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VI. — THE CARNIVORA AND INSECTIVORA OF THE BRIDGER
BASIN, MIDDLE EOCENE.

By W. D. MATTHEW.

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(Continued from 3d page of cover.)

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VOLUME IX, PART VI.

THE CARNIVORA AND INSECTIVORA OF THE BRIDGER BASIN,
MIDDLE EOCENE.

MEMOIRS
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY.

PART VI.—THE CARNIVORA AND INSECTIVORA OF THE BRIDGER
BASIN, MIDDLE EOCENE.

BY W. D. MATTHEW.

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I. INTRODUCTORY.

During the seasons of 1903-6 the American Museum has sent expeditions into the Bridger Basin of southwestern Wyoming to expand and complete the collections made ten years before, and extend as much as possible our knowledge of the richest and most important of the Eocene faunæ. Those expeditions were a part of a general plan for the more thorough exploration of the Tertiary continental formations of the Western States, arranged and directed by Professor Henry Fairfield Osborn, with a view not merely to add to the collections of extinct vertebrata, but by means of careful stratigraphic work and exact records, to enable us to correlate the various formations more certainly and to supply more complete and accurate data for the study of the history and evolution of the mammalia.

The expeditions in the Eocene formations were placed in charge of Mr. Walter Granger of the Department of Vertebrate Palæontology. He was assisted in 1903 by Messrs. Albert Thomson, L. S. Quackenbush and O. P. Hay; in 1904 by Messrs. Paul Miller, Geo. Olsen and the present writer; in 1905 by Messrs. Miller, Olsen and W. J. Sinclair, and in 1906 by Messrs. Miller and Olsen. Thanks to the skill and energy of Mr. Granger and his assistants, a remarkably fine series of fossil mammals and reptiles was secured from the Bridger Basin, especially rich in the smaller fauna, and containing more or less complete skeletons of many new or little known species. The Carnivora and Insectivora, forming a considerable and very interesting part of the collection, were assigned by Professor Osborn to the writer for study and description and form the subject of the present memoir. For the preparation of these specimens I am chiefly indebted to the skilful work of Mr. Albert Thomson, and to Mrs. L. M. Sterling for most of the drawings. The photographs were made by Mr. A. E. Anderson by especial methods which he has designed or adapted for the illustration of specimens of this description.

HISTORY OF EXPLORATION.

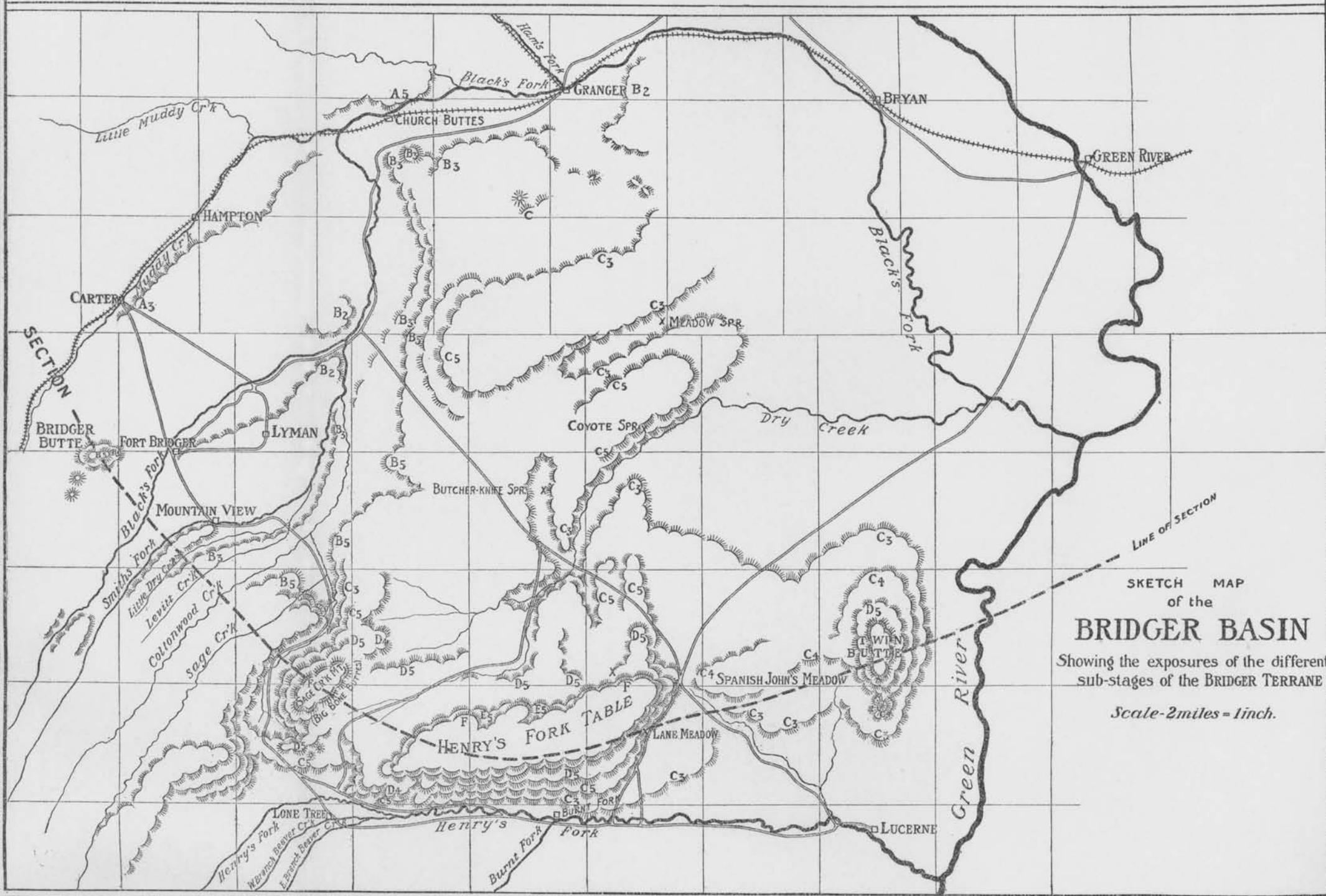
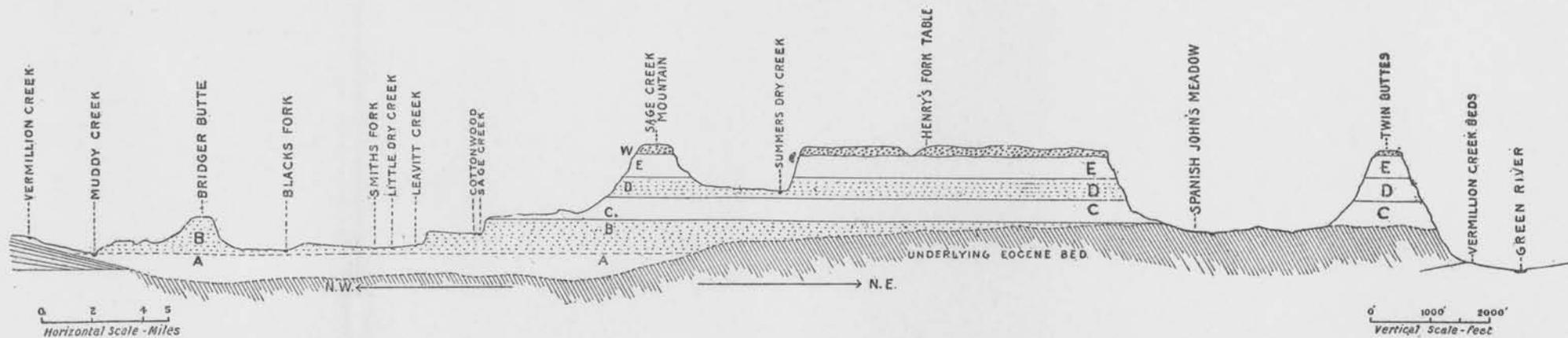
The first fossils from the Bridger Basin, discovered by Dr. J. Van A. Carter and by the Hayden Survey parties, were described by Dr. Joseph Leidy in 1868-70, and figured in his Contributions to the Extinct Vertebrate Fauna of the Western Territories (Report U. S. Geog. and Geol. Sur. Terr., Vol. I, 1873). In 1870 Prof. O. C. Marsh commenced an exploration of the Basin which he continued through various assistants for a number of years, obtaining a splendid collection, left in his will to the Museum of Yale University. Preliminary

notices of most of the new species in the collection were published by him in 1872, and in 1884 his monograph of the Dinocerata gave full descriptions and figures of that group. In 1872 Prof. E. D. Cope was attached as palæontologist to the Hayden Survey and obtained an important collection in the Bridger Basin, to which he added during the following year. It was purchased, with the remainder of his collections of fossils, by the American Museum, where it is now deposited. Cope's collections of 1872 and 1873 were fully described and figured in various publications, especially in his *Tertiary Vertebrata* (Report U. S. Geol. and Geog. Sur. Terr., Vol. III, 1885), but the much larger collections made by and for Professor Marsh were known up to the date of his death only from his brief preliminary descriptions, except for the Dinocerata and Tillodontia. Since then the Carnivora and a part of the Primates have been fully figured and described by Dr. J. L. Wortman (*American Journal of Science*, 1901-3).

In 1877 and 1886 the Princeton expeditions obtained a number of important types from this Basin, and in 1893 the American Museum Expedition under Dr. Wortman was very successful in obtaining complete skulls and skeletons of the larger characteristic types. Descriptions of some of the more important specimens obtained for the Princeton and American Museums have been published by Scott, Osborn, Wortman and Earle in various contributions.

The present memoir is based upon the collections made by the Museum expeditions of 1903-6. Through the courtesy of the curators of the Yale, Princeton and National Museums I have been able to compare all the type specimens of Bridger Carnivora and Insectivora with the new material to be described, and to revise the identifications and arrangement of the species. I take pleasure in acknowledging the liberal spirit with which these gentlemen have accorded me every facility possible for examination and comparison of types.

In taking up the subject it appears best to treat first of the Carnivora, since the collection is exceptionally rich in complete skeletal material of most of the genera of this order, and so admirably supplements previous collections that we can now give a fairly complete account of the osteology of nearly every genus. The Bridger Carnivora, moreover, form a comparatively homogeneous and well defined group, and a clear understanding of the essential features and scope of this group and the relationship of its members to each other and to modern Carnivora, enables us better to estimate the position and relations of contemporary groups whose characters are less fully known or less clearly understood. The Insectivora include a great variety of very dissimilar types, for the most part very imperfectly known, and apparently not nearly related to each other or to the modern representatives of the order. They approach so closely to the primitive Carnivora on one hand and to the primitive monkeys and rodents in other directions, that in many instances their true position can be decided only by a careful study of all parts of the skeleton.



Sketch Map of the Bridger Basin. Showing the Exposures of the different Horizons and the principal collecting localities. Redrawn by L. M. Stirling from the original by W. D. Matthew and Walter Granger, 1902. Published by courtesy of the United States Geological Survey and of Professor Henry Fairfield Osborn. Scale, 6 miles = 1 inch.

STRATIGRAPHY AND FAUNAL DIVISIONS OF THE BRIDGER FORMATION.

This section is based mainly upon observations made by the writer and Mr. Walter Granger during the season of 1902 and 1904, in determining faunal levels in the Bridger formation for the U. S. Geological Survey under instructions from Prof. H. F. Osborn, Palæontologist to the Survey. Through the courtesy of the Survey I have permission to abstract from the unpublished report such matter as may be desirable for publication elsewhere.

The Bridger formation consists of a series of gray and green tuffs, sandy or clayey, covering an area about forty miles wide and sixty miles from north to south, situated west of the Green River and principally to the south of the Union Pacific Railroad. Its southward limit is the foot-hill slope of the Uinta Mountains; westward, northward and eastward it thins out and has been removed by erosion from an unknown area — probably not very great — of further extension. It overlies the Green River lacustrine beds and apparently passes gradually into them at its base. The upper part of the formation is preserved only along the southern margin where it is protected by a capping of coarse conglomerate of supposed Pleistocene age, the Wyoming Conglomerate, more extensively developed on the flanks of the Uinta Mountains.

The entire thickness of the formation is about 1800 feet, as shown along the road from the railroad station at Carter southward to Henry's Fork. It consists of alternating sandy and clayey or shaly tuffs, with occasional thin-bedded calcareous layers from a few inches to four or five feet in thickness. Some of these calcareous layers are quite extensive; they are often crowded with fresh-water shells, and usually laminated, more or less siliceous, sometimes quite flinty. Toward the base of the formation they are more numerous and pass into the laminated calcareous shales of the Green River formation. The main mass of the Bridger is comparatively homogeneous; the coarser beds show a great deal of cross-bedding and are of very irregular distribution so that it is usually impossible to follow them for any considerable distance. The calcareous layers are much more constant; certain ones can be traced over a considerable part of the basin, and owing to their resistance to erosion they play an important part in the modelling of the surface topography, the country descending towards the north in a series of well marked benches. Beds of volcanic ash occur especially towards the upper part of the formation, and as Sinclair has shown, its whole mass, excepting the calcareous layers, is made up entirely of volcanic materials more or less redistributed by water. In the upper 500 feet the ash beds become more abundant and heavy, the tuffs are softer and finer, contain in some levels large quantities of gypsum, and are prominently color-banded.

Fossil vertebrates are found throughout the formation, but in the basal beds mammals are rare, although reptiles, fish, and fresh-water mollusca are

abundant. The uppermost beds are very barren of fossils but a few fragmentary mammal remains sufficiently prove that they belong to the Bridger age. The main body of the formation is fossiliferous throughout, although certain levels and localities have proved especially rich.

It had been recognized for some time that the fauna in the upper levels differed more or less from that in the lower beds, and in 1899 the writer tabulated the localities from which the then known Bridger species had been obtained, with a view to providing data for faunal division so far as the records would permit. Wortman in 1901 recognized a division into Upper and Lower Bridger according to the localities of the specimens under description. The reconnaissance by the writer and Mr. Granger in 1902 was planned by Professor Osborn as a preliminary to a more thorough search for fossils and accurate recording of the levels of the materials found. The division of the formation for this purpose was found to be most conveniently made by means of the more widespread calcareous layers and the benches which they supported, the inconstant alternations of sandstone and clay being of little use. The Bridger was accordingly divided as follows, beginning at the top:

Horizon E, 500 feet. Soft banded tuffs with heavy volcanic ash layers. Nearly barren of fossils and with large gypsum content.

Horizon D, 350 feet. Harder gray and greenish gray sandy and clayey tuffs with one or more ash beds. Defined inferiorly by a persistent calcareous stratum, the Lone Tree White Layer. Another persistent stratum, the Upper White Layer is about 75 feet from the top. Fossils abundant and varied.

Horizon C, 300 feet. Tuffs very similar to the preceding. Defined inferiorly by a heavy and persistent calcareous stratum, the Sage Creek White Layer, shown at Sage Creek Spring. Another persistent stratum of flinty lime, the Burnt Fork White Layer, lies about the middle of the horizon. Fossils abundant and varied.

Horizon B, 450 feet. Tuffs similar to the above. Includes two principal benches separated by the Cottonwood White Layer. Fossils abundant and varied, especially in the lower part of this horizon in which the largest number of well preserved skeletons have been found.

Horizon A, 200 feet. Predominant calcareous shales alternating with tuffs like the preceding. A few fragmentary mammals have been found in this horizon, fish, crocodiles and turtles are common and fresh-water mollusca very abundant, many layers being shell limestones.

Horizon E appears only in the southern part of the basin on both sides of the divide between Henry's Fork and Dry Creek. Horizon D has much the same occurrence, but extends all along the divide to the north of Henry's Fork. Horizon C underlies it on the south side and extends further to the north, in the basin of Dry Creek, and as far as Sage Creek Spring on the stage road between Lone Tree and Fort Bridger. Horizon B is not present in the southern part of the basin but is extensively exposed in the central and northern parts, westward as far as Bridger Butte, eastward nearly to Green River, and north of the railroad as far as Opal. Horizon A underlies it, appearing south of Carter, in the valley of Muddy Creek and around the eastern, northern and western margins. Neither Horizon A nor B can be recognized in the

southern part of the basin, the three upper horizons in the section cut by the valley of Henry's Fork resting upon thin bedded lignitic shales, which might be regarded as equivalent in age to the Green River or to Green River and Lower Bridger, but have no correspondence to the typical development of the lower horizons. They may be a marginal phase of the lacustrine Green River, and rest in their turn upon the Vermillion Creek beds. The relations and identity of these underlying formations were outside the scope of the reconnaissance, of which the aim was merely to determine the faunal levels within the Bridger formation.

Since the upper horizons, C, D and E, are found only in the southern part of the basin and the lower ones, A and B, only in the central and northern part, the recorded localities of the numerous described fossils partially settle their level. For the more exact recording of the collections made by the American Museum parties, the horizons were further divided into five numbered levels corresponding to the basal, lower, middle, upper and top levels of each horizon.

At Grizzly Buttes, an escarpment along Smith's Fork four or five miles south of Fort Bridger, the lower half of Horizon B is exposed. This is the richest collecting ground in the basin; thousands of specimens have been taken from it, and many skulls and skeletons more or less complete. Nearly all of them have come from the lower part of the escarpment, and are recorded as B₂. The escarpment along Cottonwood Creek, at a slightly higher level, up to the middle of Horizon B, has furnished a number of the most complete skeletons, recorded as B₂ and B₃. A few miles south of Granger station on the Union Pacific Railroad the lower and basal levels of Horizon B were found rich in fossils, the level being chiefly B₁.

In the southern part of the basin Horizons C and D are mostly exposed in association and are fossiliferous at all levels, the various white levels being especially rich in small species. The numerous described species recorded as coming from Henry's Fork or Twin Buttes are all from Horizon C or D, but there is no way to ascertain their level more exactly.

With these and various further data, which need not be detailed here, I have compiled the following list of the Bridger fauna, with the level of each type, and range of the species so far as it can be ascertained. Except for the Carnivora and Insectivora the list is a provisional one; and it will be considerably extended when the various groups have been more thoroughly studied.

LIST OF THE BRIDGER MAMMALS WITH HORIZONS AT WHICH THEY ARE FOUND.

PRIMATES (Lemuroidea) ¹		Type sp'm.	Ref'd sp'ms in Am. Mus.
ADAPIDÆ			
<i>Notharctus tenebrosus</i> Leidy		B	} B
" (<i>Tomitherium</i>) <i>rostratus</i> (Cope)		B ₂	
" (<i>Limnotherium</i>) <i>tyrannus</i> (Marsh)		?C	
" " <i>affinis</i> (Marsh)		B ₂	
" (<i>Thinolestes</i>) <i>anceps</i> (Marsh)			
" (<i>Telmatolestes</i>) <i>crassus</i> (Marsh)		C or D	C & D
<i>Pelycodus</i> sp. indesc.		B ₂	B ₁ , B ₂
ANAPATOMORPHIDÆ			
<i>Omomys carteri</i> Leidy 1869		B ₂	B
<i>Hemiacodon nanus</i> Marsh 1872			
<i>Palæacodon vagus</i> Marsh 1872			
<i>Omomys</i> (<i>Hemiacodon</i>) <i>puccillus</i> (Marsh) 1872		B or C	
" <i>ameghini</i> Wortman 1904			
<i>Hemiacodon gracilis</i> Marsh 1872		C or D	C & D
" <i>pygmaeus</i> Wortman 1904		C	
<i>Euryacodon lepidus</i> Marsh		B	?C
<i>Anaptomorphus æmulus</i> Cope		B	
" sp. indesc.			D ₄
<i>Washakius insignis</i> Leidy 1873			C & D
" sp. indesc.		C ₂	
Gen. indesc.			B ₁
Gen. indesc.			B ₁
? <i>Smilodectes</i> (<i>Hyopsodus</i>) <i>gracilis</i> (Marsh) ² 1871			
MIXODECTIDÆ			
<i>Microsyops</i> ³ (<i>Limnotherium</i>) <i>elegans</i> (Marsh) 1871		B ₂	} B
<i>Microsyops gracilis</i> Leidy 1872			
<i>Mesacodon speciosus</i> Marsh 1872		B ₂	
<i>Palæacodon verus</i> Leidy 1872			
<i>Microsyops</i> (<i>Bathrodon</i>) <i>typus</i> (Marsh) 1872		B ₂	} C & D
" " <i>annectens</i> (Marsh) 1872		C or D	
" <i>schlosseri</i> Wortman 1903		C or D	
INSECTIVORA			
APATEMYIDÆ			
<i>Apatemys bellus</i> Marsh 1872		C or D	D
" <i>bellulus</i> Marsh 1872		C or D	C
<i>Uintasorex parvulus</i> , gen. et sp. nov.		D ₂	
<i>Trogolemur myodes</i> , gen. et sp. nov.		B ₁	

¹ Anthropoidea auct. Wortman; Mesodonta of Cope and Osborn. The synonymy in this group is mainly upon Wortman's authority.

² "Microsyopsidæ" (= Mixodectidæ) auct. Wortman.

³ Provisionally referred to the Mixodectidæ. This genus, and *Mixodectes* as well, may pertain to the Insectivora. See p. 546.

INSECTIVORA (<i>Continued.</i>)		Type sp'm	Ref'd sp'ns in Am. Mus.
TALPIDÆ			
<i>Nyctitherium velox</i> Marsh 1872		C or D	D
“ (<i>Talpavus nitidum</i> (Marsh 1872)		C or D	C
“ <i>priscum</i> Marsh 1872		C or D	
“ <i>curtidens</i> , sp. nov.		C ₃	C
“ (<i>Nyctilestes serotinum</i> (Marsh 1872)		B	
<i>Entomacodon minutus</i> Marsh 1872		C or D	C
<i>Centracodon delicatus</i> Marsh 1872		C or D	
<i>Myolestes dasypelix</i> , gen. et sp. nov.		B ₂	C and D
<i>Entomolestes grangeri</i> , gen. et sp. nov.		B ₂	?C and D
(<i>Entomacodon angustidens</i> Marsh 1872)		B ₂	
<i>Centetodon pulcher</i> Marsh 1872		C or D	
“ <i>altidens</i> Marsh 1872		C or D	
LEPTICTIDÆ			
<i>Phenacops incerta</i> gen. et sp. nov.		C ₄	
HYOPSODONTIDÆ			
<i>Hyopsodus paulus</i> Leidy 1870		B ₂	B
<i>Microsypops vicarius</i> Cope 1872		B ₂	
<i>Lemuravus distans</i> Marsh 1875			
<i>Hyopsodus minusculus</i> Leidy 1873		B ₂	B ₁
“ <i>marshi</i> Osborn 1902		C	C
“ <i>despiciens</i> , sp. nov.		D ₄	C and D
“ <i>lepidus</i> , sp. nov.		C	C and D
PANTOLESTIDÆ			
<i>Pantolestes longicaudus</i> Cope 1872		B ₂	B, C, D
<i>Passalacodon littoralis</i> Marsh 1872		C or D	
<i>Pantolestes natans</i> sp. nov.		C ₃	C & D
“ <i>phocipes</i> sp. nov.		D ₂	C & D
“ <i>intermedius</i> sp. nov.		B ₂	B
“ (<i>Anisacodon elegans</i> (Marsh 1872)		C or D	C, D
CARNIVORA (including Creodonta)			
MIACIDÆ			
<i>Viverravus gracilis</i> Marsh 1872		B ₂	B, C, D
<i>Harpalodon vulpinus</i> Marsh 1872			
<i>Viverravus minutus</i> Wortman 1901		B ₂	B
“ <i>sicarius</i> sp. nov.		B ₂	B
<i>Miacis parvivorus</i> Cope 1872		B ₂	B
“ (<i>Harpalodon sylvestris</i> Marsh 1872		C or D	C
“ (<i>Vulpavus harger</i> Wortman 1901		C or D	
<i>Uintacyon edax</i> Leidy 1873			
“ <i>vorax</i> Leidy 1873		?C	B
“ (<i>Miacis bathygnathus</i> (Scott) 1887		C ₄	
“ <i>jugulans</i> sp. nov.			C & D
“ <i>major</i> sp. nov.		C ₃	C & D
<i>Oödetes herpestoides</i> Wortman 1901			
“ <i>proximus</i> sp. nov.		B ₂	B

300 MATTHEW, CARNIVORA AND INSECTIVORA OF THE BRIDGER BASIN.

CARNIVORA (Continued)		Type sp'in.	Ref'd sp'ns in Am. Mus.
<i>Vulpavus palustris</i> Marsh 1871	.	B ₂	B
" <i>profectus</i> sp. nov.	.	B ₂	B
" <i>ovatus</i> sp. nov.	.	B ₂	B
<i>Palæarctonyx meadi</i> gen. et sp. nov.	.	C	C & D
OXYÆNIDÆ			
<i>Patriofelis ulta</i> Leidy 1872	.	B	B
" (<i>Limnofelis</i>) <i>ferox</i> Marsh 1872	.	C or D	C & D
<i>Limnofelis latidens</i> Marsh 1872	.		
<i>Patriofelis leidyani</i> O. & W. 1892	.		
<i>Ælurotherium bicuspis</i> Wortman 1901	.	C or D	
<i>Limnocyon verus</i> Marsh 1872	.	B ₂	B, ?C
<i>Limnocyon riparius</i> Marsh 1872	.	B ₂	
<i>Thinocyon velox</i> Marsh 1872	.	B	B
" <i>medius</i> Wortman 1902	.	C or D	C & D
" <i>minimus</i> sp. nov.	.	B ₂	
<i>Machairoides eothen</i> gen. et sp. nov.	.	B ₁	B
HYÆNODONTIDÆ			
<i>Sinopa rapax</i> Leidy 1871	.	B ₂	B
" (<i>Stypolophus</i>) <i>pungens</i> (Cope) 1872	.	B	B
" <i>major</i> Wortman 1902	.	?B	D
" <i>minor</i> Wortman 1902	.	B	B
" <i>grangeri</i> Matthew 1906	.	B ₃	
<i>Tritemnodon</i> (<i>Limnocyon</i>) <i>agilis</i> (Marsh) 1872	.	B ₂	B
MESONYCHIDÆ			
<i>Mesonyx obtusidens</i> Cope 1872	.	B ₂	B
<i>Synoplotherium</i> (<i>Dromocyon</i>) <i>vorax</i> Marsh 1876	.	D	
<i>Harpagolestes macrocephalus</i> Wortman 1902	.	B ₂	
RODENTIA			
ISCHYROMYIDÆ			
<i>Paramys delicatus</i> Leidy	.	B	} B, C, D
" <i>delicatior</i> Leidy	.	B	
" <i>delicatissimus</i> Leidy	.	B	
<i>Pseudotomus hians</i> Cope	.	B	} B, C, D
" <i>robustus</i> Marsh	.	B	
" <i>superbus</i> O., S & S.	.	B	
<i>Sciuravus nitidus</i> Marsh	.	B ₂	} B, C, D
" <i>undans</i> Marsh	.	B ₂	
" <i>parvidens</i> Marsh	.	B ₂	
" sp. div.	.		
<i>Mysops fraternus</i> Leidy	.		
" <i>minimus</i> Leidy	.	B	
<i>Colonymys celer</i> Marsh	.	C or D	
<i>Taxymys lucaris</i> Marsh	.	C or D	
<i>Tillomys senex</i> Marsh	.	C or D	
" <i>parvus</i> Marsh	.	B	

	Type sp'm.	Ref'd sp'ns in Am. Mus.
TILLODONTIA		
ANCHIPPODONTIDÆ		
<i>Trogosus castoridens</i> Leidy	B ₂	
" (<i>Palæosyops</i>) <i>minor</i> Marsh	B ₂	
<i>Tillotherium hyracoides</i> Marsh		
" <i>fodiens</i> Marsh	C or D	
" <i>latidens</i> Marsh		
TÆNIODONTA		
STYLINODONTIDÆ		
<i>Stylinodon mirus</i> Marsh		
EDENTATA		
METACHEIROMYIDÆ		
<i>Metacheiromys marshi</i> Wortman		
" <i>dasypus</i> Osborn	B ₂	
" <i>tatusia</i> Osborn	B ₂	
" sp.		D
AMBLYPODA		
EOBASILEIDÆ (UINTATHERIIDÆ)		
<i>Uintatherium robustum</i> Leidy	C	} C & D
" <i>latifrons</i> Marsh	C or D	
" <i>leidyanum</i> Osborn, Scott & Spier	C ₅	
" (<i>Tinoceras</i>) <i>anceps</i> (Marsh)	C ₁	
" " <i>crassifrons</i> (Marsh)	C or D	
" " <i>hians</i> (Marsh)	"	
" (<i>Dinoceras</i>) <i>mirabile</i> (Marsh)	"	
" " <i>agreste</i> (Marsh)	"	
" " <i>laticeps</i> (Marsh)	"	
" " <i>lucare</i> (Marsh)	"	
PERISSODACTYLA ¹		
HYRACHYDONTIDÆ		
<i>Hyrachyus agrarius</i> Leidy	B	
" <i>eximius</i> Leidy	C or D	
" <i>intermedius</i> Osborn, Scott & Spier	C or D	
" <i>crassidens</i> Osborn, Scott & Spier	C or D	
" <i>paradoxus</i> Osborn, Scott & Spier		
" <i>princeps</i> Marsh	C or D	
" <i>imperialis</i> Osborn, Scott & Spier	"	
<i>Colonoceras agrestis</i> Marsh		
LOPHIODONTIDÆ		
<i>Helaletes boöps</i> Marsh	B	} B
" (<i>Hyrachyus</i>) <i>nanus</i> Leidy	B	

¹ All genera are arranged according to Osborn's classification. All the Bridger Perissodactyls are, however, quite nearly related and present no such diversity of structure in teeth, skull or skeleton as the specialized Perissodactyls of the later Tertiary. In the type of classification adopted by Gill and Cope and generally by English authors, these primitive Eocene types would be grouped under the single family Lophiodontidæ.

PERISSODACTYLA (Continued)		Type sp'm.	Ref'd sp'ms in Am. Mus.
TAPIRIDÆ			
<i>Isectolophus (Helaletes) latidens</i> (S. & O.)	.	C or D	C or D
" <i>modestus</i> (Leidy)	.	C or D	
EQUIDÆ			
<i>Orohippus</i> ¹ (<i>Lophiotherium</i>) <i>ballardi</i> Marsh	.	B	} B, C, D
" (<i>Lophiodon, Helohippus</i>) <i>pumilus</i> (Marsh)	.	B	
" <i>pumilus</i> Marsh	.	B ₂	
" (<i>Helotherium</i>) <i>procyoninus</i> (Cope)	.	B	
" (<i>Lophiotherium</i>) <i>sylvaticus</i> (Leidy)	.	C or D	
" <i>agilis</i> Marsh	.	C ₅	
" <i>major</i> Marsh	.	B	
" (<i>Orotherium</i>) <i>wintanus</i> (Marsh)	.	C or D	
" (<i>Oligotomus</i>) <i>cinctus</i> Cope	.	B	
" (<i>Hyracotherium</i>) <i>osbornianus</i> Cope	.	B	
TITANOTHERIIDÆ ²			
<i>Palæosyops paludosus</i> Leidy	.	B ₁	} B, C, D
" <i>major</i> Leidy	.	B ₂	
" <i>humilis</i> Leidy	.	C or D	
" <i>junius</i> Leidy	.		
" <i>fontinalis</i> Cope	.	B	
" (<i>Limnohyops</i>) <i>robustus</i> Marsh	.	C or D	
" (<i>Limnohyus</i>) <i>diaconus</i> (Cope)	.	"	
<i>Telmatherium validum</i> Marsh	.	C or D	
" (<i>Leurocephalus</i>) <i>cultridens</i> S. & O.	.	"	
" <i>megarhinum</i> Earle	.		
ARTIODACTYLA			
HOMACODONTIDÆ			
<i>Homacodon vagans</i> Marsh	.	C or D	} B, C, D
" sp.	.		
<i>Microsus cuspidatus</i> Leidy	.	?B	
<i>Sarcolemur pygmaeus</i> Cope	.	B	B
" <i>furcatus</i> Cope	.		
<i>Nanomeryx caudatus</i> Marsh	.		
<i>Stenacodon rarus</i> Marsh	.	C or D	
<i>Antiacodon venustus</i> Marsh	.	C or D	
HELOHYIDÆ			
<i>Helohyus plicodon</i> Marsh	.	B ₂	B
" (<i>Elotherium</i>) <i>lentus</i> (Marsh)	.	C or D	D
" <i>validus</i> Marsh	.	"	
? " <i>Platygonus</i> " <i>zieglerei</i> Marsh	.		

