out this view, if allowance be made for the difference in geologic

Fig. 13. Tomarctus brevirostris; top view of skull shown in Fig. 12.
age, which has brought about much more progressive modification in the modern Canis than in the early Pliocene Elurodon. The skull shows a very considerable difference from Canis but mostly, if not altogether, in primitive characters. The much smaller brain-case and strong sagittal and occipital crests are doubtless primitive; Elurodon in this respect comes nearer because it represents a Lower Pliocene stage of evolution. The special features that distinguish the modern genera of Canidæ, considered in the narrower scope, are not yet differentiated in the species of Tephrocyon, so far as any really conclusive evidence goes. Without doubt one might single out individual characters distinctive of the modern genera and find them foreshadowed in the Miocene species. But we do not find an association of characters in each species that foreshadows in all points the association of characters distinctive of each modern generic group; and that, in my opinion, is necessary to constitute proof; otherwise, we may be dealing with parallelism.

_Tomarctus brevirostris_ Cope, 1873

Type: a lower jaw fragment, A. M. N. H. No. 8302, from the Upper Miocene Pawnee Creek beds of northeastern Colorado.

_Tephrocyon hippophagus_ Matthew and Cook, 1909, is a synonym. Its type, A. M. N. H. No. 13836, is a lower jaw from the Snake Creek beds.

To this species are referred three fine skulls, various upper and lower jaws and a large series of teeth and other fragmentary specimens, all from the lower zone of the Snake Creek.

The skull is about the size of that of a jackal. It is comparatively broad and short-muzzled.

**DESCRIPTION OF SKULL.**—Based upon three nearly complete skulls, Nos. 18242, 18243, and 18244, collected by the Museum expedition of 1921. These three skulls, while differing slightly in almost every detail of construction, are clearly conspecific, and the lower jaw associated with one of them agrees very well with the type jaw. All are somewhat larger individuals than the type of _T. hippophagus_, but probably not specifically distinct.

The skull is of about the size of the larger "species" of coyote, but is much more like a timber-wolf in proportions. The muzzle is shorter and broader posteriorly than in the timber-wolf; the frontals somewhat wider relatively, the sagittal crest somewhat longer and about equally high, the occipital crest decidedly different in form, being expanded laterally at the top into a square-topped occiput, quite unlike the tri-
angular-topped occiput of wolf and coyote. Some South American Canidae (C. aquilus, etc.) show this character. The position of the orbits is considerably further back than in wolf or coyote or any other modern species which I have compared. The front of the orbit is above the posterior half of p4, the postorbital processes above m2. In the modern species the front of the orbit is above or behind the line between p4 and m1; the postorbital processes are quite back of the molar teeth. The position of the infraorbital foramen is less changed; in Tomarctus above a line between p3 and p4, in Canis above the posterior part of p3. The
superior branch of the premaxilla is much longer and stronger than in modern *Canis*, and is met by a corresponding anterior extension of the frontal, wholly excluding the nasals from contact with the maxillaries. I have not found this character in any modern Canidæ but it is nearly approximated in some South American species, *C. urostictus, C. aquilus*.

It is a characteristic feature in the skull of *Ælurodon*.

The zygomatic arches are as deep proportionately as in the timberwolf; the postorbital processes are nearly as prominent as in this species, much more so than in the smaller modern Canidæ.

In the basicranial region the bulla has completely the character of the modern *Canis*. It is more inflated, especially posteriorly, than in *C. occidentalis*, slightly more than in *C. latrans*, about as in the South American *C. aquilus*. The postglenoid processes are relatively farther apart, the bony meatus more extended outwardly, the postglenoid foramen more prominently defined by the lip of the meatus. The paroccipital process is sutured to the back of the bulla, nearly to its tip, as in modern *Canis*. The alisphenoid canal is somewhat longer than in *Canis* (except some South American skulls among those that I have examined). The position and relations of the remaining basicranial foramina agree closely with the wolves and coyotes.

The palate is somewhat broader and shorter than in *C. occidentalis*, much broader than in the coyote and most other species of *Canis*; and

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Fig. 15. *Tomarctus brevirostris*; No. 18243, palatal view of skull, three-fifths natural size.
the premolars are fully as massive as in the wolf. The carnassial is somewhat smaller relatively and the molars are relatively larger, especially $m^2$. The carnassial shows that slight obliquity of shear which is still seen in several of the modern South American species of Canis, but wholly lost in the species of the northern world. The relative proportions of carnassial and molars is nearly that of the coyote, but the premolars are very different from the slender, compressed, spaced premolars of C. latrans, and the triangular-based carnassial is more like C. aquilus, etc. The parastyle on the carnassial is a distinct cusp, a feature
not found in any modern species, characteristic of *Ælurodon*, in which the cusp is decidedly larger. It shows a wide variation in the different individuals referred to this species; in some it is quite rudimentary, stronger in others. Development of this cusp appears to be partly associated with reduction in relative size of the carnassial and enlargement of the molars; and it is possible that in the rather wide range of variation that has been included under *T. brevidens* there are in fact two species, one the true *hippophagus*, the other closer to the typical *T. brevidens* of the Pawnee Creek.

**Measurements in Millimeters, and Percentages of Basal Length**

No. 18242, Quarry B.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal length, premaxillae to condyles</td>
<td>156</td>
<td>100</td>
</tr>
<tr>
<td>Dentition, total length, including alveoli to m²</td>
<td>86</td>
<td>55.1</td>
</tr>
<tr>
<td>Width of skull across zygomata</td>
<td>111</td>
<td>71.2</td>
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<tr>
<td>Width of palate across m¹</td>
<td>60</td>
<td>38.5</td>
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<tr>
<td>Width of basicranium across post-glenoid foramina</td>
<td>53.5</td>
<td>34.3</td>
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<tr>
<td>Width of basicranium across mastoid process</td>
<td>63</td>
<td>40.4</td>
</tr>
<tr>
<td>Width between orbits</td>
<td>33</td>
<td>21.2</td>
</tr>
<tr>
<td>Length of muzzle (anterior border orbit to pmx, slant measurement)</td>
<td>62.5</td>
<td>40</td>
</tr>
<tr>
<td>Width of cranium, postorbital process to occipital crest</td>
<td>96</td>
<td>61.6</td>
</tr>
<tr>
<td>Postorbital constriction</td>
<td>25.5</td>
<td>16.4</td>
</tr>
<tr>
<td>Molar teeth, m¹-²</td>
<td>19.5</td>
<td>12.5</td>
</tr>
<tr>
<td>Carnassial, length</td>
<td>18.5</td>
<td>11.8</td>
</tr>
<tr>
<td>Premolars, length</td>
<td>23.5</td>
<td>15.7</td>
</tr>
<tr>
<td>Width across canine alveoli</td>
<td>35.3</td>
<td>22.6</td>
</tr>
<tr>
<td>Width across incisive alveoli</td>
<td>25</td>
<td>16</td>
</tr>
<tr>
<td>M², diameters, antero-posterior × transverse</td>
<td>7.3×12</td>
<td></td>
</tr>
<tr>
<td>M¹</td>
<td>13.1×18</td>
<td></td>
</tr>
<tr>
<td>P³</td>
<td>19 ×8.9</td>
<td></td>
</tr>
<tr>
<td>P⁴</td>
<td>11.2×5.4</td>
<td></td>
</tr>
<tr>
<td>P⁵</td>
<td>9.5×4.3</td>
<td></td>
</tr>
</tbody>
</table>
**PERCENTAGE COMPARISONS OF *Tomarctus* WITH MODERN CANIDAE**

<table>
<thead>
<tr>
<th></th>
<th><em>Tomarctus</em></th>
<th><em>Canis occident.</em></th>
<th><em>Canis microdon</em></th>
<th><em>Canis aquaticus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>brev.</em></td>
<td>(Wolf)</td>
<td>(Coyote)</td>
<td><em>Dog-fox</em></td>
</tr>
<tr>
<td>No. 18242</td>
<td></td>
<td>No.—</td>
<td>No. 22776</td>
<td>S. Amer. No. 14637</td>
</tr>
<tr>
<td>Skull, actual basal length</td>
<td>156</td>
<td>217</td>
<td>178</td>
<td>130</td>
</tr>
<tr>
<td>Skull, percentage length as above</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Dentition, length, $i^2-m^2$</td>
<td>55.1</td>
<td>53.8</td>
<td>55.9</td>
<td>55.4</td>
</tr>
<tr>
<td>Skull width, across zygomata</td>
<td>71.2</td>
<td>57.9</td>
<td>51.4</td>
<td>53.0</td>
</tr>
<tr>
<td>Palate width, across $m^1$</td>
<td>38.5</td>
<td>34.7</td>
<td>28.5</td>
<td>30.1</td>
</tr>
<tr>
<td>Basicranial width between post-glenoid foramina</td>
<td>34.3</td>
<td>27.9</td>
<td>26.4</td>
<td>30.5</td>
</tr>
<tr>
<td>Basicranial width across mastoid processes</td>
<td>40.4</td>
<td>36.3</td>
<td>32.7</td>
<td>35.5</td>
</tr>
<tr>
<td>Width between orbits</td>
<td>21.2</td>
<td>20.9</td>
<td>16.5</td>
<td>19.7</td>
</tr>
<tr>
<td>Muzzle, preorbital length$^1$</td>
<td>40</td>
<td>47.5</td>
<td>47</td>
<td>43.3</td>
</tr>
<tr>
<td>Cranium, postorbital length$^2$</td>
<td>61.6</td>
<td>52.1</td>
<td>50</td>
<td>47.5</td>
</tr>
<tr>
<td>Postorbital constriction, width across</td>
<td>16.4</td>
<td>17.5</td>
<td>20</td>
<td>25.4</td>
</tr>
<tr>
<td>Molars, length $m^1$</td>
<td>12.5</td>
<td>9.7</td>
<td>9.7</td>
<td>13.0</td>
</tr>
<tr>
<td>Carnassial, length</td>
<td>11.8</td>
<td>11.1</td>
<td>10.2</td>
<td>9.7</td>
</tr>
<tr>
<td>Premolars, length $p^1$</td>
<td>15.7</td>
<td>15.9</td>
<td>19.6</td>
<td>16.8</td>
</tr>
<tr>
<td>Muzzle, width across canine alveoli</td>
<td>22.6</td>
<td>21.5</td>
<td>16.9</td>
<td>16.5</td>
</tr>
<tr>
<td>Incisors, width across</td>
<td>16</td>
<td>14.5</td>
<td>13.1</td>
<td>11.5</td>
</tr>
</tbody>
</table>

**Tomarctus confertus** Matthew

I refer to this species a finely preserved skull No. 18253, from the lower zone of the Snake Creek beds. It may be compared in detail with the skull of *T. hippophagus* and *Tephracyon rurestris*. The construction is, as one might expect, more delicate throughout; the cranium has no sagittal crest and the occipital crest is rudimentary; the arches are not preserved but were evidently quite slender. The most distinctive feature is the notable shortness of both muzzle and cranium. To some extent this was indicated by the short and thick lower jaw, but it is more marked in the skull.

The short, deep muzzle is in marked contrast with the longer slender, delicate muzzle that is indicated by the correspondingly long and slender lower jaw of *Leptocyon*. The latter exaggerates one of the distinctive characters of the foxes and coyotes; but there is nothing else to connect it with these modern species.

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$^1$Slant length, $i$ to anterior border of orbit.

$^2$Postorbital process to occipital crest.
Fig. 17. *Tomarctus confertus*; skull, natural size, top, side and palatal views. No. 18253, Snake Creek beds, *M. paniensis* zone.
Tomarctus temerarius Leidy

The status of this species is not clear. Leidy based it in 1858 upon two specimens, a fragment of an upper jaw with m1 and part of p4 and a fragment of lower jaw with m3, mentioning them in that order. In 1869 he figured the second specimen but not the first. The second specimen has been referred to as the type by several subsequent authors, but not expressly so designated to the exclusion of the first. In the U. S. National Museum catalogue of types it is listed as though both fragments were supposed to belong to the same individual. This is hardly possible; they differ too much in size. The upper jaw fragment belongs to an animal only slightly smaller than the small variant of T. brevirostris. The lower jaw fragment belongs to an animal one-fifth smaller, and only a little larger than T. confertus. Peterson and Merriam have referred fragments of lower jaws to T. temerarius, stating that they agreed closely in size with the type lower jaw figured by Leidy. But in fact they do not; they are about one-fifth larger; they conform rather closely with the unfigured upper jaw fragment but it is decidedly doubtful whether they are in either case co-specific with the lower jaw fragment figured by Leidy, and with various specimens which I have referred to T. temerarius at different times, relying upon their accord with that figured lower jaw.

If Osborn's usage be adopted, of considering as type (lectotype) the first-mentioned specimen of the original description, then the unfigured upper jaw fragment will be the type of T. temerarius, and the specimens referred by Peterson and Merriam agree with it. I cannot find any sanction save Osborn's personal preference for this usage and many authors would consider that the figuring of the lower jaw fragment by Leidy and its implicit selection as type by Matthew, Peterson and Merriam constitute a selection of type which must stand, in accordance with the rules.

Tomarctus optatus, new species

Type.—No. 18916, a pair of lower jaws with complete dentition.
Horizon and Locality.—Sheep Creek A, Stonehouse draw.
Characters.—Intermediate in size between T. brevirostris (Tephrocyon hippoplagus) and T. temerarius.

This species is represented by a considerable number of topotypes which agree closely in size. It does not differ much in construction or proportions from the type of T. temerarius on one hand and of T. brevirostris on the other, and agrees closely in size with the cotype upper jaw.
Fig. 18. *Tomarctus optatus*; lower jaw, natural size, external and superior views. Type specimen, No. 18916. Sheep Creek beds, *M. primus* zone.

Fig. 19. *Tomarctus optatus*; upper jaw fragment, natural size. No. 14176, Sheep Creek beds, collection of 1908.
of *T. temerarius* and with specimens referred to that species by Peter-
son and by Merriam. They differ from the species here identified as *
temerarius* in larger size, longer jaw and narrower teeth, and from *brevi-
rostris* in the smaller size and somewhat slenderer proportions. They 
are closely allied, however, and it is very probable that *T. optatus* is 
a primitive mutant of *T. brevirostris*. Until the evidence is adequate 
to prove this relationship it appears better to hold the names distinct. A 
skull found in 1923 but not yet carefully studied probably represents this 
species.

*Ælurodon haydenianus validus* Matthew and Cook

To this subspecies is referred an upper jaw with p^4^-m^1, left side, 
from the Upper Snake Creek beds, Quarry No. 1.

Characters.—Inner cusp of p^4 absent, but inner root strong. Crown of 
p^4 elongate, of uniform width in front and behind. The surface is so worn that the 
three cusps are indicated only by the color of the dentine—yellowish-white where 
more deeply worn under the cusps, bluish-gray elsewhere. M^1 almost as large as p^4, 
its transverse width somewhat less than the anteroposterior diameter of p^4 but its 
anteroposterior diameter greater than the transverse width of p^4. Inner half of m^1 
nearly as wide as outer half, giving this tooth also a subquadrate outline. The tooth 
is nearly symmetrical on a transverse axis, the inner half lacking the backward twist 
characteristic of most Canidae. Hypocone somewhat larger than protocone, heavy 
but somewhat obsolete anterointernal cingulum; protocone-metacynule crest heavy, 
anterior wing of protocone crescent obscure; outer half of tooth much worn.

P^3 appears to be a rather small tooth and m^2 is also somewhat reduced, so far as 
one can judge from the imperfect alveoli.

This upper jaw is probably the same as the lower jaw from Snake 
Creek described in 1909 as a mutation of *Æ. haydenianus*. It is broadly 
similar to various upper denticions that have been referred to that 
genus. It is, however, the most specialized of the genus.

So far as one can judge from Merriam's figure and description, 
*Ælurodon aphanobus*\(^1\) of the Ricardo Pliocene is closely related to this 
species and may also be a subspecies of *Æ. haydenianus*, which, curiously, 
is the only one of the described species with which the author does not 
compare it.

*Hymnognathus direpator*, new species

Type.—No. 18919, left ramus of mandible, complete except for incisor and 
anterior premolar teeth, from Upper Snake Creek beds, *Pliohippus* draw.

Characters.—Size of *Ælurodon szevus*, premolars reduced in number and size, 
heel of m\(_1\) and whole of m\(_2\) shortened, m\(_3\) reduced compared with that genus. Denti-

Fig. 20. *Humagomys director*: lower jaw, natural size, external view and crown view of teeth. Type specimen, No. 18919, Upper Snake Creek beds.
tion $3.1.3$. Incisors probably rather large, to judge from size of alveoli; the second and third have much longer roots than the first. Canine rather small, about as in $\mathcal{E}$. sævus. First premolar absent, no postcanine diastema; $p_3$ with a single round, rather shallow root. $p_4$ also single-rooted, with a distinct external groove; both teeth appear to have been obliquely set in the jaw. $p_4$ very like that of $\mathcal{H}$yanognathus $pachyodon$ and $\mathcal{A}$lurodon $sævus$, short and stout, the principal cusp stout and high, pitched backward and curved inward, crowded back against the posterior accessory cusp and heel so that its point lies directly above them at a certain stage of wear.

$M_1$ very like that of $\mathcal{A}$lurodon, the heel somewhat shorter but with the characteristic bicuspid construction of the typical dogs. $M_2$ decidedly shorter than in $\mathcal{A}$lurodon and subquadrate, the paraconid well developed but apparently without entoconid. $M_3$ small and circular in outline, cusps worn to a flat surface. Jaw much as in $\mathcal{A}$lurodon but shorter and more massive, with deeply excavated masseeeric fossa, heavy angle, short symphysis. The symphysis is by no means so heavy as in $H$. pachyodon, nor is the jaw so massively proportioned, especially toward the symphysial region. It is about two-thirds as large.

Affinities.—The species appears to be intermediate between $\mathcal{A}$lurodon $sævus$ and $\mathcal{H}$yanognathus $pachyodon$ but agrees more nearly with $\mathcal{H}$yanognathus in the extent and character of premolar reduction and in the form and proportions and cusp construction of $m_2-3$, the carnassial construction being about the same in the two genera. It differs from $Aræocyön$ Thorpe, which has some points of resemblance in the general proportions and in the premolar reduction, in the bicuspid heel of $m_1$, as also in retention of $p_2$ and $p_3$ and somewhat different heel and accessory cusp upon $p_4$. Doctor Thorpe makes as characteristic of his genus a long $m_2$ and absence of $m_3$. Neither tooth is preserved in the type and to judge from his figure the ascending ramus back of the molars is split off too far down to allow of any certainty as to whether $m_3$ was present or not, while the direction of the split also would tend to make the posterior alveolus of $m_3$ appear much longer than the real length of the alveolus at its natural border. I do not think Doctor Thorpe’s specimen warrants any conclusion on the length of $m_3$ or the absence of $m_3$; it might in these respects be like $\mathcal{H}$yanognathus. The difference in the premolars, while considerable, is of a kind notoriously variable with age or individuals in the modern wolves. On the other hand, the median crested heel of $m_1$, if positively and unmistakably present, would exclude the genus from the Canineæ. It would fall into the Simocyonine, whether or not it be at all nearly related to Simocyon, if this be so, it clearly can have no bearing on the $\mathcal{H}$yanognathus phylum. $H$. direptor appears, on the whole, to be a fairly close intermediate, indicating the derivation of $H$. pachyodus from $\mathcal{E}$. sævus.

Mr. Harold J. Cook has referred to $Porthocyon$, under the name of $P$. pugnator, a species from the Republican River horizon in Yuma
County, Col., based upon a palate and lower jaw which are also somewhat intermediate between *Aelurodon* and *Hyænognathus* but appear to me to be more properly referable to *Aelurodon*. The characters of m₃ are not known but the premolars do not appear to be reduced as they are in *H. pachyodon* and *direptor*, and the upper teeth agree more nearly with *Aë. sevus* than with the *Porthocyon* skull, whether or not this genus is the same as *Hyænognathus*.

The geological occurrence is as follows:

- *Hyænognathus pachyodon* Pleistocene or late Pliocene, Kern Co., Cal.
- *Aelurodon sevus secundus*. Lower Pliocene, Snake Creek.

*Euoplocyon prædator*, new genus and species

**Type.**—No. 18261, a lower jaw from the Miocene, Snake Creek quarries of Nebraska.

**Generic Diagnosis.**—Dentition $\begin{array}{llll} 3 & 1 & 4 & 5 \end{array}$. Anterior and posterior heel-cusps and posterior accessory cusp on all four premolars. Carnassial with trenchant heel and no metaconid; $m_2$ with crested trigonid and crested heel.

The genus is distinguished from *Cyon* and *Icticyon* by retention of $m_3$ as a small, oval, sub-crested tooth, and by the more complex construction of the anterior premolars. From *Lycaon*, by complete loss of metaconid, the more complex structure of $p_1$, more complete cresting of the tubercular teeth. From *Enhydrocyon*, by retaining $m_3$ and $p_1$, and more compressed premolars with accessory cusps. From *Temnocyon* by loss of metaconid, different character of premolars, etc. It belongs unquestionably to the same group of the Canidae as the above genera, and is not closely related either to the typical Canidae, which include *Aelurodon*, or to the *Amphicyon* group.

This, probably, is the genus which I have heretofore called "*Cyon*," as in the very fragmentary or immature specimens previously available there was nothing definite to distinguish it from the modern genus.¹ It appears to be, in a broad sense, intermediate between *Temnocyon* and *Cyon*; *Enhydrocyon* would stand as a precocious, *Lycaon* as a persistently

primitive relative, so far as their dentition is concerned. I am unable to
determine its exact relations to certain Pleistocene South American
species, "Canis" moreni, "Palaeocyon," etc., of which there is no good
figure and no competent description of the lower teeth. They are
probably related.

**Upper Dentition.**—This is not known in the type species but a
specimen recently described by Dr. Malcolm Thorpe under the name of
*Ælurodon taxoides magnus* belongs to *Euoploycyon*, although to a much
larger species. The type consists of associated upper and lower jaws,
part of a tibia, etc. The crested heels of the lower molars immediately
exclude it from *Ælurodon* and associate it with the *Cyon* group of Cani-
dæ; the prominence of the accessory cusps, preservation of m₃, absence
of metaconid on m₁, accord with *Euoploycyon*.

The upper teeth, as shown in Dr. Thorpe's type, are, as would be
expected, near to *Cyon* in character and proportions, but distinguished
by the strong development of the accessory cusps on the premolars and a
small parastyle on the carnassial. The protocone of the carnassial is
absent; the protocone of m₁ is relatively small, as usual in the cyanine
group, but appears to be bifid.

*Canis texanus* Troxell is based upon a lower jaw, and upon upper
teeth and skeleton fragments apparently of doubtful association, from
the Rock Creek beds, Lower Pleistocene, of Texas. If correctly described
and figured it certainly does not belong to the typical group of Canidae,
and may be referable to the cyanine phylum, but probably rather to
*Palaeocyon* or *Dinocynops* than to *Euoploycyon*.

**Amphicyon** Lartet

Type: *Amphicyon major* (Blainville, 1841) from Middle Miocene
of Sansan.

This genus has been used in a very loose way by European and
American authors to include canid species which have but little in com-
mon with the type save the dental formula of m₃. How much weight
should be attributed to the retention of m₃ may be questioned. It is,
at all events, certain that the American Oligocene species referred here
by Cope belong in other genera; and it appears highly probable that the
species from the European Oligocene would also be distinguished if
more fully known.

transversus, John Day, = *Paradaphnus*.
4Amphicyon ambiguus, Phosphorites; rugosidens, Bohners; *Amphicyon lemanensis*, Saint-Gerand-
le-Puy.
Wortman in 1901 described a well-preserved upper jaw from the "Loup Fork" under the name of *A. americanus*.¹ It is distinguished from *A. major* by smaller size and more triangular and transversely extended molars (compare *A. lemanensis*, etc. and *Paradaphanis*), but it shows the double-edged canine, marked reduction of the premolars and spacing of the anterior ones characteristic of *Amphicyon*.

Matthew in 1902 described a species from the Pawnee Creek beds of Colorado more closely allied to *A. major*, based upon lower jaw frag-

Fig. 21. *Amphicyon sinapius*; lower jaw, superior and external views, two-fifths natural size. No. 18258, Snake Creek beds, *M. paniensis* zone.

ments with which a partial skeleton was provisionally associated. A number of described American species were also referred to *Amphicyon* and a complete but poorly preserved skull and jaws, with which was part of a skeleton, were described as *Dinocyon gidleyi*. The latter had but two upper molars, but was referred with grave hesitation to *Dinocyon*, which has typically much more quadrate molars. A species nearly allied to *D. gidleyi* was described by Earl Douglass² from the Lower Pliocene of

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²Douglass, Earl, 1904, Ann. Carn. Mus., II, No. 2, pp. 192-195. Although dated 1903, this paper does not appear to have been actually published until 1904.
Montana under the name of *D. ossifragus* from an upper jaw and part of the basicranial region. In 1908 Matthew and Cook described *A. amnicola* of the Snake Creek beds, from a lower jaw. In 1910 Peterson, in reviewing the affinities of *Daphaenodon*, regarded the American *Amphicyons*, *Dinocyon* and *Borophagus*, as a group distinct from the true *Amphicyons* of Europe, but did not separate them generically. Matthew in 1918 took substantially the same position and distinguished the "American Amphicyons" under the name of *Pliocyon*, with a new species, *P. medius*, as type, based upon a fairly good skull from the Snake Creek.

We now have a fine skull of *A. amnicola* from the same lower horizon of the Snake Creek as *P. medius*, and on comparison with the type of *Amphicyon major* it is at once evident that *A. amnicola* is closely allied in the tooth characters, and that it differs considerably from *P. medius* in the elongation of the muzzle, compression and spacing of the premolars, etc., as well as in absence of m₈. Wortman’s *A. americana* is a smaller species, distinguished from *A. amnicola* and *A. major* by the more triangular and transversely expanded upper molars. *A. americana* in these particulars approaches *A. lemanensis*, while *A. amnicola* must be regarded as a close ally of *A. major*, and *Pliocyon* can be held to include only those species which have but two upper molars, in most of which the premolars appear to be much more crowded than in *Amphicyon*. It is evident, however, on comparison of the details of skull structure and dentition that *Pliocyon* and *Amphicyon* are very closely allied in spite of superficial differences. *Pliocyon* is more primitive in dentition than *Dinocyon* and may be ancestral to it. The view that the American Amphicyonines were an independent parallel stock from the European Amphicyonines does not accord with the osteological facts, however plausible it may seem from a geographical viewpoint, for *A. amnicola* and *sinapius* are much more closely allied to *A. major* than they are to *A. americana*, which has some points of especial resemblance to the *lemanensis-ambiguus* group of Europe.

*Pliocyon* and *Amphicyon* are distinct genera, both represented in the American Miocene, and structurally derivable from *Daphaenodon* by divergent specialization.

Filhol has described the skull of *A. lemanensis* and discussed its affinities to *Canis*; but the more recent discoveries of the complete skulls and skeletons of *Daphaenus* and *Daphaenodon* on the one hand, of *Cynodesmus* and *Tomarctus* on the other, modify in some degree the conclusions to be drawn.

It is very evident that *Daphaenus, Daphaenodon, Amphicyon lemanensis, A. major*, form a series which, in spite of Filhol’s statements, are not
Fig. 22. *Amphicyon sinapius*; skull, palatal view, two-fifths natural size. No. 18257, Snake Creek beds, *M. paniensis* zone.
closely related to *Canis* or in any way ancestral to it. A second series is formed apparently by *Daphænodon-Pliocyön-Dinocyön*, and *Hyaænarctos* may be a further specialization of this phylum. The point to be emphasized is that this entire group has a number of distinctive features, fairly warranting subfamily separation, viz.:

![Image](A.M.18257)

(1.) Heel of m1 crested, not bicuspid; heel of m2 crested, not basined; premolars and carnassial reduced, molars enlarged, in varying degree.

(2.) Tympanic bulla small, never extending back of mastoid process1; usually a long bony meatus.

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1Filhol states that the bulla in *A. lemanensis* extends backward to the posterior lacerate foramen; but this is based upon a specimen in the Lyons City Museum, which is perhaps of doubtful reference, as it was identified as *Cephalogale* by Lortet.
(3.) Tail very long and heavy; humerus broad distally with entepicondylar foramen, lower limb bones relatively short, astragalus short and wide, trochlea broad.

These characters in the successive geologic stages show a progressive diversity from the true dogs of the Cynodictis-Cynodesmus-Tephrocyon-Canis group, with which Æurodon is closely allied.

A third group, primarily allied perhaps to the amphicyonines, but paralleling the Caninae more closely in its specialization, is the icticyonine phylum, with Daphenus, Temnocyon, Enhydrocyon, Philotrox, Euoplocyon, Icticyon, Cyon and Lycaon.

Filhol’s view that Amphicyon was ancestral to Canis, partly accepted by Boule, who regards it as ancestral to the wolves but derives the foxes from Cynodictis, is untenable on present data; both wolves and foxes are much more readily derived from species of Tephrocyon. On the other hand, the relationship between the amphicyonines and the Ursidae is suggested by the numerous intermediate types from the middle and later Tertiary. I can find no serious grounds for deriving the bears from Cephalogeale, which is closely related to Cynodesmus and is apparently a true Canine in the basicranial and other characters. Filhol’s figure of Cephalogeale geoffroyi is indeed a composite based upon several individuals, and in this instance as in his Amphicyon lemanensis, there may be doubt as to their association being correct. If, however, it be accepted, the large bulla, the fairly normal molar teeth and reduced premolar dentition compare with Cynodesmus thomsoni, to which it must be closely related; and this last species, known from a nearly complete skeleton, is certainly a true dog, though aberrant in respect to the premolar reduction.

What relationship there may be between Ursavus brevirhinus and Cephalogeale brevirostris is another question, upon which it is not necessary to enter here. The object of the foregoing discussion is to show that the Ursidae are in fact connected with the amphicyonine dogs by such a series of intermediate types as to demonstrate some degree of relationship; but until the skulls and skeletons of these intermediates are fully known and adequately described, their exact relations will remain uncertain.

**Amphicyon sinapius** Matthew

*Amphicyon sinapius* Matthew, 1902, Bull. Amer. Mus. Nat. Hist., XVI, p. 288, Fig. 2. Type from Pawnee Creek, Colorado.

*Amphicyon amnicola* Matthew and Cook, 1909, idem, XXVI, pp. 368–370, Fig. 1. Type from Snake Creek, Nebraska.
Fig. 24. *Amphicyon ingens*; part of lower jaw, natural size. No. 18272, Snake Creek beds, *M. paniensis* zone.
The following specimens referred to this species give a fair idea of the characters of skull and skeleton:

No. 18257, complete skull. Snake Creek, 1921.
No. 18258, complete lower jaw. Snake Creek, 1921.
Nos. 18259, 18260, teeth. Snake Creek, 1921.
No. 13846, lower jaw (teeth worn). Snake Creek, 1908. Type A. amnicola.
No. 9358, jaw fragment m1-2. Pawnee Creek, 1901. Type A. sinapius.
No. 9357, m1. Pawnee Creek, 1901.
No. 9356, vertebrae, ribs, humerus and ulna. Pawnee Creek, 1901.
No. 9355, parts of limb bones, astragalus, etc. Pawnee Creek, 1901.

There are in addition various separate bones, etc., that may be referable to this species. Its characters are as follows:

Size of A. major from Sansan (Middle Miocene of France). Upper teeth very like those of A. major throughout, but p4 has a more distinct protocone (inner cusp), m3 is more transversely extended. Much larger than A. americanus and the molars more quadrate, less transversely extended. I can find nothing in the teeth to separate A. amnicola from A. sinapius of the Middle Miocene of Colorado.

**Amphicyon ingens**, new species

**Type.**—No. 18272, anterior part lower jaw with damaged teeth or alveoli as far back as m1.

**Paratype.**—No. 18273, lower carnassial. Both from lower zone of Snake Creek beds.

**Characters.**—This is about the size of the large Pliocene species of *Agriotherium* (*Hyænarctos*); but the carnassial has the crested heel of the true Amphicyonines.

It is probable that to this species belong certain isolated carnivora skeleton bones from the Snake Creek; also possibly No. 9356, the para-type skeleton of *P. sinapius* from the Pawnee Creek beds.

**Amphicyon lendens**, new species

**Type.**—No. 18913, lower jaws with m1-2 emerged, c1 and m3 preformed, and upper jaw with p4-m1 emerged, m2 preformed, and m3 partly calcified.

**Horizon and Locality.**—Middle Miocene, Sheep Creek A, Stonehouse draw, Snake Creek fossil quarries.

**Characters.**—About ten per cent larger lineally than A. sinapius, the characters of the teeth approaching *Ischyrocyon* in various details; the carnassial blades sharper and higher, hypoconid crests higher, entoconid ledges reduced on m1 and absent on m2. Alveoli of four premolars are present, less reduced than in A. sinapius, the anterior ones crowded in the jaw instead of being spaced out.

An upper molar, No. 18914, is of proportionate size to the type and differs from m3 of the following species in the heavier metacone, more sym-
Fig. 25. *Amphicyon idoneus*; upper jaw, type specimen, one-half natural size. No. 18912, Sheep Creek beds, *M. primus* zone.

Fig. 26. *Amphicyon frendens*; lower jaw of type specimen, No. 18913, external view and crown view of teeth, one-half natural size.
metrical inner cingulum, the external half of the tooth relatively wider, with more massive cusps.

**Amphicyon idoneus**, new species

*Type.*—No. 18912, upper jaw with p₄–m₂.

*Horizon and Locality.*—Middle Miocene, Sheep Creek A.

*Characters.*—Size of *Pliocyon medius* and much resembling that species save for the retention of m₁, indicated by a deep and fairly large alveolus. The metacone of m₂ is distinctly smaller and the internal cingulum broader and more extended anterointernally. The inner half of m₂ is nearly as wide as the outer half.

A fine skull of this species, found in 1923, is very like that of *A. sinapius* in proportions and tooth characters but of smaller size.

**Pliocyon** Matthew

Not *Pliocyon* Thorpe 1921.¹

*Type:* *P. medius*, Lower Snake Creek beds.

The genotype is based upon a skull from the Sinclair Draw pocket. The species referred to the genus are the following:

- *Canis ursinus* Cope, 1875, Santa Fé, New Mexico. Lower jaw, no teeth.
- *Dinocyon ossifragus* Douglass, 1903. Madison, Montana. Parts of skull, etc.

To this genus or to *Amphicyon* is referred the following.

No. 2700, posterior half of skull and part of ulna, from the "Loup Fork" near Hay Springs fossil quarry, probably Valentine beds. This specimen was obtained in 1893 and identified by Dr. Wortman as a machærodont. It has always been under suspicion, as the basicranial structure was very different from any known machærodont or felid, but as the Felidae of the American Upper Miocene and Pliocene were known only from jaws and the basicranial structure of the amphicyonine dogs was wholly unknown and they differed very widely in other points of skeleton structure from the typical dogs, it was not possible to identify this cranium with certainty. It differed widely from *Ursus* or *Arctotherium* but it was not provable and indeed is not now wholly certain that it could not be *Hyænarctos.*

Comparison with the skulls of *Pliocyon medius* and *Amphicyon amnicola* shows it to agree closely in all important structural characters. It is a large species, about the size of *P. maxandrinus*, to which it is provisionally referred.

The otic bulla, although only partly preserved in this specimen, was evidently similar to that of *P. medius* and *A. amnicola*, of small size, with rather long ossified meatus external to it. The bulla is almost wholly anterior to the mastoid process, the posterior chamber being absent. The mastoid process is much more massive, broader anteroposteriorly and more prominent than in *P. medius*; the paroccipital process is broken off. The posterior lacerate foramen lies at the bottom of a large deep pit, as in *P. medius*, but the condylar foramen opens within the posterointernal margin of that pit, while in *P. medius* it is slightly outside of it. The alisphenoid canal is long and straight and posteriorly opens into the usual oval pit at the back of which the foramen ovale opens. The scars for the recti capitis muscles are prominent rugosities with a sharply defined raised margin, between which and the bulla is a shallow channel apparently for the anterior carotid artery, which does not appear to pierce the bulla but to enter the anterior lacerate foramen in front of it. The occiput is high and narrow and the sagittal crest remarkably high.

As a whole the cranium of *Amphicyon* differs widely from any felid or machærodont type; fundamentally in the construction of the bulla and the retention of the alisphenoid canal. The high narrow occiput and large sagittal crest are primitive characters partly retained by the Canidae; in the Mustelidae and Ursidae the occiput is relatively broad and low. The reduced bulla with long ossified meatus is a specialization usually associated with large size and found in Ursidae and some Mustelidae, but in the large Pliocene and later genera of these families the bulla is characteristically flattened as well as it is reduced. The development of the mastoid process and the internal position of the condylar foramen are size specializations apparently only of specific value, as they are less developed in *P. medius*. In all the basicranial features there is a marked resemblance between *Daphoenodon*, *Amphicyon* and *Pliocyon*, carrying further the lines of specialization that separate those genera from *Daphiænus*. The bulla is of identical type and relations but the meatus much longer; the mastoid process much more robust, the recti capitis scars more prominent, the paroccipital process more massive, the merger of f. l. p. and t. f. carried further.
Skeleton Characters of Amphicyonines

I have been unable to compare the cranium with *Hyænarctes* (*Agriotherium*) and *Indarctos*. I suspect that they would show closer affinities than do *Arctotherium* or *Ursus*; and the degree of affinity would have a most important bearing upon their relationship to the Amphicyonines and the entire problem of the ancestry of the Ursidae. I have heretofore indorsed the opinion very generally held by palæontologists that this family may be more intimately related to the amphicyonine dogs and less so to the Mustelidae than the comparative anatomy and osteology of the modern and Pleistocene Ursids would seem to indicate. (I do not accept Schlosser’s view that the Ursidae are descended from *Cephalogale* or *Cynodon*. The basi-cranial characters of these two genera exclude them, I think from ursid ancestry.) The cranial characters and foot construction of *Hyænarctos* would afford the critical evidence on which the question of its exact relationship to the Amphicyonines might turn; but unfortunately, although a skull of *Hyænarctos* has long been known, it is very imperfect in the cranial region, so that its basi-cranial characters apparently cannot be determined; and the foot structure of the genus is unknown. Nor have we complete data on the foot structure of any of the larger Amphicyonines. The astragalus, calcaneum, and a metapodial of *A. giganteus* and the skeletal material referred to *Pliocyon* enable us to reconstruct it in part. The fore and hind foot material described by Schlosser as *Amphicyon* belong to a much smaller animal, very different in foot proportions. More nearly related, although still much smaller and more primitive, is *Daphænodon* of Peterson. These genera may represent intermediate stages through which the large and specialized *Amphicyon* and *Pliocyon* arose from the Oligocene *Daphænus*.

In 1902 I referred to *Amphicyon sinapius* a part of the skeleton No. 9356 from the Pawnee Creek beds, which includes a humerus, ulna, nineteen dorsal and lumbar vertebrae and ribs, and a few caudals. To the same species were referred No. 9355 a number of bones found together in a wash mixed with other genera (*Dromomeryx*, etc.). These include the astragalus, parts of radius and tibia, but no skull parts. The lower jaw fragment and astragalus No. 8248, described nearly fifty years ago by Cope as a gigantic Canid are likewise to be referred here. While these remains are probably *Amphicyon*, they may very well belong to a larger species than *A. sinapius*.

In the Snake Creek beds there are isolated bones which agree very nearly with the foregoing in size and characters and belong probably to
the genus. Others, similar in type but of smaller size, are probably *P. medius*. These are, chiefly or all, from the lower horizon.

In the upper horizon at Snake Creek an equally gigantic carnivore is represented by a calcaneum and other fragments which indicate a long compressed pes. This is the horizon from which *Hyænarctos* is to be expected and an upper tooth found by Mr. Harold Cook undoubtedly represents that genus, although its horizon is not recorded. Possibly this elongate pes belongs to *Hyænarctos*, but it is not at all ursoid and I think it more likely that it is a gigantic true cat. There is also from the Snake Creek a huge scapholunar bone, too large to agree well with *Pliocyon*, possibly also referable to *Felis*. In the Republican River beds I have seen a humerus and other remains of a huge carnivore evidently distinct from *Pliocyon* and possibly this same Ursid or ? Felid.

The bones referred to *Amphicyon* and *Pliocyon* from Pawnee Creek and lower Snake Creek include therefore, vertebrae and ribs, the humerus, radius, ulna, tibia, astragalus and calcaneum, and more doubtfully, some metapodials. The humerus is of moderate length, with deltoid crest vestigial, broad inferior end with strong entepicondylar bridge, the radial facet convex, not flattened as in (?) Ursidae. The ulna and radius are massive and rather short, the olecranon rather short, not turned backward, the radius with deeply concave distal facet and massive styloid process. The tibia also is short, its trochlea of moderate depth; the astragalus is wide but not so wide and short as in Ursidae, comparable in proportions with *Smilodon* but with no trace of the astragalar foramen, neck short and navicular facet broadly convex. The calcaneum is broad, with the heel massive but not very long, the cuboid facet deeply concave. The tarsus is by no means so broad and short as in *Arctotherium*, but it is somewhat broader than in *Smilodon*, although the astragalus has a deeper trochlea and no foramen, and it is quite in contrast with the narrow, compact, elongate pes of *Canis* or *Ælurodon*.

The tail is very long and massive, as in the Oligocene Canidae and in *Daphænodon*.

The type of *Pliocyn* (*Dinocyon*) *gidleyi* from the Clarendon of Texas consists of the skull, jaws, articulated backbone and femur, described and figured in 1902. This is in very hard matrix and the basi-craniar characters could not be determined. The vertebral proportions conform with those of *A. sinapitus*.

**Affinities of the Amphicyonidae.**—The series of resemblances throughout the skeleton between the Oligocene *Daphænus*, the Lower Miocene *Daphænodon*, and the Upper Miocene *Amphicyon* and *Pliocyn*,
leave no room for serious question that they form an approximate phyletic series, with which should also be placed Dinocyon, possibly other genera.

Structurally these genera are distinguished by

1.—Progressive enlargement of molars and reduction of premolars and carnassial; metaconid of lower carnassial well developed and heel basined, but with crests rather than cusps; tendency to retain m3.

2.—Skull rather elongate, with high sagittal crest and narrow occiput.

3.—Tympanic bulla small and limited to the anterior part of the otic region; a wide space between it and the paroccipital, with a prominent lateral protrusion of the mastoid.

4.—Cervical vertebrae relatively short, dorsals small with high spines, lumbars large and moderately long. Ribs short.

5.—Limb bones massive, proportioned much as in Machærodonitæ, feet pentadactyl, rather short, probably digitigrade and symmetrical in all stages, certainly in the older ones. Claws slightly retractile in older stages, unknown in later.

From the more typical Canidæ this amphicyonine group is set off primarily by the peculiar tympanic bulla. From the known Ursidæ it is sharply distinguished by the median symmetry of the feet, much narrower and more sharply grooved astragalus, long lumbar region, high spined dorsals, high narrow cranium and different type of bulla, as well as by the well-known differences in the teeth, which are partly bridged over by Hyænarctos, etc.

From the Machærodonts and Felidæ the Amphicyonines are distinguished first by the very different teeth, then the widely different bulla and other skull characters. The skeleton is not so obviously different, but the progressive specialization of the feet seen in both felid and machærodont phyla, centering about the sharp, retractile claws, is not seen in the Amphicyonines.

RELATIONS TO OTHER GENERA OF CANIDÆ.—In contrast with this highly aberrant group of the later Tertiary may be placed the Pliocene genus Ælurodon, which, in spite of its aberrant upper carnassial, is a typical dog, closely related to Canis in all details of skull and skeleton construction. The late Miocene genus Tomarctus is intermediate and ancestral to both genera, so far as the skull characters show.

The Lower Miocene Cynodesmus, also known from complete skulls and skeletons, is decidedly more primitive as to dentition than Tomarctus, the carnassial shear oblique and not yet showing the anteroposterior direction characteristic of typical Canidæ. The feet also are much more
primitive, moderately long, pentadactyl, metapodials little appressed, claws acute; and the brain is much smaller and simpler. The basicranial structure shows a large inflated bulla, reaching back to the paroccipital process, and in general may stand as ancestral to the typical Canidae.

Among the Oligocene Canidae, *Pseudocynodictis* of the White River and John Day is the most typical and best known; the skull and skeleton have been described by Cope, Scott and the writer, and it has been regarded as not far from the typical phylum. The tympanic bulla in this genus also is large and reaches back to the paroccipital, but it is not so solidly united as in later Canidae and is not infrequently lost in the fossil skulls. It appears on the whole to be decidedly nearer to the ancestry of *Cynodesmus* and *Tomarctus* than is *Daphænus*, with its small bulla and amphicyonoid teeth.

*Temnocyon* and *Enhydrocyon* of the John Day may be considered as representative of a line leading into *Cyon* and its relatives; and for this there is much to be said, although neither appears to be in the direct line of descent; but a more critical study of their basicranial and foot structure, and a better knowledge of the very fragmentary remains, apparently intermediate, found in the American Miocene, would place this phylogeny upon safer ground. *Mesocyon* of the John Day appears to be intermediate between *Temnocyon* and *Cynodesmus* but more nearly related to the latter. Both are supposed to be descended from the White River genus *Daphænus*, which, in that case, would be the common ancestor of both the typical and the amphicyonine dogs. But it has not been shown that *Pseudocynodictis* can be excluded from the direct ancestry of the Canidae, which it approaches more nearly than does *Daphænus* in the loss of m4, the basined heel of the lower carnassial, the large bulla and the more slender limbs and compacted metapodials. A thorough and impartial anatomical study of the abundant material of Oligocene and Lower Miocene Canidae now available would be necessary to decide upon these relationships.

Professor Boule has maintained the view that *Cynodictis* is ancestral to the foxes and *Amphicyon* to the wolves, a view involving an incredible degree of convergent evolution. In his recent memoir⁴ he indicates, however, that it is not from the typical Amphicyons of the later Miocene and Pliocene that he would derive the Canidae, but from the primitive ancestral forms (presumably *A. ambiguus*, etc.), which are, in fact, closely related to the better known *Daphænus*; but he still appears to

maintain the foxes as independently derived from *Cynodictis*. Even this appears to me wholly improbable, and no real evidence has ever been adduced in support of it. It is of course quite possible to select species of fox and wolf respectively, displaying the superficial adaptive characters that belong with their respective sizes and food-adaptations, at every stage of the later Tertiary history of the Canidae, and if these are imperfectly known and only the fragmentary dentition is studied, one can construct therefrom parallel series more or less plausible. But when one studies carefully the dentitions, skull and skeleton construction of modern wolves and foxes, they are evidently very closely related indeed, and their common ancestor cannot be very distant geologically. The diversity in dentition between different species of *Tomarctus* is quite as wide as among the wolves, jackals and foxes; and any one of these is more readily derivable from one or another species of this genus than from any other known Canid of the later Tertiary. The basicranial and other skull characters of *Tomarctus* are close to those of the modern wolves and foxes—the larger species to the wolves, the smaller to the foxes, those of intermediate size to the jackals. There is no reason to go outside of this genus for the ancestry of the group. *Galecyens*, which M. Boule specifies as an independent ancestor for the foxes, is decidedly more remote in what is known of its dentition and skull characters, and its feet are very different from those of any of the modern Canidae. While the feet are not known in *Tomarctus* from any positively associated materials, there is every reason to refer to this genus various fragmentary remains like those of *Ælurodon* but smaller; and the feet of *Ælurodon*, a genus known to be closely related to *Tomarctus* (see p. 90) are quite modernized and differ but little from those of the wolf.

The modern South American Canidae, with the exception of *Icticyon*, likewise appear to be directly derivable from *Tomarctus* or from the closely related *Leptocyon* (a doubtfully distinct genus). *Icticyon*, along with *Cyon* and *Lycaon*, are more distantly related; their crushing teeth are reduced in numbers and size, the lower carnassial has a trenchant heel (always bicuspid in the typical dogs) and no metaconid, the skull is short and the limbs and feet of less cursorial type (except *Lycaon*). The ancestry of the *Cyon* group has been traced back to *Temnocyen* of the Upper Oligocene and Lower Miocene, thence to *Daphæns*. *Temnocyen*, however, is perhaps less directly in line than *Enhydrocyen*, although this genus is somewhat precociously specialized in reduction of the teeth. The imperfectly known *Philotrox* of the John Day is perhaps more directly ancestral. The group may in my opinion be better derived from *Pseudocynodictis* than from *Daphæns*. 
Paleontology gives no evidence as to the ancestry of Otocyon. This genus, while unique in the extra upper and lower molar, and peculiar in the development of the crushing dentition, is not so aberrant in other osteological features as one might expect; and probably represents not so much a stock of ancient differentiation from the rest of the Canidae as a peculiar aberrant adaptation based upon an abnormal "mutation." In this connection it may be noted that the type of Amphicyon fremdens shows on one side a partly preformed fourth lower molar (not shown in the figure) probably a reduplicated m3. Similar reduplication among modern Canidae has been recorded several times.

The relationships of the Ursidae turn, in my opinion, upon more adequate data and study of the skull and skeleton of Hyænarctos and other Tertiary genera. The phylogeny proposed by Dr. Boule (loc. cit., p. 254) derives them, following Schlosser's views, from Cynodon and Cephalogale. The evidence in its support is wholly derived from the dentition and it is not at all in accord in many particulars with the evidence from cranial and skeletal characters where these are known. The basicranial characters of Cephalogale are cynoid, those of the Amphicyonine dogs are sub-ursoid. Arctotherium in Dr. Boule's view is derived, along with Æluropus, from Hyænarctos, while the true bears are derived from Ursavus. But Arctotherium, even in its dentition, and very clearly in all the essential details of its basicranial features, foot-construction, etc., is a true bear, very close to the typical group; Hyænarctos is much more remote. There is no reason why Arctotherium should not be derived from Ursavus or even a later stage of typical Ursidae. Dinocyon and Hemicyon are too little known for any positive conclusions as to their real affinities; and Cephalogale has less apparent affinities to the bears than have some of the amphicyonine dogs. The real ancestry of the Ursidae is probably to be found in future discoveries in Asia, not in the known genera of Western Europe or of North America, in both of which countries they appear after the manner of immigrants from a common intermediate region of dispersal, not as the result of evolution in loco.