¹ The synonymy and relations of these species will be cleared up in an article by Mr. Walter Granger now ready for publication. I have provisionally referred them all to *Orohippus*.

² The synonymy and relationships of this group will be cleared up in the monograph on the family by Professor Osborn now well advanced towards completion. The published species are listed under the two genera to which they have usually been referred.

RELATION OF UPPER AND LOWER BRIDGER FAUNÆ.

On the basis of the above list the faunæ of the Lower and Upper Bridger may be distinguished as follows:

Lower Bridger Horizon B	Upper Bridger Horizons C and D
PRIMATES	
<i>Pelycodus</i> }	{ <i>Notharctus</i>
<i>Notharctus</i> }	{ <i>Telmatolestes</i>
<i>Omomys</i>	<i>Hemiacodon</i>
<i>Anaptomorphus æmulus</i>	<i>Anaptomorphus</i> sp.
<i>Smilodectes</i>	
<i>Microsypops elegans</i> }	{ <i>Microsypops annectens</i>
" <i>typus</i> }	" <i>schlosseri</i>
INSECTIVORA	
<i>Troglemur</i>	<i>Apatemys, Uintasorex</i>
<i>Nyctitherium serotinum</i>	<i>Nyctitherium velox, nitidus, priscus, curtidens</i>
<i>Myolestes</i>	<i>Entomacodon</i>
<i>Entomolestes</i>	<i>Phenacops</i>
<i>Hyopsodus paulus</i>	<i>Hyopsodus despiciens</i>
" <i>minusculus</i>	" <i>lepidus</i>
	" <i>marshi</i>
<i>Pantolestes longicaudus</i>	<i>Pantolestes elegans</i>
" <i>intermedius</i>	" <i>natans, phocipes</i>
CARNIVORA	
<i>Viverravus gracilis</i>	<i>Viverravus ? gracilis</i>
" <i>minutus</i>	
" <i>sicarius</i>	
<i>Miacis parvivorus</i>	<i>Miacis sylvestris, hargeri</i>
<i>Uintacyon ? vorax</i>	<i>Uintacyon major, jugulans</i>
<i>Oödectes</i>	
<i>Vulpavus</i>	<i>Palæarctonyx</i>
<i>Patriofelis ulta</i>	<i>Patriofelis ferox</i>
<i>Limnocyon verus</i>	<i>Limnocyon ? verus</i>
<i>Thinocyon velox</i>	<i>Thinocyon medius</i>
<i>Machairoides</i>	
<i>Sinopa</i> sp. div. (common)	<i>Sinopa</i> sp. div. (rare)
<i>Tritemnodon</i>	
<i>Mesonyx</i>	<i>Synoplotherium</i>
<i>Harpagolestes</i>	
TILLODONTIA	
<i>Trogosus</i>	<i>Tillotherium</i>
AMBLYPODA	
	<i>Uintatherium</i>

The data as to the faunal distinctions in the remaining groups are not yet available. The above list, however, will suffice to show that the fauna of Horizon B is mostly distinct from that of Horizons C and D, only a few species passing through. A few genera are peculiar to the lower beds, a much larger number of new forms first appear in Horizon C and continue through to the top of D. In a few of the more abundant animals (*e. g.*, *Hyopsodus*) we are able to trace with some approximation to certainty the actual course of mutation from one species to another; and in cases where there is fair reason to believe the species or genera of the upper beds to be the direct descendants of those of the lower, I have connected them by dotted lines. But the more marked distinctions between the upper and lower faunæ are more probably due to migration rather than mutation¹.

The Dinocerata are strictly limited to the upper beds; no Amblypoda whatever have been discovered in the abundant and varied fauna of the lower Bridger. This is the most obvious faunal distinction. *Isectolophus* appears to be peculiar to the upper beds, and several of the genera of Primates, Insectivora and Carnivora; some others are peculiar to the lower beds; but in the less abundant genera this may be merely a matter of accident. With the more abundant forms we find in general that the species of the lower beds are represented by well distinguished species in the upper, sometimes by distinct genera, and that the difference is emphasized as we approach the uppermost levels, although there is a sharp faunal break between B and C.

CONDITIONS OF DEPOSITION.

It is only within the last few years that the character and origin of the continental Tertiary formation of the Rocky Mountain States and of corresponding formations in the interior of other great continents has been at all clearly understood — perhaps the modern view is hardly yet generally appreciated outside of the small contingent of field workers in this region. The hypothesis that they were deposited in vast lakes, universally accepted ten years ago, is still to be found in text-books, but as far as I know nearly all the field workers accept the view that they are in the main of sub-aërial origin,— flood-plains and channel deposits of rivers and in part of æolian origin. True lacustrine deposits are subordinate in extent and thickness, and are more sharply distinguished by the absence or extreme rarity of terrestrial fauna than by the abundance of aquatic types. In the subaërial formations lacustrine beds occur but appear to be mostly bayou, lagoon and backwater deposits, due to a local and temporary flooding of parts of the deposit plain, incident to the accumulation of the formation itself, and not caused by crustal deformation or mountain making processes.

¹ I use this term as defined by Waagen and commonly used in invertebrate palæontology, and not to express any belief in saltatory evolution. See under *Hyopsodus* p.

These processes are of course the prime cause of the accumulation of the formation, whatever the conditions of its deposition. A slow uplift either above or below a given area of drainage basin will cause accumulation of sediment within that area, in the one case by increasing the sediment load of the streams beyond their carrying capacity, by the more active erosion towards their sources, in the other by decreasing their carrying power owing to the lessened fall down to the point of obstruction. If the obstruction ridge below rises rapidly or the erosion in the upper part of the basin is slow, the combined processes of cutting through the obstruction and filling in behind it may be insufficient to prevent the reversal of the drainage slope, and an actual lake may be formed. But even when this is the case there will be in general a much more extended area of checked drainage above the lake and most of the sediment will be dropped within this area.

The part played by true æolian deposits in these formations and the criteria for their recognition are not yet clear. There is a general tendency to confuse æolian *deposits* with residual formations due to wind sorting. Most desert regions are covered in part with wind-blown sands, and the term æolian deposits is often but erroneously assumed to mean something analogous to these. In fact, such sand is the residuum of wind sorting of the superficial covering of exposed areas and the finer material is carried elsewhere and deposited as loess in areas where the surface is at least partially protected by vegetation.

The important part which æolian action has played in the origin of the Tertiary continental formations is enhanced by the discovery that their material is in large part volcanic ash. It has been known for many years that there were beds of unaltered or little altered ash in these formations.¹ But it was not until the elimination of the lacustrine theory² that the way was clear to appreciate the circumstances of deposition of the volcanic material. Merriam in 1901 concluded that the John Day formation was largely made up of volcanic dust more or less rearranged and sorted by stream action. Sinclair in 1906 found the Bridger formation to be of precisely similar origin, substantiating his view by microscopic examination of a large series of rock specimens. The similar Santa Cruz formation was shown by Hatcher in 1903 to be also of volcanic origin. Mr. Sinclair is now engaged upon a study of the proportion of volcanic ash in the composition of the principal Tertiary mammal-bearing formations of the West, and has already obtained some remarkably interesting results.

It will be very evident that a volcanic ash cannot be carried long distances

¹ The volcanic origin of the "lacustrine" Tertiaries of Idaho, Nevada and Oregon was recognized by the geologists of the Fortieth Parallel Survey, and volcanic ash beds were observed in the Tertiary of Montana and of the Great Plains. The latter were regarded by all writers as chiefly of normal sedimentary materials.

² *I. e.*, of the lacustrine theory as generally held twenty years ago, and especially developed in King's Fortieth Parallel Report (Vol. I, Systematic Geology) — the deposition of all or nearly all of the stratified non-marine Tertiary formations of the West in vast lakes of almost continental extent.

by water without becoming more or less unrecognizable. The Bridger beds show likewise a very imperfect sorting, seldom complete, but actual ash-beds are exceptional. We may suppose that the ash was scattered over the drainage basin by wind, but that the preservation and accumulation of the beds within the deposition area was due to the lessened gradient of the streams caused by obstruction in their lower course — if the drainage was on its present lines, by a rise in the Uinta Mountain range through which the Green River cuts its way to the south. This rise, early in the Eocene, blocked the basin and caused at first an extensive lake in which the Green River shales were deposited; as the river gradually cut its way through the Lodore cañon, the lake gave way to a broad flood plain in which were deposited the volcanic ash brought directly by the wind and that washed down from the slopes of the mountains to the southward, the whole being partially worked over and sorted by the streams flowing across the plain. As the deposit accumulated it banked up the streams within the basin and caused the area of deposition to extend further upstream and overlap the lower beds to the south and west. The presence of a large arboreal element in the fauna indicates that the Bridger Basin was heavily forested during the deposition of the fossiliferous beds; and the thin but extensive layers of shell-limestone that it was subject to repeated overflows which caused widespread but shallow lakes of clear water over considerable areas. Likewise we may infer from the presence of these lakes that the falls of volcanic ash were intermittent, not continuous, and from the amount of organic change in different races of animals we may infer that the accumulation of the beds was a slow process, extending over a considerable fraction of the Middle Eocene. If we should estimate the Cenozoic as three million years, the Eocene as one-third of that time, and the Bridger as one-tenth of the total Eocene, the fossiliferous beds of the formation, 1100 feet thick, would have accumulated at an average rate of thirteen inches per century. The average rate of volcanic fall within the deposition area would be but a fraction of this, since the deposit was doubtless greatly augmented by the volcanic material brought down by streams from the slopes of the basin. A deposit growing at some such rate as this, with a warm moist climate such as is generally held to have prevailed through the Eocene, would furnish the most favorable conditions for a rich forestation and an abundant fauna.

In Horizon E the conditions appear to have changed. Heavy and frequent beds of unsorted ash indicate a final and violent burst of volcanic activity, and the large amount of gypsum and absence of fossil remains that vegetation was destroyed and animal life thereby driven away and the district converted into a barren plain alternately submerged and desiccated. It is possible that climatic change was responsible for the barrenness and gypsum content of this horizon, but as the beds are distinguished throughout by a lack of sorting and settling, it appears probable that they were all rapidly deposited, and may

have accumulated fast enough to block the streams, which then, as now, carried a considerable content of dissolved lime and alkali salts derived from the leaching of the cretaceous beds through which they passed. The blocked streams would spread out into shallow and rapidly desiccating lakes and, partly by help of the fresh ash-beds, deposit their lime as sulphate, to be covered up by further falls and thus escape being re-dissolved.

RELATIONSHIP AND ADAPTATION OF THE FAUNA.

We cannot discuss the relationships of the Carnivora and Insectivora which form the subject of this memoir without some consideration of the fauna as a whole. Thanks to the recent explorations, this is now the best known of the Eocene faunæ, and so many of its characteristic types are known from the complete skeleton, that their position and relations can be quite certainly determined. The following list shows the extent of our acquaintance with the principal types.

PRIMATES (Lemuroidea):	
<i>Notharctus</i>	skull and most of skeleton.
Anaptomorphidæ	jaws and fragments of skeleton.
INSECTIVORA:	
<i>Hyopsodus</i>	skull and most of skeleton.
<i>Pantolestes</i>	skull and most of skeleton.
The remaining genera from jaws only.	
CARNIVORA:	
<i>Mesonyx, Sinopa, Tritemnodon</i>	complete skeleton.
<i>Limnocyon, Thinocyon, Vulpavus</i>	skull and most of skeleton.
<i>Patriofelis, Miacis</i>	parts of skull and complete skeleton.
<i>Oödectes, Palæarctonyx, Uintacyon</i>	jaws and part of skeleton.
<i>Viverravus</i>	skull, etc.
TILLODONTIA:	
<i>Tillotherium</i>	skull and skeleton (Yale).
RODENTIA:	
<i>Paramys, Pseudotomus, Sciuravus</i>	skull and complete skeleton.
EDENTATA:	
<i>Metacheiromys</i>	skull and complete skeleton.
TÆNIODONTA:	
<i>Stylinodon</i>	jaws and part of skeleton.
AMBLYPODA:	
<i>Uintatherium</i>	skull and complete skeleton.
PERISSODACTYLA:	
<i>Orohippus</i>	skull and skeleton complete.
<i>Helaletes</i>	skull and feet.
<i>Isectolophus</i>	skull.
<i>Hyrachyus</i>	skull and skeleton complete.
<i>Palæosyops</i> }	skull and all parts of skeleton.
<i>Telmatherium</i> }	

ARTIODACTYLA:

<i>Homacodon</i>	skulls, jaws and parts of skeleton.
<i>Helohyus, Sarcolemur</i>	} jaws and fragments of skeleton.
<i>Microsus, etc.</i>		

Taking the fauna group by group we may observe:

(1.) The Primates are all Lemuroids and include two principal groups, related to the typical Lemurs and the Tarsiidæ respectively. They have already assumed the unique peculiarities of the feet characteristic of the typical and tarsioid Lemurs.

(2.) The Insectivora form the most numerous element of the fauna. Out of 1007 catalogued specimens in three years' collections (1903-5), one third (337) were Insectivora. They include the largest members of the order, and a greater number of genera than any other group. The best known genera belong to primitive or archaic groups, not nearly related to the modern families, but with suggestive points of resemblance to Primates and Carnivora.

(3.) The Carnivora are both abundant and varied, mostly small species with teeth little specialized. The Adaptive Carnivora in particular appear to be a very flexible and progressive group; the Inadaptive types show less variety, and the archaic Mesonychidæ are rare and highly specialized.

(4.) Rodentia are abundant but not varied; two genera in a broad sense, cover all the species. *Paramys* is sciuroid and probably nearly related to the squirrels; *Sciuravus* is also rather unfortunately named, since it probably is not so near to the squirrels as to the Geomyoid group and to *Ischyromys*. No ancestral Hystricomorpha, Myomorpha nor Lagomorpha are recognizable, but the Sciuromorph families are probably traceable to a common beginning in the Eocene of North America.

(5.) Edentata and Tæniodonta. The remarkable little armadilloid form *Metacheiromys*¹ is no doubt of common ancestry with the true armadillos, but its highly specialized dentition does not point to any near relationship, and the common origin may well date back to pre-Tertiary times. The hardly less curious Stylinodontidæ are, as Scott² and Ameghino³ have shown, not at all near to the Ground Sloths and probably are not true Edentates; a comparison with the Effodientia shows some singularly close resemblances in the foot-structure, and they may represent an archaic group of this order. They can hardly have anything to do with the Condylarthra, where Ameghino is disposed to place them.

(6.) The Condylarthra have completely disappeared at the time of Bridger, and are not found in its fauna. The Amblypoda are represented only by the huge and highly specialized *Uintatherium*, which lasted into the Upper Eocene,

¹ Osborn, Bull. A. M. N. H., 1904, p. 163.

² Rep. Princeton Exped. Patagonia, Palæontology, Vol. I, p. 631.

³ Ann. Mus. Nac. Buenos Aires, 1906, ser. 3, Vol. VI, pp. 230-235.

but the order was evidently following the Condylarthra to extinction. These pseudo-ungulate orders, more nearly akin to Creodonts than to Perissodactyls and Artiodactyls, are typically Lower or Basal Eocene.

(7.) The Perissodactyls on the other hand are in their most flourishing condition, plastic, varied and abundant, but have not yet assumed the large size and high divergent specializations of the later Tertiary. All are functionally tetradactyl in the manus, tridactyl in the feet; all have short-crowned teeth of a rather similar pattern; and the characters of skull and skeleton show throughout their near relationship.

(8.) The Artiodactyla are in a very early stage of their evolution. They are of small size, rare and very incompletely known; all are bunodont, very similar in tooth pattern, and apparently nearly related. Their relationship to the early Selenodonts is as yet uncertain, but the little that is known indicates them as the common ancestral type from which the selenodont and bunodont Artiodactyls of the later Tertiary have diverged.

The knowledge of the complete skeleton in so many Bridger genera puts us in a position to estimate with some accuracy the habitat and adaptation of the fauna as a whole, and the conditions of life at that epoch. In the first place we may consider the arboreal, terrestrial, fossorial or aquatic adaptation. The fauna may be classed on these lines into:

- | | | |
|-------------------|---|--|
| I. Land animals | { | 1. Aerial.
2. Arboreal.
3. Terrestrial (Cursorial or Ambulatory).
4. Fossorial.
5. Amphibious. |
| II. Water animals | { | 6. Aquatic (fresh-water).
7. Marine. |

1. *Aerial*. Remains of birds are rare and fragmentary in the Bridger formation, and very little is known about them. It does not follow that birds were rare in the fauna, for their remains, on account of small size, habits, light and fragile bones, are comparatively rare in nearly all geological formations, and preserved in abundance only under certain exceptional conditions.

2. *Arboreal*. All the Primates belong to this group, all the adaptive Carnivora except *Viverravus*, and quite probably *Hyopsodus* and some of the smaller Insectivora, also the Rodentia in part at least. Out of 1007 specimens belonging to 46 genera of Bridger mammals, 13 genera, 184 specimens, may be regarded as certainly, and 11 genera, 485 specimens, as probably arboreal.

3. *Terrestrial* (Cursorial and Ambulatory). In this group I would place *Viverravus*, *Patriofelis*, all the Hyænodontidæ and Mesonychidæ, the Amblypoda, Perissodactyla and Arctiodactyla; altogether, 17 genera, 314 specimens of mammals. The lizards and some of the Chelonia are also probably to be classed here.

4. *Fossorial*. Some of the Insectivora may be fossorial, but there are no means of determining whether this is so. There do not appear to be any fossorial Carnivora or rodents. *Tillotherium*, *Stylinodon* and *Metacheiromys* are apparently the only fossorial mammals in the Bridger, and all three are extremely rare, although the conditions are favorable for preservation of fossorial animals. Total, 3 genera, 8 specimens.

5 and 6. *Amphibious* and *Aquatic*. It is practically impossible to recognize in a fossil skeleton the early stages of aquatic adaptation, and it is very likely that a part of the terrestrial fauna was more or less amphibious. The only mammal which I can recognize as certainly aquatic is the Insectivore *Pantolestes*; *Limnocyon* and other Carnivora may, however, be suspected of partly amphibious habits, from their parallelism in structure to the Mustelines. *Patriofelis* I regard as probably terrestrial of ambulatory adaptation, as will be discussed later. While aquatic mammals are rare, crocodiles, aquatic turtles and fish form a large element of the Bridger fauna, and fresh-water shells are very abundant throughout the formation. No marine animals are found.

The Bridger fauna then includes a large arboreal element, a large terrestrial element, in which the ambulatory types form a relatively large proportion, the cursorial types are but little specialized, and fossorial types are rare, and a large aquatic element mostly of reptilia, fish and invertebrates. It corresponds to the fauna of a heavily forested flood-plain, and may be compared most nearly to those found in the deltas of the great tropical rivers of modern time. The large arboreal and aquatic elements, the rarity of fossorial types, and the slight development of cursorial specializations among the terrestrial mammals, are in marked contrast to the fauna of an open plains country, in which arboreal types are absent, amphibious and aquatic types restricted in range and relatively scarce, fossorial types abundant, cursorial types numerous and highly developed, and ambulatory types uncommon. The secular progress from the one type of climatic and regional adaptation to the other, is very beautifully illustrated in the faunæ of the successive Tertiary formations of the Western States.

BRAIN DEVELOPMENT.

Professor Marsh and other authorities have already pointed out the small size and inferior organization of the brain in Eocene mammals, and its steady increase in size and complexity during the successive epochs of the Tertiary. His illustrations are drawn from the larger mammalia, but the principle is equally obvious in the smaller forms, and as the succession is more directly known in these, the increase in each race is more clearly apparent. Even in the inferior orders of Insectivora and Rodentia we find the brain case smaller than in their modern representatives of equal size. In the higher groups the advance is more noticeable. In every group indeed, there are laggards, and we may

find even among Primates or Carnivora modern survivors scarcely superior in brain capacity to the highest Bridger representatives. But if in each order we compare the highest developments reached in each successive epoch of the Tertiary, we find a marked and continuous increase, especially in the complexity and the relative size of the cerebral lobes. The modern arboreal mammals differ but little in the structure of limbs and feet from their Eocene progenitors, but in brain structure they show the same striking advance as do the modern terrestrial mammals which differ widely in adaptation of limbs and feet from their Bridger ancestors. Closely related to the development of the brain are the basicranial structures, widely diverged and much specialized in all the higher modern orders, but in the Bridger rapidly approaching a common type which must have characterized the early Eocene ancestors of all the placental mammals.

In no Bridger mammal does the cerebrum extend to any considerable extent under the frontal bones; in most of them it is entirely contained within the parietals. In all of them the brain-capacity compares fairly well with that of modern marsupials of corresponding size.

We may observe, however, certain important differences in the *proportions* of the cranial region between the more progressive and less progressive types. *In the former the cranial region is elongate, in the latter it is short.* This difference is independent of the length of the facial or of the middle portion of the skull, and appears to be of fundamental importance in *conditioning the progressiveness of the brain.* It is well illustrated by comparing the skull of a primitive Eutherian carnivore, such as *Didymictis* or *Viverravus*, with that of a carnivorous marsupial of corresponding size. The apparent brain capacity does not differ materially. But in the former the brain-case is elongate; the parietals are long and narrow; the basicranial region is long; the antero-posterior space enclosed between the sphenoidal group of bones bounding the brain-case anteriorly, and the occipital group bounding it posteriorly, is very considerable; the glenoid articulations are far in advance of the occipital condyles. In the latter the brain-case is short; the parietals above and the basicranial region below are short; the frontals extend far backward; the sphenoidal group are set much closer to the occipital group of bones; the glenoid articulations are but little in advance of the occipital condyles.

This difference in length of brain-case appears to be directly proportioned to the varying capacity of different races for progressive evolution. Among the types that we shall have occasion to take up we will find that the Insectivores rank next to the Marsupials; that the ancestors of the modern carnivora (Miacidæ) stand at the other extreme; and that the remaining groups of primitive carnivora form an intermediate series in which the length of the brain-case can be directly correlated with the progressiveness of the brain and the persistence of the phylum in geological time.

The meaning of this correlation will be clear if we consider the amount of

displacement and rearrangement of the other parts and organs of the head involved in any considerable increase in brain capacity, in the long-brained type of skull on the one hand, in the short-brained on the other. In the former the brain has abundant room for lateral expansion, and can fill up and occupy very considerable spaces in the occipital region, and press forward to a considerable extent, without serious disturbance or rearrangement of other parts and organs of the head, and without interfering with the action of the powerful jaw muscles in front and neck muscles behind. In the short-brained type the brain growth is hindered by the necessity for much more extensive rearrangement of other parts and organs of the skull in order to provide the necessary space for accommodation of the larger brain, and is very probably directly limited by the pressure from the temporal muscles in front and occipital muscles behind. Whether or no these are the controlling causes, the fact is quite clear that the dolichocranial type of skull is much more progressive, and that the brachycranial races show a more limited and retarded evolution in brain capacity.

I believe that the progressiveness and dominance of the higher groups of Eutherian mammals was very largely conditioned by this initial advantage in their greater capacity for brain development, and that the elongate cranial region was a principal, though by no means the only factor in facilitating the evolution of the brain.

The progressive increase in brain capacity is the underlying cause of numerous changes in the proportions and arrangement of the bones of the entire skull. The lateral expansion of the parietals and squamosals increases the area for attachment of the temporal muscles of the lower jaws — always exceptionally powerful in carnivorous animals — and consequently reduces the need for high sagittal and occipital crests to furnish additional attachment for these muscles. The postorbital constriction, bounding the cerebrum anteriorly, moves forward and increases in width with the progressive enlargement of this organ. The concave overhanging occiput is filled out from beneath and broadened considerably at the base, by the crowding backward of the cerebellum to make room for the larger cerebrum. The frontals are pushed forward and encroach upon the nasals, which in turn are shortened and narrowed in their posterior half. The orbits are moved further forward, in order to leave room behind them for the jaw muscles as well as to retain the normal relation of the orbit to the several cranial nerves which make their exit at its base. In consequence, the anterior margin of the orbit encroaches in its turn upon the facial expansion of the lachrymal and the adjoining parts of maxillary, jugal and frontal bones, until the lachrymal is wholly within the orbit. These, and numerous minor changes in the construction of the skull, are illustrated in detail in the comparisons of primitive with modern carnivora in this memoir. They are equally well shown in the evolution of other groups of mammals. It is as well to point out in advance that their fundamental cause and chief importance in the economy of the race is as adaptations to increasing brain capacity.

II. CARNIVORA.

GENERAL CHARACTERS OF THE ORDER.

This order includes, typically, the predaceous placental mammals, and a variety of related forms more or less omnivorous or frugivorous. Unlike the Insectivora or Ungulata these form a fairly compact homogeneous group, which has not yet lost its plasticity. Intermediate and generalized forms are dominant; extreme specialization is unusual, and in almost all respects there is a great deal of individual variation among species and adaptability to a change of habitat or environment. The various adaptive radiations within the order have not usually gone so far as to result in extinguishing the more generalized and intermediate members, and these have persisted with but little alteration or have in turn specialized in various directions paralleling the earlier adaptations. This process has been repeated several times in the more generalized families and on a minor scale in the more central genera in each family. In consequence the order presents numerous intermediate stages and variants towards its several adaptive specializations while the disentanglement of the various phyla and classification of the group are unusually difficult, although our acquaintance with fossil carnivora is relatively extensive. Unlike most of the herbivorous mammals, the specialization of the teeth has been chiefly in the direction of simplifying their structure instead of complicating it. It is therefore not so easy to distinguish in their modifications between resemblances which indicate relationship and those due to analogous variation, since in proportion as their structure is simpler the parallelism may be more exact. The feet likewise retain their generalized structure to a much greater extent than among most herbivorous mammals, and, as in the teeth, their conservatism and the frequency of parallel adaptations, make it often difficult to distinguish relationship from analogy. On the other hand the Carnivora are highly progressive in brain structure, ranking next to the Primates in this respect, and in the lack of satisfactory criteria in the more obvious characters of teeth and feet, the structure of the brain, and of the basicranial region of the skull, which is most directly dependent upon it, may assume a relatively high importance in the study and classification of the group.

Adaptive Radiation of the Teeth. The main lines of adaptation in the order have been from primitive partly insectivorous types, toward more directly predaceous types on the one hand and omnivorous or frugivorous types on the other, as shown in the specializations of the teeth; and from a more or less arboreal habitat to a more strictly terrestrial life and thence into various cursorial, fossorial or aquatic specializations as shown especially in the limbs and feet. The teeth in the primitive type consist of tritubercular upper and tuberculo-

sectorial lower molars, trenchant premolars, large piercing canines, and small incisors. The triangular upper molars and the trigonids of the lower molars alternate so as to produce a succession of small notched shearing edges, an oblique and a transverse shear to each pair. The heels of the lower molars impinge on the surfaces of the upper molars, mortar-and-pestle fashion, so as to produce a series of small crushing surfaces. In the predaceous adaptations the shearing edges and especially the oblique shear, are enlarged and extended, the tubercular dentition reduced, and one pair of shearing teeth enlarged and specialized so as to assume the chief work of flesh-cutting. In the omnivorous adaptations the tubercular teeth are enlarged and flattened, the shears reduced or converted into low crushing crests, the premolars more or less reduced.

Adaptive Radiations of Limbs and Feet. The feet in the primitive type of the Carnivora are five-toed with sharp claws, flexible wrist and ankle, and plantigrade gait. The astragalar trochlea is flat, the inter-carpal and inter-metapodial joints loose and the distal metapodial and phalangeal joints of ball-and-socket type, the feet being used for prehension as well as locomotion, as required in an arboreal animal. In the terrestrial modifications they may remain plantigrade or become more or less perfectly digitigrade, mainly in accord with the adaptation of the feet to various subsidiary purposes or their use solely for locomotion. In no case has the cursorial adaptation been carried so far as to produce an unguligrade type, but the parallelism with the digitigrade herbivora is more or less clearly marked in the deepening of the astragalar trochlea, compacting of the wrist and ankle, elongation and appression of the metapodials and conversion of their ball-and-socket distal joints into hinge joints, and in the broadening of the claws; also in the reduction of the first digit, producing a tetradactyl foot, or of the first and fifth producing a functionally tridactyl foot. Additional strength is given to the wrist, at the expense of some of its flexibility, by the consolidation of the scaphoid lunar and centrale into a single bone. The limbs elongate and the power of supination is reduced or lost, the femur and humerus compacted into the flank; the tail is reduced from its primitive importance as a balancing and perhaps prehensile organ, to subserve quite minor functions.

When the limbs and feet are adapted to fossorial habits their bones, especially in the fore limb, become short, stout and powerful, the feet very short and wide with powerful muscular attachments, short phalanges with ball-and-socket joints, and claws of great size slightly curved, and of round or oval section. In the aquatic adaptations the proximal parts of the members likewise become short and powerful but the distal parts are relatively elongate, the metapodials spreading, the phalanges especially long, the ball-and-socket joints are converted more or less completely into hinge joints, and the claws are flattened and reduced in size.

Progressive Evolution of the Brain. The brain of the earliest Carnivora¹ was small and of low type, inferior in size and apparently in organization to that of modern marsupials. Throughout the Tertiary there was a continuous increase in the size and complexity of the brain, which was probably the most important factor in securing the persistence and dominance of the more progressive races. As the evolution of the brain results in elaboration and complication of its structures, its various developments in the different families of carnivora might furnish important evidence as to their interrelationship. But we know very little about the brain structure of fossil carnivora.

The basicranial region affords characters of high importance, both as being less directly affected by adaptive modifications, and more directly dependent upon the structure of the brain. In the primitive type it is comparatively long and narrow, the foramina are all well separated, the tympanic bulla is not ossified, the paroccipital process is short spatulate and directed backward, and the mastoid process is distinct but small. The later carnivora show various modifications of the primitive type conditioned by growth of brain, width of skull, length of jaw and other factors. The tympanic bulla ossifies after two distinct plans; the chamber is formed either by expansion of the tympanic ring, or from a distinct ossification of the *os bullæ*, the tympanic remaining ring-shaped.

Classification. The Carnivora are usually divided into:

I. *Fissipedia* including the modern and later Tertiary land carnivora.

II. *Creodonta* including the Eocene land carnivora and a few specialized Oligocene survivors.

III. *Pinnipedia*,—seals and walruses.

To these have been recently added by some authors:

IV. *Archæoceti* or Zeuglodonts, a marine Eocene group formerly regarded as more nearly akin to the Cetacea.

The inclusion of the Zeuglodonts in the order is based upon the discovery in the Middle Eocene of Egypt of a primitive genus of this family which shows some marked points of resemblance to the Creodont *Hyænodon* and the inference made thereupon that they must be due to relationship. The most obvious resemblances are: (1) the backward extension of the molar series upon the zygomatic arch; (2) the shearing molars and trenchant premolars, singularly like those of *Hyænodon*; (3) the closing in of the postnareal gutter by approximation of the pterygoid plates, thus carrying the posterior nareal opening backward to the basicranial region. There are various other points of resemblance to primitive mammals generally, but as they are not peculiar to Carnivora they are no evidence of relationship. The chief objection to regarding the three characters cited as evidence of relationship is that they are specialized characters of *Hyænodon*, an Oligocene genus of cursorial adaptation and are not present in its more generalized ancestors of the early Eocene, nor in any primitive Creodonta.

¹ Compare *Arctocyon* and *Triisodon* of the Basal Eocene, *Didymictis* and *Sinopa* of the Lower Eocene.

Their presence in a marine mammal of Middle Eocene time cannot be due to relationship, for if it were it would be shown equally or more clearly in *Sinopa*, the early Eocene ancestor of *Hyænodon*. On the other hand the resemblance between *Protocetus* and the more generalized Creodonts does not indicate any very near relationship, except such as we should expect a primitive cetacean to show to the primitive members of other orders.