The Phylogeny of the Canidae

As a preliminary to any remarks on this subject, I must express my total disbelief in the fundamental classification of the Canidae into an "alopecoid" and a "thoöid" series proposed by Huxley in 1880 and accepted by Boule, Scott, and various other later writers. In the main this distinction is one due to size; the thoöids are medium and large, the
alopecoids medium and small, Canidæ. The larger Canidæ have relatively smaller brains and relatively larger muscular attachments, as is necessarily and for excellent mechanical reasons the case in any contemporary series of species in any group of mammals or reptiles, living

or extinct. There is, therefore, in the Canidæ a necessity for building out the skull at certain points to provide suitable attachments for the muscles, and a vacant space results, which is usually filled by separating the inner and outer table of the bone and providing sinuses or other skull spaces. It is for this reason that the sagittal and occipital crests, the
zygomatic arches, the postorbital processes, are built out and relatively prominent in the larger species. The brain is relatively smaller than in smaller related species in the same grade of evolutionary development.

But the brain is also relatively smaller in species of the same size but in a lower stage of their evolution. Such species may be earlier geologically, inhabiting the same zoological regions. Or they may be contemporary geologically but inhabiting more marginal portions of the area of dispersal of the group. We should expect therefore to find that both the Canidæ of the later Tertiary in the northern world, when directly or approximately ancestral to the modern species, and also the existing Canidæ in the marginal southern continents, although smaller in size, resembled larger existing species of the northern world in those features which are due to building out of the skull and relative smallness of the brain.

This is exactly what we find in such obvious characters as the sagittal crest, the width and weight of the zygoma, prominence of the postorbital processes, etc., and I think it sufficiently explains the distinction on which Professor Huxley laid so much weight in the presence or absence of frontal sinuses. They are present in all the large modern Canidæ, absent in all small modern Canidæ. That they are present in South American and in certain African and Oriental Canidæ of medium size, while absent in Holarctic Canidæ of equal size, was taken by Huxley to be proof that it was not due to size and must therefore represent a real taxonomic distinction. But, as I interpret it, this is merely an indication—one of many—of the somewhat primitive character of these species of marginal regions in the geographic range of the group. If it were practicable to section skulls of all the extinct Canidæ, I have little doubt that such sinuses would be found to be present in the larger species and not in the smaller species of each of the earlier stages, but that, like the sagittal crest and other external characters, they would be found more prominent in species of the same size but at an earlier stage of evolution.

*Tomarctus brevirostris*, about the size of the coyotes, has the sagittal crest and other building-out features of the skull quite as prominent as in the timber-wolf. *T. confertus*, about the size of the fennec, has these features as much developed as in the coyotes. In the Oligocene one finds the smaller Nothocyons, *N. gregarius, lemur, latidens*, without sagittal crest, but they are much smaller than any modern Canids; and *N. temnodon* or *geismarianus*, although comparable in size to the fennec, have well-developed sagittal crests. I do not doubt that the smallest species of *Cynodictis*, *Nothocyon*, *Cynodesmus*, and *Tomarctus* are “alope-
coid” throughout, as they obviously are in the external features of the skull, while the larger species of each genus are as obviously “thoöid.” But when the larger and the smaller species in each genus are obviously closely related by innumerable constructive details in the teeth, skull and skeleton, the simple mechanical explanation which I have outlined appears to be the only one reasonably possible. To suppose that the larger and smaller species of each genus are successive representatives of phyla distinct since the Eocene would involve an incredible degree of parallelism in their evolution, violently in contrast with the divergent evolution of numerous other phyla in the Carnivora and other groups and altogether unnecessary to believe, as the evidence adduced in support of it appears to be unsound.

On the other hand, there is throughout the species of both thoöid and alopecoid Canidæ—excepting Cyon, Lycaon, Icticyon and Otocyon—a remarkably close accord in the details of construction of the teeth, extending also to the skull and skeleton, which appears to me to afford very strong evidence for their near relationship.

It is to be observed that when Professor Huxley wrote, in 1880, very little of the present evidence from the geological record was available. Had he had before him the series of skulls of Tertiary Canidæ which it has been my privilege to study and compare in recent years, one may presume that he would have given first place to their evidence, interpreting the “thoöid” and “alopecoid” characters on lines conforming to it.

Huxley’s deservedly high authority has, however, afforded what I believe to be a wrong starting-point for the later researches of two very able palæontologists, Professor Boule and Professor Scott, both of whom have been disposed to attach great importance to the distinction between the alopecoid and the thoöid Canidæ. Boule has been disposed to derive the thoöid division from Amphicyon, the alopecoid division from Cynodictis. Scott, while deriving the thoöids from Daphænus through Cynodesmus, has been somewhat obscure as to the derivation of the alopecoids. The present writer has consistently taken the view (since 1899) that the distinction between thoöids and alopecoids is an unnatural division and that the real division among the modern Canidæ lies between the genera Cyon, Icticyon and Lycaon on the one hand, and the remainder of the Canidæ on the other, which form a nearly related natural group, exclusive of the peculiarly aberrant Otocyon.

It very frequently happens in mammalian taxonomy, especially in dealing with fossil material, that some minor characters in the dentition are found to run very constant through a large series of species or speci-
mens, and to be regularly associated with other much more important characters which are either less constant or less often observable, particularly in the fossils. Such is the case in the Canidae with the character of the heel of the lower carnassial. It can be observed on a very great number of specimens and certain constructions found to run constant throughout a large series of species which vary widely in size, in superficial skull characters, in proportions of the teeth, etc.; while certain differences in this construction are as constantly associated with differences in the number and construction of other teeth, in the proportions of the skull, in the construction of the basicranial region, in length of limbs and tail, length and characters of the feet, etc., which are of much more importance in the economy of the animal but are either less constant or less often observable, especially in extinct species. For this reason such minor distinctions are practically convenient in tracing the relationships and evolution of the species, although they are quite incidental or of minor importance in the adaptive specialization of the phyla.

All the typical modern Canidae have a bicuspid heel on m₁, the outer cusp or hypoconid being more or less tetragonal or rounded, while the inner cusp or entoconid is a fairly distinct cusp, with or without a marginal crest enclosing a "basin." On the other hand, in Cyon, Icticyon and Lycaon the heel of m₁ is crested, the hypoconid almost median in position; it is an anteroposterior crest instead of a tetragonal cusp and the entoconid and inner cingular ridge are absent, so that the heel is not at all basined. This is associated in these genera with a reduction of the tubercular part of the dentition (behind the carnassial shears), a tendency to reduce the second lower molar to a similar longitudinal crest, to drop the last lower and last upper molar, absence of the conules of the upper molars, prominence of the heels and accessory cusps on the premolars and incisors, a relatively short face and short high skull and (except in Lycaon), shorter limbs and feet less specialized in the direction of cursorial adaptation. Lycaon, however, is more and not less specialized in some of its cursorial adaptations, notably the reduction of the pollex. In all the modern Canidae the tympanic bulla is of characteristic type, large, inflated, nearly simple, without bony auditory meatus, extending from the eustachian opening and anterior lacerate foramen to the paroccipital process, which is long, rather slender, points downward, and is s guturally united to the back of the bulla.

Tracing the palæontologic record of the family we find that nearly all the Pleistocene species belong to the typical group; but that in the
South American Pleistocene skulls and jaws have also been found of the
*Cyon* type. Fragmentary remains were described by Lund as *Paleocyon*
and *Speothos* and a good skull was figured by Lydekker as *Canis morenoi*. Remains of *Cyon* have been found in the Pleistocene of southern Europe. *Lycaon* has been wrongly identified in England from an uncharacteristic fragment, but occurs in the Pleistocene of France and Italy.

In the Pliocene and later Miocene many species of the typical
group of Canidae are known. The most completely known are *Canis megamastoides* of the later Pliocene of France, a fox-like type which Doctor Boule has considered, probably correctly, as a fairly direct ancestor of the foxes; and *Elurodon* of the lower Pliocene of this country, which is aberrant in certain features, notably the strong development of the parastyle on p4 and the short, massively proportioned premolars. In these particulars it parallels the hyænas; in the marked prominence of the frontal region it parallels the domestic dogs as opposed to all wild species, and in the comparative reduction of the tubercular dentition it tends toward the *Cyon* group (as do also the modern true wolves). But in the basicranial characters, the proportions and specializations of the limbs and feet, *Elurodon* is a perfectly typical Canid and it is evidently closely related, although not directly ancestral, to the modern typical Canidae.

Perhaps related to *Elurodon* but more aberrant, is the California Pliocene *Hyænognathus*, known from an imperfect skull and a lower jaw (*Porthocyon*) doubtfully identical.

A little older than *Elurodon*, in the later Miocene, we find the genus *Tomarctus*, which appears to be more directly ancestral to the typical Canidae, but also to *Elurodon*, for it displays in a minor degree all the peculiarities which *Elurodon* has accentuated and the modern dogs have lost. The skeleton of *Tomarctus* is not fully known, but in the skull and what is known of the skeleton it appears to be a typical Canid, although less specialized in numerous details.

A few jaws and teeth in the upper Miocene of this country appear to be related to the *Cyon* group. They have the characteristic crested heel and absence of metaconid on m1, agree also in reduction of the tubercular teeth, prominence of accessory cusps on the premolars, etc., but the skull and skeleton are unknown.

Another questionable type, known only from an immature lower jaw, is *Ischyrocyon*, in which m1 has the crested heel without metaconid, but the tubercular dentition is very large relatively and the premolars much reduced in size and simple in construction. This may perhaps belong rather to the *Amphicyon* group.
A second important group of Canidæ of the later Tertiary is the Amphicyon group found both in Europe and this country. These are distinguished by a heel on $m_1$ that has a large crested hypoconid but more external in position, and an inner entoconid crest more or less strongly developed; the metaconid of $m_1$ is large and the heel and all the tubercular dentition very large, while the carnassials and premolars are proportionately reduced. $M^3$ is present on Amphicyon, lost in the related Pliocyón and Dinocyón.

The skull and especially the skeleton of Amphicyon differ widely from the typical dogs and the Cyón group. The skull has various primitive characters but the most important distinction is in the tympanic bulla, which is much more suggestive of bears or mustelids than of dogs. It is small, only partly inflated, with a long bony auditory meatus and it covers only the anterior half of the otic area, being wholly in advance of the mastoid process and at some distance from the paroccipital process.

The skeleton of Amphicyon is still less like that of the dogs; in most characters it has rather specialized in an opposite direction from the primitive carnivore type. The back and neck are heavy, arched somewhat as in the bears; the tail is very long and massive, more so than in almost any living carnivore; the limbs are short and powerful, the feet broad and spreading, five-toed, apparently digitigrade (unlike the bears), the claws compressed and sharp, somewhat between cat and bear in type. This was a very extraordinary animal, as different from living dogs as a badger or an otter from a weasel, and not much like any other carnivore.

Nearly related to Amphicyon are Pliocyón and Dinocyón, in which the last molar has been lost.

In view of such wide differences from the typical dogs of the Mio-cene, the earlier opinion of Dr. Boule that modern thoöid Canidæ are descended from Amphicyon and the foxes only from the typical Tertiary Canidæ appears quite untenable, and he has more recently modified it to the extent of deriving the thoöids from smaller and more primitive Oligocene species referred to Amphicyon by European writers. This has been considered above (p. 121).

In the Upper Oligocene and Lower Miocene we find at least three groups of Canidæ, which are ancestral apparently to the true dogs, the Cyons, and the Amphicyons, and fortunately we have skulls and skeletons of all three. The first is represented by a considerable number of species referred to two closely allied if not identical genera, Cynodesmus Scott and Nothocyón Matthew. These range in size from a fox to a marten
and, although typically canid in the bulla, are decidedly more primitive in many features of their dentition and still more so in skull and skeleton. With these are larger and more robust animals, *Enhydrocyon* and *Temnocyon*, which have the *Cyon* peculiarities in the dentition but are more primitive than *Cyon* in skull and skeleton. They also have the typical bulla. The third is *Daphnodon*, which is in all respects allied to *Amphicyon* but smaller and less specialized throughout. There are also smaller related species referred to *Paradaphænus*.

In the Middle and Lower Oligocene we find two genera, likewise known from the entire skeleton, *Pseudocynodictis* and *Daphænus*. The first has the large bulla of the true dogs, the second has the bulla like that of *Amphicyon* save for lack of ossified meatus. In both genera the bulla is very loosely attached to the skull and often lost. There is not any wide difference between them in dentition, skull and skeleton, but each shows the early stages of the characteristics of the true dogs and amphicyonine dogs respectively. *Daphænus*, which seems to be the ancestral type of the *Amphicyon* group, retains the last upper molar but in "*Cynodictis*" this last upper molar is already lost.

In the Eocene we have a common ancestral type in *Miacis* and possibly in different species of *Miacis* we can trace the earliest division between true and amphicyonine dogs, in the vestigial m³ of *M. sylvestris* and the more functional m³ of *M. medius* and other species. Unfortunately, the bulla is no longer available to confirm this suggestion, as it does not appear to have been ossified in the Eocene Miacidae; and while the parts of the skeleton known in each conform to the distinctions between *Cynodictis* and *Daphænus*, they are not sufficiently diagnostic to be decisive.

**Mustelidae**

The number and variety of mustelids in the Miocene and Pliocene is very large and the species incompletely known, mostly from lower jaws, so that it is very difficult to systematize or even to correlate them. They do not appear to be in any large proportion closely related to the modern types. Some have been referred to existing genera, but usually because there are no sufficient generic distinctions apparent in the lower jaw. Among the dozen complete lower jaws in our Snake Creek collections, hardly two are enough alike to be considered conspecific; and the correlation of the upper with the lower dentition is by no means certain in some cases.

The Oligocene Mustelidae all have sharply trigonal viverroid dentition and their true relations to the contemporary viverroid and cynoid
genera are by no means certain. Père Teilhard's very able and thorough revision of the Quercy genera presents a conservative estimate of the possible and probable relationships of the various groups.1 The relationship of the American Oligocene genera (Oligobunis, Bunanurus, Parictis) is less open to question, but turns mainly upon the musteloid characters of the carnassials (protocone of p4 sharply offset, crest of heel of lower carnassial external), the simple structure of the premolars and the degree of reduction of the molars.

In the Miocene Mustelidæ the tendency to broaden the inner half of m1, so characteristic of the later genera, becomes progressively apparent; and the characters of the basicranial region are clearly differentiated from those of Canidæ, Viverridæ or Felidæ. The family relationships are no longer in doubt; but the more exact systematic arrangement, even of the modern genera, is by no means agreed upon, and the position of the extinct genera is more or less provisional in many instances.

The following key is intended to set forth the more obvious distinctive characters in the teeth, especially of the American Tertiary genera, but does not always show even the provisionally accepted affinities. The first group, Mustelidæ with two functional molars, is believed to be a natural one; the second, of primitive Mustelidæ, probably represents, in the main, the ancestral group of the family but some of the genera are of doubtful affinities and may well be, as Teilhard shows, composites of variously related species. The third division includes all the modern Mustelidæ and is subdivided into three groups, the first comprising the wolverene, ratel and extinct associates, the second, the weasels, martens, etc., the third including a rather wide variety of insectivorous and piscivorous adaptations. These in turn are grouped into (1) the otters and skunks—which are obviously related in their dentition, however diverse in their food and habits; (2) the badgers, with a number of extinct genera more or less related, the most divergent of the extinct genera being Leptarctus, whose affinities are discussed later in this paper.

**Key to the Principal Genera of Mustelidæ**

I.—Two upper molars.

A.—Metaconid of m, distinct, heel smaller, trenchant.

1.—M1 not expanded on lingual side, m² very small . . . . +Oligobunis.

2.—M1 expanded on lingual side, m² larger . . . . . . . . . . . . +Canimartes.

3.—Upper teeth unknown; near Canimartes . . . . . . . . . . . . +Sthenictis.

B.—Metaconid of m, large, heel large, basined.

+Paroligobunis, +Brachypsalis.

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II.—M² vestigial or absent, small primitive types with sharply triangular m¹.
   A.—Metaconid of m₁ small or absent, sectorial dentition compressed and sharp, tubercular dentition reduced, m¹ more extended transversely.
   1.—A small metaconid on m₁.
       +Stenogale, +Stenoplesictis, +Paleoprionodon, etc.
   2.—No metaconid on m₁.
       a.—A minute m².............................. +Bunathurus.
       b.—M² absent.............................. +Paleogale.
   B.—Metaconid of m¹ well developed, teeth more robust with tubercular dentition larger, m¹ less transverse.
   1.—Protoconid of m₁ considerably higher than metaconid.
       +Plesictis, +Parictis.
   2.—Protoconid of m₁ only slightly overtopping metaconid; m₄ elongate, procyonoid.............................. +Amphictis.
III.—One upper molar (except for a vestigial m³ in Megalictis, Ælurocyon and Potamotherium). Lingual half of m³ more or less expanded and other characteristic mustelid features.
   A.—Premolars compressed, carnassials of shearing type, m¹ narrow, transverse, no metaconid on m₁; large animals with robust preaceous teeth. Wolverene group.
   1.—Inner half of m¹ slightly expanded, m² vestigial.
       a.—Three lower premolars, skull very short............ +Megalictis.
       b.—Four lower premolars, skull more elongate........ +Ælurocyon.
   2.—Inner half of m¹ considerably expanded, m² absent.
       a.—Premolars somewhat compressed, unreduced........... Gulo.
       b.—Premolars robust, p₁ absent........................... Mellivora.
   B.—Sectorial teeth sharp, compressed, tubercular teeth reduced, m¹ narrow, transverse; mostly small animals with preaceous teeth and vermi-form bodies. Weasel group.
   1.—Metaconid on m₁ of moderate size, premolars reduced.
       a.—Talonid of m₁ crested.............................. +Plionictis.
       b.—Talonid of m₁ basined.............................. +Propulorius.
   2.—Metaconid of m₁ small, low set.
       a.—Premolars unreduced.............................. Mustela.
       b.—First premolar absent............................ Galictis.
   3.—No metaconid on m₁, premolars shortened and reduced in number.
       Ictonyx, Putorius.
   C.—Premolars robust, carnassials with reduced shear, large metaconids and heels, tubercular dentition enlarged, m¹ more or less quadrate.
   1.—Upper carnassial trigonal, no hypocone; heel of lower carnassial basined. Otters and skunks.
       a.—Premolars ¾; m² vestigial............................. Potamotherium.
       b.—Three lower premolars (upper dentition unknown)..... +Mionictis.
       c.—Premolars ¾; teeth more specialized throughout. Lutra, Pteronura.
       d.—Premolars ¾; teeth very massive and extremely specialized.
       Latax.
       e.—Premolars reduced, shortened, acutely pointed.
       Spilogale, Mephitis, Conepatus, etc.
Matthew, Third Contribution to the Snake Creek Fauna

f.—Muzzle elongate, slender, teeth much reduced...........\textit{Mydaus}.
2.—Upper carnassial becoming tetragonal, with hypocone. Badgers.
a.—M\textsubscript{1} much wider than long; hypocone of p\textsubscript{4} small, four premolars, strong postorbital crests..................\textit{Helictis}.
b.—M\textsubscript{1} fully quadrate, hypocone of p\textsubscript{4} strong, p\textsubscript{1} absent; heel of m\textsubscript{1} basined, strong postorbital crests..................\textit{Leptarctus}.
c.—M\textsubscript{1} much expanded lingually, tubercular teeth more or less multi-cuspid, p\textsubscript{1} absent; a sagittal crest and wide occiput.
\textit{+Trochotherium, +Promeles, Arctonyx, Meles, Taxidea}.
d.—Four lower premolars, skull unknown...............\textit{+Trochictis}.

\textbf{Brachypsalis}

This genus is still imperfectly known but it appears probable that it represents an extinct phylum, derived from \textit{Oligobunis} through the Lower Miocene \textit{Paroligobunis}, characterized by progressively more robust teeth, shortened jaws, enlargement of the tubercular and reduction of the sectorial dentition. Peterson has described part of the skeleton of \textit{Paroligobunis}, which shows clearly that it is not related to the otters, to which the dentition suggests affinity.

In the Lower Snake Creek \textit{B. modicus} is represented by a number of jaws and teeth and the larger and more massive \textit{B. obliquidens} is also probably from this level. In the upper horizon a large species is represented by an upper jaw, No. 18268, with p\textsubscript{4}-m\textsubscript{1} and alveolus of m\textsubscript{2}. This may be \textit{B. pachycephalus} but the materials are not sufficient for positive identification. It belongs more probably with the lower dentition described below.

\textbf{?Brachypsalis pristinus} (Matthew and Gidley)


The type of this species is a lower jaw from the Valentine beds, No. 10811. A lower jaw from Quarry C, Upper Snake Creek, No. 18922, agrees closely with the type and is referred definitely to the species but the generic reference is provisional, as the very incomplete type of Cope’s genus differs considerably in the proportions of the teeth indicated by their shattered remnants or alveoli. The premolars are much more robust, the carnassial shorter and the second molar more elongate and two-rooted, as compared with \textit{?B. pristinus}.

\textit{B. pristinus} differs equally from \textit{B. modicus}, in which the heel of the carnassial is not so decidedly basin-shaped, p\textsubscript{4} has a distinct posterior accessory cusp, and the premolars are less crowded and reduced. If the upper jaw No. 18268 from the same quarry and level is \textit{B. pristinus}, the
Fig. 29. *Brachypsalis pristinus*; upper and lower jaw, natural size, from Upper Snake Creek beds, Olcott Hill. No. 18268, crown view of upper teeth; No. 18922, external view of lower jaw of a smaller individual.

Fig. 30. *Brachypsalis modicus*; lower jaw, external view, natural size. No. 17209 (reversed), Snake Creek beds, *M. paniensis* zone.

upper teeth show corresponding differences of specialization from those of *B. modicus*. The carnassial is relatively short and massive, with posterior blade reduced and inner cusp broadened but still retaining its anterointernal position. The first molar is shorter transversely, more massive and quadrate. The second molar is relatively larger in No. 18268 than in *B. modicus* No. 17210, so far as one can judge from the alveoli.
? *Brachypsalis matutinus*, new species

**Type.**—No. 18921, parts of upper and lower jaws from Stonehouse draw quarry, Lower Sheep Creek beds.

**Characters.**—One-seventh smaller than ? *B. modicus*. Premolars more reduced and crowded than in ? *B. pristinus*, much more than in *B. modicus*, the space between canine and p₄ scarcely exceeding the length of that tooth. P₄ simple, without accessory cusp; carnassial proportions as in *B. modicus*, but heel simply basined as in *B. pristinus*, lacking any separate entoconid. M₂ oval, the trigonid cusps still distinct and with normal basined heel, unlike the round crown of *B. pristinus*.

Length from back of canine alveolus to m₁, inclusive 28

<table>
<thead>
<tr>
<th></th>
<th>a–p X tr.</th>
<th>m₁</th>
<th>m₂</th>
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<tbody>
<tr>
<td>Diameters of p₄</td>
<td>8 X 4.3</td>
<td>13.3 X 6.3</td>
<td>6.3 X 4.5</td>
</tr>
<tr>
<td>Depth of jaw beneath m₁</td>
<td>15.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameters of p₄</td>
<td>9.2 X 12.7</td>
<td>7.3 X 12.4</td>
<td></td>
</tr>
<tr>
<td>Transverse diameter of alveolus of m₂</td>
<td>8.3</td>
<td></td>
<td></td>
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</tbody>
</table>

P₄ has the inner cusp somewhat more anterior in position than in *B. modicus*. The anterointernal flange of m₁ is more rudimentary and the parastyle crest is not developed, the whole tooth having a narrower and more pointed-oval form than in *B. modicus*. The difference from *B. pristinus* is much greater, but it resembles that species, as against *B. modicus*, in the lack of parastyle on m₁.

This species might be referred to *Paroligobunis*, if Peterson’s genus were not so imperfectly known. It differs widely from *B. pachycephalus*;
B. pristinus and modicus are intermediate stages but the latter is clearly off the direct line of descent, if the series be considered as such, having a longer jaw, accessory cusp on $p_4$, entoconid on heel of $m_1$ and metastyle on $m_1$ to distinguish it. Better knowledge of the dentition of the four species would probably show that they represent at least two, probably three distinct phyla.

**Fig. 34.** Sthenictis dolichops; lower jaw, type specimen, natural size, external, superior and internal views. No. 18264, Snake Creek beds, *M. paniensis* zone.

**STHENICTIS** Peterson

The type of this genus is *Stenogale robusta* Cope. It appears to be related to *Brachypsalis* and to *Canimartes* Cope of the Blanco, but the data are so fragmentary that the genera cannot be clearly distinguished. The type of *S. robusta* is a lower jaw from the Valentine beds at Fort
Niobrara, Nebraska; it is distinguished from *Brachypsalis* by the somewhat narrower jaw with more compressed premolars, heel of carnassial narrower, smaller, with no entoconid, \( m_2 \) proportionally smaller.

**Sthenictis dolichops**, new species

**Type.—**No. 18264, lower jaw with \( p_2-m \) and alveoli of canine \( p_1 \) and \( m_1 \), from lower level of Snake Creek beds, Sheep Creek Quarry, Expedition of 1921.

**Generic Characters.—**Dentition \( 1.4.2. \). Canine large, incisors small or none. Premolars moderately compressed, a little spaced, \( P_4 \) with distinct heel and posterior accessory cusp. Carnassial compressed, metaconid small but somewhat less reduced than in *Mustela americana* and the whole tooth more massive. Posterior crest of metaconid continued down and around inner margin of talonid as in the preceding genus, but much less prominent. Hypoconid robust, somewhat external, slightly crested.

**Specific Characters.—**Size of *Cyon alpinus*, c-\( m_2 \) about 67 mm. Alveolus of \( m_2 \) round-oval, much larger than in *Sthenictis robustus*, more as in *Brachypsalis*. This is a peculiar type for a Mustelid, resembling the *Cyon* group in proportions of the jaw but with the simple premolars and sub-external hypoconid on \( m_1 \) that indicate its mustelid affinities.

The upper dentition is unknown and the genus may prove to belong in the group with two upper molars, near *Canimartes*.

**Plionictis**, new genus

Between *Sthenictis* and *Mustela* intervene a considerable number of Miocene species, known almost wholly from lower jaws, whose association and affinities are very doubtful. The only one adequately known is *Mustela ogygia* of the Pawnee Creek beds; type, a skull and lower jaws. This differs from the true martens in the more distinct metaconid of \( m_1 \), reduction of the anterior premolars and absence of \( p_1 \) on both sides of the lower jaw, of \( p_1 \) on one side of the upper jaw and other details; but it appears to be nearly related to the martens although, apparently, it should be distinguished generically.

*M. glarez* Sinclair is closely related to *M. ogygia* but distinguished by retaining a minute \( p_1 \) and an accessory cusp on \( p_4 \), both distinctions being perhaps obliterated by age on the type of *M. ogygia* and not valid specific distinctions.

*M. parviloba* from the Pawnee Creek is of larger size but otherwise nearly related, if the reference of No. 17208 from the Lower Snake Creek to this species is correct.

These three species may be associated as a genus of Mustelinae related to the martens but with strong metaconid, less expansion of the inner half of \( m_1 \), jaw shortened and premolars reduced and crowded or \( p_4 \) absent, a distinct sagittal crest. *P. ogygia* is the type of the genus.
Mionictis incertus, new genus and species

Type.—No. 18263, lower jaw with c-m₃ and root of m₂ from lower horizon of Snake Creek, Quarry A, Expedition of 1921.

Generic Diagnosis.—Dentition 71.3.2. Premolars robust with sharp posterior crests but no accessory or heel cusps, apices well forward, especially on p₂ (as in Lutra), carnassial stout, trigonid low but somewhat larger than talonid, metaconid strong with posterior crest extending downward and backward, continuous with internal and posterior marginal crest of talonid. Hypoconid external, crested, a small cusp at back of protoconid and directly in front of hypoconid. M₂ with double or semi-double root, crown unknown.

Specific Characters.—Size larger, c-m₂ = 41.5, p₃-m₂ = 34.5, carnassial = 12.3. Premolars more robust, shear of carnassial more transverse than in the following species, m₂ with semi-double root.
Mionictis incertus; lower jaw, twice natural size, internal, superior and external views. Type specimen, No. 18263, Snake Creek beds, M. paniensis zone.

Mionictis elegans, new species

Type.—No. 18267, lower jaw with p2-m3 and alveoli of m3, p3 and part of canine alveolus; from lower horizon of Snake Creek beds, Quarry B, Expedition of 1921.

Specific Characters.—Size smaller, p3-m3 = 31.0, carnassial = 11.0. Premolars more compressed, shear of carnassial more anteroposterior, m3 with two separate roots.
LEPTARCTUS Leidy

In 1856 Leidy described under the name of *Leptarctus primus* a tooth obtained by Doctor Hayden from the upper Tertiary at Bijou Hills, Mo. The tooth was found along with the type of *Merychippus insignis* and other specimens that indicate its probable age as Upper Miocene. Leidy referred it to the Ursidæ (probably including the Procyonidæ in this family), and compared it to the coati, which he seemed to regard as its nearest living relative. It has been generally considered as a procyonid. In 1894 Doctor Wortman described a lower jaw with canine, p3 and p4 preserved, which he referred to *L. primus*; it appeared to confirm the reference of *Leptarctus* to this family, as the premolars had the characteristic double main cusp of the Procyonidæ. Wortman concluded that the affinities of the genus lay between *Cercoleptes* and the more typical Procyonideæ. In 1899 Matthew described a nearly complete carnivore skeleton from the Lower Miocene of Colorado under the name of *Phlaocyon leucosteus* as an intermediate between the primitive Canids (*Cynodictis, etc.*) and the raccoons; it showed a less developed stage of the characteristic upper and lower carnassials of the Procyonidæ and was intermediate in most other features of the skull and skeleton. It was regarded as an early stage in the evolution of the Procyonidæ, and the very incompletely known *Leptarctus* was assumed to be a later and more typically procyonid genus.

The procyonid affinities of both these genera have been challenged by Ameghino and von Ihering. So far as I have been able to find, Ameghino never adduced any reasons or evidence for his assertions. Von Ihering states that "Matthew was led into error as regards *Phlaocyon* because he supposed *Bassariscus* to be a Procyonid, whereas it is in truth a Canid." On this point I shall merely observe that several authorities on modern systematic zoölogy who have in recent years revised and discussed the genera of Procyonidæ, have regarded *Bassariscus* as related to the raccoons, although with undoubted points of resemblance to the Canidæ; that the position assigned to *Phlaocyon* is based upon a multitude of characters in all parts of the skeleton; and that Doctor von Ihering's objections relate only to a single feature of the dentition and his interpretation of this feature would carry as a necessary corollary

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3Bull. Amer. Mus. Nat. Hist., XII, p. 54; idem, p. 131, Fig. 10.
that the Procyonidae had nothing to do with the remainder of the Carnivora but were of wholly independent origin. Until some more serious objections are raised, it is hardly worth while to reconsider the affinities of Phlaocyon.¹

As regards Leptarctus, von Ihering states that in his opinion it is a Mustelid, not a Procyonid.² Apparently this statement is based solely upon an examination of Leidy’s figure of the type upper p₄, which does suggest the corresponding tooth in certain Mustelidae (some of the Melinae, e.g. Taxidea, Helictis, Meles). Leidy’s description, however, would indicate that the figure is inaccurate, for he specifically states that the posterointernal cusp is stronger than in Nasua, whereas it is scarcely visible in the figure; in other points also his description would indicate a much more procyonoid character in all the cusps than is shown in the figure.

As a result of a careful reading of Leidy’s description and of comparison of various fragmentary specimens of lower jaws in the American Museum collections referred, like the one described by Wortman, to Leptarctus, I had quite confidently regarded this genus as a fairly typical Procyonid.

In the collections secured by Mr. Thomson last summer from the Snake Creek quarry is a finely preserved little carnivore skull which, after a careful comparison, I refer to Leptarctus. It proves to be a very remarkable type, characterized primarily by the complete loss of m₂ and by very prominent lateral temporal crests on the cranium. While it has thus the dental formula of a Mustelid, it agrees with the Procyonines in details of tooth construction, in the basicranial region, etc., but in most of these particulars it agrees equally well with certain mustelid genera, especially of the badger group.

Leptarctus primus Leidy, 1856

Type.—An upper carnassial, p₄ 1., from the Tertiary of Bijou Hills, Mo., presumably Upper Miocene as it was found in company with Merychippus, etc.

Neotypes.—A nearly complete skull, Amer. Mus. No. 18241 and a lower jaw, No. 18270, from the lower horizon of the Snake Creek quarries, found by Albert Thomson, Amer. Mus. Exped., 1921.

¹The real underlying reason for the attempt to exclude Leptarctus, Phlaocyon and Bassariscus from the Procyonidae, is that the existence of Tertiary ancestors of the family in North America would tend to disprove the paleogeographic hypotheses of these writers.

Fig. 37. *Leptarctus primus*; skull, natural size, top, side and palatal views. No. 18241, Snake Creek beds, *M. paniensis* zone.
Author's Description.—"A left superior molar tooth, nearly resembling in size and construction the fourth upper molar of the Coati, of South America.

"As in the latter animal the tooth has a trihedral crown and three fangs holding the same relative position.

"The crown has nearly the same proportions as in the Coati but is rather longer in relation with its other measurements. As in the Coati it is constituted of three tubercles externally and two internally. In the fossil the median outer tubercle or cusp is the largest of the five. The posteroexternal tubercle is proportionately larger than in the Coati. The summits of the median and posteroexternal tubercles are continuous, through a trenchant curved edge. The anteroexternal tubercle is rather less well-developed than in the Coati, and is not conical, but crescentoid, with an acute edge or summit continuous with the bases of the median external and the anterointernal tubercle. The latter is smaller than in the Coati and is rather trihedral than conical, while the posterointernal tubercle is proportionately larger, so that the internal tubercles in the fossil are comparatively small and nearly equal in size, whereas in the Coati the anterointernal tubercle is not only much longer than the one behind but is nearly or quite equal to the median external tubercle."

Leidy gives the following measurements:

<table>
<thead>
<tr>
<th>Description</th>
<th>Lines</th>
<th>mm.</th>
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<tbody>
<tr>
<td>Anteroposterior diameter of crown</td>
<td>3½</td>
<td>7.4</td>
</tr>
<tr>
<td>Transverse diameter of crown</td>
<td>3</td>
<td>6.3</td>
</tr>
<tr>
<td>Length of crown</td>
<td>2½</td>
<td>5.2</td>
</tr>
</tbody>
</table>

Revised Diagnosis (based upon neotypes).—Dentition \(3.1.3.1\). \(3.1.3.2\). The teeth compare most nearly with *Procyon* and *Nasua* in structure, but \(m^2\) and \(p^1\) are absent, \(p^2-3\) much reduced in size and the entire tooth row very short, more as in the badgers. The molarization is somewhat less advanced than in *Procyon* and somewhat more than in *Nasua*; the details of the cusp construction correspond very closely with these two modern genera and are not in any degree intermediate between them and the other Procyonids. Skull with very short, deep, wide muzzle, elongate cranial region, prominent temporal crests diverging backward to meet the occipital crest at the superior angles of a nearly square occiput. Bullae oval, simple, convex, the long axes of the ovals converging strongly backward, carotid foramen midway on inner border. Anterior end of bulla fully consolidated with the very low and weak postglenoid process which does not project separately behind it; auditory meatus very short,
as in Canidae and some Procyonidae; no approach to the long bony meatus and irregularly flattened bulla of modern Mustelidae and Ursidae. Basicranium of moderate width. Zygomatica very heavy; postorbital processes on jugal and frontal unusually prominent, partly closing the orbit posteriorly.

**Leptarctus primus** Leidy  
Upper Miocene  
Lower dentition, c—m₂ = 33 mm. (No. 18270)

**Leptarctus wortmani**, new species  
Lower Pliocene  
Lower dentition, c—m₂ = 38 mm.

Type No. 2575, lower jaw, Valentine beds near Hay Springs, Neb., referred by Wortman to *L. primus*.

The fine preservation and peculiar character of the *Leptarctus* skull from Snake Creek has enabled me to identify a skull and jaws which I collected near Pawnee Buttes in 1901 but have not heretofore been able to identify, owing to the badly damaged teeth. This specimen, No. 8390, has both arches preserved, the top and sides of the skull intact and the lower jaws complete at the back, but fracture and weathering had so damaged the dentition that but little of it is left; sufficient however, when compared with the Snake Creek skull, to show that the teeth were the same. The entire agreement in the top of the skull, the zygomatic arches, and in such other parts as can be compared, leaves no doubt that it is the same species. It adds but little to the characters. The upper and lower canines are preserved and the posterior part of the lower jaw is more complete than in the Snake Creek specimens.

**Affinities of Leptarctus**

Wortman concluded that *Leptarctus* was between *Procyon* and *Bassaricyon* in characters. Von Ihering, as already noted, considers it a Mustelid.

The absence of m₂ is a mustelid character. All procyonid genera have m₂ well developed, although considerably smaller than m₁. The absence of the first premolar and reduction of the second and third occur in both Mustelidae and Procyonidae, as well as in other families of Carnivora. The characters of p₄ are decidedly procyonid, resembling *Procyon* and *Nasua*, to a less degree *Bassaricyon* and *Potos*, least of all *Bassariscus*. Some Mustelidae have a similar adaptation of p₄, reduction in size and conversion from a shearing to a chopping and crushing type. But the hypocone postero internal cusp does not develop in the Mustelidae save to a limited degree in *Taxidea* and *Helictis*, and still less in *Meles*. There is, however, a certain tendency in *Leptarctus* to obliteration of the notch
between the blades of the upper carnassial, and this, as Wortman has pointed out, is a distinctive mustelid character. It is mentioned in Leidy's description of the type p* quoted above. On the other hand, *Leptarctus* has no sign of the characteristic mustelid construction of m*

the expansion of the inner half in anteroposterior direction, well developed in the more predaceous genera and indicated in most of the genera with more crushing teeth; but the m* has the quadrate type of the Procyonidae and is in detail very like that of *Procyon*. The complete absence of m* is not an individual peculiarity, for it is accompanied by a marked shortening of the skull throughout, in comparison with *Procyon*;
and by the relative reduction of \( m_2 \) which, however, has the elongate character of Procyonidæ, unlike the round peg style of most of the bunodont Mustelidæ.

The bulla has no bony meatus, a character of all Canidæ and some Procyonidæ, an inheritance from the Oligocene and early Miocene Cynoids, all of which have swollen bullæ without bony meatus; it is also found in Bunælurus and some other primitive Mustelidæ. Its peculiar relations to the postglenoid process are unique, so far as I can find, but the position of the bulla in Canidæ and Procyonidæ is further forward than in Aeluroids, and the bulla less reduced than in most Mustelids and Ursids, a condition which brings the Canid-Procyonid group nearest to the extreme anterior extension of the bulla seen in Leptarctus. The temporal crests are more or less indicated in all the Procyonid genera, but never so prominent as in Leptarctus. Similar crests are developed in a few Mustelidæ—occasionally in badgers, etc., normally in Helictis, Plesictis and some other Tertiary genera. They are developed in a few other Carnivora but never that I have seen to the prominence attained in Leptarctus.

It appears on the whole that Leptarctus is related both to the Melinæ and to the Procyoninæ, but very aberrant in certain characters (lack of \( m_2 \), prominent temporal crests, peculiar bullæ) which exclude it from anything like the direct ancestry of any of the later genera. The massive zygomata resemble Phlaocyon much more than any modern genus of Procyonidæ or Mustelidæ. Leptarctus has, however, very little of the primitive and intermediate characters of Phlaocyon, which is a true link between Procyonidæ and primitive Oligocene Cynoids. It is a fully developed but decidedly aberrant type, representing a distinct intermediate phylum. Whether this phylum should be included in Procyonidæ or in Mustelidæ requires careful consideration.

The proportions of the skull are different from those of any modern carnivore that I have compared with it. The heavy zygomata and strong postorbital processes are most like those of Proteles; in Felis the zygomatica are deeper under the orbits, not as deep behind, and the postorbital process of the jugal is much more developed, while that of the frontal is rather less so. Among the Mustelidæ, Taxidea shows some degree of approach in the zygomatic arches, but these are far more slender in other Mustelidæ or Procyonidæ. The extreme shortness of the muzzle is paralleled in several genera among the Mustelidæ, but the shortening of the basicranial region, also more or less marked in both Procyonids and Mustelids and even more extreme in Felis, brings about a different
relation of the component parts in all modern genera, none of which show
the fusion of the postglenoid process with the antéríor face of the tym-
panic bulla. In all of the modern carnivora the shortening of the basis-
cranial region brings the postglenoid process too far external to the
swollen portion of the bulla to fuse with it. In part this may be due to
the very general tendency for the external portion of the bulla to sub-
side into a bony meatus even though the internal portion be still inflated.
In part it may be due to the outward shifting of the squamosal and with
it the glenoid articulation, to accommodate the much increased cerebral
lobes of modern carnivora. Other mechanical reasons might also be
suggested, but to test their validity fully would require a larger number of
complete skulls of diverse types of Oligocene and Miocene Carnivora than
is at present known. The fact remains that this complete fusion of
postglenoid process and tympanic bulla is unique among Carnivora.

The double temporal crests are equally exceptional as compared
with modern Carnivora. It is true that similar crests are developed in
Helictis and other modern genera, but they are by no means so promi-
nent, and for comparison in this respect one must turn to Plesictis of
the European Oligocene and Miocene. They are certainly no indication
of especial relationship to Plesictis, for the dentition of this genus is
quite normally musteline, with no approach to the procyonid type, such
as is seen in Helictis and other Melinae. The crests in Plesictis are
nearer to the median line, but their position varies considerably in
different species of the genus. In Helictis the position and character of
the temporal crests is not unlike those of Leptarctus, except that they are
much weaker and more widely separated, owing to the relatively larger
braincase.

The dentition is that of the Mustelidæ but the construction of the
teeth is closer on the whole to Procyon and Nasua. The construction of
p₄ is approached by several of the Melinae, most nearly by Taxidea; but
the molar of Taxidea is widely different. Again, the form and construc-
tion of m¹ is approached by Mephitis; but p₄ in Mephitis is widely
different. The bicuspid p₄ and the anterointernal cusp of p₄ are found
in all Procyonidæ and in some but not all of the Melinae. The bicuspid
p₃ is unique. The reduction of the premolars is characteristic of the
majority of the Mustelidæ and some Procyonidæ (p₃ lost in Cercoleptes,
p₁ in Procyon). The loss of m₂ and reduction of m₃ is characteristic of
nearly all Mustelidæ, unapproached in Procyonidæ; but in the majority
of the Mustelidæ m₁ is much reduced in anteroposterior diameter; less
frequently it is also reduced in transverse diameter so as to be quite a
small tooth. Most later Tertiary and modern Mustelidæ show a widening of the inner half of \( m^1 \) which is very characteristic and peculiar to the family; but it does not occur in any Oligocene genera and is quite rudimentary in the earlier Miocene genera; hence its absence in *Leptarctus* would not argue against derivation of that genus from Oligocene mustelid ancestry. Another mustelid tooth characteristic is the tendency to union of the two crests of the carnassials, \( p^4 \) and \( m^1 \) into a single crest by obliteration of the deep notch that separates them in other Carnivora. The Procyonidæ show no trace of this; but a tendency towards it in *Leptarctus* was observed by Leidy in the type tooth and is seen in \( p^4 \) of our skull.

The above data appear to show affinities on the one hand to the Procyonine group of the Procyonidæ, on the other hand to the Meline group of the Mustelidæ, with some specializations distinct from either. They are open to somewhat varying interpretation as to the exact phyletic relationship but it will hardly be questioned that *Leptarctus* represents a distinct phylum intermediate between the typical raccoons and the badgers. Whether its affinities are closer to the Procyonidæ or to the Mustelidæ is not easily decided. Both families include a number of distinct phyla, whose precise relations to the Oligocene ancestral stocks are not yet wholly cleared up. One school of taxonomists is apt to solve all such problems by assigning separate family rank to such genera, representing evidently distinct phyla. Thus in the Procyonidæ, *Ælurus*, *Cercoleptes* and *Bassariscus* have each been placed (by different authors) in separate families; and a similar treatment of the Mustelidæ or Viverridæ would result in splitting them up into at least a dozen distinct families (not all of them recognized by any one author). This procedure appears unnecessary and objectionable. To create new families for each of the minor groups into which the Carnivora are divisible merely serves to obscure the broader affinities which the families were intended to represent. The smaller groups may be well enough distinguished as subfamilies or as phyla without whittling down the scope of the families of current usage.

As the absence of \( m^2 \) is a specific and formal distinction between Mustelidæ (typical) and Procyonidæ, I refer *Leptarctus* to the former family.

**FELIDÆ**

True cats and machæroodonts occur in the Snake Creek faunas but are rare. In the upper beds a large machærodont has been identified from a lower jaw and a few fragments. Three lower jaws of *Pseudælurus,*
a cat somewhat smaller than a puma, have been secured from the Lower Snake Creek. No Felidae have as yet been positively identified from the Sheep Creek beds.

**Pseudaelurus**

Two lower jaws in the American Museum and one in the Princeton collection are referred to this genus. They agree rather nearly with Leidy's type of *P. intrepidus*, save for minor differences of perhaps subspecific rank. All are from the lower Snake Creek beds in Sinclair draw.

![Image](image_url)

**Fig. 39.** *Heterofelis catocopis*; lower jaw, one-half natural size, outer view and crown view of teeth. No. 18920, Upper Snake Creek beds, *Aphelops* draw.

**Machærodus (Heterofelis)**1 *catocopis* Cope

No. 18920, a right lower jaw with complete dentition is referred to this species. The type, No. 8310, Cope Coll., is from the Republican River beds of Phillips Co., Kansas. It is the symphysial portion of a lower jaw, showing the character of symphysis and flange but nothing of the postcanine teeth.

The type of *Machærodus* is *Ursus cultridens* Cuvier from the Val d'Arno Pliocene. The genus is principally known, however, from the species *M. megantereon* of the Perrier Pliocene, which seems to be iden-

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tical with *M. nestianus* of the Val d’Arno and with the fine machærodont skull and skeletal material recently secured by Stehlin from the Pliocene of Senèze. It does not appear to differ much from *M. cultridens* but I have failed to find record of any really good toptype of Cuvier’s species. The Perrier species is the type of the genus *Meganterion* Croizet and Jobert, which, although proposed only provisionally, antedates *Machærodus* Kaup 1833 by five years.

The lower jaw here described I take to be the same species as the palate and jaws recently described by Mr. Cook under the name of *Machærodus (Heterofelis) coloradensis*, from the Lower Pliocene of Yuma County, Colorado. As compared with *M. megantereon* this would appear to be subgenerically or generically distinct, the entire absence of flange leaving only an angulation in the lower jaw, as in *Aeluropus*, the larger size of *p*₂, but little smaller than *p*₃, also resembling that genus, while in the absence of *p*₂ and *m*₂, talonid of *m*₁ almost or entirely absent, and relatively large size of accessory premolar cusps, it resembles the other Pliocene and Pleistocene machærodonts.

"*Heterofelis*" is an unfortunately chosen name, being a hybrid of Latin and Greek. But the genus is very probably valid even among the fifteen or twenty names¹ that have been proposed for the (probably) three or more really valid genera of Pliocene and Pleistocene sabre-tooth cats. I accept it provisionally, awaiting a revision of the European Machærodonts based on the Senèze and other material, for a final settlement as to the proper nomenclature and affinities of the several phyla.

The lower jaw from the Snake Creek is a little larger and more robust than Mr. Cook’s specimens. It compares quite closely with them, except that he ascribes to his specimens a vestigial metaconid on the heel of *m*₁. According to his statement, however, they are all damaged at that point, so that it is not certain that a metaconid was present. In our specimen, which is undamaged, there is no metaconid.

The Snake Creek jaw also agrees closely in size and characters with the type of *Felis aphanista* Kaup, a supposed synonym of *Machærodus cultridens*. If this agreement be confirmed by toptypes of *aphanista*, it will follow that *Heterofelis = Machærodus*, and that this genus is distinct from *Megantereon*.

As to the species name used for the Snake Creek jaw, I cannot find any valid distinction between *M. coloradensis* and *M. catocopis*. The Snake Creek specimen certainly agrees with the former, and presumably

therefore belongs to the latter species, with which it accords in size, characters of canine and incisors, and various correlated characters, although the flange is not preserved.

Part of an upper canine, broad and much compressed, is provisionally referred to *M. catocopis* and it is probable that some of the large carnivore bones from the Upper Snake Creek belong to this animal, but we are not able to distinguish them with certainty from true Felidae, *Amphicyon* or other Carnivora.

**EDENTATA**

**Megalonyx curvidens**, new species

The most characteristic edentate specimen found in the Snake Creek beds is a well-preserved lower molar, No. 17601, probably the last (see Leidy, J. 1855. 'Memoir on the Extinct Sloth Tribe of North America,' Smithson. Contrib., VII, Pl. vi, fig. 10) of the left side, found by Mr. Thomson in 1918 in the upper level (Quarry No. 1). To this species may also belong an incomplete claw found in 1908 and a more complete one in the Princeton collection; also navicular described by Sinclair.

**SPECIFIC CHARACTERS.**—Smaller than *M. jeffersoni leidyi*, *whelleyi*, etc., of the Pleistocene and *M. leptostomus* of the Blanco, m₄ of less transverse diameter and distinctly more curved (hence probably shorter). Diameters of m₄ antpost. 15× trans. 17.8 mm., (Note: m₄ of *M. leptostomus* not known).