The Pinnipedia have always been included in the order Carnivora, but stand well apart from the land carnivora, and very little is known of their geological history. They were already well specialized in the Miocene. Their derivation has long been a subject of controversy and is likely to remain so. As I have elsewhere observed, we should not expect to find their ancestral series in the continental formations of the interior, but in the marine and semi-marine strata along the borders of the continents, and in these strata fossil mammals are rare and mostly fragmentary. From the morphologic point of view they present certain similarities to the Arctoidea, and Mivart, Huxley, Flower, and more recently Weber,¹ have regarded them as allied to that group and especially to the bears. Cope at one time suggested their derivation from *Synoplotherium*,² but this view was not repeated in his later discussions of the affinities of that genus. Wortman regards the seals as derived from the Oxyænidæ.³

So far as the relationship to the Arctoidea is concerned, there are several important similarities in the soft anatomy enumerated by Weber, which furnish a weighty argument for this derivation, and in addition the following skeletal characters may be cited in its support. The lachrymal is reduced or absent, as in Adaptive Carnivora, especially Ursidæ. The dentition is P₁, M₁, but a small M² sometimes present. P₁ are one-rooted. The dentition is therefore readily derivable from a type in which M₁ were large, and the molars behind it reduced and tending to disappear (Fissipedia and Adaptive Creodonta) but not from a type in which the posterior molars were larger than the anterior ones (Inadaptive Creodonta). The paroccipital process is short, stout and directed backward — as in the Ursidæ, the larger Mustelidæ, and all Creodonta. The astragalus is more like that of the Ursidæ, Mustelidæ and Amphicyons than like any known Creodont astragalus.

The relationship to the bears cannot be very close, since the Pinnipeds of the Miocene⁴ were already almost like their modern descendants, and the gap between them and Miocene land carnivora is wide. The derivation from the Oxyænidæ appears to be precluded by

(1.) The Oxyænidæ have a large lachrymal with a considerable semicircular expansion on the face.

¹ Die Säugethiere, p. 551.

² Proc. Am. Phil. Soc., 1873, p. 207.

³ Bull. A. M. N. H., 1894, p. 157; Am. Jour. Sci., 1902, Vol. XIII, p. 119; Science, July, 1906.

⁴ Known from the Antwerp basin and the Atlantic and Pacific coasts of this country.

(2.) The second lower molar in Oxyænidæ is progressively enlarged and specialized, while the first tends to reduction and early loss. If the seals were descended from this group the second molar should be the largest of the series, and invariably present, instead of invariably absent.

The supposed evidence for derivation of the Pinnipedia from the Oxyænidæ will be more fully discussed under that family. The objections apply to the other Inadaptive Creodonta with equal or greater force. In the present writer's opinion there is no evidence of any real weight to offset the several important morphologic resemblances to the Arctoid Carnivora, and it seems best to regard them provisionally as derived from this group.

EOCENE CARNIVORA: RELATIONSHIP TO FISSIPEDIA, ETC.

The Fissipedia are usually divided into seven families, Canidæ, Procyonidæ, Ursidæ, Mustelidæ, Viverridæ, Hyænidæ and Felidæ. *Cercoleptes*, usually placed in the Procyonidæ, is accorded family rank by many authorities, and *Proteles*, *Cryptoprocta* and other aberrant genera have been placed in distinct families by various authors. These families were distinguished primarily on tooth characters but are supported to a varying extent by characters of the skull and skeleton. They have been grouped into Arctoidea (Canidæ, Procyonidæ, Ursidæ and Mustelidæ) and Æluroidea (Viverridæ, Hyænidæ and Felidæ) mainly upon characters of the basicranial region, supported to some extent by characters of the soft anatomy. The family and group classification of the modern Carnivora is very ably discussed and clearly presented by Weber (*Die Säugethiere* p. 515-538).

All the post-Eocene carnivora, except a few Oligocene Creodont genera, fall into one or another of the modern families. Many of them appear to be annectant types so far as the dentition is concerned, but only in a few cases is the evidence of the teeth adequately supported by characters of skull and skeleton. The family relationships indicated by these annectant series are in some instances not in accord with the relationships indicated by the morphology of the modern genera. But it must be remembered that most of the extinct genera are known only from the jaws and teeth, and many of the phyla proposed upon tooth characters have broken down in the light of more complete knowledge. It will be shown in the course of this memoir that the supposed derivation of the Felidæ from *Palæonictis* is erroneous, and that several other supposed phyletic series are either doubtful or demonstrably incorrect in the light of more complete knowledge of the skulls and skeletons of Eocene Carnivora.

The Eocene Carnivora include the ancestral types of the more recent groups and a number of side branches which have not survived. They are distinguished from the Fissipedia by a number of primitive characters which are mostly common to all Eocene mammalia and to some of the more archaic modern orders,

especially the Insectivora and Marsupials. They were at first regarded as Marsupials, later as Insectivora, but with more complete knowledge of the group its affinities to the true Carnivora have been generally recognized. They form the sub-order Creodonta of Cope, Carnivora Primigenia of Lydekker and Winge. Some authorities have preferred to place the group from which the modern Carnivora are derived (Creodonta Adaptiva of Schlosser) with the Fissipedia, and restrict the name Creodonta to the Inadaptive groups. This arrangement is open to two objections:

(1). The name Creodonta is not applicable in this sense without an entire change of its meaning and scope.

(2). The Adaptive Creodonts are more closely related to some of the inadapative families than the inadapative groups are to each other; the latter do not therefore form a natural group to the exclusion of the adaptive forms.

APPLICATION OF THE TERM CREODONTA.

Cope's original definition of the Creodonta¹ was as follows:

"Animals which fulfilled the functions of the existing Carnivora were abundant in North America during the Eocene period. The Wahsatch beds of New Mexico have yielded remains of more than a dozen species . . . they agree in possessing characters which distinguish them from the true Carnivora. I have already pointed out (Syst. Catal. Eoc. Vert. New Mex., 1875, p. 7) that in the genera *Ambloctonus*, *Oxyæna*, *Stypolophus* and *Didymictis* the tibio-tarsal articulation differs from that of the existing Carnivora, and suggested that these forms might prove to be gigantic Insectivora. Further investigation has satisfied me that they cannot be included in the order Carnivora, and their systematic position proves to be of considerable interest.

"A greater or less part of the cranial chamber is preserved in specimens of *Oxyæna forcipata* and *Stypolophus hians*. In these animals it has a long narrow form like that of the opossum, and in the first named, where the interior form can be seen, it is evident that the cerebral hemispheres were small and narrow and that the olfactory lobes were relatively large, and were entirely uncovered, projecting beyond the hemispheres.

"In *Ambloctonus*, *Didymictis* and three undetermined forms" [one of these, "*Creodus incertæ sedis* No. 1" of subsequent description and figures by Cope, is a species of *Vulpavus*], "the femur supports a third trochanter. In all the genera . . . the ilium has an angulate or convex external face, as in Insectivora and Marsupialia, and does not display the usual expansion . . . there is a strong tuberosity in the position of the anterior inferior spine which . . . marks the position of the origin of the rectus fembris muscle.

"The glenoid cavity of the squamosal is transverse and well defined anteriorly and posteriorly, as in the Carnivora . . . In the genus *Synoplotherium* which probably belongs to this group the scaphoid and lunar bones are separate . . ."

"The above characters point to the Marsupialia or the Insectivora . . . and the evidence is much more weighty in favor of the latter order as their true position.

"The astragalar articular surface of the tibia . . . is uninterrupted and more or less oblique in the transverse direction . . . the astragalus presents a corresponding trochlear face. That is, instead of a groove it presents an open angle upward, which separates the superior from the oblique internal face.

¹ Proc. Phila. Acad. Sci., 1875, p. 444.

"The dentition of this group is consistent with its reference to the sarcophagous Marsupialia or to the Insectivora. It has, however, decided resemblances in the form of the molars and the deficiency in the number of inferior incisors to such genera of Insectivora as *Mythomys* [= *Potamogale*] and *Solenodon*, while in the large canines it more nearly approaches Sarcophaga and Carnivora.

"I propose to include the genera *Ambloctonus*, *Oxyæna*, *Stypolophus* and *Didymictis* in a special division under the name of Creodonta. This division may be regarded as a suborder of the Insectivora. It is possible that the genus *Diacodon* Cope belongs here The genus *Mesonyx* cannot be referred to the Creodonta as here constituted since the trochlear face of the astragalus is completely grooved above as in the true Carnivora, and its distal end presents two facets, one for the cuboid and the other for the navicular bones. It represents on this account a peculiar family, the Mesonychidæ.

"To the Creodonta must be referred the genera *Pterodon* and *Palæonictis* . . . here also doubtless belong supposed Carnivora from the Wyoming Eocene stated by Marsh to be allied to the Viverridæ [this refers to *Viverravus*, *Limnocyon* and *Harpalodon* [= *Miacis*]

"The definitions will be as follows:

Insectivora. Mammalia with small cerebral hemispheres which do not cover the olfactory lobes nor the cerebellum; with numerous clawed digits and a third trochanter of the femur; with a transverse glenoid cavity for the mandible.

Superior incisors normal, not growing from persistent pulps; canines large; premolars compressed. Astragalus not grooved above, articulating with the cuboid as well as with the navicular; five toes on the hind foot: Creodonta

"Superior incisors large, growing from persistent pulps and without enamel on the sides, superior canines small when present; premolars wide or tubercular Tillodonta."

From the description quoted above it will appear that

- I. The Creodonta were defined upon
 - (1) Small primitive brain.
 - (2) Femur with third trochanter.
 - (3) Articulation of jaw transverse.
 - (4) Astragalar trochlea flat.
 - (5) Five toes on the hind foot.
 - (6) Canines large, premolars compressed, incisors small, not scalpriform.

- II. The typical genera were
Ambloctonus, *Oxyæna*, *Stypolophus* (= *Sinopa*) and *Didymictis*.

The referred genera were

Vulpavus ("undetermined form" subsequently figured and now identifiable),
Synoplotherium, *Diacodon*, *Pterodon*, *Palæonictis*, *Viverravus*, *Limnocyon* and
Harpalodon (= *Miacis*).

It is quite clear therefore that Cope, in his original description as in all his subsequent descriptions, regarded them as a primitive group, defined them exclusively upon primitive characters, and used as types both adaptive and inadapative Creodonts. Of the four typical genera the first three are inadapative and the last adaptive Creodonts; of eight referred genera three are of the adaptive group. The Mesonychidæ were at first excluded on account of their advanced type of astragalar trochlea. Cope subsequently included them in the order, with amended definition as follows:

“Unguiculate ?placental Mammalia with separate scaphoid and lunar bones, narrow cerebral hemispheres and very large and exposed olfactory lobes; and the ankle joint generally not trochlear The differences from the Insectivora are less numerous, the only trenchant distinctive character is the peculiar tibio-tarsal articulation.” (Tertiary Vertebrata, p. 251.)

It will be observed that the definition of the suborder Creodonta is in accord with the general views of its author upon classification and phylogeny, according to which the suborder represented a structural group, defined by the possession of certain common characters indicative of relationship. The alternate theory of classification, that an order, family or other division represents a phylogenetic line, including animals often of widely different structure but which in the opinion of the classifier are genetically connected, will of course involve a radical change in our conception of the Creodonta, regarding the inadapative forms as pseudo-Carnivora, and transferring the adaptive group to the Fissipedia. According to the rules of nomenclature, the term Creodonta cannot then be applied to the former group, as it is widely different both in scope and meaning.

Subsequent research has tended to emphasize the relationship of the Creodonta to the true Carnivora rather than to the Insectivora. Lydekker makes them a suborder of Carnivora under the name Carnivora Primigenia. Schlosser in 1888 divides them into Adaptiva and Inadaptiva, the former group giving rise to the modern Carnivora; but in general this author includes the adaptive Creodonts in the Carnivora and distinguishes the Creodonts as a separate although closely related order. Scott, Osborn, Wortman and Matthew have usually regarded the Creodonts as a distinct order including the ancestral types of modern carnivora, but Wortman in 1901 included the Creodonta as a suborder of Carnivora, restricting the name to the inadapative groups, and re-defining it upon a single negative character,¹ the adaptive group being included with the Fissipedia under the name Carnassidentia.

The present writer is indisposed to follow to extremes either the group or linear theory of classification and regards a combination of the two as more practical and convenient, and as best expressing the relationships of groups from both the morphological and phyletic standpoints. As regards the Eocene Carnivora it appears better to retain the generally accepted arrangement as more natural and convenient. They form a natural and readily definable suborder, divisible into three groups of about equal value, besides a few primitive forms of uncertain affinities. One of these groups gave rise to the Fissipedia by assumption of a number of progressive characters; the others became extinct without assuming these progressive characters.² The conversion of the adaptive Creodonts into Fissipedia and the disappearance of the inadapative groups nearly coincide with the end of the Eocene. If on the other hand we place the Adaptive

¹“ Carnassial teeth when present not on P⁴ and M₁.”

² With individual exception as noted below.

Creodonts in the Fissipedia, we not only remove them from their nearest relatives, and make it difficult to adequately define the Inadaptive groups so as to exclude them, but we obscure, as it seems to me, the real relationships of the Eocene Carnivora to each other and to adjoining orders, as well as to the more modernized group. The attempt to distribute the adaptive genera into the modern families is open to more serious objections, as even with a complete knowledge of the skeleton it is not always possible to be sure of their exact relationship to the living carnivora, and to associate the closely allied Eocene genera with the widely separated modern families to which they may be ancestral, not only obscures their real relations, but makes their position dependent upon very transitory and uncertain theories of phylogeny.

CRITERIA OF CLASSIFICATION.

In order to arrive at a natural classification of the Creodonta we must first distinguish between the adaptive and specialized characters of each group and those more fundamental points of likeness or difference which indicate the position of its early generalized ancestors among the primitive group from which all the Carnivora are descended. It is equally necessary that the arrangement be based not upon teeth alone, nor upon any one character, but upon all the important diagnostic features of skull and skeleton so far as they are known to us. A correct perspective of the time relations of each group is hardly less necessary.

1. *Teeth.* In the primitive type the teeth are tuberculo-sectorial as above noted. In the development of shearing teeth out of the primitive tuberculo-sectorial type one pair of teeth are usually enlarged and specialized to assume the chief shearing function, and are termed carnassials. In the Adaptive Creodonta and Fissipedia these carnassials are P^2 and M_1 . In the Oxyænidaë they are M_2 and in the Hyænodontidaë M_3 . In most of the modern Carnivora the carnassials become the sole shearing teeth, but in the Hyænodontidaë and Oxyænidaë, in most of the Adaptive Creodonts and many of the Oligocene Fissipedia, and even in some of the modern Viverridaë, the other molars retain a subordinate shearing function. In the omnivorous specializations (Arctocyonidaë, Miacidaë in part) the tubercular dentition is enlarged, the sectorial and premolar dentition reduced and the crowns of the molars finally become round and flat-topped. A third and very peculiar specialization is seen in the Mesonychidaë, where the molars assume the triconodont type with high blunt-pointed cusps and no trace of shear. The history of this family proves that their peculiar type of teeth is derived from the typical primitive tuberculo-sectorial pattern.

The location of the carnassial is determined not so much by the relative *size* of the teeth as by their form and relative position. The upper teeth in the primitive tritubercular mammals form a series of triangles with the base outwards, the lower teeth a series of triangles with the base inwards, fitting into sockets be-

tween the upper triangles, and provided with heels which fit over the surface of the upper triangles and serve to limit the closing of the teeth and prevent their projecting points from striking on the bone of the opposite jaw. In the carnassial specialization one of these sockets becomes especially wide and deep, to accommodate a lower tooth usually, though not at first always, larger than the adjoining lower teeth. The upper triangles in advance of this socket, and especially the one immediately in front of it, become extended at the postero-

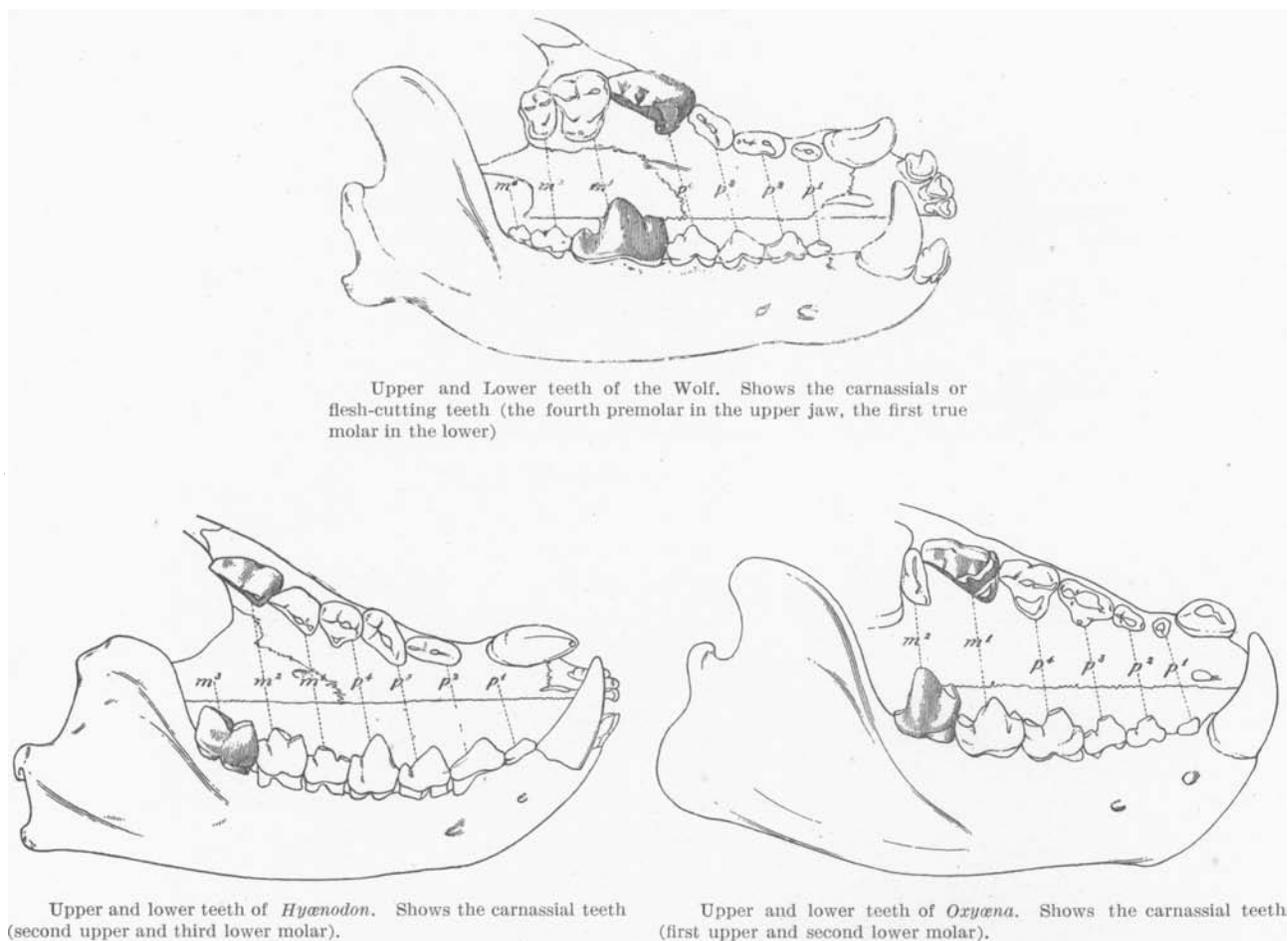


Fig. 1. Carnassial Teeth in Creodonta and modern Carnivora, showing the three pairs of teeth which in different groups have been specialized for the purpose of flesh-cutting.

external angle, developing a shearing blade at that point. The teeth behind the socket, and especially the tooth immediately behind it, become extended at the antero-external angle. In consequence there develops a more or less marked outward angulation in the outer border of the tooth row, the apex of the angle being at the carnassial socket. In the further progress of the carnassial specialization, the teeth in advance of this angle tend to become longitudinal, those behind it tend to become transverse shears and ultimately disappear, or else to lose their

shearing function and become flat-topped crushing surfaces. The chief shearing

action lies between the anterior border of the lower tooth which fits into this principal socket and the posterior border of the upper tooth immediately in front of it. It is upon these two teeth that the emphasis of specialization in shearing function must of necessity fall, and they ultimately become the sole shearing teeth.

The position of the external angle of the upper tooth row, and the consequent location of the point where carnassial specialization must take place, affords the most reliable character for classifying the primitive carnivora. In the Adaptive Creodonts and modern Carnivora it is between p^4 and m^1 . In the Oxyænidæ it is between m^1 and m^2 ; in the Hyænodontidæ between m^2 and m^3 . In the Mesonychidæ there is no defined angle and no development of shearing teeth. In the Carnivorous Marsupials it is between m^3 and m^4 .

2. *Feet.* Our more complete knowledge of

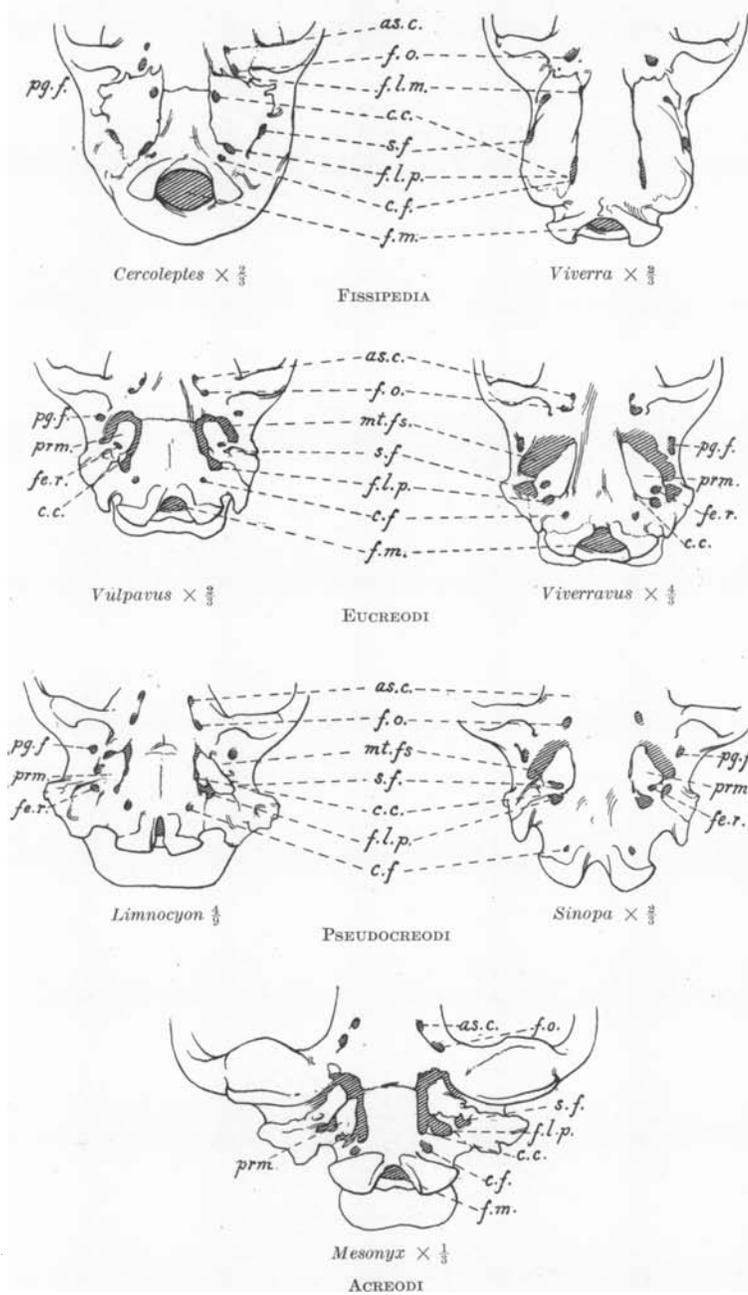


Fig. 2. Basicranial foramina in Creodonta and Fissipedia. Lettering: *as.c.*, alisphenoid canal; *c.c.*, carotid canal; *c.f.*, condylar foramen; *fe.r.*, fenestra rotunda; *f.l.m.*, foramen lacerum medium; *f.l.p.*, foramen lacerum posterius; *f.m.*, foramen magnum; *f.o.*, foramen ovale; *mt.fs.*, mesotympanic fossa; *pg.f.*, postglenoid foramen; *prm.*, auditory prominence of the petrosal; *s.f.*, stylomastoid foramen.

the skeleton has brought to light certain foot-characters which appear to be of

fundamental importance. In all the Adaptive Creodonta the claws are compressed, pointed and never fissured at the tip. In the Fissipedia, although often broadened, they are never fissured. In the Hyænodontidæ and Oxyænidæ they are always fissured at the tip whether broad or compressed.¹ In the Mesonychidæ they are flattened and hoof-like and more or less deeply fissured.

The symmetry of the manus and pes appears to be equally important. In the Adaptive Creodonts and Fissipedia, and in the Mesonychidæ, the symmetry is paraxonic. In the earliest types the first digit is semi-opposable; in the more advanced types it is reduced or vestigial and has lost its opposability more

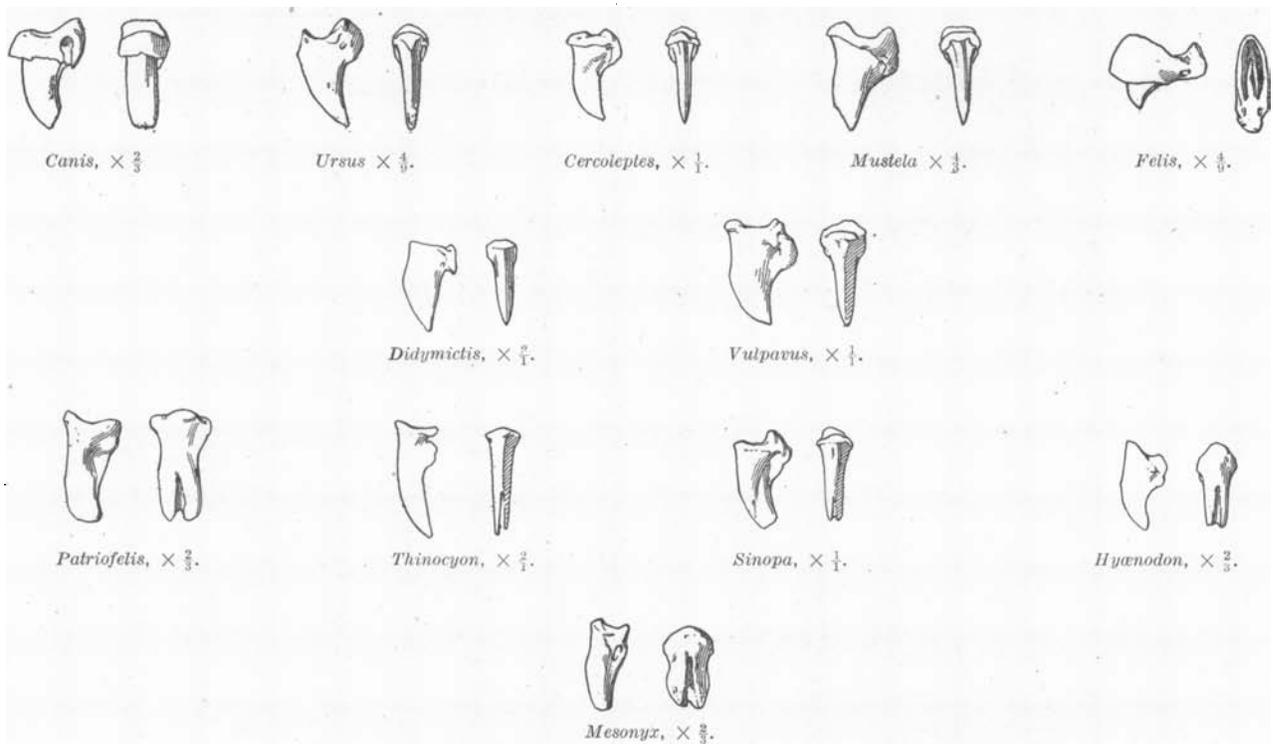


Fig. 3. Claws of Creodonta and Fissipedia. Superior and lateral views of ungual phalanx.

or less completely. In the Hyænodontidæ and Oxyænidæ the symmetry is approximately mesaxonic, the first digit being primarily less opposable, and the first and fifth being simultaneously reduced in the most specialized phylum. In these two families the fibula has a considerable articulation with the calcaneum, as also in the Viverravinæ and the primitive or archaic Creodonts generally.

3. *Skull*. The expansion of the lachrymal bone upon the face is least in the Miacidæ, and greatest in the Mesonychidæ. In the Hyænodontidæ and Oxyænidæ it is of intermediate size, and more nearly semicircular form. The

¹ Wortman's statement that they are not fissured in *Sinopa* is erroneous.

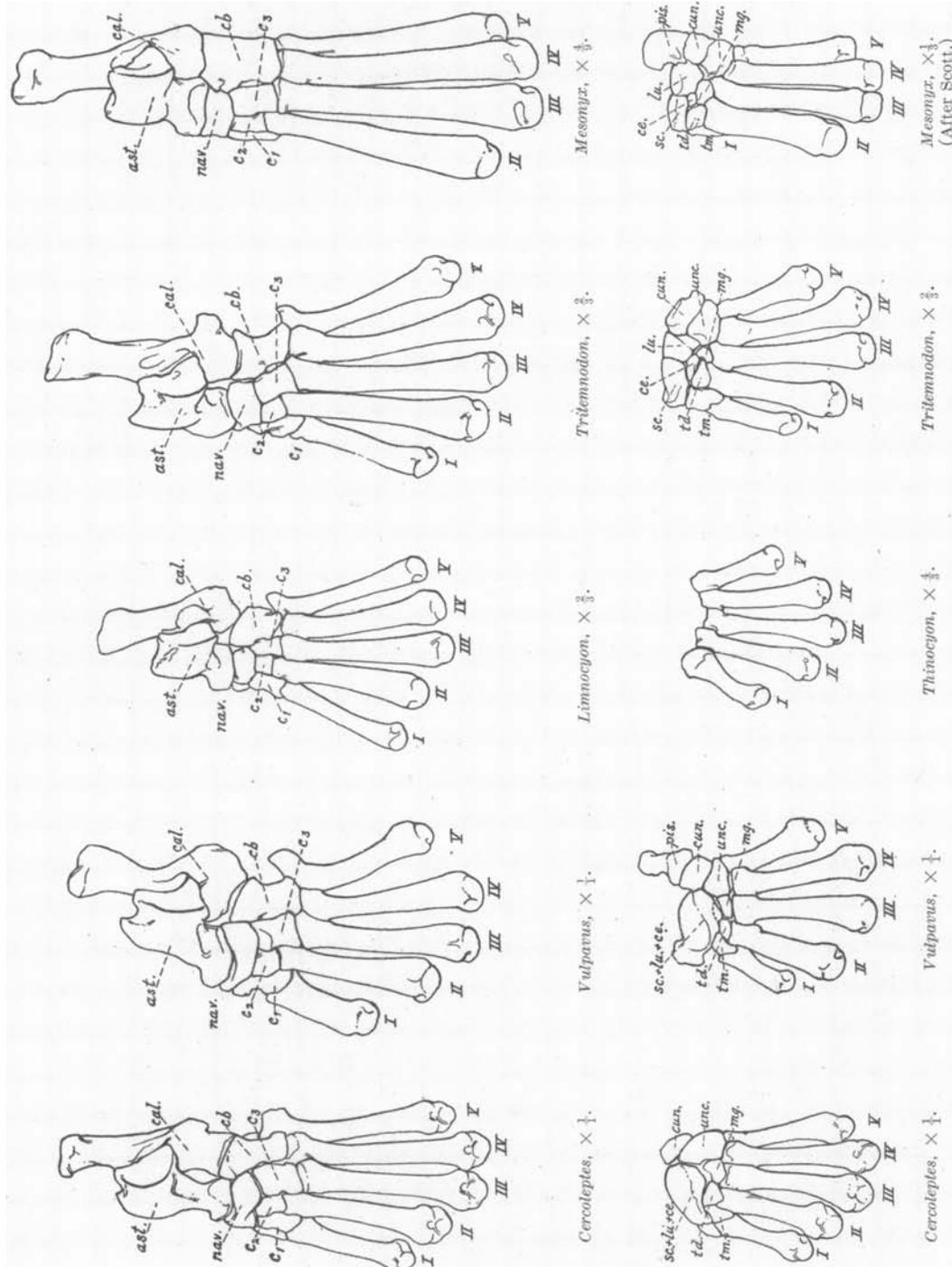


Fig. 4. Fore and Hind Feet of Creodonts and Fissipedia. Lettering: *ast.*, astragalus; *c₁*, *c₂*, *c₃*, ento-, meso- and ectocuneiforms; *cal.*, calcaneum; *cb.*, cuboid; *ce.*, centrale; *cun.*, cuneiform; *lu.*, lunar; *mag.*, magnum; *nav.*, navicular; *pis.*, pisiform; *sc.*, scaphoid; *td.*, trapezoid; *tm.*, trapezium; *unc.*, unciform; *v.*, I, II, III, IV, V, first, second, third, fourth and fifth digits.

posterior expansion of the nasals is greatest in the Mesonychidæ and least among the Miacidæ. In these and in numerous characters of the base of the skull etc., the Mesonychidæ are most remote and the Miacidæ nearest to the Fissipedia. The tympanic bulla is not completely ossified in any of the Creodonta except Mesonychidæ, perhaps in certain species of *Hyænodon*. The form of the petrosal prominence appears to be of considerable importance; the arrangement of the carotid circulation appears to be much the same in all, and represents probably the primitive condition, from which the arrangement in Fissipedia on one hand, Insectivora on the other is derivable. The arrangement of the basicranial foramina generally represents the primitive conditions most nearly retained by the Arctoid Fissipedia especially Mustelidæ and Procyonidæ.