The characters indicate a more primitive species more nearly allied to *Eucholeops* of the Patagonian Santa Cruz formation. Its relations to *Sinclairia*¹ are wholly doubtful.

It is generally believed that *Megalonyx* is derived from the South American Tertiary ground-sloths and is an immigrant from the Neotropical region like *Mylodon*, although arriving at an earlier date. *Eucholeops* (including *Megalonychotherium* of the Santa Cruz) appears to be an

¹Name given by Ameghino to a supposed megalonychid claw described and figured by Sinclair but not named and supposed to be from the Mascall formation, but perhaps from the overlying Rattlesnake in the John Day basin of Oregon.
approximate or direct ancestor both of Megalonyx and of the smaller and less known Antillean genera of the Pleistocene (Megalocnus, Acratocnus, etc.). M. leptostomus of the later Pliocene (Blanco) is slightly, and M. curvidens of the earlier Pliocene (Snake Creek) is distinctly nearer to Eucholoeops, so far as the fragmentary material shows. Sinclairia is known only from the claw and throws no light on the matter. If this claw is really from the Mascall we must conclude that an edentate from South America managed in some way to colonize the northern continent in spite of the barrier which prevented any northern animals from reaching South America.

PERISSODACTYLA

Rhinoceroses are fairly common at all levels in the Snake Creek series and horses are overwhelmingly abundant, constituting eighty to ninety per cent of the material as found. No tapirs have been identified. Chalicotheres are found, although very rare, in the Sheep Creek beds, but not in the Snake Creek.

RHINOCEROTIDÆ

Only one really good skull has been found in the Snake Creek quarries, although many jaws and teeth and skeleton bones are in our collections. This skull belongs to a species nearly related to Aphelops malacorhinus. A skull of Peraceras was found in beds of probably the same formation several miles to the eastward, and is noticed in an earlier article.1 In the M. paniensis zone occur species close to or identical with the more primitive Aphelops megalodus and Teleoceras medicornutus of Pawnee Creek. In the M. primus zone are found jaws, teeth, a fragmentary skeleton, etc., of a rhinoceros provisionally identified as A. megalodus.

Aphelops malacorhinus mutilus, new subspecies

TYPE.—A. M. N. H. No. 17584, a skull from the Snake Creek beds, Quarry No. 1, found by Mrs. Albert Thomson in 1918.

SUBSPECIFIC DIAGNOSIS.—Closely allied to A. malacorhinus Cope but distinguished by longer and broader nasals, posterior nares farther back, cranium less elevated above facial portion of skull, and nasals less convex.

The skull compares with the type skull of A. malacorhinus from the Republican River beds of Hitchcock County, Nebraska, and with a more complete skull recently discovered by the Denver Museum expedition in Yuma County, Colorado.

Fig. 41. *Aphelops mutilus*; skull, side views, one-sixth natural size. No. 17584, Upper Snake Creek beds, *Aphelops* draw.

The Snake Creek skull is of about the same size and, although a little distorted by crushing, is very nearly complete. The nasal bones are moderately long and peculiarly broad and thin, as in *malacorhinus*, approaching *Peraceras superciliosus* in type, but apparently longer and more sharply differentiated from the truncated nasals of *P. troxelli*. The occiput has the same high narrow form as in *A. malacorhinus*, a marked contrast to *Peraceras*; but the peculiar concave forehead of the two *Aphelopes* approaches *Peraceras*. 
Fig. 42. *Aphelops mutilus*, palatal view of type skull, No. 17584, one-sixth natural size.

Fig. 43. *Aphelops mutilus*; top view of type skull, one-sixth natural size.

**CHALICOTHERIIDÆ**

A lower molar and an ungual phalanx serve to prove the existence of a chalicotherium in the Lower Sheep Creek beds. It is not *Moropus*; the ungual is shorter and much broader than any of the unguals of *Moropus*. Nor, so far as one may judge from published figures and descriptions, is it referable to *Macrotherium* or *Chalicotherium*. It might be congeneric
with “Moropus” matthewi Holland, which is nearer to Macrotherium than to Moropus but very likely distinct from either. Pending the discovery of better specimens I refrain from naming it.

No Chalicotheres have been recognized in the Lower Snake Creek beds, although they occur in the contemporary Pawnee Creek of Colorado ("M." matthewi) and Virgin Valley of Nevada ("M." merriami). Whether the family survived into the Pliocene in North America is doubtful; an upper jaw figured by Osborn in 1890 is supposed to be “Loup Fork” but it may have come from an earlier horizon. It has not been recognized in any of the later collections from known Pliocene horizons.

**Equidae**

As a result of the expeditions of 1918–1922 the species of the different horizons are definitely located and distinguished. The great amount of material available for comparison has, however, brought into relief the questionable validity of many of the species of Tertiary Equidae.

The broad facts of the distribution are as follows.

1.—In the two older horizons (Sheep Creek, Snake Creek A) Merychippus is the dominant form, Parahippus and Hypohippus are scarce. In the upper levels (Snake Creek B and C) Merychippus does not occur, save for a few specimens that are suspected of being redeposit from the older channel-beds. Hipparion, Pliohippus and Protohippus (absent in the older zones) are the dominant forms in the order of abundance as listed, Hypohippus is rare and Parahippus absent.

2.—In the *M. primus* zone the Merychippi are chiefly a small and slender-footed species with primitive teeth and narrow skull. In the *M. paniensis* zone they are chiefly a larger and more progressive form which agrees best with *M. paniensis*.

3.—In the highest beds of the Snake Creek series (Hor. C) the large Pliohippi appear to be relatively common, while Hipparion is more prevalent in the lower part of the upper division (H. affine zone, Hor. B).

4.—The Equidae of the upper horizons are chiefly Pliohippus and Hipparion; there are at least two common species of each genus. “Protohippus” placidus is scarce and *P. perditus* doubtfully present. Hypohippus is very rare (possibly due to redeposit), Parahippus is absent and Merychippus rare and doubtful, as above noted.

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3Bull. Mus. Comp. Zool., XX, p. 100, Fig. 18.
Validity of Species

It is not the purpose of the present contribution to revise critically the species and genera of American later Tertiary Equidae, but comparisons with all of them have been necessary for the purpose of identifying the material at hand. This represents many thousands of individuals, no two of them exactly alike in the complex details of tooth construction. If the standards of species distinction that have been accepted by most American students of fossil Equidae were applied conscientiously to this great collection, the result would be to place upon record scores if not hundreds of "new species" from this one locality. But the thousands of isolated teeth or other fragmentary specimens would clearly show that there are no really constant and uniformly associated distinctions between such "species." They are merely individual differences and it is the scanty or fragmentary character of the material or a failure to make a thorough and impartial study of all materials available for comparison, the natural tendency to compare only the types or best preserved specimens, or to use drawings in place of the originals, that have been responsible for maintaining many of these species as distinct.

It is, of course, quite probable that equally abundant material from many localities would show that the average or typical character of these closely allied "species" differed in much the same way as the geographical variants among modern mammals that it is now customary to describe as "new species." But it is only very rarely that the palaeontologist has enough material really to establish such species and the proposal of them is almost always to be regarded rather as a tentative claim than a proof of their existence. Unfortunately such claims serve as the foundation for elaborate superstructures of hypotheses of geographic distribution and migration, whose tenuous and doubtful foundation is not in the least appreciated by the ambitious builders. It would serve far more for the advancement of real and permanent knowledge of fossil vertebrates to adopt a more conservative attitude in this, as in some other matters, and so far as the Snake Creek fauna is concerned, that is the present writer's aim.

Parahippus integer, new species

Type.—H. C. 310, upper jaws in collection of Harold J. Cook.

Paratypes.—A. M. N. H. Nos. 17567, 17568, lower jaws.

Characters.—This is a species of medium size in the genus, rather brachyodont, but with the crochet well developed. Comparison with the type of the genus P. cognatus can be made only by inference, as the milk dentition of the present species has not been recognized in the Snake Creek collections and as Gidley has stated the type of P. cognatus consists of milk teeth.
Fig. 44. *Parahippus* near *cognatus*; skull and jaws, one-half natural size. No. 14305. Miocene, near Marsland, Nebraska.

The milk and permanent dentitions of this genus are, however, positively associated in the small and primitive species *P. pristinus*, Lower Rosebud, and in an undescribed *Parahippus* skull and jaws, No. 14305, from the Miocene near Marsland, Nebraska. The *P. pristinus* has very brachyodont milk teeth with simple construction, much like those of *Mesohippus* and far more primitive than the *P. cognatus* teeth. In No. 14305 the milk teeth are quite near to those of *P. cognatus*, although not so progressive in the *Merychippus* direction, while the permanent molars are of the long-crowned, progressive type seen in *P. coloradensis* but distinctly further advanced towards *Merychippus*. It is to be presumed therefore,
Fig. 45. *Paranthropus robustus*: upper teeth of No. 14305, showing the milk premolars with the permanent incisors and first premolar and first molar of right side.
à fortiori, that the permanent dentition of *P. cognatus* was of very progressive type, somewhat more so than in the Marsland specimen and decidedly more so than in any described species of the genus. *P. brevidens* would perhaps make the nearest approach, but although long-crowned and heavily cemented, the pattern of this species does not show the marked approach to that of *Merychippus* that must inferentially have been shown by the permanent teeth of *P. cognatus*. It may be that some of the materials from Snake Creek and other equivalent horizons, that have been regarded as primitive species of *Merychippus*, are really the permanent dentition of *P. cognatus* or closely allied species.

Fig. 46. *Parahippus* near *cognatus*; lower teeth No. of 14305, showing the milk premolars and first molar partly emerged.

On the other hand, *Parahippus integer* belongs to what has been usually regarded as "typical" *Parahippus* but is really better represented by *Anchippus* Leidy and *Desmatippus* of Scott. It is sharply distinct from *Merychippus*, about equivalent to *Hypohippus* or *Anchitherium* in progressiveness, but with the transverse crests less continuous, a small crochet, rugose enamel, metastylid and metaconid well separated. The feet are not known; presumably, as in other species of *Parahippus*, they are Protohippine, whereas in *Hypohippus* they are Anchitheriine. *Hypohippus pertinax* of the Snake Creek fauna is of nearly the same size as *P. integer*, and looks much like it superficially; but they are not in fact closely related, as the comparison of complete skulls (were they known) or feet would demonstrate.
It is not far removed from *P. (Archæohippus) mourningi* of the Barstow Miocene of California1 but the crochet is more developed and the parastylid more separated.

**Archæohippus penultimus**, new species

**TYPE.**—No. 18950, fragment of lower jaw with p₃–m₃.

**PARATYPE.**—No. 18951, isolated lower molar. Both from Sheep Creek beds of Stonehouse draw quarry.

**CHARACTERS.**—Size of *Mesohippus bairdii* but with much higher crown. Construction of lower teeth nearly as in *Parahippus* but metaconid and metastylid separated only at extreme tip, as in *Hypohippus*. No external or internal cingula; molar slightly narrower than premolars. Enamel obscurely rugose.

**MEASUREMENTS**

<table>
<thead>
<tr>
<th></th>
<th>No. 18950, type</th>
<th>No. 18951</th>
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<tr>
<td>Length, p₃–m₃</td>
<td>31.8</td>
<td></td>
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<tr>
<td>P₄, diameters, a–p × tr.</td>
<td>10.1 × 9.0</td>
<td>10.7 × 9.2 × 12.6 × 8.8</td>
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<tr>
<td>M₁, “ “ “ “</td>
<td>10.2 × 8.1</td>
<td></td>
</tr>
<tr>
<td>Depth of jaw beneath m₁</td>
<td>23</td>
<td></td>
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</tbody>
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**AFFINITIES.**—The reference of this species to *Archæohippus* is provisional in absence of the upper teeth. Except for the type and paratype no specimens from the Sheep Creek beds have been recognized as referable to it. It has not been found in the Snake Creek beds; but a specimen from the Pawnee Creek beds, No. 6305, a lower jaw fragment with m₃, is tentatively referred by Gidley and myself to this genus. The Pawnee Creek specimen accords in size with *A. ultimus* of the Mascall but is not directly comparable; in the m₃ the relatively smooth enamel and absence of metastylid agree with *Hypohippus*, but the crown is much higher and the third lobe large, as in *Parahippus*. This is the construction that one would expect to find in *Archæohippus* from the characters of the upper molars. A metapodial, No. 8799 from the Martin Cañon beds of the same locality, may also belong to *Archæohippus*. It is about the size of *Mesohippus bairdii* metapodials but shorter, heavier and more compact, with a distinct though narrow facet, facing proximad, for the inner cuneiform. In these and some other particulars it approaches *Hypohippus* and *Anchitherium* and differs from *Mesohippus*, *Miohippus*, *Parahippus* or *Merychippus*.

*Parahippus mourningi* of the Barstow is apparent close to *Archæohippus*, as pointed out by Doctor Merriam, and has been definitely referred by Osborn to the genus.

1*Merriam, J. C., 1919, loc. cit.*
The geologic range of the phylum, if these references are correct, is from Lower to Upper Miocene as follows:

Barstow, Cal. *A. mourningi*, parts of upper and lower jaws.
Pawnee Creek, Col. *A.* sp., part of lower jaw.
Snake Creek, Neb. Not found.
Mascall, Ore. *A. ultimus*, part of skull, teeth.
Sheep Creek, Neb. *A. penultimus*, part of lower jaw.
Martin Cañon, Col. *A.* sp., metatarsal.

**Merychippus paniensis** Cope

To this species I refer the great bulk, about ninety to ninety-five per cent, of the Equidae from the Lower Snake Creek. The *Parahippus* and *Hypohippus* material constitutes perhaps two per cent, the remainder consists of *Merychippus* specimens of doubtful reference, differing so much from the usual type that they must represent either distinct species or abnormal variants of the common form.

Within the material that I have referred to *M. paniensis* there is a wide range of variation, in size, length of crown and other proportional characters, in the degree of union of the protocone, the development of hypostyle, thickness of external styles, complication of the enamel on the lake borders, etc. Where these characters are associated with differences in geologic or geographic position it is advisable to distinguish them as varieties or mutants. In the Snake Creek material they are all found in a few small pockets and probably lived at the same time and place. It is to be concluded that the species was a variable one. Some specimens are as large and progressive as *M. calamarius*, others as small and primitive as *M. seversus*. Among the scarcer variants are a few doubtfully referred to *M. eohipparion*, *M. proparvalus*, *M. sphenodus* and *M. sejunctus*, and a few very primitive, small, short-crowned, the crescents incomplete and the milk dentition practically inseparable from *Parahippus cognatus*, perhaps referable to that species or to *M. brevidens*. Nor is it always easy to draw the line between *Merychippus* and *Protohippus* in the permanent teeth; but in all the collections that are known to be from the older pockets there is no milk molar of the *Protohippus* type. All are broad and low-crowned, though often heavily cemented at a certain stage of wear.

From the great variability of the Snake Creek *Merychippus* the inference might be drawn that the number of species of this genus recognized by Osborn should be very greatly reduced. This may be so, but the proof is wanting. Most of the described species are based upon a single or a very few specimens. The Pawnee Creek Colorado collections
Fig. 47. *Merychippus paniensis*; skull, half natural size. No. 18297, the muzzle completed from No. 18299. Snake Creek beds, *M. paniensis* zone.

Typical adult skull of the most abundant and characteristic animal of this faunal zone.
and those from the Barstow Miocene of California are the only ones at all comparable to those from the Snake Creek and Sheep Creek locality. The former include a good series of skulls and partial skeletons and, while Professor Osborn has made but little mention of these referred specimens, they appear to fall into a number of closely allied species or subspecies rather than a single widely varying one. The distinctions in the teeth are at least partially confirmed by more marked differences in skull and feet. As to the “Sheep Creek” Merychhipi they show a progressive change corresponding to their stratigraphic position that is supported by far too much material to be accidental.

The Barstow collections are more fragmentary and, although less abundant, the material presents a very similar problem to that seen in the Snake Creek Merychhipi. Dr. Merriam has solved it somewhat differently, recognizing three supposedly distinct species, and in the earlier studies on the Snake Creek Merychhipi I was disposed to recognize at least two distinct species and three or four more as doubtful.
Additional material, however, shows the variability of many of the characters at first thought distinctive and (contrary to Dr. Merriam's expectation in such cases) it has not enabled me to find new distinctions of a more constant kind to take their place.

**FACIAL FOSSÆ.**—The fossæ in *Merychippus* vary widely with age and apparently the individual or sex differences are great; nevertheless, some differences appear to be specific. In the Pliohippoid group the lacrymal and malar fossæ are both deep and extensive; in the *paniensis* group the lacrymal is deep, the malar absent; in the *sejunctus* (Protohippoid) group both fossæ are shallow. Ontogenetic changes appear to result in filling of the malar and contraction of the lacrymal, the filling being partly due to shallowing of the bottom of the pocket, partly to contraction of its margin, and by no means constant in its course or uniform in its effects. The adult skulls of *M. isonesus*, however, still show an extensive although rather shallow fossa, chiefly in the lacrymal fossa area. The deep, restricted, sharply outlined lacrymal fossa of *M. paniensis* and *sphenodus*, the obscure shallow fossæ of *M. sejunctus* and *republicanus*, etc., are probably valid specific characters; at all events, they are not age variations.

It should be observed, however, that the distinction of *Pliohippus* from *Protohippus* or *Hipparion* by the facial fossæ cannot be maintained, as the malar fossa disappears in adult *Pliohippus*, in some species at least.

**Merychippus insignis primus** (Osborn)


Type: a series of upper teeth, No. 14187, Lower Sheep Creek beds, Olcott Hill.

Neotype: No. 18944, a nearly complete skull, Lower Sheep Creek beds, Stonehouse draw. See Figs. 48, 55.

Topotypes: numerous skulls, palates, jaws, limb and foot bones from the same quarry as the neotype.

The type was provisionally placed as a subspecies of *M. isonesus*, the milk dentition and the skull being then unknown. The series obtained in 1922 shows every stage in age and defines the limit of individual variation exhibited by the animals that then frequented that locality. About two hundred upper milk dentitions are at hand for comparison and it is impossible to find in them any constant distinctions from the type of *M. insignis* from Bijou Hills, Missouri. Whether this species in
turn is distinct from the type of *Hippodon speciosus*\(^1\) from the same locality may be questioned; but a number of upper teeth from Bijou Hills, referred to *H. speciosus* by Leidy, are pretty certainly distinct from the present species. Until adequate series of toptotypes are obtained at Bijou Hills, the species described by Leidy from that locality cannot be fully validated.

The range in size among the teeth is considerable; some specimens are as large as Leidy’s type of *M. insignis* or even somewhat larger; the great majority are distinctly smaller. All of them show a rather close approach in pattern to the type and are distinguished by relatively primitive pattern, the ancestral transverse lophs being unusually distinct, the median valley between them comparatively open, the enamel-folds rather simple and inconspicuous, disappearing in well-worn teeth. In all structural details the teeth approach *Parahippus*.

**Ontogenetic Stages in *M. primus*.—**The very large series of jaws, juvenile and adult, from the Stonehouse draw quarry fall quite exactly into six definite stages in the growth of the teeth.

1.—Milk premolars fully emerged but unworn; no permanent teeth have broken through the jaw.

2.—Milk premolars considerably worn; m\(_1^+\) emerged but almost unworn.

3.—Milk molars in course of replacement, dp\(_{2-2}\)\(_2-2\) usually out, dp\(_1\) usually still present, the permanent premolars not fully emerged, m\(_{1-2}\)\(_1-2\) emerged and m\(_1^+\) a little worn.

4.—All the permanent teeth in place, m\(_3^+\) unworn and not always fully emerged.

5.—All the permanent teeth moderately worn.

6.—Teeth heavily worn, p\(_2\) sometimes worn to base and lost.

The latter two stages may perhaps be divisible into two additional stages, but there is no mistaking the unity of the first four. There is little variation from the normal; anything like an intermediate is not to be found.

When compared with the modern horse these growth stages correspond, the first to a colt a few days or weeks old, the second to a colt a little over a year old, the third to a colt between two and three years old, the fourth to a four-year-old horse, and so on.

The explanation of these curiously limited growth stages would seem to be as follows:

\(^1\)Figured by Leidy in 1869, Journ. Acad. Nat. Sci. Phila., VII, Pl. xix, fig. 23. The original is in the American Museum collections.
a.—The young were all born at about the same time of year, presumably in the early summer.

b.—The trapping and entombment of the animals in these channel-bed formations occurred chiefly or wholly at a definite season of the year, presumably the middle or latter part of the summer season, when the stream was reduced to a string of scattered pools to which the animals resorted to drink and were destroyed by carnivora, caught in quicksands or met with other misadventures, their remains accumulating only during the few weeks of low water, and buried by the floods of the next rainy season.

Fig. 49. *Merychippus primus*; adult skull with well-worn teeth. No. 18944, one-third natural size. Sheep Creek beds, *M. primus* zone.

If this interpretation be correct, then our stages are the stages of annual growth of *Merychippus*, beginning with colts a few days or weeks old, then year-old colts, two-year-olds, three-year-olds and so on. The evidence would prove that *Merychippus* developed somewhat more rapidly than the modern horse, a three-year-old *Merychippus* being as fully grown as a four-year-old horse. It would indicate with less certainty that the period of its adult life was relatively short, not over four or five years at most, in contrast to the fifteen or twenty years that a horse ordinarily lives after it is full-grown. The later stages, however, are not so clearly distinct; in adult life the individuals varied in wear, so that the stages approach or even overlap, and could only be separated by finding the nodes in average measurements of a very large series of specimens.

The validity of these conclusions turns upon the soundness of the two stated assumptions, *a* and *b*. The first will hardly be questioned, as
seasonal parturition is generally prevalent among the larger mammals, and among plains-living herbivora the season is usually early summer. The second will be regarded as doubtful or improbable by many—perhaps most—geologists who are obsessed by the traditional text-book idea that fossil remains were animals drowned by rivers during flood, whose remains were washed down by the stream to their present location. There is no doubt that the Snake Creek quarries were chiefly river-channel fillings, and that a large part of the bones have been more or less water-worn; but I think it doubtful whether they have been carried very far, and so large a proportion is wholly unworn that one can hardly assume more than a certain amount of scattering and redeposit at a few feet or yards distance from the original location of the carcass. The scattering and breaking of the bones may be largely due to carnivora or to trampling by other animals, and the accumulation during dry seasons in and around waterholes and pools in streams at the present day is a matter of common observation, whereas I do not know of any recent or verified observations of the accumulation of a large number of carcasses of animals at one point as a result of flood conditions. Animals drowned and carried down by floods would be buried in the midst of such vastly greater quantities of vegetation, mud and sand, that the remains would be fossilized as isolated skeletons in a great mass of sediment and rarely, if ever, in the form of a fossil quarry.

It will be obvious at all events that the definite growth stages in the Miocene material indicate that it was accumulated in the Stonehouse draw quarry during a limited season of the year, and similar stages observed in other quarries indicate that Quarries A and B of 1921 were similarly limited; and the analogies of modern observed conditions conform best with the interpretation here placed upon it. Whether the whole of the fossils in each quarry were accumulated during the dry season of a single year, or represent regularly or occasionally recurrent conditions during a succession of years, I do not know.

Loomis has observed1 similar growth stages in the large series of Stenomylus remains which he described from the "Stenomylus quarry" near Agate, Nebraska. He interprets them in a similar manner, save that he ascribes the quarry accumulation to a sudden flood which had drowned a large herd of the animals at one time. An alternative explanation that has been suggested is based upon analogy with the habits of modern guanacos and assumes that the quarry is an old "bedding-

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ground.” In either case, or under other possible explanations, the definite growth stages point probably to a seasonal limitation, within a few weeks at most, and not to continuance of the conditions of deposition through any large part of the year. The fact that they are recognized in two different animals (and apparently are present in others) would eliminate the possibility that they might be due to special susceptibility of *Merychippus* to disease or accident at certain critical periods of its growth.

**Pliohippus** Marsh

The type of the genus is *P. pernix* Marsh, which if not identical with "*Merychippus*” mirabilis Leidy, is at least very closely allied to it. This species is unfortunately a marginal one in the genus, hardly distinct from *Merychippus*. The group included under the generic name *Pliohippus* is much better represented by the two fine skeletons that form the types of *P. leidyanus* Osborn and *P. lullianus* Troxell. The first, an adult (?), female, has the lacrymal fossa partly obliterated by crushing of the skull, but probably originally deep and extensive; the malar fossa absent. The second, a young individual, has both malar and lacrymal fossae wide and deep; it shows the deciduous molars narrow, subhypsodont and heavily cemented, clearly distinct from the broad brachydont and imperfectly cemented type of *Merychippus*.

The permanent dentition is distinguished from that of *Merychippus* by large size, greater hypsodonty and heavy external styles. The protocone is united at its anterior end to the protoloph almost to the summit of the crown; the enamel is little or not at all plicated, the protocone is oval or but little flattened, the metaconid is not reduced postero-internally, the teeth are relatively broad, strongly curved, the enamel lakes large. These characters are shared by certain species of *Merychippus* and distinguish *Pliohippus* from *Equus* and *Neohipparion*.

It is commonly said that *Pliohippus* is monodactyl, *Hipparion* and *Neohipparion* persistently tridactyl, and that the latter cannot therefore be ancestral to the monodactyl *Equus*. But in fact the lateral digits are

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1The protocone is united in *Equus*, but less broadly, less completely and at a different point. In *Hipparion* proper the protocone is oval; in *Neohipparion* it is flattened in the same manner as in *Equus*. The *Neohipparion* molar is directly converted into that of *Equus* by upgrowth of the bridge between protocone and protoloph; an intermediate stage in this upgrowth is seen in *N. princeps* of the Florida Pleistocene, which is a typical *Neohipparion* near the summit of the crown but when sectioned becomes *Equus fratermus*. Other undescribed specimens of *Neohipparion* are in varying degrees intermediate in this character. The conversion of *Pliohippus* into *Equus* requires more considerable and varied changes, including a partial reversion to the semi-separate protocone. Merriam has, however, described from the Pacific Coast species which, so far as the very imperfect material indicates, appear to bridge the gap between *Pliohippus* and *Equus*. Whether *P. procerus* should be referred to this genus or to *Equus* is a question, just as it is a question whether *N. princeps* properly belongs in *Neohipparion* or in *Equus*. 

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known only in one species of *Neohipparion*,¹ in which they are very greatly reduced, and it is only the Old World Hipparions that show any indication of persistent tridactyly. And while certain species of *Pliohippus* are apparently monodactyl, it must be remembered that there is at least one large Texan species in which the lateral digits are complete and well developed. Probably in both *Pliohippus* and *Hipparion* some species were tridactyl and others monodactyl.

**Relationship to *Equus* and *Hippidium***

The foot-bones which can be positively associated with *Pliohippus* have, however, a much nearer approach to the robust proportions of *Equus* than any which can be positively associated with *Neohipparion*, nor are there any known species of *Neohipparion* save *N. princeps* which approach *Equus* in size anywhere nearly as closely as do the larger Pliohippi. I suspect that these two facts are interdependent² and that until or unless large Pliocene species of *Neohipparion* are discovered, the gap between this genus and *Equus* will not be filled. But it is unfortunate that the writers who have insisted upon the relationship of *Pliohippus* to *Equus* have paid no attention to the much closer approach seen in the large monodactyl species of this genus to *Hippidium*, and especially to *Onohippidium*.

Upon the evidence as it stands I should regard *Equus* as directly descended neither from *Pliohippus* nor *Hipparion*, as represented by the typical or better-known species, but from unknown or slightly known Pliocene species intermediate between the two genera, referable to the one or to the other genus, or to *Equus*, according to the generic definitions accepted. I believe, however, that the hard and fast lines of distinction that it is customary among palaeontologists (and zoologists) to draw between "species" are not justified by the evidence; that when one deals with very extensive series of specimens from many closely succeeding stages and many localities, the amount and character of intergrading and mixture of their species characteristics is only explicable as the result of continual admixture of numerous interbreeding strains, so that the "species" is merely a more or less arbitrary selection of material representing approximations to a strain locally and temporarily dominant. It is to be pointed out in this connection that interbreeding

¹ *Neohipparion* proper, exclusive of the species with oval protocone.
²The large species of *Hipparion* proper from the Mediterranean and Indian regions show this approach to *Equus* in proportions of skull, foot-bones, etc., but they belong to the group with oval protocones, large lateral digits, etc., not in the line of *Equus* ancestry, although they parallel it in these characters, mainly functions of size.
does not produce exact intergradation in the characters of a series of specimens but various admixtures of more or less distinct and definite characters. The indirect effects of such interbreeding as shown in the fossil record may be far more extensive than one would at first suppose, as I have elsewhere attempted to point out.1

From this viewpoint the more detailed affinities of the later Equidae are matters of degree of relationship or dominance of one or another ancestral stock in a complexity of intercrossing strains which only slowly and gradually take on that complete infertility between progressively diverging groups which brings about definite and permanent distinctness.

The South American group of one-toed horses of which Hippidium, Onohippidium, Hyperhippidium, etc., are known to us, appear to be approximate derivatives of the large monodactyl species of Pliohippus, but have little if any Hipparion blood in them. The various Pliocene and Pleistocene species which are referred to Equus are derivable from a group of intermediate more or less interbreeding species which had various proportions of Hipparion and Pliohippus blood in them, the Hipparions being mostly unknown "species" of the Neohipparion group, the Pliohippi of a group represented by P. proversus, so far as our very slight knowledge of that "species" goes. Since Equus appears in the later Pliocene of the Old World but only in the Pleistocene of the New World, it would seem to be derivable in the main from early Pliocene Old World Equidae, but obviously not from any of the described forms; presumably therefore, its ancestry is to be traced mainly to an unknown Lower Pliocene fauna of northern or northeastern Asia, extending probably over northern North America. P. proversus might be provisionally regarded as an outlier of this fauna; Hipparion princeps, as an Equus which showed Hipparion blood in its ancestry by its semi-separate protocone, although otherwise a typical Equus fraternus. But conclusions based upon such slight evidence as we have of these two species are highly provisional and scarcely worth being taken seriously. The substance of what we know is that Equus shows an admixture, somewhat varying in its different species, of progressive characters, some of which are assumed earlier by typical Pliohippi, some by typical Hipparions; there is nothing in the generic characters of either genus to exclude it from the ancestry of Equus2 but all the better-known species of each are off the direct line, although some are perhaps not excluded from participation in some degree in the ancestry of the modern horses.

2The separate protocone of Hipparion is due simply to the lagging of upgrowth of the commissure between protocone and protoloph in relation to the progressive hypodonty of the rest of the tooth. Further progress could, and does in some degree, repair this structural defect of the tooth.
Fig. 50. *Pliohippus leidyanus*; skull, No. 18972, one-third natural size. Upper Snake Creek beds, *Pliohippus* draw.
Pliohippus leidyanus Osborn

This genus is unknown in the Lower Snake Creek, but is abundant in the upper beds. The fine (female) skeleton type of *P. leidyanus* Osborn is the best specimen secured. A fine (male) skull, a few jaws and parts of jaws, great numbers of teeth, many foot bones, etc., are referable to this species. They vary considerably in size, in proportions and pattern of the teeth, etc., but the rather characteristic form of the protocone, the amount of complication of the enamel borders (more than usual for the genus) and other distinctions of the species run fairly constant.

The male skull, No. 18972, is distinguished by the large canine teeth. The cheek teeth and skull construction accord with those of the type in most respects, but the lacrymal fossa is more clearly defined. It is a small shallow oval pit with well-defined borders, lying wholly in advance of the lacrymal bone and close above the preorbital foramen. It is chiefly in the maxilla, but the upper posterior end is excavated in the nasal bone.

The premaxilla ends abruptly just back of the nareal notch, as in the types of *P. leidyanus* and *lullianus*. This is probably a generic character of *Pliohippus* and constitutes an approach towards the conditions seen in *Hippidium*. In the Oligocene and Miocene horses the premaxilla sends a rather long, pointed process backward between maxilla and nasals behind the nareal notch. The latter is the primitive condition and is retained by *Protohippus*, *Hipparion*, and *Equus*, with certain minor but probably characteristic modifications in each group of species.

Pliohippus supremus (Leidy)

A smaller species than *P. leidyanus*, with simpler tooth pattern, smaller and rounder protocone, is represented in the Upper Snake Creek pockets by upper and lower jaws and parts of jaws and great numbers of teeth. It agrees very well with *Pliohippus pernix* Marsh when specimens in a corresponding stage of wear are compared; but it also seems to be identical with the earlier described *P. supremus* Leidy. The species is more easily distinguished from the large *leidyanus* than it is from the somewhat smaller and shorter-crowned *P. mirabilis*. Many of the isolated teeth I am unable to assign with certainty to *supremus* or *mirabilis*.

If *P. pernix* Marsh is really identical with this species it affords a secure basis for correlating the foot bones, which are associated with the dentition in the types of *pernix* and *leidyanus*. The foot bones which I have correlated with the Snake Creek *P. supremus* are so much larger
than those of Marsh's type that I can hardly believe that they are the same species. They agree more nearly with *P. lullianus* Troxell, so far as comparisons can be made between adult and immature bones. This species in dentition is not far removed from *P. supremus*, and inferentially from *P. pernix*, but the much more elongate skull and larger skeleton shows it to be distinct from the latter; but I cannot find satisfactory distinctions from *P. supremus* as represented by the neotypes described by Gidley. None are cited by either Dr. Troxell or Professor Osborn.

**Pliohippus mirabilis** (Leidy)

A considerable number of isolated teeth accord with this species as represented by the type and Mr. Gidley's neotypes, but they grade so much into the larger and more hypsodont *P. supremus* that I doubt whether they afford any real proof of the presence of the species in the Upper Snake Creek fauna. If *P. pernix* be a synonym of *P. mirabilis* it is still more doubtful, for none of the *Pliohippus* foot bones in the collections of 1908 and 1918 are as small or as slender as the type of *pernix*.

**Pliohippus sp. max.**

A single metatarsal III, No. 17600, is much larger than those of *P. leidyanus*, equal in size and robustness to many of the *Equus* metatarsals from the Lower Pleistocene of Hay Springs quarry, but agreeing with *P. leidyanus* in the character of the cuboid and ectocuneiform facets, distal keel and some other details. No teeth conformant in size to this metatarsal are to be found in the Snake Creek collections and it may prove to be merely a gigantic individual of *P. leidyanus*.

**Hypohippus**

There are many fragmentary jaws and numerous teeth in the Lower Snake Creek pockets, some, Nos. 18322–4, 18326, and various specimens not numbered, about the size of *H. osborni*, while others are a little smaller, about the size of *H. equinus*, but differing from that species in a number of minor characters so that I have separated them under the name of *H. pertinax*. The type of this species, No. 17232, is a lower jaw with p2–m3 complete, and Nos. 17233–4 agree closely. They are, however, very near to *H. osborni* and may prove to be only a small variety. These specimens enable me to compare the milk and permanent premolars in the upper and lower jaws. There is little difference in size but the upper permanent premolars are broader as well as higher-
crowned; $p_2$ is considerably shorter than its predecessor but of the same width, and $p_{2,4}$ are slightly broader, higher-crowned but not longer anteroposteriorly.

In No. 18324 the protoloph is separate from the ectoloph on $m_2$ but united on $m_3$; on all the other upper teeth it is united at the base and usually nearly to the apex of the crest, although in a few teeth the union is imperfect. It is at least partially united in such milk teeth as I have examined. This character appears therefore to be subject to individual variation and can hardly serve to distinguish Merriam's subgenus *Drymohippus*, unless supported by further evidence.

In the Sheep Creek fauna *Hypohippus* is very rare, the few teeth obtained agreeing with *H. pertinax*.

Affinities of the Species of *Hipparion*

The typical species of *Hipparion* are from the Pliocene of France and a large number of species have been described from the Old World—Europe, India, China, Western Asia and Northern Africa. The Old World species have always, so far as I have seen, an oval to round-oval protocone, moderate to extreme complexity of enamel plication, premolar and molar crowns both moderately high. The round-oval protocones are shown in the Pikermi species, which is so widely known and figured that it has come to be considered (erroneously) as the type of the genus; and in this species are also shown the deep lacrymal fossa and the exceptionally large lateral digits that are attributed to the genus by most writers. Other species of *Hipparion* from Samos, France, Persia, China, India, have an oval or lenticular protocone, moderate enamel plication, and one (*H. antilopinum*) is stated to be monodactyl; the lacrymal fossa is variable, but there is no true malar fossa even in the young. None of the Old World species show the extreme hypsodonty of the true molars characteristic in varying degree of *Hipparion gratum*, *lenticulare*, *plicatile* and other species of the *H. gratum* group, but in other respects they are much alike. The Californian species *M. mo-havense* is distinctly nearer to the Old World species than any other American form, as pointed out by Merriam.

The American species of the *occidentale* group, namely, *H. occidentale*, *affine*, *whitneyi*, *sinclairi*, are distinguished by a marked flattening and anteroposterior elongation of the protocone, which assumes the shape of *Equus*. The premolars and molars are more nearly equal in

1Very wide, deep and extensive with a large maxillary fossa in advance of it in the young; restricted and shallowed in adult skulls.
size and in height of crown as compared with the *H. gratum* group; the plication of the enamel varies, as it does in the European species. The protocone is almost always separate to the base, while in *H. gratum* and its allies, as also in the European *H. minor* from Samos, the protocone is frequently united with the protoloph near the base.

I am quite unable to find any adequate basis for Mr. Gidley's conclusion that the *Hipparion* teeth from Florida and South Carolina are more nearly related to the Old World Hipparions than those of the western United States. His statement that the protocones are round to round-oval seems to be based upon an early illustration by Leidy of a South Carolina tooth that has since been lost. With this exception all the specimens that I have seen show the usual oval form, lenticular in early stages of wear, characteristic both of most Old World species and of the *H. gratum* group in the western United States. His ascription of exceptional hypsodonty to the Floridan and South Carolina species appears to be correct so far as the true molars are concerned; it is not clear that the premolars are especially hypsodont. But this is a point of resemblance to the American *H. gratum* group and not to the European species, in which the molar teeth are not unusually hypsodont. The fact is that the Hipparions of the southeastern United States are near allies, probably quite inseparable specifically, of the group of western and southwestern species that I have called the *H. gratum* group, but are not close to the Old World Hipparions, which find their nearest relative in California.

**Palæogeographic Speculations Based Upon Supposed Affinities of the Species of Hipparion**

Unfortunately Mr. Gidley's view of nearly twenty years ago, cited without criticism by Professor Osborn, has been seized upon by Professor Joleaud as evidence for the "Atlantis theory" so strongly advocated by many French writers. Professor Joleaud has evidently failed to notice the real Old World affinities of *H. mohavense*, also noted in Osborn's memoir, but from the supposed affinities of the "Floridan" species of *Hipparion* to Old World forms he has concluded that the genus must have reached Europe from Florida by means of a transatlantic bridge between the Antilles and Spain and North Africa, whose existence in the Eocene and Oligocene he considers to be well demonstrated and whose persistence to the Pliocene is proven by this evidence. In subsequent papers, starting from the above conclusions as proven facts, M. Joleaud proceeds to detail the migrations of various other Pliocene mammals.
upon equally tenuous data, also in many instances wholly erroneous as to facts, or their significance quite misunderstood. It is to be regretted that in discussing a subject in which such wide diversity of opinion prevails, M. Joleaud has thought fit to ignore altogether the present writer's contributions (although he is not unaware of their existence) as they are based upon a detailed practical knowledge of American fossil mammals, of the character and distribution of the formations in which they are found, which are essential to the proper evaluation of the evidence, but which, naturally a European writer does not possess. This criticism is without detriment to his practical acquaintance with North African fossil mammals, which has led to some suggestions of real value that are discussed elsewhere.

Hipparion affine Leidy

A moderately large species of Hipparion with flattened protocone is the most abundant of all the Equidae of the Upper Snake Creek beds. It is represented by numerous parts of upper and lower jaws and multitudes of unassociated teeth. These show a wide range in size and in practically every detail of construction, but their average character agrees best with H. affine. Only a few are as large and as complex in enamel folding as H. occidentale; on the other hand, there is some intergrading with the smaller oval-protoconed, less plicate H. gratum, but the two types can usually be readily separated even among the isolated teeth.

The enamel foldings are sometimes quite as complex as in H. occidentale, and on the other hand, they are very often as simple as in H. whitneyi and many of the teeth are indistinguishable from the type of this species. Some of the milk teeth agree equally well with the milk dentitions found with the type skeleton of this species. A number of metapodials and other foot bones also agree very closely with the corresponding parts of the type skeleton of H. whitneyi. It appears probable that this species is a synonym of H. affine and somewhat doubtful in my mind whether the latter is fully distinct from H. occidentale.

Hipparion (?) gratum Leidy

This species was based upon a few teeth but Gidley has referred to it a number of palates and jaws which serve as neotypes. To it may be provisionally referred a large number of teeth from the Upper Snake Creek beds. These are characterized by small size, usually oval protocone, simple to moderately plicate enamel, premolars of moderate
length but molars relatively small and often very hypsodont, external styles tending to be narrow on both molars and premolars (lacking the heavy premolar styles characteristic of the flat-protocone group).

I am by no means certain that these teeth all belong to one species, or that the species to which the bulk of them belong is really *H. gratum*; but they are not at present distinguishable from it. A few of the teeth are quite as long-crowned, small in cross-section, and indistinguishable in enamel pattern from the little Florida species *H. minor*; others are like the type of *H. venustum*; and others resemble *H. lenticulare* of Texas. It is rare, however, to find any specimens that have such round protocones as the California species *H. mohavense*, although a similar pattern of enamel plications is common enough.

**Protohippus placidus** Leidy

A few teeth in the 1918, 1921 and 1922 collections and a larger number in the 1908 collection are comparable with this species. The distinctive characters are the small size, very hypsodont molars, contracted lakes, partial restriction of the union between protocone and inner crescent, lake borders simple or with a few plications, external styles narrow, especially on the molars, premolars relatively brachyodont, p very short anteroposteriorly. The curvature of the teeth is decidedly less than in *P. perditus* or in *Pliohippus*, more as in *Hipparion*. Most of the characters of the species are shared by the *Hipparion gratum* group but in these the protocones are separate to near the base of the tooth, the enamel usually more complexly folded and the transverse diameters of the teeth average less and they are less curved.

**Protohippus perditus** Leidy

A few jaws and teeth are doubtfully referred here. They are not distinguishable from the type of *P. perditus*, nevertheless they may be merely extreme variants of *Pliohippus mirabilis*, to which *P. perditus* is probably nearly related.

**ARTIODACTYLA**

Camelidae are the most abundant Artiodactyla in all levels of the Snake Creek beds, with *Merycodus* a rather close second in the lower

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1Not the paratype, in which alone the round protocone is displayed. Both these specimens are lost and the comparisons are from Leidy's figure. This figure is the sole evidence on record of a round protocone in any American *Hipparion*. The other species and such undescribed specimens as I have seen have the normal oval protocone of the *H. gratum* group of this genus. *H. placidus* has a distinctive pattern of enamel plications, but does not otherwise show anything exceptional, although its combination of very heavy mesostyle with oval protocone is unusual and more often to be found in premolars of the *H. affine* material from Snake Creek than in that of *H. gratum*. 
horizons but scarce in the upper levels. Oreodonts are scarce in the lower levels, quite rare in the upper. Palaeomerycids and true deer are fairly common, especially in the lower divisions. Peccaries are scarce but found in all levels. A number of rare and imperfectly known types from upper or lower levels are placed provisionally; the occurrence of true antelopids in the upper horizons is probable but not yet conclusively demonstrated.

The artiodactyls of the lower beds are not so sharply distinguished from those of the upper beds as is the case with the Equidae; but certain broad distinctions may be made as to prevalent types in the camels and ruminants. The difficulty in distinguishing the faunas is only with fragmentary specimens.

**DICOTYLIDÆ**

The evolution and affinities of the genera and species of this phylum and its relations to the Old World Suina have been little studied. Following is a brief summary of certain data bearing on the subject.¹

1.—The Eocene Suina, both of Europe and America, have teeth related in construction to the Anthracotheres, preserving what is presumably the primitive pattern—upper molars five-cusped with the protoconule distinct, much broader than the four-cusped lower molars, the protocone somewhat crescentic; the upper premolars with the usual primitive pattern, an inner cusp on p³ and p⁴.

$$\begin{align*}
\text{Cebocentrus} & \quad \text{Cheropotamus} \\
\text{Charomoropus} & \quad \text{Helohyus} \\
\end{align*}$$

Whether any of these are especially related to the later Suinae and Dicotylidæ, or whether some or all are related to the Eocene entelodonts (*Achænodon*, etc.) is not fully known.

2.—The Oligocene Suina of Europe and America are immediately distinguished by the subequal width of upper and lower molars. The premolars are still simple. The tusks are peccary-like, the upper pair dagger-like, projecting downward. The incisors are unreduced, the muzzle not elongate.

$$\begin{align*}
\text{Palaëochærus} & \quad \text{Suinae} \\
\text{Perchærus, Thinohyus, Bothrolabis} & \quad \text{Subfamily} \\
\text{Chænohyus} & \quad \text{Palaëochærinæ} \\
\end{align*}$$

¹The following discussion was written before Miss Pearson had made the very thorough and able comparative study of American Museum Dicotylidæ published in this bulletin, XLVIII, pp. 61-96, Sept. 19, 1922. I have thought best to leave it unchanged, as a basis for a more extended discussion of the phylogeny based upon her recent studies, which I hope she will find time to publish.
These are all probably nearly related and, like the greater part of the Oligocene fauna of western Europe and the United States, they represent a new invasion, presumably from central or northern Asia, which reached these two countries at about the same time.

This Oligocene group is the source of a large number of phyla, some in the Old World, some in the New, which specialize in various lines. The Old World group, or Suinae, are nearly all distinguished by an outward growth of the upper canine. The New World group, or Dicotylinæ, never show this feature.

A.—Suinae:

(1.) *Hyotherium.* Simple premolars, bunodont molars, upper canine premolariform, subverted.

(2.) *Listriodon.* Simple premolars, tapiroid molars. The upper canine is everted in this and the following Old World phyla.

(3.) *Xenocharus.* Molariform premolars.

(4.) *Hippothyus.* Molars hypsodont, cemented, the cusps elongated into anteroposterior crests.

(5.) *Phacochowrus.* Last molar hypsodont, cemented, polybunodont, premolars much reduced.

(6.) *Potamochoerus, Sus, Babirussa.* Molars of the characteristic suid type.

B.—Dicotylinæ:

The Dicotyline group includes the American Miocene and later genera. Of these, *Desmathyus* of the Lower Miocene is an obvious connecting link with the Oligocene genera, which it nearly resembles. The remaining genera have all lost the external upper incisors (*i³*); the median pair (*i¹*) is considerably larger than the lateral pair (*i²*).

In *Prosthennops* the premolars are submolariform, in *Dicotyles* slightly more so and in *Mylohyus* completely molariform. In *Prosthennops* and *Mylohyus* the muzzle is progressively elongate and the incisors become vestigial; in *Dicotyles* the muzzle remains short. Two species of *Prosthennops* whose skulls are known show very remarkable bony expansions of the zygomata, quite diverse in type, and associated with an equal diversity in other skull characters, while the teeth differ but little. As the zygomata and back of the skull are unknown in *Mylohyus*, there is no evidence to show whether one or the other, or neither, of these species, *P. crassigenis, P. serus*, are ancestral to *Mylohyus*, but the genus *Prosthennops* probably stands in that relation. It is not ancestral to *Dicotyles*, unless through primitive unknown species in which the lengthening of the muzzle, reduction of incisors and peculiar
expansions of zygomata had not yet begun. And it clearly is not ancestral to *Platygonus*, which derives its peculiar type of premolars from the lower Miocene *Desmathyus* stage (see p. 180), with bicuspid bunodont premolars, tetracuspid molars and two incisors and, like *Dicotyles*, retains the normal zygomatic arch. Species of *Platygonus* occurring in the Blanco are limitrophe forms in which the cross-cresting of the teeth is very imperfect. Three other Tertiary species which have been referred to the genus are imperfectly known, *P. rex* of the (?) Rattlesnake, known only from the molars, *P. condoni* of the (?) Mascall, *P. ziegleri* of unknown horizon (recorded as Bridger but that is impossible) are known from premolars which I have not seen.

The relations of the genera are as shown in the following table.

<table>
<thead>
<tr>
<th>Recent</th>
<th><em>Dicotyles</em> (Neotr.)</th>
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<tbody>
<tr>
<td>Pleistocene</td>
<td><em>Dicotyles</em> (Neotr.)</td>
</tr>
<tr>
<td>Pliocene</td>
<td><em>Prosthennops</em></td>
</tr>
<tr>
<td>Miocene</td>
<td><em>Prosthennops</em></td>
</tr>
<tr>
<td>Oligocene</td>
<td><em>Perchærus</em></td>
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*Pediohyus* Loomis differs from the type species of *Desmathyus* in absence of $p_1$; but this may be an age character and is not alone entitled to generic rank. The type is an old individual, whereas the type of *Desmathyus* is a young adult. They are from the same horizon.

*Desmathyus*.—I$^1$ much reduced, premolars nearly simple, large dagger-like upper canine. *Desmathyus* s.s. with 4, *Pediohyus* with 3 pms. Lower Miocene.

*Prosthennops*.—I$^1$ much reduced, $i^3$ absent, muzzle elongate, premolars partly molariform, zygomata expanded into great ring-like processes. Upper Miocene and Pliocene.

*Mylohyus*.—I$^{1-2}$ vestigial, $i^3$ absent, muzzle greatly elongate, premolars fully molariform, zygomata unknown, ? expanded into ring processes. Pleistocene.

*Dicotyles*.—I$^{1-2}$ unreduced, $i^3$ absent, muzzle not elongate, premolars molariform, no expansions of zygomata. Pleistocene and Recent. All Neotropical.

*Platygonus*.—I$^{1-2}$ unreduced, $i^3$ absent, muzzle of moderate length, premolars simple, molars tapiroid, no expansion of zygomata. Pliocene and Pleistocene.