4. *Skeleton*. The number of dorso-lumbar vertebræ is said to be 19 in *Dromocyon* (Wortman) while in the closely allied genus *Mesonyx* it is 20 according to Scott. In *Sinopa*, *Tritemnodon*, *Oxyæna*, *Hyænodon* and *Patriofelis*, the only other Creodont genera in which it is known, the dorso-lumbar formula is 20, as it is, with rare exceptions, among all the Fissipedia. The reduction to 19 in *Dromocyon* is probably individual, and not, as Wortman supposes, an indication of the Marsupial affinities of the Creodonta.

The lumbar zygapophyses in the Adaptive Creodonts are comparatively flat, as they mostly are in the Fissipedia. In the Hyænodontidæ and Mesonychidæ they are strongly convex, semi-cylindrical, as in some Fissipedia; and in *Patriofelis* they are revolute as in many Ungulata. This character would seem to be adaptive; on the other hand the dorso-lumbar formula is of high importance as an ordinal or group character, although subject to some individual variation.

The deltoid crest of the humerus in Arctocyonidæ and Miacidæ (except *Didymictis*) is peculiarly high and ends abruptly. In Hyænodontidæ, Oxyænidæ and Mesonychidæ it is more like that of the Fissipedia. The latter is probably an adaptive character of terrestrial or cursorial specialization, the Arctocyonidæ and Miacidæ retaining the primitive arboreal type in accordance with their general structure and probable habits. The supra-trochlear foramen is absent in adaptive Creodonts and Oxyænidæ but present in Hyæodontidæ and Mesonychidæ, an important approximation to Insectivora.

The above characters with many others of less importance in the arrangement of the Creodonta will be considered more in detail in the description and discussion of the families and genera of Bridger Carnivora. So far as our present knowledge enables us to estimate their relative importance they indicate the following as the most natural and convenient arrangement of the suborder.

CLASSIFICATION AND GEOLOGICAL DISTRIBUTION OF THE CREODONTA.

Suborder CREODONTA Cope. Brain small, narrow, the cerebral lobes smooth or with one principal sulcus and entirely covered by the parietal bones. Tympanic bulla not ossified.¹ Scaphoid lunar and centrale separate.² Astragalar trochlea flat (exc. *Didymictis*, *Viverravus* and the later Mesonychidæ). Digits 5-5³. An entepicondylar foramen on the humerus⁴ and usually a third trochanter on the femur.

- | | |
|--------------------------|---|
| Adaptive
Creodonta | <p>A. EUCREODI. Carnassials P₄, M₁ or none. Claws compressed, pointed, not fissured. Manus and pes paraxonic. No fibulo-calcaneal facet.⁵ No supra-trochlear foramen of the humerus. Lumbar zygapophyses flat.</p> <p>I. <i>Arctocyonidæ</i> Gerv. No carnassials, molars flattened, premolars reduced. Scaphoid and centrale united. Brain very small, not convoluted.
<i>Clænodon</i>, <i>Arctocyon</i>, <i>Anacodon</i>.</p> <p>II. <i>Miacidæ</i> Cope. Carnassials variously developed. Carpals generally separate. Brain progressively larger.
<i>Miacis</i>, <i>Uintacyon</i>, <i>Oödetes</i>, <i>Vulpavus</i>, <i>Palaearctonyx</i>, <i>Vassacyon</i>, <i>Didymictis</i>, <i>Viverravus</i>, ? <i>Prodaphænus</i>.</p> |
| Inadaptive
Creodonata | <p>B. PSEUDOCREODI. Carnassials M₁ or M₂. Claws fissured at the tip. Manus and pes mesaxonic. A fibulo-calcaneal facet. Lumbar zygapophyses cylindrical or revolute.</p> <p>III. <i>Hyænodontidæ</i>. Carnassials M₂. Skull long, basicranial region narrow, jaws long with loose symphysis. A supra-trochlear foramen on the humerus. Feet becoming cursorial in the principal phylum.
<i>Sinopa</i>, <i>Tritemnodon</i>, <i>Proviverra</i>, <i>Quercytherium</i>, <i>Cynohyænodon</i>, <i>Apterodon</i>, <i>Pterodon</i>, <i>Hyænodon</i>.</p> <p>IV. <i>Oxyænidæ</i>. Carnassials M₂; third molar absent. Skull robust, basicranial region wide, jaws stout with strong symphysis. No supra-trochlear foramen on the humerus. Feet spreading, probably amphibious in one phylum, terrestrial-plantigrade in another.
<i>Oxyæna</i>, <i>Patriofelis</i>, <i>Palæonictis</i>, <i>Ambloctonus</i>, <i>Limnocyon</i>, <i>Thinocyon</i>, <i>Oxyænodon</i>, <i>Thereutherium</i>, <i>Machairoides</i>.</p> |
| Primitive
Creodonta | <p>C. ACREODI. No shearing teeth. Molars primitive or with high blunted cones, tritubercular above, tuberculo-sectorial or triconodont below.</p> <p>VI. <i>Mesonychidæ</i>. Claws flattened, hoof-like, fissured. Manus and pes paraxonic. No fibulo-calcaneal facet. A supra-trochlear foramen on the humerus. Lumbar zygapophyses cylindrical or revolute.
<i>Dissacus</i>, <i>Pachyæna</i>, <i>Mesonyx</i>, <i>Synoplotherium</i>, <i>Harpagolestes</i>, <i>Haplodectes</i>, ? <i>Triisodon</i>, <i>Sarcothraustes</i>, <i>Goniacodon</i>, <i>Microclænodon</i>.</p> <p>? VII. <i>Oxyclænidæ</i>. Molars primitive, tritubercular above, tuberculo-sectorial below, with sharp angular cusps. Skull and skeleton mostly unknown.
<i>Oxyclænus</i>, <i>Chriacus</i>, <i>Deltatherium</i>, <i>Tricentes</i>.</p> |

¹ Except *Mesonyx*, and certain species of *Hyænodon*.

² Scaphoid and centrale united in *Clænodon* and *Palaearctonyx*; scaphoid, lunar and centrale in one species of *Vulpavus*, and exceptionally in *Hyænodon*.

³ Except in Mesonychidæ where the first digit is vestigial in both fore and hind foot.

⁴ Except *Mesonyx*.

⁵ Except *Didymictis* and ? *Viverravus*.

Geological Distribution of the Creodont Families.

The figures indicate the number of genera in each formation. (European genera are not included in this table.)

	Basal		EOCENE						OLIGOCENE		
	Puercu	Torrejon	Lower	Middle	Upper	Lower	Middle	Upper			
			Wasatch	Wind R. and L'r Huerfano	L'r Bridger and Up. Huerfano	Up. Bridger and L'r Washakie	Up. Washakie and L'r Uinta	Up. Uinta			
<i>Eucreodi</i>											
Arctocyonidæ	1	2	1
Miacidæ	1	5	6	6	6	?1	= Fissipedia
<i>Pseudocreodi</i>											
Hyænodontidæ	2	2	2	2	2	1
Oxyænidæ	3	3	4	3	2	1
<i>Acreodi</i>											
Mesonychinæ	1	2	1	2	2	1	1
Triisodontinæ	1	3
Oxyclænidæ	2	2

RELATIONSHIP AND ADAPTATION.

The above classification and distribution appears to be best explained by the following hypothesis of the course of evolution of the order.

The Cretaceous ancestors of the Carnivora were a group of small arboreal mammals resembling the opossum in size and habits, but more nearly allied to the primitive Insectivora. The pollex was semi-opposable, the hallux somewhat opposable, the feet five-toed and plantigrade with highly flexible carpus and tarsus. The limbs were loose jointed with relatively long proximal segments; the radius having a high degree of rotation on the ulna, and the tibia to a less degree rotating on the fibula. The neck was of a moderate length, the body slender and flexible, especially in the lumbar region, the tail long and more or less prehensile. The teeth resembled those of the opossums and were adapted to a mixed diet largely insectivorous; but the cusps were at first conical, and later acquired the angular form and series of small notched shears characteristic of insectivora and shown in the opossums and other small animals of similar habits. Dentition $\frac{3.1.4.3}{3.1.4.3}$. Angle of jaw not inflected. All teeth except true molars preceded by milk teeth. Dorsolumbar formula 20. Skull elongate in both facial and cranial region, brain small, cerebrum not convolute. Carotid canal not perforating basisphenoid. Vertebral artery perforating arch of the axis and not that of the seventh cervical. Lunar large and magnum small; astragalus

with distinct neck and convex head and with flat tibial and fibular facets at right angles to each other; tibia and fibula not in contact distally but fibula articulating with calcaneum.

The members of this primitive group differed in adaptation, some being more clearly adapted to arboreal life, as shown in compressed claws, probably retractile to a slight degree, larger, more opposable first digit, more flexible wrist and ankle. Others had more or less fissured claws, non-retractile, stiffer wrist and ankle, less opposable first digit, and in many other respects approximated the early Insectivora. The entire group was advancing in brain development,¹ losing the rotability of the tibia and reducing the size of the fibula, and losing the opposability of the first digit.

The earliest specializations from the primitive type were the Mesonychidæ on one hand, Arctocyonidæ on the other. The former separated at a point in their development when the pollex and hallux were so far opposable that they could not pair with the fifth digit in walking on the ground, and in the adaptation of the family to terrestrial and subsequently to cursorial habits the first digit degenerated without losing its opposition, and the symmetry of the foot was and remained paraxonic. The peculiar development of the teeth may be supposed to represent an early predaceous adaptation before the tritubercular molars of the primitive type had acquired their small shears.

The Arctocyonidæ represent a frugivorous adaptation derived from the most arboreal and least Insectivore-like members of the primitive group, with semi-opposable first digit, compressed unfissured claws and precocious tendency to union of the carpals. The fibula is still large enough to retain connection with the calcaneum, and there are no indications of this specialized group losing its arboreal habitat.

The remainder of ancestral Creodonts at the beginning of the Tertiary were divisible into three groups, all of which had developed the primitive insectivorous shears in the molar teeth, as in the modern opossums, etc. The most arboreal group, furthest from the Insectivora, and highest in brain development, had the posterior molars reduced in size. In a second group, nearest to the Insectivora and probably of more amphibious habits, the molars were reduced in number m_3^2 being absent, but m_2^2 were not reduced in size. In a third intermediate group of more terrestrial habit, the molars were not reduced either in number or size.

From each of these three groups were developed predaceous terrestrial forms with shearing teeth. In the first group the shear specialized upon p^4 , m_1 , in the second upon m_2^1 , in the third (intermediate) group upon m_2^2 . In the first group (Miacidæ), as earlier in the Mesonychidæ, the more opposable first digit was unable to pair with the fifth in its reduction, and the symmetry of the foot became paraxonic. In the second and third groups (Oxyænidæ and Hyæno-

¹ As in general, the arboreal life was most favorable to advance in brain structure, and the most arboreal types stand highest in this respect.

dontidæ) the opposability was too slight to prevent its pairing with the fifth, and the symmetry of the foot became mesaxonic. The Miacidæ remained predominantly arboreal in adaptation through the Eocene, but early gave rise to one predaceous terrestrial type (Viverravinæ) paralleling the modern Canidæ to a limited degree. In this type the fibula still retains connection with the calcaneum. The Oxyænidæ early gave rise to terrestrial predaceous types (Oxyæninæ, Machairoidinæ) paralleling the Hyænidæ and Felidæ in dentition, while the more conservative (amphibious) part of the group survived to the end

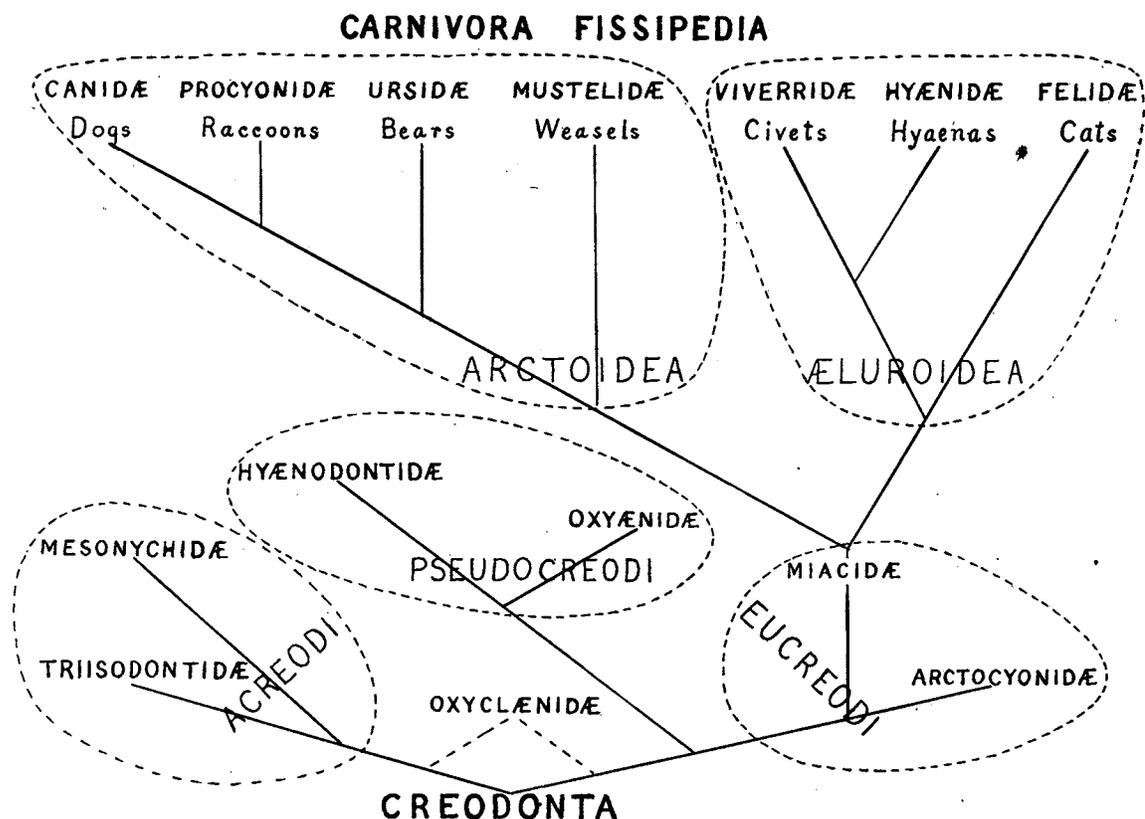


Fig. 5. Relationship of the Families of Creodonta and Fissipedia.

of the Eocene with comparatively little change. The Hyænodontidæ developed more gradually during the Eocene into cursorial predaceous types parallel to cats and hyænas in dentition, which survived to the middle Oligocene, and in the old world gave rise also to amphibious types (*Apterodon*).

From the Miacidæ are descended the various Fissiped families, the Canidæ, Mustelidæ, Procyonidæ and Ursidæ, most probably from the Miacinæ, while the Viverravinæ may have given rise to the modern Viverridæ and perhaps, through unknown members of the group, to the Felidæ. The Hyænidæ are generally supposed to be derived from the Viverridæ through *Ictitherium*. If these rela-

tions of the Fissipedia to the Miacidæ be true, the commencement of the differentiation into Arctoidea and Æluroides dates back to the beginning of the Tertiary, and the commencement of the family differentiation took place, in part at least, during the Middle or later Eocene, as will appear in the discussion of the Miacidæ. The progressive specialization of the Fissipedia has been towards predaceous types on the one hand, omnivorous types on the other, and for the most part towards a terrestrial habitat. The most strictly terrestrial types (Canidæ, Hyænidæ) have departed the most from the primitive skeletal structure, the fossorial and amphibious types hardly less, while the arboreal or semi-arboreal types are generally primitive, and *Cercoleptes*, the most strictly arboreal of the modern Carnivora, is the nearest to the Eocene Miacidæ in skeletal construction.

ENVIRONMENT AND ADAPTATION OF THE BRIDGER CREODONTA.

The number and variety of the Bridger Carnivora, as compared with their numbers in the modern American fauna, is very remarkable. Thirty-four well-distinguished species have been discovered in the sediments of the Bridger formation, in an area only forty miles in diameter, a considerably larger number than now inhabit the State of Wyoming, taking Elliot's 'Synopsis' as our guide. It can hardly be supposed that our knowledge of the Middle Eocene fauna of Wyoming compares in completeness with our knowledge of the modern fauna, and we must assume that the remains which have been exhumed from the Bridger sediments represent but a fraction of the species which inhabited that region of North America during the Middle Eocene. Nor can it be allowed that the lines of specific distinction have been drawn finer in the ancient than in modern carnivora, thus admitting a greater number of valid species; for in fact the reverse is the case, many modern species being almost indistinguishable on the characters of the teeth, the principal criterion of distinction among the fossil species. Hence we must conclude that the Eocene Carnivora were really much more varied than the modern ones, in this region at least. On the other hand the Bridger carnivores are far from exhibiting the extent of differentiation and specialization seen in the modern representatives of the order. Their diversity and progressiveness in reduction and specialization of the teeth, special adaptations of the limbs and feet, etc., is much less; all retain the small low-organized brain, most of them the primitive number of forty-four teeth, and nearly all retain the five-toed feet. The species exhibit a high degree of individual variability in the most critical parts, especially in the form and arrangement of the molar cusps, in which modern species are very constant.

These facts I interpret as meaning that, owing to secular changes in climate and environment, to the occupation of new fields owing to migration or to the extinction of competing types, or to other unknown changes affect-

ing their habitat, the order Carnivora was undergoing a very rapid expansion and evolution during the Eocene. Each of the several phyla which had been differentiated by an earlier radiation, branched out into a number of specializations, for the most part paralleling the contemporary or later specializations of other phyla more or less exactly. In the Oligocene the specializations of the Inadaptive Creodonts became extinct, while those of the adaptive Creodonts, converted into True Carnivora (Fissipedia) by their parallel assumption of a number of features of general advancement, underwent a further expansion and specialization during Oligocene and Miocene, giving rise to the different groups of modern carnivora. During the Pliocene and Pleistocene these groups attained a comparative fixity of type, and most of the intermediate forms were weeded out amongst the more specialized phyla, so that the dominant groups of modern carnivora are comparatively circumscribed in their range of structure, and their species exhibit much less individual variation than do the Creodont of the Middle Eocene or the Fissipedia of the Oligocene.

The principal trends in this adaptive radiation and the parallelism which resulted from the superposition of new adaptive divergences upon those already defined or completed are more or less clearly traceable in the geological history of the Carnivora as known to us. The primitive type of the order we take to have been fitted to an arboreal habitat and an insectivorous diet; from this diverged the predaceous types on the one hand, the omnivorous on the other, the terrestrial forms in either group becoming larger and more dominant. A primary divergence partly upon these lines give rise not later than the end of the Cretaceous to the Adaptive Creodonts and to the several groups of Inadaptive Creodonts. During the Eocene a second adaptive divergence was in progress in the different Creodont families, especially in the Hyænodontidæ and Oxyænidæ, while the Adaptive Creodonts by a third radiation, principally of later date, although its beginnings must have been in the Eocene, gave rise to the modern families of Carnivora. It will be observed that the lines of divergence in Eocene Hyænodonts and Oxyænids parallel only the persistent and predaceous adaptations among the later Carnivora, and not the omnivorous and cursorial adaptations; this is explained by the fact that the Arctocyoniidæ and Mesonychiidæ already occupied these fields during the Hyænodont-Oxyænid radiation, but had become extinct before the evolution of Ursidæ, Procyoniidæ and Canidæ from the main Miacid stock.

RELATIONSHIP OF THE CREODONTA TO OTHER PLACENTAL ORDERS.

Dr. Ameghino (1901) has expressed the opinion that most of the so-called Creodonta of the Basal and Lower Eocene should be removed to the Condylarthra, and distinguished from the true Creodonta typified by *Didymictis* and *Dissacus*, and more recently Professor Gaudry has lent the weight of his great

authority to the indorsement of this view. The principal argument in favor of this rearrangement is in the undoubted resemblance in the teeth between the supposed Condylarthra of the Basal Eocene and their supposed Creodont contemporaries, for very little is known of the skeleton in either group. I agree with my distinguished confrères in the belief that this resemblance does indicate a real relationship, perhaps not very remote, but I place a somewhat different interpretation upon the facts. I may observe in the first place that the current belief that Condylarthra are ancestral to the higher Ungulata and the less generally accepted view advocated by M. Gaudry, that they are ancestral to the Primates, are not in accord with present evidence.

We have in the Lower Eocene, Perissodactyla and Artiodactyla which, if we judged from the teeth only, might be supposed to be rapidly approximating the Condylarthra, and were thought to be directly derived from them when only the teeth were known. But the characteristic parts of the skeleton show no corresponding approach. As we follow back the different Perissodactyl phyla we find them converging in the Middle and Lower Eocene towards a single type, and in the Wasatch beds it is difficult to tell either from the teeth or the foot structure, to which of the Perissodactyl families a species should be referred. The same may be said of the Artiodactyla. But the *ordinal* characters of the skeleton show no such approximation. A Perissodactyl or Artiodactyl astragalus from the Wasatch is just as distinctly Perissodactyl or Artiodactyl as in any later formation, and shows no approach whatsoever towards a common ancestral type or towards the Condylarth type. Nor do any of the Basal Eocene mammals, as far as known, show the least degree of approach in the characters of the astragalus, to the Perissodactyl or Artiodactyl type.¹ So also with numerous ordinal characters of the skull, with those of the carpus and other parts of the skeleton when known. They are clearly distinct and characteristic in the Eocene as now. On our present evidence therefore, we must regard Perissodactyla and Artiodactyla as being remotely related to the Condylarthra, and having evolved their characteristic peculiarities in some region unknown to us before the beginning of the Tertiary period.

The Primates are of at least equally antique origin. For the complete skeletal material of Middle Eocene Primates now accessible to students in this museum, shows that the characteristic ordinal peculiarities of the manus and pes were as fully developed then as now, and the approach towards the Condylarthrous type which, as Professor Gaudry shows, is indicated by the teeth, does not appear in the foot-structure. Nor does any Basal Eocene mammal, as far as known, exhibit an approach towards the characteristic features of the astragalus, the peculiar pollex, nailed phalanges, etc., of *Pelycodus*, *Notharctus*, *Hemiacodon* and other less known Primates of the Middle Eocene.

On the other hand the approximation between the less specialized Creodonts

¹ See appendix on the importance of the astragalus in ordinal classification.

and Condylarths is equally marked in the characters of the teeth, of the skull, of the feet and other parts of the skeleton. These resemblances, extending to all parts of skull and skeleton, will bear the most careful scrutiny and comparison, and indicate a common origin of Creodonta and Condylarthra at no remote period. I expressed this conclusion in 1897 by deriving the Condylarthra from the Creodonta. Another expression of the same view would be to derive the Creodonta from the Condylarthra. The essential fact is that the two groups are closely related and had a common origin about the beginning of the Tertiary.

These resemblances, however, are common to *all* Creodonta. The transference of the Creodont genera with tritubercular molars to the Condylarthra finds no support in the characters of the skull and skeleton. The manus and pes of *Clænodon* (*Arctocyon*) described by Matthew in 1901 show that it is an adaptive Creodont nearly related to the Miacidæ and to the true Carnivora, and very far removed from the Condylarths to which Ameghino and Gaudry would transfer it. And the genera *Vulpavus*, *Phlaodectes* and *Palæarctonyx* described in this paper, with low-crowned tritubercular teeth like those which Ameghino and Gaudry would refer to the Condylarthra, and especially like those of *Arctocyon*, are likewise adaptive Creodonts, as is quite conclusively shown by all the characters of skull and skeleton.

The low-crowned tritubercular molar is equally shown in primitive Artiodactyla (*Trigonolestes*) and Perissodactyla (*Eohippus*, *Hyracotherium*), Primates (*Pelycodus*, *Microsyops*, etc.), Insectivora (*Pantolestes*), and in fact is present in every group that we are able to positively recognize from adequate and certainly associated skeleton materials. But the well marked and characteristic ordinal features shown in the skeletal parts of Perissodactyla, of Artiodactyla and of Primates, show that these three groups, although resembling Creodonts, Condylarths and early Insectivora in dentition, were nevertheless not closely related, and had separated from these groups at a much earlier period than the Eocene. It is an unfortunate fact that the attention of palæontologists has been so exclusively centred upon the teeth of fossil mammals, that they have often failed to realize that these alone are an unsafe guide, especially in ordinal relationships.

In a later section of this memoir I shall discuss more in detail the position and characters of the primitive Insectivora and point out the evidence supporting the view that this order represents more nearly than any other the common ancestral group from which the Placental Mammals are derivable. It is quite true, as Wortman observes, that the modern Insectivora are all highly specialized forms. But the order as a whole is defined principally by primitive characters, and its Eocene representatives are much more generalized. They indicate a very early differentiation of the primitive Insectivore stock, probably far back in the Cretaceous Period. The three principal Eocene families, Lepti-

tidæ, Pantolestidæ and Hyopsodontidæ, show a marked resemblance in certain respects to the primitive Creodonts, the two first in the teeth and skull, the last in the astragalus and other features. On the other hand the Creodonta show marked resemblances to the Insectivora, especially in the basicranial region, and the dentition in the primitive type Oxyclænidæ is so like that of the earlier groups of Insectivora that their position is more or less in question, as most of them are very incompletely known. So far as I am able to judge from present evidence, the Creodonta, Condylarthra and Amblypoda stand in rather close relationship to the primitive Insectivora.

RELATIONSHIP OF THE CREODONTA TO THE MARSUPIALS.

The relationship to the Marsupials requires more careful consideration. Many of the Creodonts, both primitive and specialized, show certain marked points of resemblance to the carnivorous Marsupials. Partly on this account, and partly on à priori grounds — viz., that the Placental mammals were descended from the Metatheria and therefore the early ancestral types of the Carnivora ought to be Carnivorous Marsupials — most of the first described Creodonta were referred to the Marsupialia. More complete knowledge and more exact studies upon the group led to their being referred to the Insectivora, and finally to the Carnivora. Dr. Wortman, however, in his recent studies has emphasized the Marsupial relations, especially among the earlier members of the group. He regards the different dental formula of the Marsupials as secondarily acquired by the partial suppression of the second set of teeth, and the inflection of the jaw as equally so. Against the latter view it may be observed that the angle in the Cretaceous and Eocene Marsupials is inflected in exactly the same manner and to the same extent as in the Tertiary and modern forms. The marsupial dental formula may have been in part secondarily acquired, but as regards the pre-molar-molar series there is no evidence that this is so, and the Jurassic mammals afford several types of dental formula from which that of the Marsupials might have been derived without any such repression. The earliest Creodonts do not show any approximation to the Marsupials in either of these characters. Dr. Wortman lists in addition a series of characters which he regards as primitive characters of the Marsupials and displayed to a greater or less extent by some members of the Creodonta. These are:

1. Narrow, more or less elongated type of skull, much constricted behind the orbits.

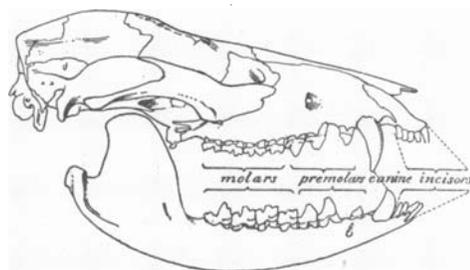


Fig. 6. Skull of the Opossum. Shows the peculiar dentition of the marsupials. Half natural size.

2. Stout, heavy zygomata.
3. Large lachrymal, spreading out upon the face.
4. Prominent sagittal crest terminating in a rather high overhanging occiput.
5. Relatively large, downwardly projecting paroccipitals.
6. Double condyloid foramen.
7. Peculiar thickening of the posterior border of the palate.
8. Large hatchet shaped neural spine of the axis.
9. Large size of the lumbar vertebrae as compared with the dorsals, and their tendency in some forms (Opossums) to develop the double tongue and groove articulations.
10. Large deltoid crest and characteristically broad distal end of the humerus.
11. Fusion of the scaphoid and centrale (Opossums, *Myrmecobius* and Dasyures).
12. Subequal size of ulna and radius.
13. Large size of the lesser trochanter of the femur.
14. Large size of the fibula and its extensive articulation with the proximal surface of the astragalus instead of its outside.
15. Very primitive form of the astragalus.
16. Small size of the brain.
17. Dorsolumbar formula of 19.
18. Posterior spreading of the nasals so as to exclude contact between frontals and maxillary in front.

As to the significance of the above list, we may observe that

(1) and (4) are conditioned by (16), the small size of the brain, equally shown in all primitive mammals. (2) The zygoma is not exceptionally heavy in the more primitive Creodonts nor in other primitive placentals. In the Marsupials it is peculiar in the heavy extension of the posterior branch of the jugal, forming a part of the glenoid fossa. No Creodonts show any approach to this peculiarity. (5) The paroccipitals in the Creodonta are short and spatulate and project backward. This appears to be chiefly coördinated with the long basicranial region. In Marsupials, Insectivores and Rodents the paroccipital processes project more downward, the basicranial region being shorter.

6. The foramen which Wortman homologizes as the "accessory condyloid" occurs only among the more primitive Hyænodonts¹ and its position and direction are so different from that of the anterior condylar in the Marsupials, that it does not appear probable that there is any homology between the two. It is not present in any other Creodonts as a distinct foramen, but apparently becomes merged in the posterior lacerate.

7. Common to the Marsupials, many Insectivores and other mammalia, but it is not clear to what extent it is a primitive character. A slight approach to it is seen in some Creodonta.

¹ It appears to be present in the Artiodactyl *Helohyus*.

8. The Creodonta do not afford any particular approximation to this character, but are more like the Fissipedia. It is probably not primitive.

9, 10. Common to most primitive mammals of arboreal adaptation. The high deltoid crest is peculiar among Creodonts to the Adaptive Creodonta (Carnassidentia of Wortman).

11. Not a primitive character and not peculiar to Marsupials. Among the Creodonta it is found only in the adaptive group.

12, 13. Common to most primitive mammals.

14. The fibula is less reduced in the Marsupials than in any of the known primitive Placentals. The Adaptive Creodont *Claenodon* offers the nearest approach among the Creodonta.

15. The astragalus of the earliest Creodonts differs quite widely from that of the Marsupials. Whether or no the latter represents the original primitive type may be open to discussion, but there can be no doubt as to the much closer resemblance among the astragali of the earliest known Creodonta, Insectivora, Condylarthra and other Placentals to each other than to the Marsupial type.

17. The normal dorso-lumbar formula in the Creodonta, as I have shown above, appears to be 20 as in Fissipedia, not 19 as in Marsupials, most Artiodactyla, Rodents and some Edentata and Insectivora. It is also 20 in Condylarthra and Amblypoda and in some Insectivora, and said to be 20 in the Titanotheres and Oreodonts.

3, 18. The posterior spreading of the nasals is present to a varying degree in the Creodonta, to an equal extent in primitive Insectivora, to a greater extent in most primitive Ungulates. It appears to be a function of the elongate face and is pretty accurately coordinated with the spreading of the lachrymals upon the face and the enlargement of the upper branch of the jugal.