**Prosthennops serus** Cope

No. 17582, a fragmentary skull with the dentition excellently preserved, enables me to describe the cranial construction of this species, hitherto known only from the jaw described by Cope in 1878 and from
other fragmentary jaws. The reference of the skull is somewhat provisional. Two species of peccary occur in the Snake Creek beds, represented by lower jaws, one of which I have identified with *P. serus*. This agrees in size and in the degree of molarization of the premolars with the skull here described, but positive proof is lacking of identity with Cope's type from the Republican River. The skull differs to a remarkable degree from that of *P. crassigenis* described and figured by Gidley, so that I have grave doubts of the propriety of leaving them in the same genus, despite the apparently near resemblance between the dentitions of the two species. Sub-generic distinction at least must be made between them, as follows:

**Prosthennops.**—Zygomatic arch expanded into a broad flat plate. Sagittal and occipital crests well marked. Type, *Dicotyles serus* Cope 1878.

**Macrogenis**, new subgenus.—Zygomatic arch expanded into a massive lateral knob. No sagittal crest. Type, *Prosthennops crassigenis* Gidley, 1904.

The skull when found was broken into fragments by weathering, the palate less damaged than the rest, and the teeth fortunately intact except for the crowns of the canines. The fragments have been pieced together in great part, so that the original is reconstructed save for some uncertainty as to the exact relations of parts that could not be accurately fitted together, and the destruction of some of the more delicate regions.

The general proportions are most like those of *P. (M.) crassigenis*, especially as to the palate and facial portion of the cranium. The length of the muzzle is about the same, less than in *Mylohyus* but much greater than in *Dicotyles*. The premaxillae are united by suture; in *Mylohyus* they are solidly coossified. The frontals are broad, nearly flat, the superior aspect defined posteriorly by distinct postorbital ridges which converge sharply to a short but prominent sagittal crest. The occipital crests diverge nearly at right angles to the sagittal crest and like it are high, sharp and narrow, and quite short, ending inferiorly in a thin warped plate. Owing to missing fragments, the relations of the occipital to the lambdoidal crest are not clear; these are formed apparently at the sutural union of mastoid and squamosal, and are rather heavy and massive. The mastoid exposure is broad, the bone being large, solid, and heavily sutured to the squamosal. The latter is also comparatively thick and heavy, the zygomatic process is broken off so that little can be seen of its character. The bulla is of moderate size, ovoid with sub-vertical major axis, and filled with cancellous tissue, as in all Miocene and later peccaries. The basioccipital is of comparatively light construction, the condyle like that of *crassigenis*. 
The palate is of moderate width and considerably although not excessively elongate; the proportions as in *crassigenis*. The cheek teeth form a straight row with a diastema in front of the premolars; the canine is large, prominent, projects downward and a little outward and in front of it is a deep notch for the reception of the lower canine.

Two pairs of incisors are present, the median pair about twice the diameter of the lateral pair; they are considerably larger than in *P. crassigenis*, much smaller than in *Dicotyles* and set much further in advance of the canines. The canine is a stout heavy tusk with oval root about a centimeter in its major (anteroposterior) diameter; the crown is mostly broken off but it was evidently much larger than in *P. crassigenis* and accords in size with the lower canine of the type of *P. serus*. Three premolars are present, of which *p2* has three cusps and three roots, *p3* and *p4* have four main cusps and four roots, but the posterior pair of cusps is lower and smaller than the anterior pair, unlike *Mylohyus* in which they are equally developed. The molars are also quadricuspid, the third with a small heel. All the cusps of premolars and molars are round, blunt-conical, and show no tendency towards cross-cresting. They lack any tendency to polybuny and have equally lost the traces of the primitive choeropotamid pattern still distinguishable in the Oligocene peccaries and in *Desmathyus*.

The most remarkable feature of the skull is the expansion of the jugal into a broad plate with concave upper surface facing upward, outward and somewhat forward. There is some suggestion in it of the broad jugal plate of some of the larger Oreodonts, but no near resemblance. The postorbital process of the jugal is a prominent broad-based spine, which does not reach the frontal; the external border of the plate is convex, somewhat thickened and rugose, the whole upper surface being slightly roughened. A nearer approach in type, although less specialized, is seen in some of the Suinae, e.g., *Hylochoerus*.

**Dicotylid, cf. Desmathyus**

No. 18952, a badly smashed upper jaw from Stonehouse draw quarry, retains dp³ and m¹ nearly complete and shows that a large peccary existed in the *Merychippus primus* fauna. It is readily distinguished from the described species of *Desmathyus* and *Prosthenrops* by the greater size and breadth of the teeth, which have the same general construction as in these genera. As it is probable that other and better specimens will be found by future explorations, I do not name it at present.
A second upper jaw fragment found in the same quarry in 1923 shows dp³-m¹, with p³-p⁴ preformed in the jaw. The premolars are simply bicuspid, as in Platygonus; the molar retains the primitive bunodont quadricuspid construction of other Tertiary dicotylids, and is about as wide as it is long. This appears to be a possible ancestor of Platygonus.

Fig. 51. Pronomotherium siouense; skull, palatal view, two-fifths natural size. No. 18333, Snake Creek beds, M. paniensis zone. 18244 by error in figure.

AGRIOCHÆRIDAÆ (Oreodontidae)

This family is represented in the Lower Snake Creek horizon by the extraordinary genus Pronomotherium, by at least two well-defined species of the Merychys group and probably by others. In the upper level we have positive evidence of one species, described from a lower jaw in 1909 as Merychys (Metoreodon) profectus. Upper jaws can now be correlated with the type and indicate that it is identical with Merychys major Leidy, based upon an upper jaw with p³-m². The horizon of Metoreodon relictus is doubtful, probably Lower Snake Creek.

Metoreodon major (Leidy)

Syn.: M. profectus Matthew and Cook

The type of Leidy's species is from some point on the Niobrara River and the fine skull from Devil's Gulch, Brown County, Nebraska, recently described and figured by Barbour and Cook,¹ may be a topo-

type and is certainly not far removed in locality and horizon. For this reason it seems advisable to assume that the Snake Creek species is really, as it appears to be, identical with Leidy's type as well as with the Devil's Gulch skull which has been referred to M. profectus. There is, at all events, no question of the close alliance between them and of the generic distinctness of Leidy's type, along with the Snake Creek M. profectus material and the Devil's Gulch skull, from Merycochoerus, Pronomotherium, Ticholeptus, or Merychys.

Metoreodon was based upon the more complex construction of the lower premolars as compared with Merychys or Merycochoerus. This is confirmed by the upper premolars, which are quadrate in outline, longer than wide, the anterointernal and posterointernal crests equally developed on both p² and p³, united with the outer crescent respectively by anterior and posterior marginal crests, separated from each other by a medial internal crest running inward from the apex of the outer crescent to the internal basal cingulum.

The incisors in this genus are pointed and not broadly spatulate, the upper canine of moderate size, a slight diastema behind it, the upper premolars close set, narrow transversely, relatively hypsodont; the premaxillae are solidly coossified, the infraorbital foramen is above p² or the anterior end of m¹.

As Loomis has observed,¹ Metoreodon is probably nearest to Mesoreodon and Ticholeptus, and is not close to Merycochoerus and Pronomotherium, in spite of the considerable resemblance in teeth.

I suspect that Pronomotherium californicum² belongs in this genus rather than in the one to which Dr. Merriam has provisionally referred it. The upper premolars agree more closely with Metoreodon than they do with Pronomotherium and the infraorbital foramen has the same position as in P. profectus and relictus, whereas in Pronomotherium it is much further back, approximately over m² or m³.

**Metoreodon relictus** Matthew and Cook

Two small oreodonts are represented in the Lower Snake Creek fauna besides the large Pronomotherium. They are alike in size and in most other respects, except for the characters of the premolars, which in one are simple, p₁ large, and agree with Merychys; in the other they are decidedly more complex, p₁ is small and premolariform and the details agree with the type of M. relictus. But no specimens of Metoreodon

relictus are included in the 1918 material from Quarry 1 (upper level) and in default of this positive evidence (which was to be expected) of the species belonging to the later fauna, it must be retained as doubtful.

Fig. 52. Pronomotherium siouense; side and top views of skull No. 18333, two-fifths natural size. 18344 by error in figure.

**Pronomotherium siouense** Sinclair

**Type.**—No. 12057 Princeton Mus., a lower jaw from Horizon A of the Snake Creek beds, at Sinclair draw.

**Neotype.**—No. 18333, a finely preserved skull from the lower Snake Creek, Quarry B, expedition of 1921.

**Specific Diagnosis.**—Somewhat smaller than *P. laticeps*, considerably smaller than *P. altiramum*, and intermediate between the two in form of muzzle.
The neotype is compared with the skulls of *P. laticeps* in the Carnegie Museum and of *P. altiramum* in the American Museum. It is more perfectly preserved than either, but lacks an associated lower jaw. Four lower jaws from the same quarry are referred to the species.

The nasals have been lost but the position of the naso-frontal sutures, flush with the superior surface of the frontal bones, shows that the nasals projected sharply upward as in *P. laticeps*; the recession of the nares is less extreme than in that species, the skull is flatter, the superior border of the maxillaries and premaxillaries is less convex and shorter.

The generic characters, great recession of the nares, which are extended from the principal opening above downward and forward in a long slit between the superior border of the maxillary and premaxillary to within a short distance of the front of the skull, are evident in this skull as in *P. laticeps* and *altiramum*. The basicranial region is peculiarly shortened and bent sharply downward relatively to the basifacial plane, the paroccipital process, bulla and postglenoid process greatly crowded together, the bulla of very small diameter but extended downward as an elongate finger-like process filled with cancellous tissue, somewhat as in the Suidæ. The condyles face largely downward in relation to the palatal plane. Other features peculiar to the genus have been described in detail by Douglass¹ in the skull of *P. laticeps*.

*Pronomotherium* appears to be in most respects an extreme specialization along the lines of *Merycochoerus* but has not the broad lateral expansion of the occiput formed from the lambdoid crest of the squamosal, as described by Matthew in that genus.² It had, undoubtedly, some peculiar type of proboscis developed. The skull has some analogies to the type of *Saiga* and others to the tapir, but a careful study and reconstruction of the facial musculature is necessary before its character can be scientifically restored.

**Pronomotherium siouense**, variety

A number of upper and lower jaws from the Sheep Creek beds at Stonehouse draw (Sheep Creek, Hor. A.) are referable to the genus and not positively distinguishable from *P. siouense*. I regard them provisionally as a variant, and specify as type No. 18344, upper jaw. The size is a little larger throughout, the premolars, especially the anterior ones, proportionately larger and more robust but not showing any clearly distinctive construction.

¹Douglass, Earl, 1900, Amer. Journ. Sci., X, pp. 428–438 [*Merycochoerus* *laticeps*].
Fig. 53. *Pronomotherium siouense*; lower jaw, half natural size, external, superior and internal views. No. 18334, Snake Creek beds, *M. paniensis* zone.
CAMELIDÆ

The large progressive *Megatylopus gigas* is now known to be from the Upper Snake Creek beds. While not so far advanced as are some of the Blanco camelids, it approaches them and is probably in their line of ancestry. It is allied also to the Pleistocene *Camelops* but cannot be ancestral to this form, as it is decidedly more cushion-footed, equalling the modern camel in this respect. On the other hand, the small and primitive *Protolabis princtontianus* (= *P. fissidens*) and other species of *Protolabis* and *Procamelus* come from the Lower Snake Creek beds. These are more nearly related to the Pawnee Creek species. *Alticamelus*, which is a side branch with very elongate limbs, progressive as to feet and front teeth, conservative as to cheek teeth, is present in all three horizons. This was to be expected, as it occurs in the Republican River fauna and also in the Pawnee Creek Miocene, and is probably quite directly descended from certain species of *Oxydactylus* of the Lower Miocene of Nebraska.

A considerable number of skulls and a large series of upper and lower jaws, limb and foot bones from each of the three horizons is available for comparison. There is, with a few exceptions, no association of skull and foot parts. The type of "*Alticamelus*" *procerus* Matthew and Cook, 1909, includes considerable part of the skeleton in association with skull and jaws. The type of *A. priscus* infra, and a few other specimens out of the Sheep Creek beds, also have skull and skeleton parts associated. *Megatylopus gigas*, Matthew and Cook, 1909, has an ulnoradius rather doubtfully associated with the skull. The Pawnee Creek beds, with a fauna largely identical, have supplied the positive evidence on correlation of skull and feet in some other species.

*Alticamelus procerus* Matthew and Cook

The type of this species, No. 14070, consists of the skull, jaws, hind limb and parts of the fore limb and a number of vertebrae. Re-examination in 1922 of the point where this specimen was excavated shows that it is from the *M. paniensis* zone in Sinclair draw. It is always a possibility that a small pocket from the upper channel-beds was let into the lower horizon at this point but there is no evidence of it and the specimen must be recorded as of the *M. paniensis* zone, although the referred specimens are chiefly from the *Hipparion affine* zone.

The absence of incisors 1 and 2 is demonstrated in the type, the cheek teeth being only moderately worn.

A number of additional specimens, upper and lower jaws, found in 1916 and 1921, agree with the type, besides various limb and foot bones.
Alticamelus leptocolon Matthew

The type, No. 9115, consists of parts of the lower jaws and feet from the Pawnee Creek beds. The species is quite common and characteristic in that formation. In the Lower Snake Creek it appears to be equally common and is represented by one or more skulls and many upper and lower jaws, limb and foot bones. It is distinguished from A. procerus by smaller size, molars with less relative transverse width, inner crescents of premolars less developed, the inner crescent usually incomplete on p₃ and wholly absent on p₂.

Alticamelus priscus, new species

Type.—No. 14189, a skull with atlas and axis vertebrae, tibia and pes.

Horizon and locality.—Sheep Creek beds, Merychippus draw, probably Horizon A, Exped. 1908.

Characters.—Skull with the elongate proportions, broadly excavated facial fossa and other characters of A. procerus and A. leptocolon but of smaller size throughout. Axis, tibia and metatarsus extremely long and slender, metatarsals completely united but not expanded distally. Premolars unreduced. Molars and incisors 1–2 not preserved in the type.

An incomplete skull, a number of upper and lower jaws, limb and foot bones found in 1922 are referred to this species.

Protolabis angustidens Cope

The type is a lower jaw from the Pawnee Creek Miocene, A. M. N. H. No. 8294. P. heterodontus Cope, the type of the genus, is not clearly distinguishable although somewhat larger and more robust. Both have the large caniniform teeth and heavy muzzle which I assume to be distinctive of the male, the supposed females having very much smaller front teeth, although not different in premolars and molars.

I refer to this species No. 18348, skull of an old male, and 18349, front of skull and lower jaws of adult female, besides a number of palates, jaws, limb and foot-bones. The skull is about the size of A. leptocolon and very similar in general proportions; the premolars are much smaller but the molars are scarcely distinguishable from those of A. leptocolon. The condyles of the skull are smaller, as befits the smaller skeleton, and the limbs and feet are relatively smaller and less stilted. The association of the feet is based upon the proportions of referred specimens of the species from Colorado, Nos. 9100, 9425, which show the metapodials partly united in the proximal half, but never solidly united as they are in Alticamelus.
Fig. 54. Alticetus cf. lepidocon, skull, half natural size, Snake Creek beds, M. pantiensis zone.
Fig. 55. *Merychippus primus*; skull, half natural size. No. 18944, Sheep Creek beds, *M. primus* zone. See p. 162.
A palate, No. 18963, and various upper and lower jaws, limb and foot-bones from the Sheep Creek beds, chiefly from Stonehouse draw quarry, are provisionally referred to *P. angustidens*. A larger series and more complete material from the *M. primus* and *M. paniensis* zones might demonstrate constant distinctions in the two horizons.

**Protolabis fissidens** Cope

**Synonym:** *P. princetonianus* Sinclair

The type of *P. fissidens* is a lower jaw, parts of both rami, from the Pawnee Creek beds of Colorado, A. M. N. H. No. 8297, Cope Coll. With this specimen a number of lower jaws in our collection agree very closely. The fine skull which Sinclair used for type of his species accords in size, proportions and character of premolars and molars with the lower jaws referred to *P. fissidens*, and the lower jaw referred by Doctor Sinclair to *P. princetonianus* agrees quite exactly. A complete skull and various parts of skulls, palates, jaws, and limb and foot-bones from Stonehouse draw are referred to *P. fissidens*. It appears to have been the most abundant of the camels of this horizon.

This apparently fixes the affinities of this species as one of the *Protolabis* group related most nearly to *P. longiceps* of the Pawnee Creek and like it retaining i^2^ unreduced, as in *Miolabis*, but with longer-crowned teeth than in *M. transmontanus* of the Mascall (genotype of *Miolabis*).

Other specimens referred to *P. fissidens* are from the Lower Snake Creek, Horizon A.

To this species should probably be referred various separate metapodials and limb bones of a small form which had previously been provisionally referred to *Procamelus*.

**Protolabis saxeus**, new species

**Type.**—No. 18960, skull from Stonehouse draw quarry, *Merychippus primus* zone.

**Diagnosis.**—Size considerably smaller than *P. heterodontus* and *angustidens*, about the same as *Miolabis longiceps* or *fissidens*, but in proportions and character of the teeth quite like the larger species. A small but rather deep facial fossa, sharply defined above, lies in advance of the lacrymal vacuily and above the premolars. The upper incisors are not preserved in the type but their alveoli indicate some reduction of i^2^, although less than in *P. heterodontus*.

Various specimens referable to this species agree fairly well in characters, but show a considerable amount of variation. A second skull, No. 18961, lacking the occiput, is an older individual of somewhat larger
size and the facial fossa is quite shallow, the roots of $p^1$ more divergent. In a number of jaws grouped under 18962, the caniniform teeth show the usual sex difference in size, accompanied by a corresponding difference in robustness of the anterior part of the jaw (both skulls are females) and some individual variation in size and details of construction of the cheek teeth.

Various limb and foot bones of appropriate size from the Stonehouse draw quarry are also referable here. They show the median metatarsals completely united, save in young individuals, while the median metacarpals are united only in the proximal half.

**Miolabis tenuis**, new species

**Type.**—No. 18965, a lower jaw, left ramus and symphysis.

**Horizon and Locality.**—Sheep Creek beds, Horizon A, Stonehouse draw.

**Characters.**—Symphysis shallow, flaring and a long sharp-crested diastema between the canine and the cheek teeth; $p_2$ absent, $p_1$ vestigial, $p_3$ and $p_4$ small and rather short, molars of normal camelid construction, the anteroexternal pillar prominent on $m_1$ and $m_2$, the anterointernal pillar prominent on $m_3$.

This species is considerably larger than *Pliauchenia minima* Wortman and the premolars are much less compressed, but the peculiar deer-like lines of the diastema are somewhat the same. It is smaller than *M. longiceps*, the premolars are relatively smaller, the diastema between canine and cheek teeth is longer and more crested, the accessory pillars are well developed on two molars while they are entirely absent in *M. longiceps*. These appear to be the nearest relatives of the present species.

The reference to *Miolabis* is provisional, based principally upon the apparent affinity to *M. longiceps*. The reduction of the premolars is carried further in No. 18966, a lower jaw with well worn teeth; the second and third premolars have disappeared and their alveoli closed; the size and characters of the remaining teeth accord with the type of *P. tenuis*, except that the anterior pillars on the molars are almost gone, probably through wear, as the pillar disappears towards the base of the crown in all Camelidae which possess it.

A skull of this species with one ramus of the lower jaw was obtained in 1923 from the same quarry as the type. The muzzle is elongate and extremely slender. The incisive alveoli indicate three teeth of moderate size projecting strongly forward; the canines are small and $p^1$ absent except for a small alveolus on one side only. The posterior premolars and $m^1$ are represented only by alveoli, but apparently $p^2$ is absent, $p^3$ two-rooted, and $p^4$ has a good-sized internal root. The premaxilla,
Fig. 56. *Miolabis latus*; lower jaw, natural size, superior and external views. Type specimen, No. 18965, Sheep Creek beds, *M. primus* zone.
though slender anteriorly, has a long and wide nasal suture. This skull evidently differs widely from the type of *M. transmontanus*, but may be more nearly related to *M. longiceps*.

**Ceridæ**

( Including Palæomerycidæ and Moschidæ)

Three distinct phyla at least are represented in the Snake Creek fauna. Of these *Dromomeryx* and *Blastomeryx* have been clearly defined by Douglass and Matthew, the former large, very brachyodont, with stout postorbital horns of giraffoid type; the latter small, semi-brachyodont, hornless, with large laniary upper canine tusks like *Moschus*. One species of the third group has been provisionally referred to *Cervavus* Schlosser, which is typical in the Chinese Pliocene (*C. oweni*, *C. kokeni*). The species described by Scott in 1890 as *Blastomeryx* is perhaps of the same type. Lull's *Blastomeryx marshi* and *Aletomeryx gracilis* also need to be considered in this connection; unfortunately, their exact geological horizon is uncertain, as is that of Scott's *Blastomeryx "gemmifer."*

**Dromomeryx whitfordi** Sinclair

There is nothing to add in regard to this genus. A number of upper and lower jaws representing a single species of *D. whitfordi* have been found in the *Merychippus paniensis* zone and various limb and foot bones of appropriate size and characters. I have not identified this phylum in the beds above or below. The horns are the most characteristic feature, long, straight, supraorbital, with a wide posteroexternal flange. The characteristic features of the teeth are their short crowns, great breadth and massiveness, strongly rugose enamel, "palæomeryx fold" well developed and traceable even on half-worn teeth, the inner heel-cusp of m₃ well developed, tending to separation from the outer heel-cusp and to union with the posterointernal cusp (entoconid); the inner pillar of p₃ extended into a wide anteroposterior crest; a corresponding but rudimentary extension on p₂.

**Blastomeryx**

The typical species is *B. gemmifer* of the Pawnee Creek and topotypes have been described by Matthew in 1901. This is a much smaller species than the *Blastomeryx gemmifer* of Scott, 1890, which is hereinafter renamed *B. scotti*. The Lower Miocene species referred to the genus cover a considerable range of variation and include apparently two phyla
whose further progress can be traced in the Miocene and Pliocene of the Snake Creek quarries. These later stages are unfortunately incompletely known; the Lower Miocene (Upper Rosebud, Upper Harrison) species B. advena and B. marshi, each known from skeletons in this museum, differ in size and proportions and may prove to belong to entirely distinct genera. The former is hornless and has a large canine tusk, the latter has rudimentary horns and a small tusk.

The two Lower Miocene species are succeeded in the Middle Miocene (Lower Sheep Creek beds) by the species hereinafter described as B. medius and B. riparius. The former is intermediate in size and characters between B. advena of the Lower Miocene and B. elegans of Upper Miocene (Snake Creek A), the latter between B. marshi and B. sinclairi of the Upper Miocene. Both lines appear to be represented in the Lower Pliocene but by very imperfect specimens.

The first phylum increases very little in size but distinct steps can be observed in the changes of tooth pattern. Cope's name Blastomeryx, type B. gemmifer, applies in a more restricted sense to this phylum. In the second phylum, which may be distinguished as a subgenus under the name Dyseomeryx,¹ there is a considerable increase in size, some changes in tooth pattern, but not any marked increase in horn development. Possibly more material would show that the horn increased in the male.

Lull's Aletomeryx does not differ widely from Dyseomeryx in teeth but has simpler premolars, much longer horns and a very different shape of skull (if Lull has correctly assembled his material). It seems likely that it represents a nearly related phylum but deserves full generic separation.

The Lower Miocene stage of Dyseomeryx is best represented in our collection by No. 14264, two skulls with part of the skeleton associated, including good fore and hind limbs. It is from the Upper Harrison beds near Agate, Nebraska, collected in 1908. It agrees very nearly with Blastomeryx marshi Lull, 1920, so that I refer it to that species, which is based upon a skull and jaws of unknown horizon and doubtful locality.

The next stage, from the Lower Sheep Creek, is represented by an upper and several lower jaws, various foot bones, etc., not associated, and is described below under the name of B. (D) riparius.

The third stage is the species which I have heretofore referred to "Cervavus" under the name of C. sinclairi: an incomplete skull together with various upper and lower jaws, teeth and foot bones and a partial skeleton, jaws and jaw fragments from Pawnee Creek beds.

¹Gr. ἀμνὸς = sunet, μοῦμος = ruminant. In allusion to its habitat in the western United States.
A fourth stage perhaps, although not clearly distinguishable from the third, is the species described by Professor Scott as *B. gemmifer* and here re-named *B. scotti*. The type is the skull fragment described by Scott and such other parts as pertain to it in the Garman "Loup Fork" collection, probably from the Valentine horizon. From this horizon there are in our collection a number of upper and lower jaws, front bones, etc., but nothing associated. Most of them are from South Dakota, some from Nebraska.

The latest stage in the series is from the *Pliohippus leidyanus* zone at Snake Creek, a large species represented by parts of jaws, teeth and other fragments. The species also appears in the Republican River fauna of that valley in Kansas, Nebraska and Colorado, but I do not know of any good specimens suitable for types.

Possibly *Odocoileus* may represent the final stage of this phylum, but I think it very improbable.