In the analysis of the above characters it appears that so far as they are primitive they are more closely paralleled among various primitive groups of placentals than among the Marsupials. The carnivorous Marsupials certainly are extremely archaic in most respects, but from the Creodonta, and from all primitive placentals, they are separated by a variety of characters which appear to be of very fundamental importance, and I do not see that Dr. Wortman has in any way succeeded in diminishing the importance of these distinctions. The Adaptive Creodonts which he refers to the Carnassidentia (=Fissipedia) show certain resemblances not found in the Inadaptive groups, but these are probably due to a more arboreal habitat, as they are in other respects the furthest removed from Marsupials.

In his excellent memoir on the Santa Cruz Marsupials Sinclair has listed the peculiar characters of the order, and by comparison with this list it can be seen that the Creodonta and all other placentals are separated from it by numerous and important distinctions which bespeak a very remote relationship between the Marsupials and the Eutherian Groups. He has demonstrated very clearly that the

so-called "Sparassodonta," supposed to be a connecting link between Marsupials and Creodonts, are in fact typical carnivorous Marsupials, and do not in any important respect bridge the gap between Eutherian and Metatherian orders.

I have elsewhere¹ discussed the relationships of *Sinopa*, one of the most typical of the Creodonta and the comparisons based upon the whole of the Bridger carnivora only serve to extend and confirm the conclusions there expressed.

What we know of the palæontology of Marsupials has considerable bearing upon the nearness of their relationship to Creodonta. It will be evident that if, as Wortman asserts (1901, p. 336), the Fissipedia, Creodonta, and Insectivora are independently² derived from the (upper) Cretaceous Marsupials exemplified by (the Laramie genus) *Didelphops*, the approximation between the early Tertiary members of these placental groups and the contemporary Marsupials should be as marked as their approximation to one another. On the other hand, if the Metatherian-Eutherian divergence was much more ancient than the differentiation of the Eutherian orders, and the resemblances between the modern carnivorous Marsupials and the Eocene Eutherian mammals are due to their being at an equivalent stage of development and not to any near relationship, then the characters which distinguish modern Marsupials from the Eutheria should be nearly as marked and constant in their early Tertiary ancestors as in the living forms. The best known Tertiary Marsupial fauna is that of the Santa Cruz beds in Patagonia. Dr. Ameghino, who regards these as Eocene, is of the opinion that some of the specimens which he has described indicate a more complete tooth replacement in the carnivorous Marsupials, and regards them as representing an intermediate group (Sparassodonta) between Sarcophaga and Creodonta. The much more complete material of Santa Cruz marsupials studied by Dr. Sinclair fails to substantiate this view, or to show any marked approximation to the Creodonta, and Sinclair has shown that they are in almost every respect typical Marsupials, showing considerable approximation between the Diprotodont and Polyprotodont divisions of the order, but none to the Eutheria. The age of this fauna is, however, probably much later than Eocene; it is Middle or Upper Miocene, according to Ortmann and Scott. In the northern hemisphere Marsupials are known from the Lower Oligocene of Europe (Gyps de Paris; Phosphorites de Quercy, etc.) which are hardly distinct generically from the modern opossums, and in dentition, inflection of the angle of the jaw, characters of the basicranial region, presence of marsupial bones, etc., are quite as distinct from any Eutheria as is the living genus *Didelphys*. In the Oligocene of Tasmania is found *Wynyardia*, which again combines Polyprotodont and Diprotodont characters, but does not approach the Eutheria. Eocene marsupials and those of the Laramie formation are so incompletely known that they are of

¹ Bull. U. S. Nat. Mus., 1906.

² "Present evidence points to the fact that the two groups [Fissipedia and Inadaptive Creodonta] probably arose side by side from the Mesozoic Marsupials." Wortman, 1901, Vol. XII, p. 282. See also Vol. XI, pp. 335-337.

little assistance. The dentition, skull and skeleton are mostly unknown; in the conformation of the angle of the jaw they are entirely like the modern representatives of the order. A single lower jaw from the Bridger Eocene (Pl. L, fig. 9) is referable to the Marsupialia and so far as the evidence goes is very like the small *Peratheria* of the European and American Oligocene. It has three premolars and four molars, and in the inflection of the angle and all details of conformation of the jaw it is typically opossum-like. It is quite probable that the Allotheria (Multituberculata) of the Mesozoic and Basal Eocene are an archaic group of Marsupials, but as they show no approximation toward the placental orders (unless it be the Rodents) they need not be considered in this connection. Another jaw, Pl. XLIX, Fig. 4, is more doubtfully referred.

It would appear therefore that the distinctive characters of the marsupials, whether primary or secondary, were at all events fixed and constant as far back as the early Tertiary, at a time when the various Placental orders show a marked degree of approximation to one another.

1. FAMILY MIACIDÆ Cope, 1880.

Historical Review.—This family was proposed, and used by all authors until 1899, to include the Eocene carnivora with cynoid or viverroid dentition. The reference of the family to the Creodonta was based upon the characters of the astragalus in *Didymictis*, for with this exception the genera were known only from teeth and jaws, but it has been generally so referred, and regarded as ancestral to some or all of the modern land carnivora. In 1899 Wortman and Matthew separated *Viverravus* (including *Didymictis*) as the type of a distinct family, and referred the remaining genera to the Canidæ; and in 1901 Wortman retained this arrangement and referred the new genus *Oödictes* to the Viverravidæ. In 1902 Hay renamed the cynoid group Uintacyonidæ, without definition.

The material for comparison is now far more complete than that accessible to earlier workers. We have a more or less complete knowledge of the skull or skeleton or both of almost every genus. We can therefore estimate the position and relationship of these genera with much greater certainty than heretofore. All of them are distinguished from modern carnivora by those primitive characters on which the Creodonta were originally defined, and must be included in this group if we are to use the term in a way at all corresponding to its original significance. But their ancestral relationship to modern carnivora, inferred from the dentition, is confirmed by several important peculiarities of skull and skeleton. The Viverravine group, including *Viverravus* and *Didymictis* but excluding *Oödictes*, represent a very distinct phylum whose characters both in teeth and skeleton were marked out very early in the Eocene. The remaining genera present considerable diversity in dentition but are much alike in skeletal structure, and are evidently quite nearly related. The rehabilitation of Cope's *Miacis* makes it possible to retain the term Miacidæ for this group. The Miacidæ and Viverravidæ are, however, more nearly related than modern families of

Carnivora, or the remaining Creodont families, and it seems better to regard them as subfamilies Miacinæ and Viverravinæ, of a single family Miacidæ.¹

The nomenclature in this family is unusually complicated. Thirteen generic and thirty-four specific names have been proposed, most of them based upon inadequate or quite indeterminate types, and the synonymy has been further confused by various erroneous identifications. The accompanying table shows the species which have been referred to this group, in order of their publication, with the date, nature of the type specimen, formation in which it was found, museum where now preserved, and the present reference of the species. Most of the types are either in the American Museum of Natural History or the Peabody Museum of Yale University. Through the courtesy of Dr. Schuchert I have been able to make a careful examination of all the type specimens at Yale and compare with those in the American Museum collection.

The first species on the list is *Canis montanus* Marsh, based upon what was supposed to be the upper carnassial of a dog-like animal, but is in fact an anterior lower premolar of a Titanotherid, probably *Telmatherium*. This species must therefore be thrown out of the list; as its specific name is preoccupied it is in any case of no importance. Hay in 1899 re-named it *C. marshii*, which should now be *Telmatherium marshii*.

Triacodon fallax was based upon the trigonid of a lower molar, supposed to be a complete tooth, and referred to the Marsupials. Wortman has referred it to *Viverravus gracilis* (which it antedates), but it does not agree with that species, the trigonid being wider transversely and less extended anteroposteriorly than in *Viverravus*. It does not agree with *Vulpavus*, nor with *Miacis parvivorus*, the protoconid being considerably higher, but might be identified with equal propriety with *Sinopa minor*, *Thinocyon velox* or as a species related to *Harpalodon sylvestris* or *Uintacyon jugulans*. It is indeterminate, and the generic name invalid on this ground.

Vulpavus palustris was based upon an upper molar incomplete at the antero-external angle. Wortman and Matthew in 1899 referred to this species a specimen from the Washakie Basin, and Wortman in 1901 referred to the genus the fine type of *V. hargeri* from the Upper Bridger, separating the Washakie specimen as *Neovulpavus washakius*; both these identifications are quite erroneous. Wortman's figure of the type is incorrect in showing the outer border less complete than it really is, and the tooth did not have the extended parastyle which characterizes *V. hargeri*, *Neovulpavus* and the other Cynoid Miacidæ. On the other hand it

¹ According to many authors the name of the family should be based upon the first described genus. But in this case the first genus which might be referred here, *Triacodon*, is wholly indeterminate, even as to family; the second, *Vulpavus*, is determinate and if the family name must be based on the first described genus, *Vulpavidæ* would take precedence of *Miacidæ*. *Viverravus* is the third genus, but the name *Viverravidæ* was proposed with a quite different scope, and is here considered as of subfamily rank. The name *Miacidæ* was based upon the fourth genus, but was the first family name given, its scope the same as here used, and has been in exclusive use for twenty years to designate this group. The last consideration in the present writer's mind is the most important, but the previous ones may assist in convincing purists of the desirability of continuing to call the group *Miacidæ*.

FAMILY MIACIDÆ.

List of Described Species.

Formation.	Original Name.	Date.	Description of Type.	Location of Type.	Present Reference.
Bridger	<i>Canis montanus</i> Marsh	June 21, 1871	Lower premolar	Yale	<i>Telmatherium</i> sp.
"	<i>Triacodon fallax</i> Marsh	" "	Trigonid of lower molar	"	Indet., cf. <i>Uintacyon</i> , <i>Limnocyon</i> and <i>Sinopa</i>
"	<i>Vulpavus palustris</i> Marsh	" "	Incomplete M ¹	"	▷ <i>Vulpavus</i>
"	<i>Viverravus gracilis</i> Marsh	July 22, 1872	Lower jaw, P ₂ -m ₂ ; p ⁴ .	Am. Mus.	▷ <i>Viverravus</i>
"	<i>Miacis parvirostris</i> Cope	Aug. 7, "	Part of lower jaw, m ₂ complete	Yale	▷ <i>Miacis</i>
"	<i>Viverravus nitidus</i> Marsh	" "	Lower ? milk molar	"	? Leptictidae, indet.
"	<i>Ziphaecodon rugatus</i> Marsh	Aug. 13, "	Part of lower jaw p ₂₋₃	"	▷ <i>Ziphaecodon</i>
"	<i>Harpalodon sylvestris</i> Marsh	" "	" " " p ₃₋₄ and base m ₁	"	<i>Miacis (Harpalodon) sylvestris</i>
"	" <i>vulpinus</i> Marsh	" "	" " " P ₄	"	<i>Viverravus gracilis</i>
"	<i>Triacodon grandis</i> Marsh	Aug. 17, "	Trigonid of m ₁	"	Indet. cf. <i>Uintacyon</i>
"	" <i>nanus</i> Marsh	" "	" " lower molar	"	" cf. <i>Oödetes</i>
"	<i>Uintacyon edax</i> Leidy	Feb. 11, 1873	Lower jaw, P ₂ -m ₂ , broken	Phil. Acad.	▷ <i>Uintacyon</i>
"	" <i>vorax</i>	" "	Part of lower jaw, m ₂ and heel m ₁	"	"
Wasatch	<i>Limnocyon protenus</i> Cope	Nov. 28, 1874	Lower jaw	Nat. Mus.	▷ <i>Didymictis</i>
Wind River	<i>Didymictis</i> Cope	April 17, 1875	<i>Limnocyon protenus</i> Cope	Am. Mus.	<i>Didymictis albidens</i>
"	" <i>leptomylus</i> Cope	Sept. 20, 1880	Lower jaw fragment with teeth	"	" <i>leptomylus</i>
"	" <i>dawkinsianus</i> Cope	Dec. 9, "	Lower molars	"	<i>Viverravus</i>
"	<i>Miacis canarus</i> Cope	1881	Lower jaw	"	<i>Vulpavus canarus</i>
Wasatch	" <i>brevirostris</i> Cope	" "	Lower jaw, teeth broken off	"	" <i>brevirostris</i>
"	<i>Didymictis massetericus</i> Cope	Mar. 11, 1882	Part of lower jaw	"	<i>Uintacyon massetericus</i>
"	" <i>curtidens</i> Cope	" "	" " "	"	<i>Didymictis protenus</i> juv.
"	" <i>haydenianus</i> Cope	" "	" " "	"	" <i>haydenianus</i>
Torrejon	" <i>primus</i> Cope	Nov. 18, "	Upper and lower jaw	"	"
Uinta	<i>Amphicyon vulpinus</i> S. & O.	April 17, 1883	Part of lower jaw	Princeton	? <i>Miacis vulpinus</i>
Bridger	<i>Miacis bathygnathus</i> Scott.	1887	Lower molar and premolar	"	<i>Uintacyon bathygnathus</i>
Uinta	" <i>vintensis</i> Osborn.	Oct. 10, 1887	Lower jaw without teeth	"	<i>Miacis (Prodaphænus) vintensis</i>
Wasatch	<i>Prodaphænus</i> Matthew	May 18, 1895	<i>Miacis vintensis</i> Osb.	Am. Mus.	▷ <i>Vassacyon</i>
Washakie	<i>Uintacyon promicrodon</i> W. & M.	Mar. 31, 1899	Lower jaw	"	<i>Oödetes pugnax</i>
Uinta	" <i>pugnax</i> W. & M.	June 21, 1899	" "	"	<i>Uintacyon scottii</i>
"	<i>Prodaphænus scotti</i> W. & M.	" "	Part of upper jaw	"	▷ <i>Procymodictis</i>
Bridger	<i>Procymodictis vulpiceps</i> W. & M.	" "	Upper and lower jaws etc.	Yale	<i>Miacis (Lycarion) hargeri</i>
Washakie	<i>Vulpavus hargeri</i> Wortman	May 1901	" " " "	Am. Mus.	<i>Viverravus minutus</i>
Bridger	<i>Neovulpavus washakius</i> "	June "	" " " "	Yale	<i>Miacis (Harpalodon) washakius</i>
"	<i>Viverravus minutus</i> "	Aug. "	Lower jaw	"	<i>Viverravus minutus</i>
"	<i>Oödetes herpestoides</i> "	" "	Upper and lower jaws & part skeleton	"	▷ <i>Oödetes</i>
Bridger	<i>Vassacyon</i> Matthew	Feb. 1909	<i>Uintacyon promicrodon</i>	Am. Mus.	
"	<i>Viverravus sicartus</i> infra	" "	Upper and lower jaws	"	
"	<i>Lycarion</i> (s. g.)	" "	Vulpavus hargeri Wortman	"	
"	<i>Uintacyon jugulans</i> "	" "	Lower jaws	Am. Mus.	
"	" <i>major</i> "	" "	" "	"	
"	<i>Vulpavus ovatus</i> infra	" "	Skull and large part of skeleton	Am. Mus.	
"	" <i>completus</i> "	" "	Lower jaw	"	
"	" <i>profectus</i> "	" "	Skull, jaws and large part of skeleton	"	
"	<i>Oödetes proximus</i> "	" "	Upper and lower jaws & part skeleton	"	
"	<i>Palaearctonyx meadi</i> "	" "	Upper jaw and fragments of skeleton	"	
"	<i>Miacis (Lycarion) medius</i> infra	" "	Front half of skull, jaws, etc.	"	

Total 42 species (exclusive of *Canis montanus*)
14 genera

Am. Mus. 24 types
Yale 13
Princeton 2
Phila. Acad. 2
Nat. Mus. 1

corresponds very closely with the upper molars of an incomplete skeleton in the American Museum, apparently of the same species, and less exactly with three other incomplete skeletons all of which may be referred to this genus, one of them to a distinct subgenus *Phlaodectes*.

The fourth species, *Viverravus gracilis*, is based upon an adequate type, and both genus and species are easily recognizable.

The next species is *Miacis parvivorus*, based upon a fragment of the lower jaw with m_2 and alveoli of m_1 and m_3 . Cope subsequently made this the type of the family Miacidæ. Wortman and Matthew in 1899 identified the type with *Vulpavus palustris*, and in 1901 Wortman regarded it as a smaller species of *Vulpavus*; both identifications are erroneous. A number of specimens in our collection agree sufficiently with Cope's type to be referred to the same species and give a fairly complete knowledge of the teeth and skeleton.

A second species of *Viverravus* was based by Marsh upon a supposed lower carnassial, probably a lower milk molar of some Insectivore related to the Leptictidæ, but practically indeterminate. *Ziphacodon rugatus* is wrongly identified by Wortman with *Viverravus gracilis*; it does not agree with any of the Miacidæ, and is very doubtfully Carnivore and at present indeterminate.

Harpalodon sylvestris is rather nearly related to *Miacis parvivorus*, but may be regarded as subgenerically distinct; additional specimens from the Bridger and Lower Washakie give the characters of the upper and lower dentition more completely. *Harpalodon vulpinus* is correctly referred by Wortman to *Viverravus gracilis*.

Triacodon grandis is based upon the trigonid of a lower molar agreeing fairly well with some one of the larger species of *Uintacyon*, but is not specifically determinate. The similar but smaller type of *T. nanus* may be compared with *Oödetes*, but is also indeterminate specifically.

Uintacyon edax is based upon a lower jaw with more or less damaged teeth, and shows an extra premolar, evidently abnormal. It has been generally regarded as a species of *Miacis*, but Wortman and Matthew in 1899 and Wortman in 1901 regarded it as generically distinct from *Vulpavus*, in which *Miacis* was then included. It is nearly allied to *Miacis* but may be considered as a distinct genus, although the referred species *U. vorax*, and *Miacis (Harpalodon) sylvestris* are in some respects intermediate between the two. Its relationship to *Vulpavus* is much more distant.

The next genus described was *Didymictis*, type *Limnocyon protenus* from the Wasatch of New Mexico. Cope subsequently included in the genus a number of species, *D. altidens*, *leptomylus*, *curtidens* and *haydenianus*, similar to the type, one, *D. dawkinsianus*, referable to *Viverravus* and one, *D. massetericus*, related to *Uintacyon edax*. In 1899 Wortman and Matthew identified the genus with *Viverravus*, to which it is nearly allied, but our more complete knowledge of the skull and teeth of *Viverravus* shows that the two genera are distinct.

The next genus to be proposed was *Prodaphænus* Matthew, type *Miacis uintensis* Osborn.¹ The typical specimen consists of the lower jaws with teeth badly broken; a skeleton referred to this species enables us to define the genus completely, and shows that neither *P. scotti* W. & M., nor the Middle and Lower Eocene species subsequently referred to *Prodaphænus* by Wortman, are congeneric with the type, which is rather nearly related to *Miacis*, but may be distinguished as a subgenus. "*P.*" *scotti* appears to be more nearly related to *Uintacyon*, especially to the larger species of that genus, but I do not think it necessary to give a new generic name to this group until it is more certainly known to be a homogeneous one, and distinguish it provisionally as a subgenus of *Uintacyon*.

Procynodictis W. & M. has the scaphoid and lunar united and thus belongs in the Canidæ rather than in the Miacidæ, the brain and basicranial characters being unknown. It appears to be intermediate in all known characters between *Miacis* and *Cynodictis*, agreeing with the former in the extended parastyles of the upper molars, with the latter in the equal size of paracone and metacone and complete loss of m^3 .

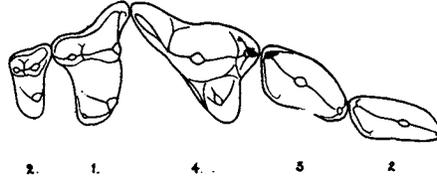
"*Vulpavus*" *harger*i Wortman, while distinct from the true *Vulpavus*, is rather nearly related to *Miacis parvivorus*, and is referable to *Miacis* as a not very distinct subgenus which may be called *Lycarion*. The type of *Neovulpavus* Wortman is closely related to *Miacis (Harpalodon) sylvestris*, distinguishable by the well developed accessory cusp on p_4 , and the larger size of p_1 which may be considered of specific value. Wortman distinguished the genus from "*Vulpavus*" (*i. e.*, *Miacis s. g. Lycarion*) by the supposed absence of m^3 , which is present in referred specimens of *M. harger*i although its presence cannot be determined in the type. A more careful examination of the type of *Neovulpavus* shows a very small alveolus for m^3 , and that this tooth was present but vestigial as in the Bridger *Harpalodon sylvestris*.

Oödetes was regarded by Wortman as related to *Viverravus*, and compared with the Paradoxures among the Viverridæ. It is much closer both in teeth and skeleton to the more typical Miacidæ than to *Viverravus*, and is intermediate between *Vulpavus* and the cynoid group.

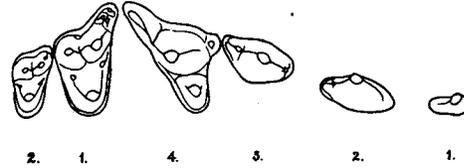
There are thus, omitting *Procynodictis* as a true Canid, six described genera of Miacidæ which appear to be valid, namely *Vulpavus*, *Viverravus*, *Miacis*, *Uintacyon*, *Didymictis* and *Oödetes*, to which may be added *Vassacyon* and *Palæarctonyx* infra. In addition there appear to be three distinguishable subgenera of *Miacis*, namely *Harpalodon*, *Prodaphænus* and *Lycarion*, one of *Uintacyon*, *Miocyon*, and one of *Vulpavus*, *Phlaodectes*. Altogether twelve genera and subgenera. I am able to distinguish thirty-three species, besides several which

¹ The publication of the genus by Matthew at this time was inadvertent, and consisted in the reference to the genus, given as a *nomen nudum* in a list of species from the Uinta formation, of a published species, *P. uintensis*. The species preceding it in the list, and intended to be taken as type, was as there noted unpublished, and was afterwards figured and described as the type of the genus by Wortman and Matthew.

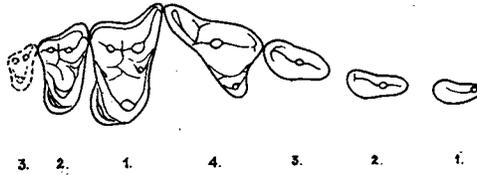
VIVERRAVUS
V. sicarius, $\times \frac{2}{3}$. No. 11521.



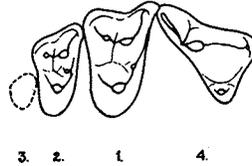
DIDYMICTIS.
D. protenus, $\times \frac{1}{4}$. No. 2831.



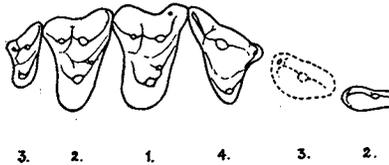
MIACIS.
M. parvivorus $\times \frac{1}{4}$. No. 11500.



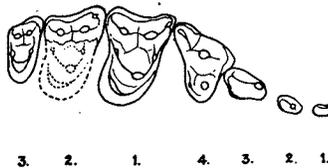
UINTAGYON.
U. vorax, $\times \frac{3}{2}$. Nos. 11507, 12620.



OÖDECTES.
O. proximus, $\times \frac{3}{2}$. No. 11495.



VULPAVUS.
V. profectus, $\times \frac{3}{2}$. No. 12626.



PALÆARCTONYX.
P. meadi, $\times \frac{3}{2}$. No. 12158.

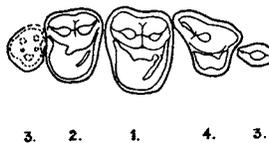


Fig. 7. Upper Teeth of Miacidæ.

are probably distinct but inadequately known. Nineteen species are found in the Bridger formation.

Classification.—The Miacidæ may be defined and classified as follows:

1. *Creodont characters*: Scaphoid, lunar and centrale generally distinct.¹ A third trochanter on femur, an entepicondylar foramen on humerus. Brain small, tympanic bullæ not ossified.² Toes 5-5.
2. *Family characters*: P⁴, M₁ carnassials as in modern carnivora. Post-carnassial teeth more or less tubercular. Metacone smaller than protocone. Ungual phalanges compressed, not fissured at the tips.³ Symmetry of digits paraxonic.

SUBFAMILY VIVERRAVINÆ.

Molars $\frac{3}{2}$. Antero-external cusp of P⁴ and posterior accessory cusp of P₄ large. Feet compact, digitigrade. Humerus with flattened deltoid crest and high greater tuberosity. Femur with small prominent third trochanter and long narrow patellar trochlea. Astragalus with narrow oblique head, the trochlea more or less excavated, the inner and outer keels well-developed. A fibulo-calcaneal facet. Skull much elongate.

1. *Viverravus* Marsh. Teeth much compressed. Oblique shear of lower carnassial more anteroposterior, heels of lower molars sub-trenchant. Upper molars without conules, parastyle continuous with paracone, anterior wing of protocone crescent extended, posterior wing undeveloped. Hypocone on M¹.

V. gracilis, minutus, sicarius, Bridger; dawkinsianus, Wind River and Wasatch.

2. *Didymictis* Cope. Teeth less compressed. Oblique shear of lower carnassial more transverse, heels of lower molars broadly basin-shaped. Upper molars with well-developed conules, parastyle distinct from paracone, anterior and posterior wings of protocone crescent equally developed, hypocone absent.

D. protenus, leptomyilus, altidens, Wind River and Wasatch; *D. haydenianus*, Torrejon.

SUBFAMILY MIACINÆ.

Molars $\frac{3}{3}$. Antero-external cusp of P⁴ and posterior accessory cusp of P₄ rudimentary or absent. Skull short or of moderate length. Feet spreading, plantigrade. Humerus with high ridged deltoid crest and small greater tuberosity. Femur with low broad third trochanter and wide short patellar trochlea. Astragalus with wide flat head, the trochlea flat without inner keel. No fibulo-calcaneal facet.

A. CYNODEI. Carnassials well differentiated; posterior molars tubercular.

3. *Miacis* Cope. Teeth $\frac{3.1.4.3}{3.1.4.3}$. Heels of lower molars basin-shaped. Carnassials and premolars large or moderate, tubercular dentition small. Jaw slender anteriorly or of moderate depth, symphysis loose.

a. *Miacis* s. s. Carnassials and premolars moderate, tubercular dentition less reduced. Jaw rather short and moderately deep anteriorly. Hypocone on m¹; m² of moderate size.

M. parvivorus, Bridger; *M. sp. div.*, Wind River and Wasatch.

¹ United in one species of *Vulpavus*, separate in another. Separate in *Didymictis*, *Miacis* and *Oödetes*. Centrale united with scaphoid in *Palæarctonyx*. Carpals not known in the remaining genera.

² In *Vulpavus* (2 species), *Uintacyon* or *Viverravus*. Unknown in the remaining genera.

³ In *Vulpavus* (3 species), *Miacis*, *Oödetes*, *Lycarion* and *Didymictis*; unknown in remaining genera.

- b. *Lycarion*¹ subgen. nov. Carnassials and premolars larger, tubercular dentition reduced. Jaw of moderate length, rather slender anteriorly. Hypocone on m¹, vestigial; m² small.
M. hargeri, Bridger; *M. medius*, Washakie.
- c. *Harpalodon* Marsh. Carnassials and premolars larger, tubercular dentition reduced. Jaw slender anteriorly. No hypocone on m¹; m² vestigial; size small; limbs long and slender.
M. sylvestris, Bridger; *M. washakius*, Washakie.
- d. *Prodaphænus* Matthew. Carnassials and premolars as in *Harpalodon*; m² ? absent; no hypocone on m¹; size large, limbs robust.
M. vintensis Osborn.
4. *Uintacyon* Leidy. Teeth $\frac{3.1.4.3}{3.1.4.3}$. Carnassials reduced and post-carnassial teeth enlarged; m² one-rooted and comparatively small; premolars reduced, p₂₋₃ of equal size. Heels of lower molars trenchant. Jaw more robust anteriorly than in *Miacis*, with heavy symphysis.
- a. *Uintacyon* s. s. Premolars moderately reduced, tubercular dentition smaller.
U. edax Leidy, *vorax* Leidy, *massetericus* (Cope), *jugulans* infra.
- b. *Miocyon*² subgen. nov. Premolars much reduced, tubercular dentition large.
U. major infra, *bathygnathus* (Scott), *scotti* (W. & M.).
5. *Vassacyon*³ Matthew. Molars proportioned as in *Uintacyon* but with basin-heels. Premolars considerably reduced but decreasing uniformly in size. Jaw deep, symphysis abrupt, canine flattened.
V. promicrodon, Wasatch.
- B. CERCOLEPTOIDEI. Carnassials little differentiated, molars all of similar form.
6. *Oödetes* Wortman. Teeth $\frac{3.1.4.3}{3.1.4.3}$. Lower molars all of similar form, decreasing in size from first to third, composed of high trigonid and trenchant heel. P⁴ carnassiform with small antero-internal cusp. Premolars short and high.
O. herpestoides, *proximus*, Bridger; *O. pugnax*, Washakie; *O. sp.*, Wind River.
7. *Vulpavus* Marsh. Teeth $\frac{3.1.4-3.3}{3.1.4-3.3}$. Lower molars all of similar form, decreasing in size from first to third, composed of a low trigonid of three subequal cusps, and broad basin heel. P⁴ not carnassiform, no antero-external cusp. Premolars robust, short and high.
V. palustris, *ovatus*, *completus*, *profectus*, Bridger; *V. brevirostris*, *canavus*, *minor*, Wind River; *V. sp. div.*, Wasatch.
8. *Palæarctonyx*⁴ gen. nov. Premolars much reduced, molars with low flattened crowns; otherwise as in the preceding genus.
P. meadi, Bridger.

The accompanying diagrams of upper and lower teeth of the eight genera (Figs. 7 and 8) will illustrate the principal distinctions. In order to show more clearly the relative proportions of the tubercular and sectorial teeth they have been enlarged so as to bring the first molar in each to approximately the same size, and arranged one above another on a vertical line dividing the sectorial from the tubercular dentition. The series from *Viverravus* to *Palæarctonyx* shows the increase of the tubercular and decrease of the sectorial dentition, the enlarge-

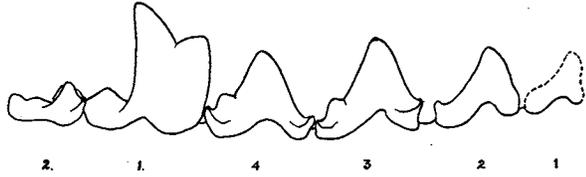
¹ Λυκαρίον a little wolf.

² Gr. μειων less, κυν dog — less typically cynoid.

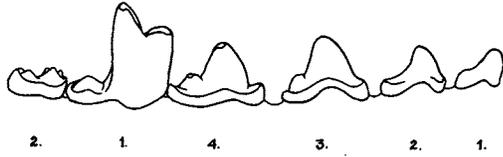
³ Wasatch, κυων dog.

⁴ Gr. παλαιος ancient, ἀρκτος bear, ὄνυξ claw.

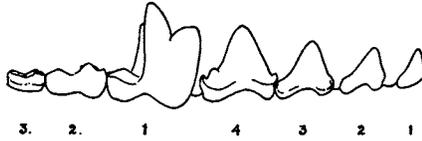
VIVERRAVUS.
V. sicarius, $\times \frac{2}{1}$. No. 11521.



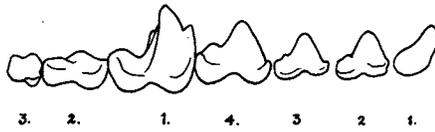
DIDYMICTIS.
D. protenus, $\times \frac{1}{1}$. No. 2831.



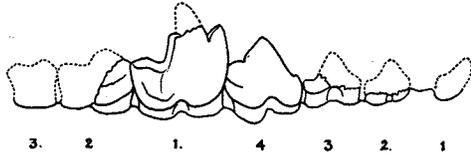
MIACIS.
M. parvivorus, $\times \frac{2}{1}$. No. 11496.



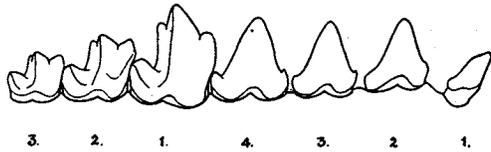
UINTACYON.
U. vorax, $\times \frac{3}{2}$. No. 11507, 12620.



VASSACYON.
V. promicrodon, $\times \frac{3}{2}$. No. 83.



OÖDECTES.
O. proximus, $\times \frac{5}{2}$. No. 11495.



VULPAVUS.
V. profectus, $\times \frac{3}{2}$. No. 12626.

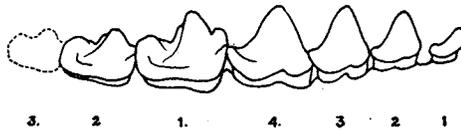


Fig. 8. Lower Teeth of Miacidæ.

ment, broadening and flattening of the molars, increase of conules and hypocone above, of entoconid and breadth of heel below, the lowering of the trigonids, decrease of carnassials and loss of shearing function, decrease of premolars and loss of accessory cusps.

Associated with the less predaceous adaptation of the teeth is a notable decrease in the relative size of the skull as compared with the rest of the skeleton. This may be illustrated by the proportion of the length of the humerus which is a fair index of the general size of the body, to the length of the lower premolar-molar dentition, a fair index of the general size of the head. These two measurements can be made upon the same specimen in the following species, and yield the results tabulated when the length of the humerus is standardized to 100.

	Length of humerus	Length of P ₁ -m ₃
Viverravinæ		
<i>Didymictis protensus</i> No. 2830	100	72.5
Miacinæ (Cynoidei)		
<i>Miacis (Prodaphænus) uintensis</i> , No. 1964	100	est. 45
" (<i>Harpalodon</i>) <i>washakius</i> , Type	"	47.2
" (<i>Lycarion</i>) <i>medius</i> , Type	"	
" <i>parvivorus</i> No. 11496	"	49.
<i>Uintacyon vorax</i>	"	46.7
Miacinæ (Cercoleptoidei)		
<i>Oödetes herpestoides</i> , Type	100	36.5
" <i>proximus</i> , Type	"	37.3
<i>Vulpavus profectus</i> , Type	"	38.2
" (<i>Phlaodectes</i>) <i>ovatus</i> , Type	"	33.3
<i>Palæarctonyx meadi</i> , Type	100	27.6

It thus appears that the skull of *Didymictis* is nearly three times as large in proportion to the skeleton as in *Palæarctonyx*, and twice as large as in *Oödetes* and *Vulpavus*. The Viverravinæ were extraordinarily macrocephalic, and *Palæarctonyx* remarkably microcephalic. The cynoid and cercoleptoid groups are intermediate, having the proportions respectively of *Bassaris* and *Cercoleptes*.

Geological Distribution of the Miacidæ.

	EOCENE											
	Basal		Lower			Middle		Upper				
	Puerco	Torrejon	Wasatch	Wind River	Lower Huerfano	Upper Huerfano	Lower Bridger	Upper Bridger	Lower Washakie	Upper Washakie	Lower Uinta	Upper Uinta
VIVERRAVINÆ.												
<i>Didymictis haydenianus</i> Cope		×										
“ <i>protenus</i> Cope			×		×							
“ <i>leptomylus</i> Cope			×	×								
“ <i>altidens</i> Cope				×	×							
<i>Viverravus dawkinsianus</i> (Cope)			×	×	×							
“ <i>sicarius</i> sp. nov.							×					
“ <i>gracilis</i> Marsh							×	×				
“ <i>minutus</i> Wortman							×	×				
MIACINÆ												
<i>Miacis</i> sp. div.			×	×								
“ <i>parvivorus</i> Cope							×					
“ (<i>Harpalodon</i>) <i>sylvestris</i> Marsh								×				
“ “ <i>washakius</i> (Wortman)									×			
“ (<i>Lycarion</i>) <i>harger</i> i (Wortman)								×				
“ “ <i>medius</i> sp. nov.												
“ (<i>Prodaphænus</i>) <i>uintensis</i> Osborn												×
“ “ <i>vulpinus</i> S. & O.												×
<i>Uintacyon massetericus</i> (Cope)			×									
“ <i>edax</i> Leidy							?					
“ <i>vorax</i> Leidy							×					
“ <i>jugulans</i> sp. nov.								×				
“ (<i>Miocyon</i>) <i>bathygnathus</i> (Scott)								?				
“ “ <i>major</i> sp. nov.								×				
“ “ <i>scotti</i> (W. & M.)												×
<i>Vassacyon promicrodon</i> (W. & M.)			×									
<i>Oödetes</i> sp.				×								
“ <i>herpestoides</i> Wortman							×					
“ <i>proximus</i> sp. nov.							×					
“ <i>?pugnax</i> (W. & M.)									×			
<i>Vulpavus</i> sp. div.			×									
“ <i>canavus</i> (Cope)				×								
“ <i>brevirostris</i> (Cope)				×								
“ <i>palustris</i> Marsh							×					
“ <i>profectus</i>							×					
“ <i>completus</i>							×					
“ (<i>Phlaodectes</i>) <i>ovatus</i>							×					
<i>Palæarctonyx meadi</i>								×				
? “ sp.							×					

Relationship to the Fissipedia.—This family has been regarded by all authorities as ancestral to part or all of the Fissiped Carnivora. The dentition approximates that of the least specialized members of the true Carnivora but is in several respects more primitive than any. The emphasis of carnassial development is placed upon p^4 and m_1 but a subordinate shear is retained by the posterior molars. The molars decrease in size from first to third but are of similar construction and more or less similar proportions, either in upper or lower jaw. The metacone is generally smaller than the paracone, but it is not clear that this should be regarded as a primitive character, since in *Vulpavus*, which in other respects presents the most primitive type of molar dentition, the paracone and metacone are sub-equal, and the greatest inequality is seen in the most specialized molar dentition, that of *Viverravus*. The three primary cusps are always present in the upper molars; the conules, cingula and styler cusps are variously developed. The lower molars always show the triangular trigonid of three well separated cusps, and a heel either basin-shaped or trenchant.

The skull displays various primitive characters as compared with Fissipedia, the most important of which are the small brain-case and absence of tympanic bulla. The cerebral lobes extend a little under the frontals, but are almost entirely contained within the parietals; correspondingly the postorbital constriction is very narrow. The nasals extend far backward, and the lachrymals are slightly expanded upon the face, but less than in the Inadaptive Creodont families. The orbit is placed further back than in most modern Fissipedia. The arrangement of the basicranial bones and foramina (see Fig. 2) is in general that of the more primitive Arctoidea, but in addition to the absence of the tympanic bulla, the ento-carotid circulation appears to be of a more generalized type, as in the other Creodont families, retaining in addition to the inner branch, which is placed as in the Arctoidea, a branch external to the petrosal prominence, passing forward to the foramen lacerum medius along the medial side of the meso-tympanic fossa. This branch apparently corresponds with the main entocarotid of Insectivora. In the Creodonta, and presumably in the primitive Insectivora as well, both branches are retained, one of which becomes aborted in the modern Insectivora, the other in the modern Arctoid Carnivora.¹ In the *Æluroid* carnivora the carotid circulation is still further modified. In this respect therefore, as in almost all characters of the basicranial region, the Miacidæ agree with the other Creodont families (especially with the less specialized members thereof) in presenting the common primitive structure which is most nearly retained among modern Carnivora by the Arctoidea, and is still more closely approximated by the early Fissipedia of the Oligocene and Lower Miocene.

¹This interpretation differs from that advocated by van Kampen in his recent monograph upon the Tympanic Region of the Mammalian Skull (Amsterdam, 1906, Dutch; Leipzig, 1906, German) but it accords better with the conditions presented by the Creodonta and Eocene Insectivora, which can hardly be brought into conformity with his hypothesis of the cause and course of differentiation between the two orders.

In skeleton structure the Miacidæ are also primitive, but, except in a few points, not more so than the most primitive of modern Fissipedia. This will be shown in detail in the comparison of *Miacis* with *Bassaris* and of *Vulpavus* with *Cercoleptes*. The neck is of moderate length, the trunk long and slender, the lumbar region highly flexible, the tail long and powerful and probably more or less prehensile. The limbs are exceptionally loose jointed, displaying, especially in the fore-limb, a very great flexibility and prehensile adaptation. The radius can be very fully rotated upon the ulna, and the tibia to some extent upon the fibula. The carpal and tarsal joints are very mobile in all directions, the feet are five toed, the pollex and hallux divergent and to a certain extent opposable, although not so much as in the Primates. The claws are sharp, compressed and curved. These characters are explainable as primitive arboreal adaptations from which the Fissipede Carnivora have departed to an extent corresponding to their more or less strictly terrestrial habitat, most of all in the Canidæ and Hyænidæ, and least of all in *Cercoleptes*, the most strictly arboreal of modern carnivora. The Viverravinæ depart from this primitive type in several respects, apparently to adaptation to more terrestrial habitat, but retain one primitive feature lost by the Miacinæ, in the articulation between fibula and calcaneum.

It appears probable that in the Miacinæ and Viverravinæ we have the beginning of the differentiation into Arctoid and Æluroid carnivora. The Miacinæ correspond with the more primitive Arctoidea (Mustelidæ) in the generally shorter basicranial region and absence or slight development of the antero-external cusp of p^4 , and in the relatively greater conservatism in the development of the manus and pes. The Viverravinæ correspond with the more primitive Æluroides (Viverridæ) in the more elongate basicranial region, prominence of the antero-external cusp of p^4 , and the earlier digitigradism and reduction of the first digit. But with our present knowledge this relationship can only be regarded as provisional. The derivation of the Canidæ from the Cynoid Miacinæ may be considered as securely established through a fairly complete series of annectant forms known from the entire skeleton. The approximation of the primitive Procyonidæ and Mustelidæ to the same type renders it reasonably certain that they are derived from this group, but their exact relations to the known genera of Miacinæ are problematic. In both families the primitive types are known from the complete skeleton and are sufficiently connected with their modern descendants by intermediate forms. The phylogeny of the Ursidæ is very incompletely known; they are connected with the Canidæ by a series of supposed intermediate forms known only from the teeth, while their morphologic characters connect them rather with the Mustelidæ, both families retaining many primitive characters displayed by the Miacinæ but early lost by the Canidæ. On the other hand one at least of the supposed primitive characters of the Ursidæ, the plantigrade feet, may be secondary, as it is in the raccoons, derived from an

earlier semi-digitigrade condition, since the astragalus is of the type usually associated with a digitigrade gait, while that of the plantigrade Mustelidæ indicates a primary plantigradism. This would overcome one of the difficulties in deriving the Ursidæ from the early digitigrade Canidæ. Whether they are more nearly related to the Canidæ or to Mustelidæ, there is no difficulty about their derivation from the Miacinæ; in the one case *Vassacyon*, in the other *Palæarctonyx*, would stand nearest among the known genera.

The derivation of the Æluroid families is much more uncertain. The Viverridæ may be derived from Viverravinæ without much change in dentition, but intermediate forms are very incompletely known, and the very considerable differences in skull structure and in certain characters of the feet are not known to be bridged over by intermediate types. The supposed Viverridæ of the European Oligocene are mostly very imperfectly known, and as far as the teeth go, appear to connect the family very closely with the Oligocene Mustelidæ. But the resemblance in teeth may not imply any close relationship, and it is quite possible that some at least of these supposed Oligocene Viverrines may be Mustelidæ with Viverrid dentition. If we admit the alleged close connection of Mustelidæ, Canidæ and Viverridæ in the Oligocene then all three families would have to be derived from the Cynoid group of Miacinæ, the Viverravinæ would be an abortive side branch paralleling the Viverridæ in teeth, skull and skeleton, the Cercoleptoid group might be ancestral to *Cercoleptes* but not to the Mustelidæ, and their very considerable approximation to Mustelidæ and Ursidæ in characters of teeth, basicranial region and feet would likewise be wholly due to parallelism. The Hyænidæ are usually considered to be derived from the Viverridæ through *Ictitherium*; a more exact study of the basicranial region of this genus would probably place their relations upon a more secure foundation. The Felidæ are morphologically more nearly related to the Viverridæ than are the Hyænidæ, but in the Machærodont division at least are of very early specialization. We should look to find connecting links with the more primitive family in the Eocene, but thus far they have not been discovered, and the various structurally intermediate forms except possibly *Proailurus* cannot be regarded as in any sense ancestral; even *Pseudæilurus* is contemporary with the most highly specialized Machærodonts (*Eusmilus*, *Hoplophoneus*) and could only be considered in relation to the Felinæ. The supposed derivation of the Felidæ from the Palæonictidæ will be discussed later.

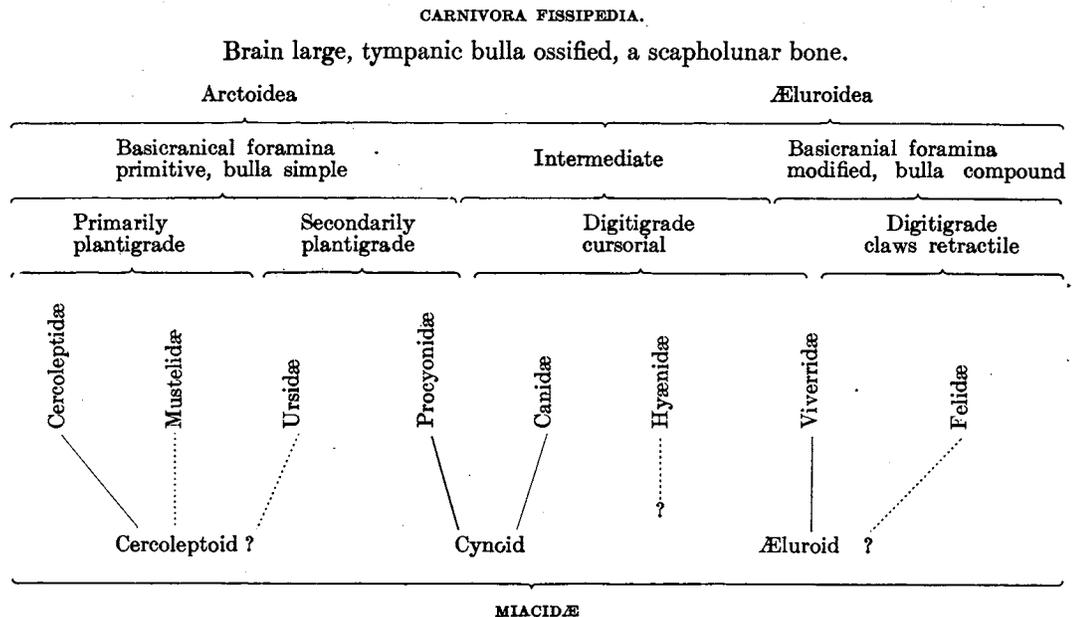
various correspondences in the teeth and jaws. The typical group of Canidæ tends to slender jaws, compressed premolars with small accessory cusps and upper molars with well developed conules and hypocone, the trenchant-heeled types to heavy stout jaws, robust premolars often reduced in number or size, with large accessory cusps, and upper molars with conules and hypocone reduced or absent. A corresponding association of characters appears to be foreshadowed in the basin-heeled and trenchant-heeled genera of the Cynoid Miacidæ. Against it must be placed the facts that the basicranial region in *Cynodictis* and *Daphænus* is almost identical in arrangement and much more cynoid than in any Miacidæ, indicating a near relationship between the two Oligocene genera. The basicranial region in the Miacinæ of the Bridger and Washakie is unknown, in *Prodaphænus* of the Uinta it is imperfectly known and apparently much as in *Vulpavus*, and it may be that the other cynoid genera were more typically cynoid in the skull, and *Prodaphænus* an aberrant form. Provisionally therefore, we may regard *Miacis* and *Uintacyon* as ancestral respectively to the typical and trenchant-heeled Canidæ, an arrangement outlined by Wortman and Matthew in 1899 and adopted by Wortman in 1902, although in a somewhat different and less comprehensive form.

Evidence as to the Natural Classification of the Fissipedia.—It will be observed that the Miacidæ are divisible upon characters of teeth, skull and skeleton, so far as these are known, into groups corresponding with the primary divisions of the modern carnivora based upon their morphologic relationships. We have first a division into Miacinæ and Viverravinæ, corresponding with the divisions Arctoidea and Aeluroidea among modern Fissipedia. The Miacinæ are further divisible into a Cercoleptoid and a Cynoid group, corresponding with the division of modern Arctoidea into Arctoidea proper and Cynoidea. The Cynoid group of Miacidæ are pretty certainly ancestral to the Canidæ, while the Cercoleptoid and Viverroid groups correspond with the most primitive of the typical Arctoidea and Aeluroidea, and are probably ancestral to them, although the annectant series have not been discovered. The structural classification of the Fissipedia, in which primary importance is given to the characters of the basicranial region, supported by the characters of the skeleton and the soft anatomy, is therefore in entire accord with the primary divisions of the Eocene group from which they appear to be descended. This correspondence is a strong argument, on the one hand for the view that in the Miacidæ we have represented the approximate ancestral types of all the primary groups of Fissipedia, on the other hand for believing that the accepted classification of the modern carnivora is a natural one and represents the true relationships of the families. It has been generally considered that this classification is not supported by palæontology, and that the relationships of the families indicated by their fossil representatives of the Oligocene and Miocene are materially different from the morphologic arrangement. The Ursidæ, which are structurally nearest to the Mustelidæ, are apparently derivable from Miocene or Upper Oligo-

cene Canidæ; the Mustelidæ and Viverridæ, wide apart structurally, are apparently very intimately connected with each other and with the Canidæ in the Oligocene; while the Felidæ are rather widely separated from the other families. But, as already observed, these annectant series are based upon characters of the teeth, and are not known to be supported by characters of the skull and skeleton. In the introductory part of this memoir I have pointed out some of the reasons why the teeth alone in the Carnivora afford an unsafe guide in classification, especially in the primary divisions of the order, as there are many admitted instances of close parallelism in different groups. The annectant types (*e. g.*, *Phlaocyon*) whose position has been estimated from a study of the entire skeleton, with especial regard to the basicranial region, indicate relationships entirely in accord with those based upon the morphology of modern Carnivora.

The fact therefore that several independent and apparently fundamental distinctions in the basicranial region concur with important characters in the skull, skeleton and soft anatomy of the modern carnivora, and with the independently based arrangement of the Eocene ancestral groups (worked out in its present form by the writer before considering their relations to the Fissiped families), in supporting the accepted primary divisions of the Fissipedia, appears to be sufficient reason for regarding these as a well established and natural arrangement, and the apparent conflict in certain points of the palæontological evidence as due mainly to our imperfect knowledge of supposed annectant series.

The accompanying diagram illustrates the apparent relationships of the Miacidæ to the various modern Carnivora.



Brain small, tympanic bulla not ossified, scaphoid and lunar separate, basicranial foramina primitive, plantigrade, arboreal.

Viverravus Marsh, 1872.

See Figs. 7 and 8.

Viverravus MARSH, Am. Journ. Sci., 1872, Vol. IV, p. 127; separates dated July 22.

This genus has been known hitherto only from the lower jaw and a single upper carnassial. We are now able to describe in addition the upper dentition and the skull, but the skeleton remains unknown, save for the astragalus and a few other fragments.

The teeth are of more sectorial type than in any of the other Miacidæ. The premolars are large, compressed, two-rooted, the carnassials large with shear more oblique and better developed than in any of the other genera; m_2^2 small and m_3^2 absent. The antero-external cusp of p_4^1 and the posterior accessory cusps of p_{3-4} are well developed. P_1^1 two-rooted. The jaws are long and slender and the skull extremely elongate in both facial and cranial regions. The brain-case is of small size, the basicranial region narrow, and the skeleton, so far as may be judged from the fragments preserved, was proportionately small, with slender

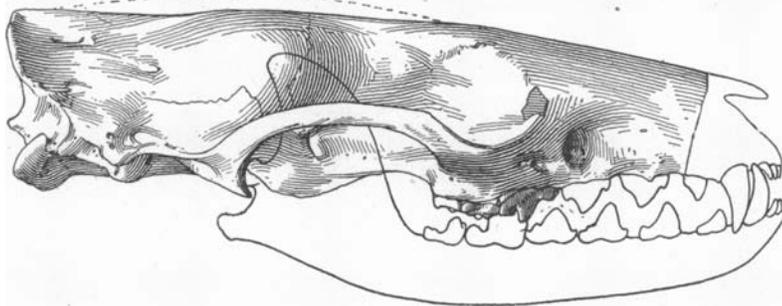


Fig. 9. *Viverravus minutus*, skull and jaws, side view, No. 12621, $\times \frac{2}{3}$. The lower jaw is restored principally from No. 13074.

digitigrade pes, and grooved astragalar trochlea.

The genus is nearly related to *Didymictis*, but the sectorial character of the dentition is more marked, the skull is less archaic, and the feet, so far as can be inferred

from the fragments preserved, decidedly more progressive. The trenchant heels of the lower molars and absence of conules and of the posterior wing of the protocone crescent in the upper molars, the compression and large angulate cusps of the tubercular teeth, the more antero-posterior shear of the carnassials, the slight development of the outer shelf of the upper molars etc. readily distinguish it from the more ancient genus, as exemplified by the typical *D. protenus*. *Didymictis* and *Viverravus* stand in somewhat the same relation as do *Viverra* and *Genetta*, although the difference is somewhat more marked. We may regard *Viverravus* as approximately derivable from some small unspecialized species of *Didymictis* (e. g. *D. haydenianus*) although not from the more typical Wasatch and Wind River species.

The typical species is *V. gracilis* Marsh, about as large as a mink. Dr.

Wortman has added a smaller species, *V. minutus*, of about the size of a weasel; a third and considerably larger species about as large as the fisher (*Mustela pennanti*) is represented by specimens in our collection.

***Viverravus gracilis* Marsh.**

Viverravus gracilis MARSH, Am. Journ. Sci., 1872, Vol. IV, p. 127, separates dated July 22; WORTMAN, *ibid.*, 1901, Vol. XII, p. 145, figs. 18, 19, (type figured).

Harpalodon vulpinus MARSH, *ibid.*, p. 217.

Fifteen specimens in our collection are referred to this species, all of them consisting of lower jaws with more or less dentition, two associated with a few fragments of the skeleton. Nos. 11512, 11514, 11515, 11517, 11520, 13075, 13076 and 13078 are from the Lower Bridger, mostly Horizon B₂. Nos. 12068, 12069, 12072, 12073, 12622 and 12624, from the Upper Bridger, do not show any constant differences to separate them from the species of the lower beds, although the teeth appear to be more compressed and the cusps sharper and more angulate than in the typical jaws from Grizzly Buttes. No. 12623, from the upper part of Horizon D, is of much larger size than the above, nearly equal to *V. sicarius*, but in form and proportion of the teeth agrees with *V. gracilis*, and may indicate a large variety or mutant of Marsh's species.

***Viverravus minutus* Wortman.**

Plate XLIII, Fig. 1, and Text Figs. 9-12.

Viverravus minutus WORTMAN, Am. Journ. Sci., 1901, Vol. XII, p. 147, fig. 21.

This species was founded upon several incomplete lower jaws in the Marsh collection. I refer to it a well preserved skull, No. 12621, found by Mr. Granger, on the ground of its appropriate size and the generic agreement of the teeth with those of *V. sicarius*. Two lower jaws in the collection, Nos. 13074 and 11516, are referable here, although of somewhat larger size than the type. There are no constant differences except size to separate this species from the foregoing, the remaining characters noted by Wortman being quite variable in our series.

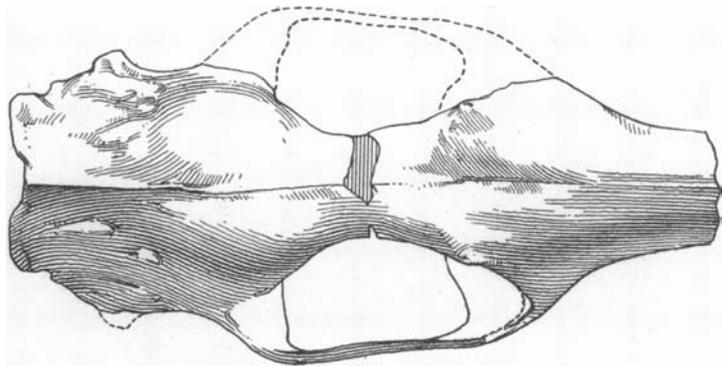


Fig. 10. *Viverravus minutus*, skull, top view, No. 12621, $\times \frac{2}{1}$.

The skull is of rather remarkable proportions and very different from *Didymictis*, although the most obvious distinctions are dependent on the great difference in size. As in the Wasatch genus it is extremely long and narrow, both in facial and cranial regions; unlike it, the occiput is low and the sagittal crest absent. The muzzle is broken off in front of the second premolar, and the sutures of the facial bones cannot be certainly distinguished; otherwise the skull is nearly perfect and quite uncrushed. The lachrymal foramen is internal and the anterior border of the orbit is defined, inferiorly at least, by a sharp crest. The infraorbital foramen is small, and situated over the posterior end of p^3 . The postorbital processes are very rudimentary, especially that on the jugal, which is indicated merely by a slight angulation. The postorbital constriction is long and narrow and there are no temporal crests. The arches are very slender and narrow. The brain-case is of very small capacity; the small cerebral lobes are indicated by swellings on the surface of the parietals, and behind them the parietals extend for some distance to the occiput with nearly flat surfaces meeting at an angle in the middle line, but without any sagittal crest. In the preparation of the specimen, however, the writer was able to trace and define a discolored parting of the matrix with the form and position of a low sagittal crest, which may indicate a cartilaginous crest of the outline indicated in the figure. The obliteration of the sutures shows that the animal was mature, so that the absence of bony crest was not a juvenile character.

The occipital crests are broad and low. The mastoid has a considerable lateral exposure at the postero-lateral angle of the skull and extends upward on the side of the cranium so as to approach quite near to the parietals somewhat as in rodents.

The mastoid process is very slight and the paroccipital process small and directed backward. The condyles face backward and are wide apart. The glenoid fossa is far forward, and the postglenoid foramen a considerable distance behind it. There are no bullæ; the petrosal prominence is pear-shaped, most prominent posteriorly, with the broad deep mesotympanic fossa antero-external to it. The grooves on the outer side of the petrosal prominence for the tympanic branches of the entocarotid artery are distinct, the groove beginning at the apex of the promontory and dividing into two branches, one leading to the *fenestra ovalis*, the other forward to the *foramen lacerum medium*. The stylomastoid foramen is at the posterior end of the tympanic fossa, defined anteriorly by a spur from the posttympanic process of the squamosal, which bridges the fossa nearly to the petrosal. The inner branch of the entocarotid enters between basioccipital and petrosal some distance in front of the *foramen lacerum posterius*, and presumably passes forward to the *for. lac. med.* as usual among primitive carnivora. The posterior lacerate foramen is, as usual among Creodonta, more external than in modern carnivora, situated at the postero-external angle of the auditory prominence. The condylar foramen is well separated from the posterior

lacerate; the median lacerate foramen is small. The foramen ovale lies opposite the postglenoid process, and a little in front of it begins the alisphenoid canal. The foramen rotundum and sphenoidal fissure appear to be united. The pterygoid plates are deep but do not overarch the postnareal gutter, which is open to a point opposite M^2 . The palatines extend forward to a point opposite the anterior end of p^4 .

Dentition.—The carnassial and molars of one side are preserved, with alveoli of the anterior premolars. There is a short diastema in front of p^2 ; this and the following tooth are two rooted. The carnassial is much like that of *V. sicarius* except for the somewhat smaller deutocone and more widely separated parastyle. The first molar has the external cusps

more symmetrical and the hypocone somewhat larger; the second molar is less symmetrical, the metacone being less external in position. The teeth have smaller, sharper cusps, with concave slopes and rather open valleys between, confirming the insectivore-like suggestions which are apparent

in the skull. I can find no evidence, however, of any real affinity to the Insectivora; the resemblance is merely a matter of small size and similar habits. The skull compares in size with the weasel or some of the smallest Viverridæ, and has the same slender arch, low cranium, broad occiput and anteriorly placed glenoid fossæ as in these small vermiform fissipeds. It is much more elongate than any of them and the brain capacity very much smaller.

I am unable to find in this skull any good reasons for associating *Viverravus*

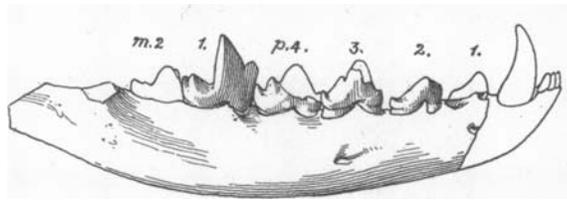


Fig. 12. *Viverravus minutus*, lower jaw, No. 13074, $\times \frac{2}{3}$.

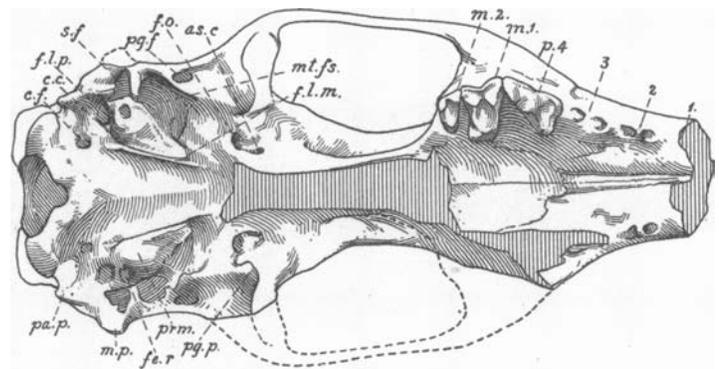


Fig. 11. *Viverravus minutus*, skull, under view, No. 12621, $\times \frac{2}{3}$. Lettering as in Fig. 2.

with the Æluroid Carnivora other than the narrow elongate basicranial region, the distinct parastyle on p^4 and the correspondence in dental formula and proportions of the teeth with the Viverridæ. The arrangement of the basicranial foramina etc.

is the same as in all the smaller Creodonta (cf. *Vulpavus*, *Limnocyon*, *Thinocyon*, *Sinopa* and *Tritemnodon*) and show no advance towards the modifications characteristic of the Æluroides. None of the above mentioned characters are entirely confined to Æluroides, but

they are exceptional in other carnivora and normal to primitive æluroids although developed to a varying extent.

***Viverravus sicarius* sp. nov.**

Text Figures 7, 8, 13 and 14.

A third species of *Viverravus* considerably larger than *V. gracilis* is represented by the upper and lower jaws, No. 11521, with well preserved teeth, and by two fragmentary jaws, Nos. 11513, 13077; all from the lower Bridger beds.

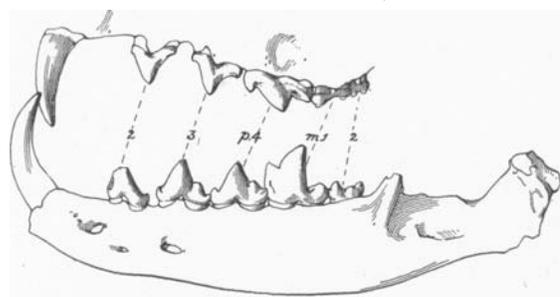


Fig. 13. *Viverravus sicarius*, upper and lower jaws, external view, natural size: Type specimen; No. 11521. Lower Bridger.

The upper premolars, except the fourth, are compressed and two-rooted, of comparatively large size and without internal cusps. P⁴ has much the same proportions as in the genet, with large antero-internal deuterocone and strong parastyle, anterior rather than antero-external in position. The upper molars are peculiar, the paracone and metacone trihedral cusps, the paracone being of larger size and its anterior face

nearly vertical; the posterior wing of the protocone crescent is undeveloped, its anterior wing extended toward the paracone, the two forming a strong notched shearing crest along the anterior border of the tooth which is continued nearly to its outer angle in the descending crest forming the antero-external angle of the paracone. There are no conules, but the hypocone is moderately developed on m¹. M² is similar to m¹ but much smaller and without hypocone. The flat cingular shelf of the external border of the molars of *Didymictis*, *Miacis* and *Vulpavus* is but little developed, and there is no distinct parastyle and no metastyle.

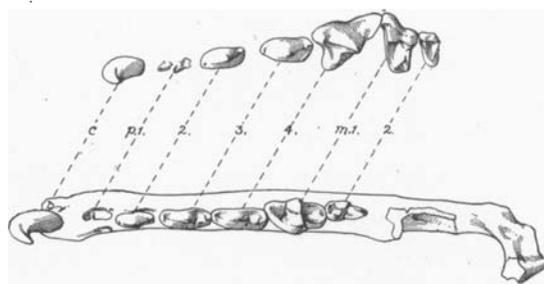


Fig. 14. *Viverravus sicarius*, crown view of upper and lower dentition, natural size. Type specimen.

The lower jaw is deeper and more massive than in *V. gracilis*, the premolars higher and less compressed with more prominent protocones and smaller basal and accessory cusps. It is about one-half larger (linear) than the type species, and twice the size of *V. minutus*.