The more typical *Blastomeryx* is represented in the Lower Miocene by the skeletons of *B. advena, primus* and *olcottii*, which I described in 1907; in the Middle Miocene by lower jaws, upper teeth and foot bones from Sheep Creek A, at Stonehouse quarry; in the Upper Miocene by *B. gemmifer* of the Pawnee Creek and *B. elegans* of the Snake Creek, and in the Lower Pliocene by *B. wellsi*.

![A.M.18955](image)

Fig. 57. *Blastomeryx medius*; lower jaw, natural size, external view. Type specimen, No. 18955, Sheep Creek beds, *M. primus* zone.

**Blastomeryx medius**, new species

**Type.**—No. 18955, a lower jaw from the Sheep Creek beds at Stonehouse draw, Hor. A, Exp. 1922.

**Distinctive Characters.**—Size of *B. advena* and resembles that and other species of the Lower Miocene in the simple construction of m₃, lacking the postero-internal pillar; but differs from the Lower Miocene species and resembles *B. elegans* in the pillar in front of middle internal crest of p₄.
Blastomeryx elegans Matthew and Cook

Type: No. 14101, lower jaw from the *paniensis* zone, Snake Creek A*figured and described by Matthew and Cook in 1909. Various jaws and skeleton bones in the collections of 1916 and 1921 are referred here.

Blastomeryx cf. wellsii Matthew

Type: No. 9823, part of lower jaw from the Valentine beds, Little White River, S. Dakota, figured and described by Matthew in 1904.

Dysomeryx, new subgenus

Dentition as in Blastomeryx but posterior end of main crest of p₄ extended inward to form a fourth transverse crest; palæomeryx fold vestigial; entoconid of m₂ more or less united to internal cusp of third lobe; size progressively larger; rudimentary horns at upper posterior angle of orbit; lateral digits of manus complete or with part of metacarpal shaft missing. Type, *B. marshi* Lull, 1920.

Blastomeryx (Dysomeryx) marshi Lull

No. 14264 is a partial skeleton with an extra skull and jaws associated, found by W. D. Matthew in 1908 in the Upper Harrison beds of Nebraska. Unfortunately, neither skull is complete and the skeleton is in bad preservation. So far as comparisons can be made, it agrees very closely with Professor Lull's type, which is believed to have been collected near the Niobrara River at a point not far east of Antelope Creek. I do not know of any Lower Miocene formation along this part of the river but the Upper Rosebud is not very far to the north of it and there is sufficient uncertainty about the record of the type to warrant the reference of the Lower Miocene skeleton to the species.

No. 14264 is a considerably larger animal than the typical Blastomeryx, has rudimentary horns, a vestigial palæomeryx fold, anterior cannon bone complete and, lateral digits of the forefoot complete, although the shaft is reduced to a thread, the lateral digits of the pes probably reduced to small, partly coossified proximal splints; at all events, no evidence remains of any distal vestiges. Ulnar shaft complete and separate throughout.

The size of the species is nearly that of the dorcas gazelle but the proportions of the limb segments are quite different, the metapodials much shorter, the humeri longer and heavier. It agrees much more nearly in proportions with the brocket but is rather smaller throughout.

Professor Lull has published a restoration of a topotype specimen of *B. marshi*, but has not described the skeleton in any detail, so that I am unable to verify the identification of our specimens.
**Blastomeryx (Dyseomeryx) riparius**, new species

**Type.**—A left upper jaw with p₄–m₃, No. 18956 from Stonehouse draw quarry; paratypes, Nos. 18958, lower jaws from the same quarry. All Hor. A of Sheep Creek beds, Exped. 1922.

In size this is a fair intermediate between *B. marshi* of the Lower Miocene and *B. ("Cervavus") sinclairi* of the Upper Miocene. The premolars are comparatively small, p₄ slightly longer than wide, with complete inner crescent, a posterointernal cingular crest, a deep external notch just behind the anteroexternal angle. The upper molars moderately brachyodont, m₂ and m₃ of equal size, m₁ somewhat smaller, the surface somewhat rugose but not as much as in *Dromomeryx*, the inner basal tubercles quite small. The posterior wings of the hypocone crescents and anterior wings of the protocone crescent unite early to the outer crescents at the posterior and anterior angles of the tooth; the posterior wing of the protoselene unites a little later to the flank of the hyposelene, while the anterior wing of the hyposelene remains separate, although close to the posterior wing of the paraselene.

In the lower jaw the molars show the moderate brachyodonty of *Blastomeryx* but the internal talonid cusp of m₃ is more or less completely united with the hypocnid, the large external talonid crescent looping around the back of the tooth in the usual manner. The basal cusp between the outer crescents of the molars is distinct and the anterior basal cingulum rather prominent.

Of the lower premolars the second is rather small but has the median and posterior transverse crests; the third and fourth have the median transverse crest expanded internally into a round pillar, the anterior one rudimentary, the posterior one well developed, while the main external crest is curved around at its anterior and posterior ends until it reaches the inner border line of the tooth (distinction from *Blastomeryx* proper and from *Merycodus*).

**Blastomeryx (Dyseomeryx) species**

The occurrence in the upper beds of a species resembling *Blastomeryx sinclairi* of the lower horizon but larger and more robust, is shown by a lower jaw fragment with m₂,₃ and some separate teeth.
Blastomeryx (Dyseomeryx) sinclairi (Matthew)

*Cervus* sinclairi Matthew, 1918

To *B. (D) sinclairi* is referred an incomplete skull, No. 18879, from Sheep Creek quarry, Sinclair draw, Expedition of 1921. The horizon is Lower Snake Creek (Hor. A).

The front teeth are not preserved and the cheek teeth are so much worn that they give little in the way of definite characters. The orbit is rather large and only moderately prominent and above it at the posterosuperior angle is a small rudimentary horn. The face is depressed upon the basicranial axis to a moderate degree, about 15°. The lacrymal vacuity is a long and narrow slot, apparently like that of *Antilocapra* but more elongate. The nasals and premaxillae are not preserved and the anterior borders of the maxillae broken. The position of the orbit also is about as in *Antilocapra*, its anterior border being wholly behind the line of the last molar. The rudiment of horn projects outward and upward from the border of the orbit; in does of *Odocoileus* slight swellings appear at the posterior angles of the frontals and about half-way between those points and the orbital margins; in female *Capreolus*, a swelling just in advance of the posterior angle of the frontal; in the present species the horn is situate as in *B. marshi* and *Aletomeryx* but the orbit is as in *Antilocapra*.

The premolars are simpler than in *Dromomeryx*; p²₃ both have strong median internal cusps but the inner crescent is not completely formed; the anteroposterior diameter exceeds the transverse in both teeth, though more considerably in p². The premolars of *Aletomeryx* are much simpler, p² wholly lacking an internal crest, while that of p³ is no more developed than in p² of the species of *Dyseomeryx*.

**ANTILOCAPRIDÆ**

*Merycodus* is fairly common in the *Merychippus primus* zone, this being the earliest record of its occurrence. The upper and lower jaws, limb and foot bones do not show any uniform distinctions from the more abundant material secured in the *M. paniensis* zone. It is quite possible that skulls or antlers might show such distinctions.

*Merycodus* appears at this point as an invading immigrant, so far as we can judge. There is nothing in the extensive and well studied fauna of the Lower Miocene that could stand as ancestral to it. It appears suddenly, just as *Blastomeryx* appears suddenly at an earlier point (Upper Rosebud and Upper Harrison).
The species of *Merycodus* are very much confused and at present can be straightened out only in a provisional way. The species from Snake Creek A appears to be distinct from *M. osborni* of Pawnee Creek, and both from *M. furcatus* of the Valentine and Republican beds. The position of *M. necatus* is not clear; it was based upon jaws from Bijou Hills, but no topotype antlers are known. The Bijou Hills fauna is probably Middle Miocene, at least as regards the specimens first collected there by Hayden; and the specimens from Horizon A, Sheep Creek, should therefore be correlated with *M. necatus*. Unfortunately, they do not include antlers. The *Merycodus* from the Upper Miocene at Snake Creek (Hor. A) has been described as a variant of *M. necatus*, *M. n. sabulonis*, M. and C., 1909, and in default of contrary evidence I continue this identification provisionally. *Cervus warreni* Leidy is closely allied to *M. osborni* and may prove identical, although presumptively from a different geological horizon (Valentine beds). The New Mexican specimens referred by Cope in 1877 to "Dicrocerus" *furcatus*, including those described in 1874 as *Cosoryx ramosus*, appear to me to be also closely allied to *M. osborni* and probably identical with *C. warreni*, but distinct from *M. furcatus*. His *D. tehuanus* is hardly distinguishable; it is known only from a number of small jaws of varying size, of which Cope selected the smallest for his type; measurements of the teeth, however, have little significance when their dimensions vary so widely with age and wear as they do in ruminants. His *D. teres* and *trilateralis* are possibly members of the Dyseomeryx phylum of *Blastomeryx*; they have not the horn characters of typical *Dromomeryx* and there is no reason to associate them with *Merycodus*, as the teeth are not known.

**Key to Species of Merycodus**

1.—Antlers with short beam, long tines, forked near the base, often three-tined.
   *M. osborni* Matthew, 1904 .................... Pawnee Creek, Upper Miocene.
   *M. warreni* Leidy, 1858 .................... Valentine, Lower Pliocene.
   *M. ramosus* Cope, 1874 .................... Santa Fé, Lower Pliocene.

2.—Antlers with long beam, short tines, never more than the single fork.
   *M. furcatus* Leidy, 1869 .................... Valentine, Lower Pliocene.
   Republican R., Lower Pliocene.

3.—Antlers with short beam and short tines, never more than the single fork.
   *N. necatus sabulonis* M. and C., 1909 ... Snake Creek A, Upper Miocene.
   *M. necatus* Leidy, 1854 .................... Bijou Hills, (?) Middle Miocene.

? *Merycodus altidens*, new species

**Type.**—A. M. N. H. No. 18981, lower jaw fragment with *m*₃; paratypes, No. 18981a, last upper molar, and No. 18981b, last lower molars.
Horizon and Locality.—All from Snake Creek beds (upper level), Quarry No. 1 and Pliohippus draw.

Specific Characters.—The chief distinctive features as compared with *M. necatus* are (1) size one-half larger lineally; (2) fourth lobe on m₃ and posterior lobe of m₄ well developed and distinct from crown to base; (3) last molar more hypsodont.

The species is very clearly distinct from any described but whether it belongs to *Merycodus* is doubtful until more complete dentition and skull are known.

Affinities of *Merycodus.*—In a previous contribution I made some comment upon the views of Doctor Winge as to the affinities of *Merycodus* and *Antilocapra*. A recent discussion by Doctor Hilzheimer¹ of the

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¹1922, Centralblatt f. Min., Geol. u. Pal., p. 745.
Markische Museum, Berlin, calls for more careful consideration. The author gives an able and well-considered argument for transference of *Merycodus* to the Cervidæ, replying in detail to the points brought forward in my paper of 1904 and making, without question, a strong case for his conclusion.

His main argument is that the existence of a burr in the *Merycodus* antlers is infallible proof that they were deciduous; that the presence of deciduous antlers is the fundamental and essential character of the Cervidæ; that it is not likely that so peculiar a character could be exactly duplicated by parallelism; that many of the characters that I cited as Antilocaprine are paralleled more or less among the Cervidæ, and of some others he is doubtful whether the described specimen\(^1\) demonstrates the characters claimed. He does not see any real correspondence between the deciduous forked horn sheath of *Antilocapra* with its permanent core, and the deciduous antler of *Merycodus*, corresponding not to the sheath but to the core of *Antilocapra*.

These strictures are warranted, at least in part, as applied to the very inadequate presentation of the evidence in my paper of 1904. There was, however, even then a good deal that I did not make clear, and much more can now be shown, against reference of the genus to the Cervidæ and in favor of its reference to the Antilocapridæ as a separate family.

I.—Character of the Antlers. There are half-a-dozen skulls in the American Museum collections, complete enough to show the association of antlers with teeth; and many more "frontlets" or crania which lack the teeth. Several hundreds of upper or lower jaws and numerous un-associated antlers, or parts thereof, are also in our collections. These serve as basis for the following characterization.

(a.) Antlers on both male and female, not in the young. This is probable from the fact that all our crania and frontlets have antlers. A young skull in the Carnegie Museum collections (type of "*Cosoryx agilis*" Douglass) lacks them but still retains most of the milk teeth.

(b.) Antlers are not more than once forked, except in one species or group of species. I have seen only three or four specimens of 3-tined antlers besides those figured by Cope.

(c.) The forking is not a progressive character, so far as the record shows. All our Pliocene specimens are single-forked. The type of *M. osborni* (Upper Miocene) is an old individual, but others of almost or quite as great wear in the molars have a simple two-tined antler.

\(^1\)He is evidently under the impression that the *M. osborni* skeleton is the only known specimen.
(d.) The “antlers” are unlike those of the Cervidae in their smooth hard surface. They differ equally from the soft-surfaced horn-cores of Bovidae, or from the rough surface of giraffid horns, but are quite exactly like the horn-cores of Antilocapride, save that they are oval and forked and provided with a burre, instead of being flattened and unforked and with no burre. They have some resemblance also to the antlers of deer “in the velvet” and do not differ so much from brocket antlers as from the larger and more complex types.

(e.) The burre at the base of the beam may be single, double or triple, in two cases quadruple. It is very easily broken off and leaves no perceptible scar beneath it, the surface of beam and stock being identical in character. The burre is the sole basis for the statement that “antlers” were deciduous. As a matter of fact they are NEVER FOUND BROKEN OFF AT THE BURRE. The fossil specimens are broken off frequently at the base of the stock, some of the orbit going with the antler and breaking off as it is knocked about. Or the antler breaks off anywhere along stock or beam. But a clean break at the burre I have never seen. This is a sharp contrast to the true fossil deer, among which the antler is customarily found broken off at the burre.

These data concerning the antler might seem open to two possible interpretations. Either the antler was NOT DECIDUOUS, but covered during life with a velvet or with a horny casing which split or peeled off periodically but not until a new protective casing had formed within it, the burre then representing the seasonal stoppage of growth and lime supply after the new growth of horn and horn-case had been completed. Or the habits of the Merycodus were such that its remains were never buried in stream-valley deposits except during the time that the antlers were in the velvet. It would seem a tenable hypothesis that the animal always retired to the mountains in late summer and autumn, drinking from the mountain brooks and never approaching the muddy streams of the plains except in the spring when the antlers were full-grown but still in the velvet.1 On the theory that the Merycodus antlers were deciduous like those of the Cervidae this hypothesis would explain the fact that the antlers are always found fossil in this condition, never rugose, and never shed. But it is very difficult under this supposition to explain the peculiar character of the three or four successive burrels all loosely attached to a beam continuous with the stock. In the deer the burre breaks off with the shed antler and a new one is formed at the base of the

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1This was, in fact, a suggestion made to me by Mr. Madison Grant when we were discussing the matter in 1902.
beam when the new antler ceases its growth. Obviously a multiple burr could not normally occur with a deciduous antler. But in *Merycodus* the multiple burr is certainly a normal character. It appears to me far more reasonable, therefore, to conclude that the bony horn-cores were not deciduous.¹

(f.) The horns are supraorbital (when the basiocular axis is horizontal) as in *Antilocapra* and many antelopes. In Cervidae the antlers are more posterior in position and the stock is usually plastered on to the side of the brain-case to some extent. In the larger and more progressive Bovidae the horns move backward during the growth of the individual and in primitive and juvenile deer the antler begins almost supraorbital, so that *Merycodus* may be said merely to retain the primitive relations of all Pecora in this respect.

II.—Characters of the Skull. The bending down of the basiocular on the basiocular axis is a progressive character developed to a marked extent in most Bovidae, to a lesser extent in some Cervidae. In *Merycodus* and *Antilocapra* it is strongly marked. This is a character that might very readily be the result of parallelism and it is not advisable to attach too much weight to it.

III.—Characters of the Teeth. The real weight of argument for relationship lies in the teeth. The molars are hypsodont, progressively so from first to third. They increase notably in size from first to third. The last upper molar tends (progressively) to establish a third lobe, and the last lower molar a fourth lobe. This is incipient in the Middle Miocene *Merycodus necatus*, variable in the Upper Miocene *M. necatus sabulonis*, established in the Lower Pliocene *M. altidens*, well established in *Capromeryx* and *Antilocapra* of the Pleistocene. The teeth have smooth surfaces and the molars no accessory cusps, resembling *Antilocapra*, Camelidae and most Bovidae, Unlike Cervidae or Giraffidae. The comparatively small simple and hypsodont premolars have the primitive pecoran construction of the crests—three inner transverse crests, one posterior outer one—from which *Antilocapra* has departed less than either Cervidae, Bovidae or Giraffidae. The construction in *Merycodus* is very close to that of *Blastomeryx; Leptomeryx* of the Oligocene presents a more primitive stage, as I have elsewhere attempted to show. There is, however, a certain angularity of outline and proportion, and relative reduction of the anterior premolars, in which *Merycodus* foreshadows *Capromeryx* and *Antilocapra*.

¹Scott in 1890, Bull. Mus. Comp Zoöl., XX, p. 84, observes that the burr of *Cosoryx* "can hardly be regarded as evidence that the antler was deciduous."
The antilocaprid characters of the teeth in *Merycodus* are far more than mere hypsodonty of the molars. But they must clearly be interpreted in light of the fact that this is a Miocene genus and must be compared with other Miocene genera in order to get a fair concept of its relative position in the phylogenetic tree. The primitive construction of the premolars is shared by *Blastomeryx*, *Dremotherium* and other early Cervidæ, as well as by the most primitive of the antelopes and giraffes. On the other hand, *Merycodus* lacks two characteristic Cervid features, the rugose enamel and the intercrescent basal pillars, already assumed by *Blastomeryx* and the *Palæomeryx* group and present in all Cervidæ and Giraffidæ, although almost lost in some modern deer. It has also already assumed certain specialized antilocaprid characters, the relative reduction of the premolars, especially the anterior ones, the increase in size and hypsodonty of the posterior molars, the third cusp on *m₃* and the fourth cusp on *m₂*, progressively developed in the later species.

There are several deer and small antelopes that have teeth quite as hypsodont as *Merycodus* but they do not assume the other characters cited, which are to be found united only in *Antilocapra*, although some of them occur sporadically among other ruminants. Thus *Rangifer* is what Doctor Winge asserts *Merycodus* to be—"merely a deer which has developed hypsodont teeth." But *Rangifer* retains all the Cervid characters in the teeth—the rugose enamel, the basal pillars on the molars, construction of the heel of *m₃*, the large size, broadly oval form, and particulars of construction of the premolars; and so do various other more or less hypsodont Cervidæ. *Merycodus* has none of them. The true antelopes include various hypsodont types, some of which approach *Merycodus* more nearly. The gazelle has the smooth molars with no basal cusps and about the same degree of hypsodonty. But the molars do not show the characteristic increase from first to third nor the tendency to form an extra posterior lobe; the premolars do not show the tendency toward a trigonal outline, the relative reduction and simplicity of the anterior premolars nor some other constructional peculiarities of detail. The several characters of the *Merycodus* teeth are seen combined in *Antilocapra* alone; they are not due to its hypsodonty nor explainable as parallelism.

For these reasons I have hitherto regarded the teeth of *Merycodus* as proving its affinity to *Antilocapra*, in spite of its supposedly cervid deciduous antlers. These constituted, after all, one character which,
remarkable as it was, could be explained as parallelism within the same large group. The teeth, on the other hand, showed a dozen or so non-correlated characters of affinity to Antilocapra and it was incredible that simultaneous parallelism could account for all of these. The antilopid or antilocaprid affinity was further confirmed by the sharp downward angulation of the basifacial axis and the supraorbital position of the horn, characters not peculiar to the antilopid division but characteristic of it as opposed to the cerviformia. The extreme reduction of the lateral digits, greater than among Cervidae and less than in Antilocapra or most true antelopes, again confirmed this view of its relationship; while the grooved back of the metapodials, to which Winge attaches great importance, was quite obviously a primitive character, both in theory and from the record, and is shown by all Miocene ruminants of any group at all, and retained by some antelopes as well as by most deer.

With many authors, however, the evidence of the antlers outweighed everything else. But if, as now appears, the "antlers" were not deciduous but their sheath periodically renewed as in Antilocapra, it does not appear that there is any evidence left for cervid affinities. All the characters conform in indicating antilocaprid relationship. On the question of whether or not the genus is a direct or approximate ancestor of Antilocapra, it is not necessary to enter here.

**Bovidae**

**Neotragocerus**

This genus was based upon a horn-core, with which were provisionally associated certain brachydont, smooth and simple antilopine upper molars. It was tentatively referred to the Tragocerine group but its affinities cannot be settled until the skull is known, or at least some positive association of horn and dentition. Dr. Joleaud in a recent publication has referred it to the Hippotragine group, which may perhaps prove to be correct; and in support of this reference it may be noted that two incomplete teeth in the 1918 collection have a rather marked resemblance to those of Hippotragus and it may be that these should be referred to Neotragocerus and the dentition provisionally associated with it in 1909 really belongs to Craniocerus or some undescribed genus.

It is at least equally probable that neither Neotragocerus nor Craniocerus have any near relationship with any of the Old World antelopes with which the imperfection of our knowledge has suggested comparison, and to discuss palaeogeographic theories based upon such flimsy
evidence appears to me an utter waste of time. The collections from the Chinese Pliocene now being studied by Professor Wiman of Upsala, together with further collections from the Tertiary of China now being made by the Chinese Geological Survey and The American Museum of Natural History, will, one may hope, provide really sound and adequate evidence as to the Tertiary distribution and migrations of the several groups of antelopes, and more complete and better associated American material may give definite and certain data as to the affinities and derivation of the New World genera. Until these data are at hand such positive and detailed conclusions as Dr. Joleaud has expressed are merely proof that he does not appreciate the inadequacy of the evidence cited in support of his theories or the amount and gravity of the objections that stand in their way.

CHELONIA

Platypeltis miocænus, new species

Type.—No. 6298, carapace lacking the nuchal bone, from paniensis zone, Sinclair draw.

Characters.—Shell comparatively narrow, as in P. ferox. Vacuity between nuchal, anterior neural and anterior costal, as in P. leucopotamica.
Fig. 62. *Platypeltis miocenus*; carapace, three-fifths natural size. Lower Snake Creek beds, *M. paniensis* zone.

This is the first carapace of a soft-shell turtle to be reported from the American later Tertiary.

**Chelydrops stricta**, new genus and species

**Type.**—No. 6297, an incomplete skull from the *paniensis* zone, Sinclair draw.

**Characters.**—Size of modern snapping turtle but skull considerably narrower, muzzle more pointed and decurved; a central ridge on the jaw-plate, much as in
Fig. 63. *Chelydrops stricta*; front of skull, side and palatal view, natural size. Type specimen, No. 6297, Snake Creek beds, *M. paniensis* zone.
Testudo. A much smaller skull, No. 6296, has a very sharply pointed and decurved beak and about the same relative width of the jaw.

This appears to be the first record of the snapping turtle from the Tertiary. It has been recorded by Doctor Hay from the Pleistocene upon fragments of the carapace. It is probable that the failure to recognize it hitherto in the later Tertiary formations is due not to its absence but to the uncharacteristic form of its shell elements and the tendency of the shell to break up into separate parts, which have been mistaken for the ubiquitous and unvalued tortoise fragments.

**Testudo orthopygia angusticeps**, new mutant

**Type.**—No. 6295, a skull with greater part of carapace and plastron doubtfully associated, from the *Merychippus primus* zone, Stonehouse draw.

**Characters.**—Skull somewhat narrower than in most large tortoises of the Miocene and Pliocene in which the skull is known; slightly narrower than in *T. osborniana*, with orbits facing more laterally, interorbital space wider, arches somewhat more massive. The shell attains a large size, up to 750 mm. according to our estimates, the width of the ? type shell being 450 mm.

Comparison of the skulls of *T. thomsoni* of the White River with the present species, *T. osborniana* of the Pawnee Creek, *T. gilberti* (? = *orthopygia*) of the Republican River, and some large modern tortoises, shows apparently a progressive lightening of the skull, expansion of the arches forward and upward shift of the direction of the eyes, etc. Our material is not adequate to test the validity of this apparent progress. I venture to remark that a more careful search for skulls of extinct chelonians, and less reliance upon the characters of the carapace and plastron might perhaps aid in clearing up the real affinities of both fossil and recent members of the order. A classification of mammals based primarily upon the number and relations of the ribs and taking no serious account of the skull would probably be as unsatisfactory as are the current classifications of fossil chelonians.

**Testudo orthopygia** Cope

An incomplete skull, many parts of the carapace and plastron from the Lower Snake Creek beds are referred to Cope's species, of which the type is from the Republican River beds. Specimens range from size approximately equal to the type shell, A. M. N. H. No. 6108, down to six inches in length. None of the shells agree at all closely either with the type or with each other, but they are somewhat nearer, on the whole, to *orthopygia* than to any of the numerous "species" of *Testudo* that Doctor Hay has described and illustrated in his monograph.