Comparative Measurements of Teeth.

	V. sicarius No. 11521 (type)	V. gracilis type.	V. minutus No. 12621
Length of upper dentition, c^1 - m^2	44.8		(est.) 21.
“ “ “ premolars	30.		(est.) 14.
“ “ “ molars	7.5		4.4
Diameters of p^4 , anteroposterior and transverse	9.1×6.0	7×3.5	4.5×2.8
Diameter of m^1 , “ “ “	4.7×8.8		2.8×4.2
“ “ m^2 , “ “ “	2.8×5.1		1.5×3.0
Length of lower dentition, C_1 - m_2	47.5		type
“ “ premolars	25.8	18.5	14.
“ “ molars	13.4	9.5	7.
Diameters of m_1 , anteroposterior and transverse	8.5×4.7	5.2×3.4	4.5×2.5
“ “ m_2 , “ “ “	5.4×3.0		

Viverravus dawkinsianus (Cope).

Didymictis dawkinsianus COPE, Bull. U. S. G. S. Terrs., 1881, Vol. VI, p. 191.

Viverravus gracilis MATTHEW, Bull. A. M. N. H., 1899, p. 35; WORTMAN and MATTHEW, *ibid.*, p. 136; WORTMAN, Am. Jour. Sci., 1901, Vol. XII, p. 145.

This species from the Wind River is somewhat smaller with less elongate jaw and more compressed premolars than the typical *V. gracilis*, but very doubtfully distinct, unless Cope's statement that the first premolar is one-rooted is correct; I am unable to certainly verify it on the type.

Didymictis Cope, 1875.

This genus was identified by Wortman and Matthew with *Viverravus*, but a more careful comparison and the more complete knowledge of the Bridger genus shows that they are distinct. The typical and best known species is *D. protenus* of the Wasatch; *D. leptomytus* is a closely related species first described from the Wind River, but apparently also occurring in the Wasatch. *D. altidens* is a larger species from the Wind River. *D. curtidens* was founded on a jaw fragment of an immature individual of *D. protenus*. *D. massetericus* proves to be a species of *Uintacyon*, agreeing with this genus in the form of the teeth and in the presence of m^3 (the alveolus of this tooth was concealed by matrix when described by Professor Cope, and erroneously supposed to be absent). *D. dawkinsianus* of the Wind River is a species of *Viverravus*, closely allied to *V. gracilis* and doubtfully distinct. The most interesting species of the group is the little *D. haydenianus* of the Basal Eocene (including *D. primus*). This is the oldest of the Miacidæ. The teeth are more compressed than in the remaining species of *Didymictis*, but otherwise it agrees with that genus, and is undoubtedly distinct from *Viverravus*.

The skull and jaws and parts of the skeleton of *D. protenus* were figured and described by Matthew in 1901. The genus is limited to the basal and lower Eocene and does not occur in the Bridger.

Miacis Cope, 1872.

See Text Figs. 7 and 8.

Miacis COPE, Pal. Bull. No. 3, dated Aug. 7, 1872; Proc. Am. Phil. Soc., 1872, Vol. XII, p. 470.

Miacis, in part, of later publications of Cope, Scott and other authors.

Harpalodon MARSH, Am. Jour. Sci., 1872, Vol. IV, p. 216, separates dated Aug. 13 (type species only).

Prodaphænus MATTHEW, Bull. A. M. N. H., 1899, p. 49 (*P. uintensis* only). Not *Prodaphænus* W. & M., *ibid.*, p. 114, nor Wortman, Am. Jour. Sci., 1901, Vol. XI, p. 449.

Vulpavus WORTMAN & MATTHEW, Bull. A. M. N. H., 1899, p. 118; WORTMAN, Am. Jour. Sci., 1901, Vol. XI, p. 341, not of Marsh.

Neovulpavus WORTMAN, *ibid.*, p. 445.

This genus includes the more typical cynoid Miacidæ with carnassial and tubercular dentition well differentiated, lower molars with basin heels, slender or moderately deep jaws with the symphyseal region comparatively shallow and loosely sutured, and typically a full Eutherian dentition, but m^3 vestigial or absent in some species. The general proportions of the skull are much as in *Cynodictis*, but the brain-case is smaller. The skeleton is decidedly more primitive than in any Oligocene Carnivora, and agrees very closely with *Vulpavus* and *Oödictes*.

The genus is structurally ancestral to the typical Canidæ and is therefore of the highest importance from a phylogenetic standpoint, since the successive stages in the evolution of the modern dogs are much more completely known than in any other group of Carnivora.

The teeth are much like those of *Cynodictis* but the tubercular dentition is less completely differentiated from the sectorial teeth, much more so, however than in *Oödictes* and *Vulpavus*, the tubercular molars retaining to a certain extent the similarity of construction to the carnassial, and the subordinate shearing function, more obviously shown in these genera. The second lower molar is less elongate than in *Didymictis* and *Viverravus*, and the third is always present though small, with either one or two roots. The third upper molar is always small, sometimes vestigial, and perhaps absent in the Uinta species. The parastyle of p^4 is small or minute, and the accessory cusps of the premolars less developed than in the *Viverravinæ*.

The general proportions of the skeleton are much as in the small "vermiform" Mustelidæ and Viverridæ, but the feet are comparatively short, the first digit less reduced than in most of the later Tertiary and modern genera, and the tail unusually long and powerful. The species vary considerably in length of limbs; in *M. sylvestris* and *washakius* they are comparatively long and slender,

in *M. uintensis* short and stout, in *M. parvivorus* and *hargeri* of intermediate proportions. All the species, however, agree in the construction of limbs and feet, differing in several important features from any Fissiped carnivora. The humerus has a long, prominent, abruptly ending deltoid crest, high supinator crest, broad distal end with shallow imperforate supratrochlear fossæ and prominent epicondyles. The ulna and radius are subequal and capable of free rotation. The scaphoid and lunar are separate (in *M. parvivorus* at least). The femur is always longer than the tibia, the lesser trochanter is on the internal side of the shaft instead of the posterior surface as in modern carnivora, and the third trochanter, absent in the fissipeds, is always present although not prominent. The astragalus is very characteristic, with flat trochlea, the inner crest undeveloped. The trochlear facet extends forward upon the neck of the astragalus and is of limited extent posteriorly; the astragalar foramen is present; the head of the astragalus is a flattened oval and very obliquely set. The calcaneum is broad with very oblique cuboid facet, short tuber, prominent peroneal tubercle and no fibular facet. The ungual phalanges are moderately compressed and are not fissured at the tip.

These characters are equally well shown in *Oödetes* and *Vulpavus*, which are not distinguishable in the skeleton from *Miacis* and *Uintacyon*. Some of them are retained by the Viverravinæ and the more primitive Fissipedia, others are lost by all the Fissipedia. None of them are present in the Canidæ, which have departed most of all the modern carnivora from the primitive limb and foot structure. Their significance as indicating a plantigrade gait and probably arboreal habitat will be more fully discussed in the description of *Vulpavus projectus* (infra). It is sufficient to point out at present that the wide departure of the modern Canidæ from this primitive type is dependent upon their strictly terrestrial and cursorial adaptation, and that the successive stages in the specialization of limbs and feet can be traced through a very complete series of intermediate genera down to the modern types.

The limbs and feet in this genus are throughout more slender than in *Vulpavus* or *Oödetes*, and the patellar trochlea is relatively narrow.

The species of *Miacis* present a considerable diversity in the form and proportions of the teeth, and the geological range of the genus is somewhat extensive. It is found in all the Middle and Upper Eocene formations, and several fragmentary specimens from the Lower Eocene (Wasatch and Wind River) may be provisionally referred to it. We are fortunately able to refer to the type species several other specimens from the same horizon and locality and to describe the complete dentition and principal parts of the skeleton. The other Middle and Upper Eocene species are also fairly well known, mostly from referred material, but the Lower Eocene specimens are too fragmentary for specific description and better material might show them to be generically different from *Miacis*. The most marked distinction among the better known species, aside from size, is in

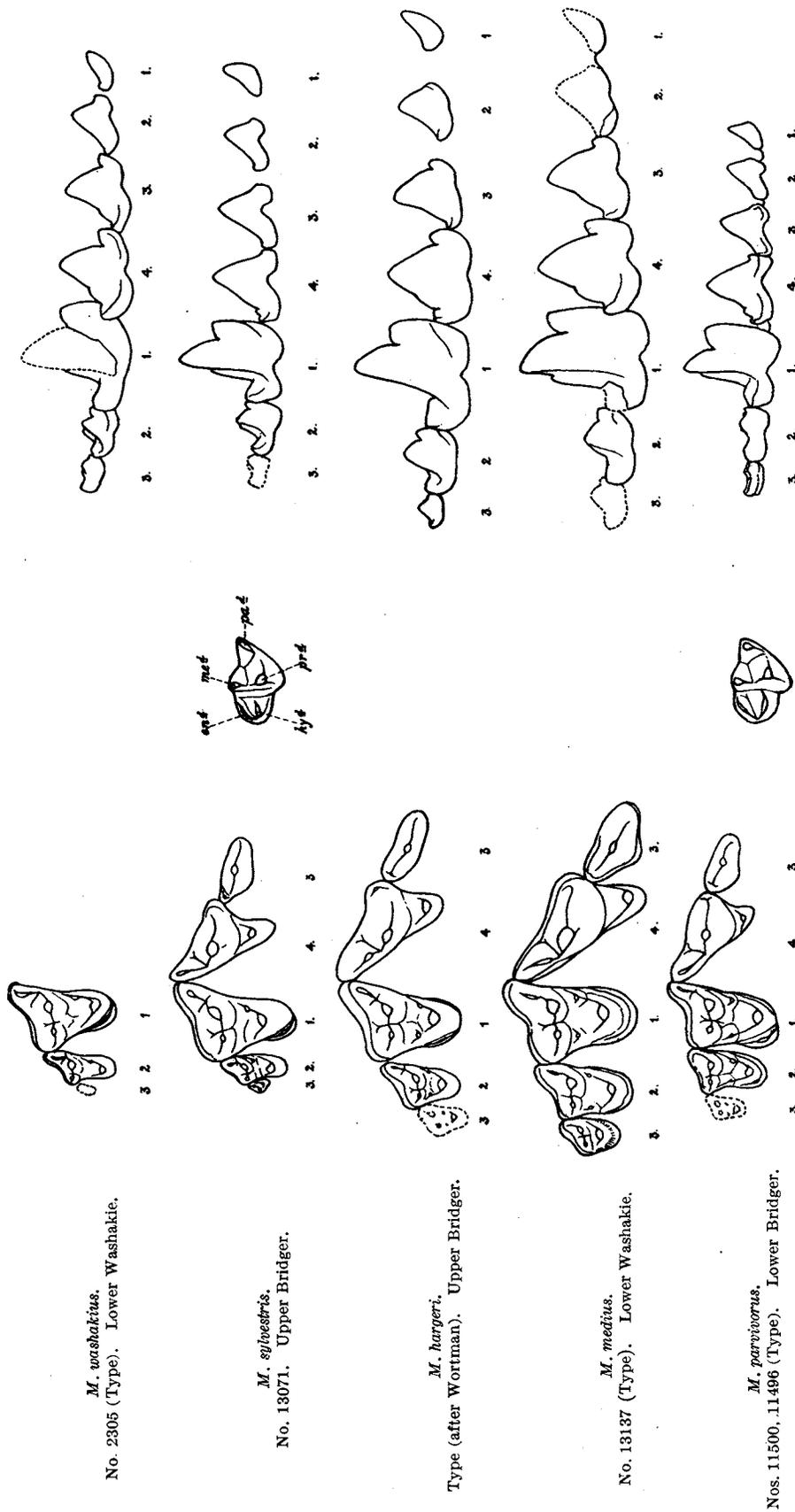


Fig. 15. Upper and lower dentition of the species of *Miacis*. All twice natural size.

the proportion of the sectorial to the tubercular dentition. In *M. parvivorus* the sectorial dentition of the lower jaw (p_{1-4} plus trigonid of m_1) is twice the length of the tubercular dentition (m_{2-3} plus heel of m_1). In *M. hargeri* the proportion is as three to one. The other species are intermediate. The varying reduction of m^3 , and the proportions of the limbs and feet, also furnish well marked specific characters. The species fall into four groups which may be regarded as of subgeneric value.

- A. *Miacis* s. s. Heels of lower molars wide.
M. parvivorus Cope. $P_1-m_3 = 27-30$ mm.; $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{2}{1}$.
 Hypocone well developed on m^1 , less on m^2 . M^{2-3} moderately reduced . Lower Bridger.
- B. *Lycarion*, s.-g. nov. Heels of lower molars compressed.
M. hargeri (Wortman). $P_1-m_3 = 39$ mm., $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{3}{1}$.
 Hypocone vestigial on m^1 , absent on m^2 . M^{2-3} smaller, not compressed . Upper Bridger.
M. medius sp. nov. $P_1-m_3 = 38$ mm.; $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{2\frac{1}{2}}{1}$.
 A heavy cingulum on m^{1-2} but no distinct hypocone. M^{2-3} moderately reduced, not compressed Lower Washakie.
- C. *Harpalodon* Marsh. Heels of lower molars compressed; m^3 vestigial. Limbs long and slender.
M. sylvestris (Marsh). $P_1-m_3 = 31$ mm.; $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{2\frac{3}{4}}{1}$.
 Hypocone vestigial on m^1 , absent on m^2 ; m^2 compressed. M^3 vestigial. No accessory cusp on p_4 Upper Bridger.
M. washakius (Wortman). $P_1-m_3 = 33$ mm.; $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{2\frac{3}{4}}{1}$.
 A small hypocone on m^1 ; m^2 compressed, much reduced, m^3 minute. Strong accessory cusp on p_4 Lower Washakie
- D. *Prodaphænus* Matthew. Teeth much as in *Lycarion* but m^3 apparently minute or absent. Limbs short and stout.
M. wintensis Osborn. $P_1-m_3 = 53$ mm.; $\frac{\text{sectorial}}{\text{tubercular}}$ dentition = $\frac{3}{1}$.
 Strong accessory cusp on p_4 Upper Uinta.
 ? *M. vulpinus* (Scott). No accessory cusp on p_4 Upper Uinta.

***Miacis parvivorus* Cope.**

Text Fig. 15.

Miacis parvivorus COPE, Pal. Bull. No. 3, dated Aug. 7, 1872, republished in Proc. Am. Phil. Soc., 1872, Vol. XII, p. 470; Tertiary Vertebrata, 1884, p. 304, pl. xxiv, fig. 12.

The type of this species is a lower jaw fragment, No. 5019 of the American Museum Cope Collection, found by Professor Cope in 1872 in the Lower Bridger beds on Black's Fork. The second molar is perfectly preserved, with alveoli of the first and third. The specimen is in itself almost indeterminate, but agrees approximately with several more complete specimens collected by the American Museum expeditions of 1903-6 in the same general locality and horizon. It is not certain that these specimens are exactly co-specific with the type or with each other, but they represent either a single variable species or a group of very closely allied species. In either case they represent approximately or exactly the structural features of *M. parvivorus* and enable us to clear up its relations to the various other members of the *Miacidæ* and to other carnivora.

The principal characters which can be derived from the type are as follows: The second molar is short, with low trigonid and large basin heel, and the alveolus of the carnassial is smaller than in *Lycarion* or *Harpalodon*, which have m_2 more elongate with compressed heel. The third molar is one-rooted. From these facts we may infer that the dentition was less sectorial in character than in these subgenera, and that the lower molars were basin-heeled (distinction from *Uintacyon*) while the nearly tubercular character of m_2 indicates that the tubercular dentition was well differentiated (distinction from *Vulpavus* and *Oödetes*). These characters, partly inferential in the type, are displayed in five more complete specimens from the Lower Bridger at Grizzly Buttes, which agree with No. 5019 except for slight differences [in size and proportions, and a variable development of m_3 , which is two-rooted in one individual and partly so in another. They are:

No. 11496. Upper and lower dentition, most of the dorsal and lumbar vertebræ and ribs, many caudals, pelvis and sacrum, fore and hind limb bones and a few fragments of the fore-foot. The greater part of this specimen was found articulated. Discovered by Walter Granger.

No. 11500. Upper jaws and part of lower.

No. 11509. Lower jaws and various fragments of skeleton.

No. 11510. Part of lower jaw with fragments of skeleton.

No. 11511. Two unassociated lower jaws.

The following description is based upon No. 11496, except as noted.

Dentition. The upper incisors (No. 11500) are small, set in a transverse row, their crowns long pointed, not expanded transversely, the lateral pair much larger than the others. Behind them is a shallow ill defined notch for the reception of the lower canines. The upper canines (No. 11496) are comparatively straight and slender, with anterior and posterior ridges moderately developed. The third upper premolar (No. 11500) is shorter and less compressed than in *M. hargeri* and has no posterior accessory cusp. The upper carnassial (No. 11496) is relatively smaller but proportionately longer antero-posteriorly than in *M. hargeri*, *medius* or *sylvestris* and the antero-internal cusp (deuterocone) smaller. The molars (Nos. 11496, 11500, 11509) differ from those of the other species in the stronger development of the hypocone and smaller parastyle; the posterior molars are less reduced than in *M. hargeri*, *sylvaticus* and *washakius*.

The lower jaw (best seen in No. 11509) is shorter and deeper anteriorly than in the three last named species, more like that of *Uintacyon* both in character and in premolar proportions. The canines (No. 11496) are slender, the first premolar one-rooted, the second and third have minute heels, the third is not much larger than the second, and lacks the posterior accessory cusp of *M. hargeri*. The fourth premolar is considerably larger, with anterior basal cusp, heel and posterior accessory cusp all of moderate size. The lower sectorial (11496, 11500) is broader than in any of the other species, with larger heel, not completely basin-shaped but intermediate between that form and the trenchant

heel of *Uintacyon*. The second molar is proportionately larger than in the other Miacides, with less prominent trigonid and broader heel. The third molar varies in the different specimens being one-rooted in Nos. 11496, 11500, 11510 and 11511, but distinctly two-rooted in No. 11509.

M. parvivorus is less sectorial in dentition and in every respect closer to *Uintacyon* than any other species of the genus. An examination of the diagram of the upper and lower teeth of the several species will show that this may readily be regarded as the primitive type from which the other species, all of later horizons, can be derived, all tending to a greater specialization of the sectorial dentition and reduction of the tubercular.

Structurally speaking, *Uintacyon* may also be regarded as a derivative of this species, the specialization being mainly in an opposite sense. *Uintacyon* is first found along with *Miacis*, in the Wasatch beds, so that it cannot be regarded as a descendant of *M. parvivorus* but rather of some Basal Eocene species of very similar dentition.

Skeleton. The three specimens—Nos. 11496, 11509—and 11510 agree quite closely in the skeleton so far as comparison is possible, except for some difference in size, the second specimen being a little larger than the others. The animal was of about the size and general proportions of *Bassariscus astutus*. The atlas (No. 11510) is short, the posterior opening of the vertebral canal is not completely posterior as in the civets, nor superior as in the dogs, but intermediate between the two. The anterior course of the vertebral artery lies in a sharply defined groove in common with the inferior branch of the first spinal nerve, as in the Felidæ. In most modern carnivora, and in *Oödetes* among the Miacidæ, this groove is converted into a foramen by a bridge of bone from the transverse process to the articular cotylus. The anterior dorsals are represented in No. 11496 by two complete vertebræ and several centra; the spines are rather short and slender but the vertebræ are not otherwise remarkable. The last two dorsals are in series with the lumbar, and close in front of them lay the vertebra prominens with the zygapophyses of dorsal type anteriorly, of lumbar type posteriorly, and the spine reduced to a small upright tubercle. The two dorsals behind it have small forwardly sloping spines, long centra, strong anapophyses, zygapophyses of lumbar type but smaller. The lumbar increase in size from 1st to 6th, the 7th being short but broad. The centra are long and flattened, the spines successively higher, the anapophyses decrease in size, the transverse processes are short and small. The zygapophyses are somewhat convex and concave in the anterior lumbar and posterior dorsal region. The sacrum consists of the usual three vertebræ. The anterior caudals are large and have powerful anapophyses, short forwardly directed spines and flat well separated zygapophyses. The middle caudals are long and slender, exceeding the lumbar in length; the posterior caudals are shorter but not slenderer.

The *humerus* is much like that of *Uintacyon*, with high compressed deltoid

crest extending about half way down the shaft, and ending abruptly. The crest is a little longer but not quite so high as in *Vulpavus* and *Oödetes*. The tuberosities are not much developed, the greater scarcely rising as high as the top of the head. The distal end is not deep, considerably expanded laterally, with entepicondylar foramen but no supra-trochlear perforation. The high deltoid crest, the much broader distal end, convex radial facet, more prominent entepicondyle and larger entepicondylar foramen are the most noticeable differences from *Bassariscus*.

The *ulna* has a sigmoid curvature from end to end, as in the viverrines. The olecranon is rather short and small, not expanded antero-posteriorly. The proximal two-thirds of the bone is strongly curved, the convexity backward. The articulation with the radius is a nearly flat facet. The external and anterior borders in the distal part of the shaft, which are rather anterior and internal respectively in position, are produced into sharp prominent crests somewhat oblique to the axis of the bone, giving an extended attachment for the pronator quadratus which lies between them. The distal part of the shaft is deep, and strongly crested posteriorly, the styloid process short, prominent posteriorly, without neck. In general construction the ulnar shaft agrees with the more primitive Fissipedia in the position and arrangement of the crests on the shaft, and affords some marked points of diversity from Pseudocreodine families. The crests are similarly placed but less prominent in Mustelidæ and Procyonidæ; in Viverridæ (*Genetta*, *Herpestes*) the crests are more marked and extended further up the shaft. The distal part of the radial and ulnar shafts are much heavier in *Miacis* than in *Bassariscus*, and both shafts display a much greater sigmoid curvature when viewed from in front; the olecranon is considerably longer, the styloid process at the distal end of the ulna shorter, broader and less distinct.

The *radius* is moderately curved, and the head oval; its distal end shows no indication of the separation between scaphoid and lunar which nevertheless existed; the styloid process is more prominent than in *Bassariscus*, the articulation for the ulna is distinct, the carpal articulation is rather oval than trihedral. The bicipital process is much more prominent than in *Bassariscus*.

The *scaphoid* is small, with little expansion on its internal side and no great vertical height. It has distinct facets for centrale and trapezium, and a small trapezoid facet. The unciform is comparatively small and its vertical exceeds its transverse diameter. The only complete metacarpal is the fourth, which has about the same proportions as in *Bassariscus*; the proximal and second phalanges are a little more slender than in the modern genus, the unguals are not preserved.

The *pelvis* is longer than in *Bassariscus* but not so deep or heavy. The ilium is somewhat more expanded at the anterior end, but is much more like the Fissiped type than that of the Hyænodonts, and entirely lacks the peculiar decurved everted iliac bar and peculiar type of flange above it which may be seen in *Sinopa*, *Tritemnodon* and their allies.

The *femur* is straight-shafted and slender, as in *Bassariscus* and the viverrines, the shaft showing scarcely any indication of the curvature characteristic of the Canidæ. As in the Miacidæ generally the third trochanter is moderately developed, and the lesser trochanter internal instead of posterior in position. The bone is nearly a sixth longer than in *Bassariscus*, the distal end less expanded, the patellar trochlea long and narrow. In these respects the femur differs from those of *Oödetes* and *Vulpavus* and agrees with *Miacis harger*i and with *Cynodictis*.

The *tibia* is straight-shafted and resembles that of the viverrines. In *M. harger*i the upper part of the tibia is considerably curved. It is rather slender, a little shorter than the femur, somewhat longer than the tibia of *Bassariscus astutus* but not more robust. The cnemial crest is long but not prominent, the upper part of the shaft much compressed, the malleolus long, as wide as in *Vulpavus* but not so thick, the astragalar facet oblique and ungrooved.

The *astragalus* is wide and the trochlea flat, without distinct internal crest separating it from the malleolar facet.

Miacis hargeri (*Wortman*).

Fig. 15, p. 364.

*Vulpavus harger*i WORTMAN, Am. Jour. Sci., 1901, Vol. XI, p. 342.

The type is the anterior half of the skull with lower jaws. The characters may be summarized as follows, from Dr. Wortman's description and figures:

Dentition $\frac{3.1.4.3.}{3.1.4.3.}$. Jaw slender anteriorly, premolars and carnassials un-reduced, tubercular teeth comparatively small. In the lower jaw the proportional length of premolar plus carnassial teeth ($p_{1-4} + \text{trigonid of } m_1$) to the tubercular teeth (heel of $m_1 + m_{2-3}$) is as three to one. Heels of lower molars small, basin-shaped. Premolars with large protocones and small accessory cusps. Parastyle of p^4 rudimentary, deuterocone well developed, antero-internal in position, metastyle blade-shaped, elongate. M^1 with broad external cingular shelf extended antero-externally and short blade-shaped parastyle within it; paracone larger than metacone, distinct from it, and both set well in from external border, paraconule and metaconule distinct, hypocone small or absent, metastyle absent. M^{2-3} like m^1 but smaller.

Dorsolumbar formula unknown (presumably twenty) lumbar zygapophyses comparatively simple, tail large. Limb bones primitive, civet-like (as in all Miacinæ). Fore foot unknown. Pes pentadactyl with paraxonic symmetry. Astragalar trochlea little grooved, astragalar foramen small. No fibulocalcanear facet. Ungual phalanges small, compressed, unfissured.

This species is not certainly recognizable in our collections. It is represented, according to Wortman, by four or more specimens from the Upper Bridger in the Marsh Collection.

Miacis medius sp. nov.

Fig. 15, p. 364.

The anterior half of the skull, lower jaws and most of the humerus, No. 13137, from the Lower Washakie, represents a species nearly allied to *M. hargeri* but differing in various particulars. It is materially larger than Wortman's species, the premolars are more robust, the second molar is less reduced and the protocones of all the molars are surrounded by heavy continuous cingula. It is in most respects intermediate between *M. hargeri* and *M. parvivorus*, but larger than either. The lower jaw is comparatively deep and robust. The nasals are long, extending back to a point opposite the anterior rim of the orbit, deeply fissured anteriorly and slightly expanded posteriorly. There is a distinct post-orbital process on the jugal as well as on the frontal.

Miacis sylvestris (Marsh).

Fig. 15, p. 364.

Harpalodon sylvestris MARSH, Am. Jour. Sci., 1872, Vol. IV, p. 216, separata dated Aug. 13; WORTMAN, *ibid.*, 1901, Vol. XII, p. 201, fig. 38, (= *Uintacyon*?).

The type is a part of a lower jaw in the Yale Museum with p_{3-4} complete and the heel of m_1 . To this species I refer No. 13071 consisting of upper and lower jaws with p^3-m^3 , p_3-m_2 , and a few foot bones; and No. 13073, a lower jaw fragment with m_2 and the heel of m_1 . The type is from Henry's Fork, Upper Bridger beds, the second specimen is from the base of the Upper and the third from near the top of the Lower Bridger.

The species is distinguished from *M. parvivorus* by somewhat smaller size, lower molars more compressed, with smaller heels, less completely basin-shaped, tubercular dentition reduced, jaw slender and elongate anteriorly, premolars relatively larger, upper molars with metacone more reduced, hypocone vestigial on m^1 , m^2 compressed antero-posteriorly and relatively small, m^3 vestigial, of minute size and in No. 13071 erupting on the posterior border of the maxilla instead of on its inferior surface. The premolars have no accessory cusps. The upper carnassial differs considerably in form, the deuterocone being large, compressed and extended inward. The fragments of the skeleton include the fourth metacarpal with parts of the third and fifth, and several phalanges. The metacarpals are slender and correspond in proportions with the slender fore limb bones in the closely allied species *M. washakius*.

Miacis washakius (Wortman).

Fig. 15, p. 364.

Vulpavus palustris WORTMAN and MATTHEW, Bull. A. M. N. H., 1899, Vol. XII, p. 118, figs. 4-6.

Not *V. palustris* of Marsh.

Neovulpavus washakius WORTMAN, Am. Jour. Sci., 1901, Vol. XI, p. 445.

Type, No. 2305, lower jaws, upper molars, parts of humeri, radius and ulna, from the Lower Washakie beds.

This species was at first referred to *Vulpavus palustris* Marsh, but subsequently separated by Wortman on the ground of the supposed absence of m^3 . A more careful examination of the type shows the alveolus for a minute third molar, about as large as in *M. sylvestris*, but situate on the posterior border of the maxilla. In other respects the teeth are very close to *M. sylvestris*, the chief difference being the slightly different proportions of m^2 , the prominent accessory cusp on p_4 , somewhat larger size of the lower jaw anterior to the carnassial, and other points of doubtful specific value. It undoubtedly belongs to the subgenus *Harpalodon* and may be identical with *H. sylvestris*. The limb-bones are considerably more slender and elongate than in *M. parvivorus*, *hargeri* or *medius*, the proportions apparently corresponding with those indicated in *M. sylvestris*.

Miacis uintensis Osborn.

Miacis uintensis OSBORN, Bull. A. M. N. H., 1895, Vol. VII, p. 77, fig. 2.
Prodaphænus uintensis OSBORN, Matthew, *ibid.*, 1899, Vol. XII, p. 49.

This species is represented by several specimens from the Upper Uinta beds. The type, No. 1896 (said to be from the top of the Lower Uinta), consists of a part of the lower jaw. An incomplete skeleton which may be referred to the same species includes the greater part of skull and jaws but the teeth badly shattered, the fore and hind limbs with most of the carpus, tarsus and metacarpus, and the cervical vertebræ. Several fragmentary jaws are also referable here, all from the Upper Uinta. The teeth, so far as I can determine, are proportioned much as in *M. hargeri* but the tubercular dentition somewhat more reduced, and m^3 may be absent. The basicranial region shows substantially the same conditions as in *Vulpavus*; the tympanic is absent, the paroccipital directed backward, the condylar foramen well separated from the posterior lacerate. It does not show any very marked approximation to *Cynodictis* or *Daphænus*.

The fore limbs are short and stout, the hind limbs heavy but rather long. The humerus is short with exceptionally high and extended deltoid and supinator crests. The ulna and radius are rather short and subequal; the carpus lacks the scaphoid lunar centrale and trapezium so that it is not possible to determine whether or not there was a united scapholunar. The metacarpals are rather short and wide spread. The femur, tibia and fibula are rather long, the fibular shaft slender. The astragalus has a flat trochlea without inner crest and is rather elongate in a proximo-distal direction. It is rather different from the usual Miacine type, but not in the direction of *Daphænus* or *Cynodictis*.

This species is much larger than any of the Bridger or Washakie species of *Miacis*, and seems to be an aberrant form not transitional to any of the known Canidæ so far as comparisons have been made.

? *Miacis vulpinus* (Scott & Osborn).

Amphicyon vulpinus S. & O., Proc. Am. Phil. Soc., 1887, Vol. XXIV, p. 225.

This species was based upon a lower premolar and carnassial from the Upper Uinta collected by the Princeton Expedition of 1886. It is distinguished from *M. uintensis* by the lack of accessory cusps on p_4 . It has never been figured and the type is lost or mislaid, so that the species cannot be further defined.

Uintacyon Leidy.

This genus was described by Leidy in December, 1872, from a lower jaw with the teeth much broken. It shows five premolars besides the canine and three true molars, but the third of the premolar series is obviously an abnormal tooth. The second molar and heel of the first, and the second, third and fourth premolars are preserved entire. It is distinguished from *Lycarion* and *Harpalodon* by the reduced premolars and enlargement of the post carnassial teeth, by the trenchant heels of the molars and the short deep jaw with abrupt chin. From *Miacis* proper it is less easily distinguished by the trenchant heels of the molars and the somewhat greater reduction of the premolars, especially P_3 , which is no larger than P_2 ; but the two genera are quite nearly related, *Miacis* being intermediate between *Lycarion* and *Uintacyon*, and structurally ancestral to either genus. A second larger species of *Uintacyon* was described by Leidy from a fragment of jaw containing the second molar entire, and alveoli of the first and third.

There are fifteen specimens in the American Museum Bridger collections which can be referred to this genus, and represent three well distinguished species. Of these the smallest, represented by five lower jaws all from the Upper Bridger, is slightly smaller than Leidy's type of *U. edax* and differs considerably from it in the proportions of all the teeth preserved, so that it cannot be referred to this species. The second, represented by six specimens from the Lower Bridger, agrees in size and form with *U. vorax* Leidy, and may be referred to this species although the type is recorded as coming from Henry's Fork (Upper Bridger). Two of these include besides the lower jaws a considerable part of the upper dentition, while two others have various fragments of the skeleton associated. The third species is represented by three lower jaws and an upper molar, all from the Upper Bridger, and is much larger than any of the preceding. It agrees in size with "*Miacis*" *bathygnathus* Scott, based on a lower jaw without teeth, associated with fragments of the skeleton and probably referable to *Uintacyon*, but differs from Scott's type in the spacing of the premolars.

From the above material we are now able to characterize *Uintacyon* as follows:

Dentition $\frac{7.1.7.3}{3.1.4.3}$. Premolars reduced, without accessory cusps, the second and third of equal size. Lower molars with trenchant heels; upper molars without hypocones. Deuterocone of p_4 of moderate size. Upper molars moderately extended antero-externally with distinct parastyle crest; paraconule strong, metaconule weak, protocone subrescenscentic with anterior and posterior horns equally developed. Paracone higher than metacone. Third upper molar small. Third lower molar small, one-rooted, flat-crowned. Lower jaw short, with robust and rather deep symphyseal region, somewhat reduced in depth and thickness under the premolars.

The specific distinctions are as follows:

- U. edax* Leidy. $P_1-m_3 = 31$ mm. Premolars short and very robust. M_2 quadrate. Heel of M_1 rather large. Jaw moderately deep.
- U. jugulans* sp. nov. $P_1-m_3 = 30$ mm. Premolars more elongate and compressed. M_1 with high trigonid and small heel; m_2 smaller, long-oval. Jaw robust, but not very deep.
- U. vorax* Leidy. $P_1-m_3 = 37$ mm. Trigonids of molars lower and heels larger than in the preceding species. M_2 broader and proportionately larger. Jaw deeper.
- U. major* sp. nov. $P_1-m_3 = 50$ mm. Trigonids of molars lower and heels larger than in *U. vorax*. M_2 large, broad, nearly flat crowned except for protoconid. Jaw deep. Premolars small, spaced.
- U. bathygnathus* Scott. $P_1-m_3 = 50$ mm. Premolars not spaced. Crowns of teeth unknown.

A number of other species have been referred to this genus by Wortman and Matthew, but a better knowledge of the typical forms shows that they belong elsewhere. *U. pugnax* is a species of *Oödetes*. *U. promicrodon*, distinguished from *Uintacyon* by the basin-shaped heels of the molars, is the type of the new genus *Vassacyon* herein described, *U. canavus* and *brevirostris* are more nearly allied to *Vulpavus*. On the other hand "*Didymictis*" *massetericus* Cope is a true *Uintacyon* as far as can be judged from the fragment of jaw by which it is known, and rather nearly allied to *U. jugulans*; removal of the matrix shows a small alveolus for m_3 , and the form of m_{1-2} corresponds with *Uintacyon* and differs materially from *Didymictis*. This extends the range of the genus from Wasatch to Bridger; it is not positively known to occur in the Uinta, but "*Prodaphænus*" *scotti* may be provisionally referred here.

Uintacyon jugulans sp. nov.

Fig. 16.

Type No. 12066, lower jaws from Henry's Fork, Horizon C_4 found by Walter Granger, Am. Mus. Exp. 1904. Referred specimens, Nos. 11505, 12070, 12067, all lower jaws of various degrees of completeness, from the Upper Bridger beds.

The crowns of all the teeth except incisors are preserved in the type. The canine has a stout root, is rather straight and slender distally, stout and strongly curved towards the base of the crown, of sub-round section without anterior or posterior crests. The first premolar has a rather stout root and low stubby crown. The second and third premolars are small, two-rooted with rather low crowns, little compressed, the third slightly smaller than the second. The fourth premolar is also reduced in size, has a rather stout protoconid, large

trenchant heel and no accessory cusps. The first molar has a large rather high trigonid and small trenchant heel, but little larger than that of p_4^2 . The paraconid and metaconid are well developed and of equal size and height, the protoconid considerably overtopping both. The second molar is of similar form and construction, but smaller size, and the trigonid low and its cusps blunt, so that paracone and metacone are almost on a level with the heel. A small antero-external cingulum is present on both molars. The third molar is one-rooted, small, with round flat-topped crown, the cusps low and more or less vestigial.

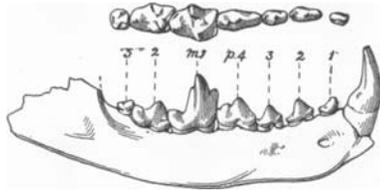


Fig. 16. *Uintacyon jugulans*, lower jaw, external view, and crown view of teeth, natural size. No. 12066 (type), Upper Bridger.

Upper teeth and skeleton unknown.

A specimen in the Marsh collection, associated fragments of upper and lower jaws referred by Wortman to *U. edax*, (1901, p. 446, figs. 12-15) may belong in part to this species. The upper teeth, however, if his figure and description be correct, can hardly pertain to *Uintacyon*, and correspond much more nearly with *Viverravus*.

Uintacyon edax Leidy.

Proc. Acad. Nat. Sci. Phila., 1872, p. 2; Ext. Vert. West. Terrs. (1873), p. 118, pl. xxvii, figs. 6-177.

The type specimen has, unfortunately, disappeared, but an excellent cast of it taken under the direction of Professor Marsh, which we owe to the courtesy of Yale Museum, enables us to compare and supplement Leidy's figures. The teeth show throughout such considerable differences in form from those of *U. jugulans* that I cannot regard them as associated with the individual peculiarity of an excess premolar in the type of *U. edax*, and am compelled to hold the two species as distinct. In *U. edax* the premolars are much more robust, the heel of m_1 larger, m_2 is much shorter and wider and its cusps lower, the jaw is heavier and deeper than in *U. jugulans*. The horizon of the type is not recorded.

Uintacyon vorax Leidy.

Figs. 7 and 8, pp. 344, 347.

Proc. Acad. Nat. Sci. Phila., 1872, p. 2; Ext. Vert. West. Terrs., p. 120, pl. xxvii, figs. 11-13.

In the Lower Bridger beds occurs a larger species than *U. jugulans*, with the generic character more accentuated. It is referred with doubt to *U. vorax*, partly because of the imperfection of the type, and the meagre description which Leidy gives of it, and partly because it appears to be limited to the lower beds,

while Leidy records the type as from Henry's Fork (Upper Bridger). The specimens are:

- No. 11507. Upper and lower jaws with several teeth preserved.
- No. 12620. " " " " " " " " " "
- No. 11504. Lower jaw without teeth, and various fragments of the skeleton.
- No. 11518. Lower carnassial, fore-limb bones and vertebræ.

The upper teeth shown in Nos. 11507 and 12620, are much like those of *Miacis* but the hypocone is absent. The antero-external corner of p^4 is not preserved, so that we cannot determine whether a basal cusp was present at this point; the deuterocone is distinct and of moderate size and antero-internal position, and the tooth is extended postero-externally in a strong shearing blade. The parastyle blade of the molars is distinct, and they are somewhat extended antero-externally, but not nearly so much as in *Lycarion*. The metastyle blade is absent. The second molar has about four-fifths the dimensions of the first; the third is not preserved, but judging from the alveolus was quite small.

The lower teeth are much like those of *U. jugulans* but more robust; m_2

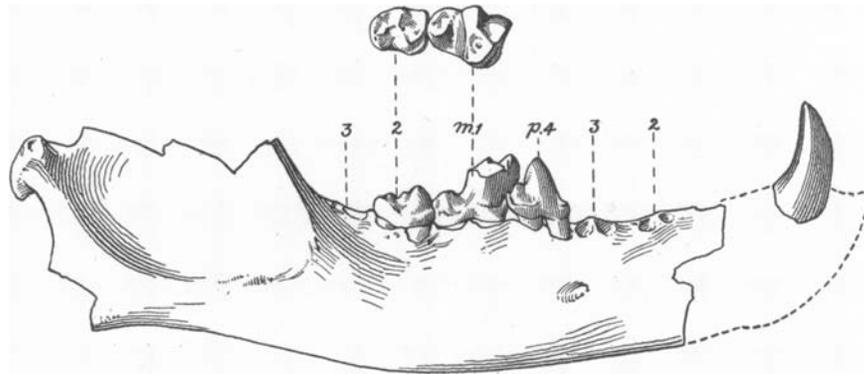


Fig. 17. *Uintacyon major*, lower jaw, external view, and crown view of molar teeth, natural size. No. 12159 (type), Upper Bridger.

and the heel of m_1 larger in proportion, and the trigonid of m^1 not so high. M_2 is considerably broader, and has a strong antero-external cingulum.

The parts of the skeleton preserved resemble closely the corresponding bones in *Miacis*, *Vulpavus*, *Oödetes* and *Lycarion*, the differences between these genera being mainly in relative proportions and robustness of the various bones. The family characters are apparent in all parts of the skeleton. The cervical vertebræ are about as large as in *V. ovatus*, but with smaller zygapophyses; the lumbar vertebræ are considerably smaller, their zygapophyses flatter, and the anapophyses better developed.

The sacrum is very like that of *Vulpavus* but somewhat smaller proximally with narrower rib on the first vertebra. The caudals preserved indicate a large powerful tail.

The humerus compares most nearly with that of *Miacis*; its shaft has more of a sigmoid flexure than in *Vulpavus*. The deltoid crest is hardly as high as in *Oödictes* and *Vulpavus*, but extends a little further down on the shaft. The ulna is somewhat more convex posteriorly in its proximal two-thirds than in *Vulpavus*, the olecranon is somewhat longer; the anterior and internal crests on the distal third of the shaft have nearly the same development. The distal end of the femur has a wide shallow rotular trochlea over which moves a remarkably small patella, flat, thin, wider than long, without spine above or below. The astragalus, Plate XLVII, Fig. 2. c, is very like that of *Miacis*; the tibial trochlea does not extend as far down on the neck as in *Vulpavus*, and the head is rather flatter; the internal crest of the trochlea is not so sharp, the fibular facet flatter and more vertical, so that the astragalus lies more directly under the tibia instead of being wedged in between the oblique distal facets of tibia and fibula. This is evidently a necessary preliminary to the reduction of the fibula. The cuboid is very like that of *Vulpavus* and as in that genus has a considerable astragalar facet, and naricular contact very imperfectly faceted. The first metatarsal is stout with large proximal facet.

Uintacyon major sp. nov.

Fig. 17.

This species is of considerably larger size than the preceding, the premolar-molar series measuring 50 mm. The teeth in the type, No. 12159, are much like those of *U. vorax*, but m_2 and the heel of m_1 proportionately larger, the spacing of the premolars wider, the cusps of all the teeth somewhat lower, the antero-external cingulum of m_2 more expanded, the depth of the jaw somewhat greater. No. 11159, an isolated upper molar is similar to m^1 of *U. vorax* except for larger size. Nos. 11508 and 12084, lower jaws, also agree with the type. An isolated m^1 referred by Wortman to *U. vorax* (1901, p. 448, fig. 16) agrees in size with this species. All the specimens are from the Upper Bridger.

Vassacyon Matthew, 1909.

Plate XLIII, Fig. 4; Text Fig. 8, p. 347.

The type of the genus is *Uintacyon promicrodon* W. & M., from the Wasatch of Wyoming. Its generic distinction from *Uintacyon* is based upon the large broad basin heel of the carnassial. The alveolus of the canine appears to indicate a flattened root, but this may be merely due to crushing. The characteristic peculiarity of *Uintacyon*, the equal size of p_2 and p_3 , is not observed in this genus, in which the premolars increase uniformly in size. The second molar is comparatively large but the third is small and one-rooted. P_4 is simi-

lar in form to the corresponding tooth in *Uintacyon*, the anterior basal cusp very rudimentary, the posterior accessory cusp well developed, and the protoconid sloping backward.

Oödectes Wortman.

Dentition $I\frac{3}{1} C\frac{1}{1} P\frac{4}{1} M\frac{3}{1}$. First upper molar symmetrical, the metastyle and parastyle equally developed. P^4 carnassiform, with inner cusp (deuterocone) anterior in position, and extended postero-external shearing blade; parastyle of p^4 somewhat larger than in *Miacis* or *Uintacyon*, smaller than in *Didymictis* or *Viverravus*. Lower molars similar in proportion and structure, composed of a high trigonid of three sub-equal cusps, and a trenchant heel. Premolars with high protocones and no accessory cusps. Skull unknown except for a few fragments. Skeleton as in *Miacis*, especially *M. parvivorus*, but larger in proportion to size of teeth and skull.

This genus was regarded by Wortman as a member of the Viverravidae (Viverravinæ), but our more complete knowledge of *Vulpavus* and *Miacis* shows without question that it is much more nearly related to these genera, and intermediate between them in almost all the characters of teeth and skeleton. The lower carnassial is much less differentiated from the posterior molars than in *Miacis* and *Uintacyon*, more as in *Vulpavus*, but the upper carnassial is a much more efficient shearing tooth than in that genus. As in *Uintacyon* the hypocones and metaconules are absent on the upper molars and the heels of the lower molars trenchant. The teeth are sharper and higher cusped than in *Vulpavus*, the premolars short, high and compressed, suggesting those of Mustelidæ. The only feature which can be regarded as an approximation to the Viverravinæ is the parastyle on p^4 ; the skeleton agrees entirely with the Miacinæ and differs from Viverravinæ in important characters which have already been mentioned in the analysis of the family.

The type of the genus is *O. herpestoides* Wortman based upon a fragmentary skeleton in the Yale Museum. A fragmentary skeleton in our collection, represents a closely allied but distinguishable species, and two or more lower jaws are referable to the genus, but uncertain as to species. "*Uintacyon*" *pugnax* W. & M. probably belongs to this genus.

The species are distinguished as follows:

- O. herpestoides* Wortman. $P_1-m_3 = 25$ mm. Parastyle of p^4 larger and more external in position, deuterocone somewhat smaller.
- O. proximus* sp. nov. $P_1-m_3 = 26$ mm. Parastyle of p^4 smaller and more anterior in position, deuterocone somewhat larger.
- O. pugnax* W. & M. $P_1-m_3 = 28$ mm. Jaw short, deep, robust.

Oödetes proximus sp. nov.

Figs. 7, 8, 18-22.

The type, No. 11495, is a fragmentary but well preserved skeleton found in the eastern part of the Grizzly Buttes bluff by Mr. L. S. Quackenbush of the Museum Expedition of 1903. It includes most of the upper and lower jaws



Fig. 18. *Oödetes proximus*, atlas from above, natural size, No. 11495 (type), Lower Bridger.

and a few fragments of the skull, the scapula, pelvis, several limb-bones, vertebræ, etc. The bones are less crushed than in the type of *O. herpestoides* but agree very nearly in size, proportions and most details of construction. The teeth are distinguished by the following characters: parastyle of p^4 smaller and anterior instead of external, deuterocone somewhat larger; parastyle of upper molars less extended, protocones wider, transverse diameter less; m^3 more reduced; lower premolars straighter, higher and less compressed.

The chief distinctions in the skeleton are the somewhat greater expansion of the distal end of the humerus, and its broader trochlea, the more robust ulna, the larger oval pit in the head of the femur, more robust calcaneum with thicker sustentacular process.

In comparison with the skeleton of *Miacis parvivorus* already described, the bones show throughout a close similarity in form. The distal end of the humerus is less expanded transversely and the deltoid crest does not extend quite so far down on the shaft. The back of the olecranon is somewhat more expanded laterally. The femur has the same nearly straight round shaft and wide patellar trochlea, and the proportions of the upper end are very similar. The curvature of the shaft is slightly greater than in *Miacis*. The calcaneum has no facet for the fibula. The course of the vertebral artery and first spinal nerve in the atlas (Fig. 18) is the same as in most modern carnivora and quite a material difference exists here between

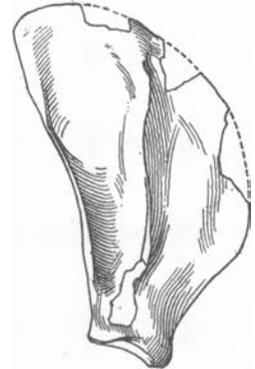


Fig. 19. *Oödetes proximus*, scapula, $\times \frac{1}{2}$. No. 11495.

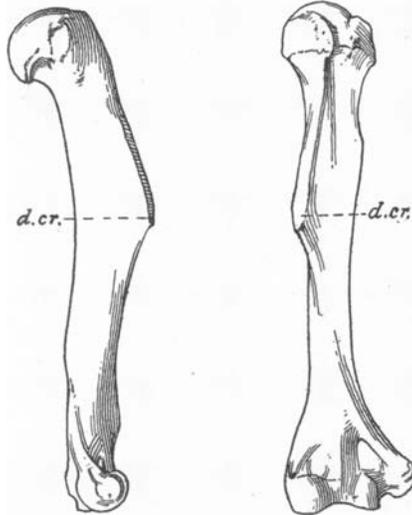


Fig. 20. *Oödetes proximus*, humerus, external and anterior views. $\times \frac{1}{2}$. No. 11495.

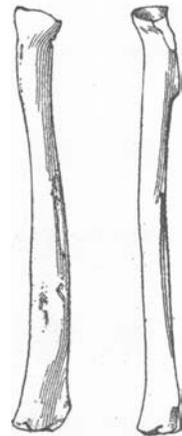


Fig. 21. *Oödetes proximus*, radius, anterior and internal views, $\times \frac{1}{2}$, No. 11495.

Oödetes and *Miacis* as in the latter the transverse process does not extend so far forward at its base, and the vertebral artery and inferior branch of the spinal nerve lie as they do in the cats, in a deep groove which is not bridged over by bone as in other carnivora. In the Inadaptive Creodonts there is neither bridge nor groove.

Vulpavus Marsh.

Am. Jour. Sci. 1871, Vol. XI, p. 124. Not of Wortman and Matthew 1899, nor Wortman 1901.

Dental formula $I\frac{3}{3} C\frac{1}{1} P\frac{3-4}{3-4} M\frac{3}{3}$. Upper molars rounded, quadrate with low cusps and no shear. P^4 not carnassiform; lower molars with low trigonids and broad basin heels, the third two rooted and of moderate size. Premolars small, short and high crowned without accessory cusps. Skull short with wide basicranial region rather wide, low sagittal and occipital crests and comparatively large brain-case. Feet five-toed; plantigrade, with high compressed unfissured claws. Scaphoid, lunar and centrale separate or united. Astragalus with nearly flat trochlea, calcaneum with small or no fibular facet. Pollex and hallux short and stout; symmetry of the foot paraxonic. Lumbar large with flat zygapophyses.

This genus has been hitherto known only by the single upper molar upon which it was founded by Professor Marsh in 1871, the additional material referred to it by Wortman belonging in another genus of quite different affinities.

The true *Vulpavus* is represented in our collections by the skull and most of the skeleton of one species; skull, jaws, fore and hind limbs and feet of a second; jaws and parts of skull, limbs and feet of a third; jaws and parts of skull of a fourth, and several isolated jaws. These give us a practically complete knowledge of the osteology of the genus, and a pretty accurate conception of its relationships. The name is somewhat unfortunate, as it has no particular Canid affinities, but is related more nearly to *Cercoleptes* among recent carnivora. It stands intermediate between *Oödetes* and *Palæarctonyx* among the Bridger carnivora.

The Bridger species are distinguished as follows:

1. Upper molars with well developed hypocone and crested metastyle. Premolars $\frac{4}{3}$. Lower molars with paraconid and metaconid of equal height, protoconid somewhat higher. Lower canines of moderate size, strongly curved and little compressed. *V. palustris* Marsh.

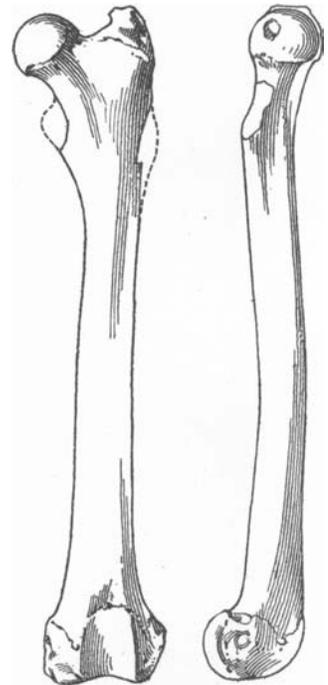


Fig. 22. *Oödetes proximus*, femur, anterior and internal views, $\times \frac{1}{3}$, No. 11495.

2. Upper molars with well developed hypocone but no metastyle. Premolars $\frac{4}{4}$. Lower jaw more slender, teeth as in *V. palustris* but m_{2-3} proportionately larger. *V. profectus*.

3. Upper molars with rudimentary hypocone and crested parastyle. Premolars $\frac{4}{4}$. Lower jaw as in *V. palustris* and teeth very similar. *V. completus*.

4. Upper molars with rudimentary hypocone on m^1 only, strong internal cingulum on m^2 , no parastyle or metastyle. Lower canines long, much compressed and little curved, upper canines trihedral, straight. Premolars $\frac{3}{3}$, smaller than in the three preceding species. Lower molars with protoconid, paraconid and metaconid of equal height. M_3 shorter than in the three preceding species. *V. ovatus*.

V. ovatus differs so much from the type and from *V. profectus* that it may be placed in a distinct subgenus, *Phlaodectes*, characterized primarily by the compressed straight dagger-like canines, and also as far as present appears by lower molars with the three cusps of the trigonid of equal height, upper molars with a strong internal cingulum but no distinct hypocone, premolars more reduced and various minor characters. The position of *V. completus* is uncertain as we do not know the canine teeth; the first upper molar has a rudimentary hypocone, the lower ones have pr^d overtopping me^d and pa^d . The remaining details of tooth construction relate it to the typical *Vulpavus* with which I place it provisionally.

Miacis canavus and *M. brevirostris* Cope of the Wind River formation, are referable to *Vulpavus*, but when better known may prove to be subgenerically distinct.

Vulpavus palustris Marsh.

The type of the genus and species is a single upper molar, almost unworn, but with the antero-external angle broken off. It was figured by Wortman in 1901, but his drawing, while accurate in the main, represents the external border as less complete than it really is, enabling him to restore the outline with a long antero-external extension as in "*V.*" *hargerii*, *Miacis*, *Uintacyon*, etc. In fact, however, the external border comes close to the paracone before it is broken away, leaving no room for such an extension at the antero-external angle. The inner part of the tooth differs in construction from that of "*V.*" *hargerii*, *Miacis*, *Harpalodon* or *Uintacyon*, being much wider antero-posteriorly but not extended transversely. The central basin of the tooth is large, broad and open, the protocone crescent continuous with the metaconule and partly with the paraconule, and there is a strong crested metastyle and a small cingular cusp directly external to the metacone. In all these distinguishing characters the type agrees with the upper molar of an incomplete skeleton in the American Museum Collection, No. 11497, including palate, jaws, parts of the skull, many limb and foot bones, etc. This specimen may be regarded as neotype of the species, and the characters drawn from it.

Specific characters. Dental formula $\frac{7.1.4.3}{3.1.3.3}$. Premolars not spaced, but a diastema in front of p_2 . P_3 trigonal in cross-section. Upper molars quadrate, with well developed hypocone and no internal cingulum. M^3 nearly as large as m^1 and m^2 . Paracone larger than metacone, parastyle and metastyle prominent. Lower molars with protoconid higher than paraconid or metaconid.

Description of Neotype. The skull and skeleton parts preserved agree quite closely with those of the much more perfect type of *V. profectus* (infra) except for uniformly larger size. The maxillaries are short, deep and rather wide, the palate broad and short. The jugal bone is proportionately heavier than in *V. profectus*, and deep posteriorly. The periotic bones are disarticulated and incomplete, but serve to confirm the characters of this region as described in *V. profectus* and *ovatus*. The auditory prominence is of rounded oval form with a curiously irregular surface. Near its posterior end is the *fenestra rotunda*, external to which is the external opening of the fallopian aqueduct (stylomastoid foramen) and antero-external the *fenestra ovalis*. The groove for the tympanic branch of the entocarotid artery is faint but unmistakable, running forward and outward a little in advance of the *fenestra rotunda*; thence the groove curves forward toward the foramen lacerum medius, but vanishes before it reaches that point. The groove for the stapedia branch is very much smaller, and is distinct only towards the lip of the *fenestra ovalis*. The inner side of the petrosal shows the internal auditory meatus enclosed in a common pit with the inner opening of the fallopian aqueduct, as in *Fissipedia*, instead of having separate openings as in *Limnocyon*.

The *lower jaw* is larger and more robust than in *V. profectus*, the coronoid process somewhat higher and much less recurved, p_1 is absent, p^3 is higher, p_4 more compressed, m_1 has a smaller heel, m_2 is considerably smaller throughout.

The *radius* is very like that of *Cercoleptes* except that the head is not quite so round. The *ulna* has a somewhat larger olecranon and considerably heavier shaft, especially toward the distal end. The first and third *metacarpals* are complete, but as they agree very closely with those in the complete fore foot of *V. profectus* they call for no separate description. The *femur* shows two marked primitive characters as compared with modern carnivora, namely, the presence of a third trochanter, and the internal instead of posterior position of the lesser trochanter upon the shaft. In other respects it agrees quite closely with the femur of *Arctictis*; less nearly with *Cercoleptes*. The *tibia* has about the same length as in *Cercoleptes* and *Arctictis*, but the distal trochlea is much more oblique and much less grooved, the internal malleolus is about half as wide and twice as thick, and more prominent; the cnemial crest is long although not very prominent, extending nearly half-way down the shaft; the upper portion of the shaft is compressed laterally. In other respects the construction of the bones agrees fairly closely with the two modern genera cited. The *fibula* has a much heavier shaft than in any modern carnivore.

The greater part of the *pes* is preserved in this specimen. Except in a few

minor features, it agrees closely with the complete pes of *V. profectus* described later. The astragalar trochlea is a little less oblique, but flatter, the neck of the astragalus is somewhat shorter and the head less convex. The peculiar deep fossa between astragalus and calcaneum noticed in the description of *V. profectus* is scarcely present at all in this species, the bones having much more the normal relations as seen in *Cercoleptes*, except for the much shorter neck of both astragalus and calcaneum. The third and fourth metatarsals are approximately a pair, as in the Miacidæ and Fissipedia generally; the fifth is missing; the second is a little shorter than the third or fourth, and less symmetric distally; the first is short and stout, considerably heavier in the shaft than any of the others but only three-fifths to two-thirds as long. Its broad convex proximal facet indicates a considerable degree of mobility, amounting perhaps to a semi-opposability. All the metatarsals are a little larger and stouter than in *V. profectus* but otherwise agree closely. They are much shorter and more spreading than in *Cercoleptes*, somewhat more so than in *Arctictis*, but their construction and symmetry is much the same, save for Mt I, which in the Bridger genus is much shorter in proportion, and the proximal facet admits of much freer lateral motion.

***Vulpavus profectus* sp. nov.**

Plate XLIII, Figs. 2; Text Figs. 7, 8, 23-31.

The type of this species, No. 12626, consists of the skull and jaws, fore and hind limbs and feet, nearly complete, and in fair preservation, found at Grizzly Buttes by Mr. Paul Miller, Am. Mus. Exp. 1905. The geological horizon is B₂ of the Lower Bridger.

The skull is a little smaller than that of the raccoon, much less robust, and with a very much smaller brain-case, making it appear rather like a reduced copy of one of the larger carnivora than like any modern carnivore of equal size. The smaller brain-case results in a moderate development of sagittal and occipital crests, a more posterior position of the postorbital constriction, in the glenoid articulations being placed much nearer together and, with the mastoid and paroccipital processes, projecting more laterally from the skull.

The nasals are long and somewhat expanded posteriorly, a primitive character retained in the Procyonidæ. The ascending processes of the premaxillæ are short, and do not nearly reach the frontals, the nasals being in contact with the maxillæ for the middle half of their length. The lachrymal is somewhat expanded upon the face, much less than in Mesonychidæ or Hyænodontidæ and somewhat less than in *Limnocyon*, but more than in any modern carnivora. The lachrymal foramen is entirely within the orbit. The maxilla is short and high, the infraorbital foramen of moderate size, situate above p³, considerably in advance of the anterior border of the orbit instead of beneath it as usually in modern carnivora. The superior branch of the jugal is both broader and longer

than in recent carnivora, reaching with almost undiminished width to the lower border of the lachrymal, and excluding the maxillary from any close approach to the orbit. The inferior branch is short and small, relatively to the superior and corresponds in size and proportions to modern carnivora. This elongation of the superior branch of the jugal is coördinated, like the expansion of the lachrymals, with a more posterior position of the orbit, whose anterior border is behind p^4 instead of above or in front of it as in modern carnivora. And this change in the modern species is probably caused by the expansion of the brain-case and consequent crowding and pushing forward of all the structures in front of it.

The frontals are of moderate size and width, moderately convex anteriorly, somewhat concave posteriorly between the postorbital crests. Their postorbital processes are moderately developed. Anteriorly they surround the posterior ends of the nasals and extend forward outside of these bones about one fifth of their length, to meet the maxillæ in a transverse suture, not splinted between nasals and maxillæ as in modern carnivora. The post-orbital constriction is near the posterior border of the frontals, but the postorbital crests behind this point, at the anterior end of the parietals.

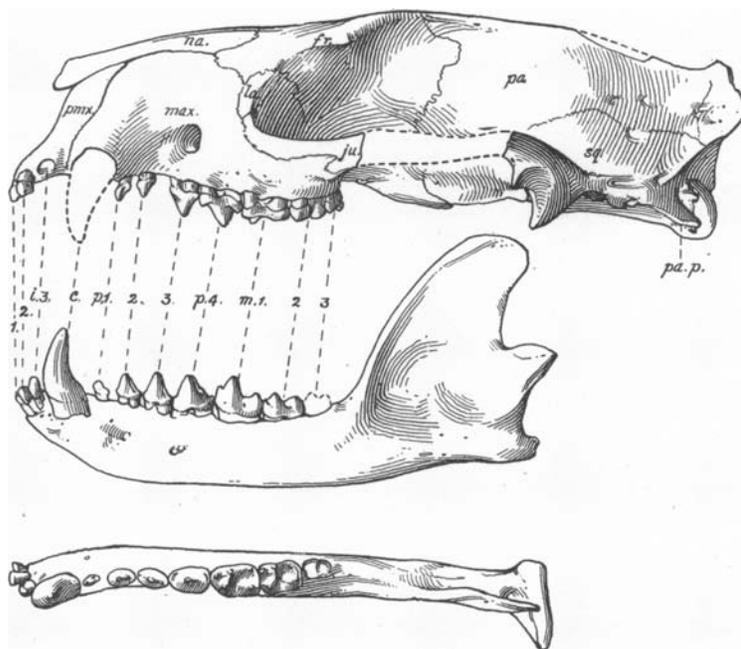


Fig. 23. *Vulpavus profectus*, skull and lower jaw, natural size, type specimen, No. 12626. Lower Bridger.

The parietals are long and comparatively narrow, and cover nearly the whole of the brain-case, except the olfactory lobes and the anterior end of the cerebrum, which project under the frontals. This is a material advance upon the usual condition in Bridger mammals, in which the cerebrum is entirely covered by the parietals, but is much more primitive than in any modern carnivores. There is no indication of any interparietal bone. The sagittal crest is of moderate height. The occiput is rather low and wide, the occipital crests moderately strong, occipital foramen large, condyles large and well separated, and above and external to the condyles is the deep fossa characteristic of primitive mam-

mals, which later becomes filled up by expansion of the brain from within. On the inferior surface of the skull the most noticeable feature is the absence of ossified bullæ. The paroccipital processes are strong and directed backward, as in primitive carnivora generally, and in many modern forms. The mastoid processes are not prominent. The auditory prominence of the petrosal is oval, strongly convex and separated by deep fossæ from the occipital, sphenoid and squamosal bones around it. Along its inner side the fossa appears to be continuous with the brain-cavity, and includes the median and posterior lacerate foramina. This is probably due chiefly to some displacement of the petrosal. The wider fossa on the outer side is the mesotympanic fossa and is excavated in the periotic; it has anteriorly a large foramen bounded in front by the posterior border of the alisphenoid, and posteriorly the stylomastoid foramen traversing the periotic bone, partly separated from the rest of the fossa by a bridge extending inward from the posterior border of the squamosal towards the fenestra

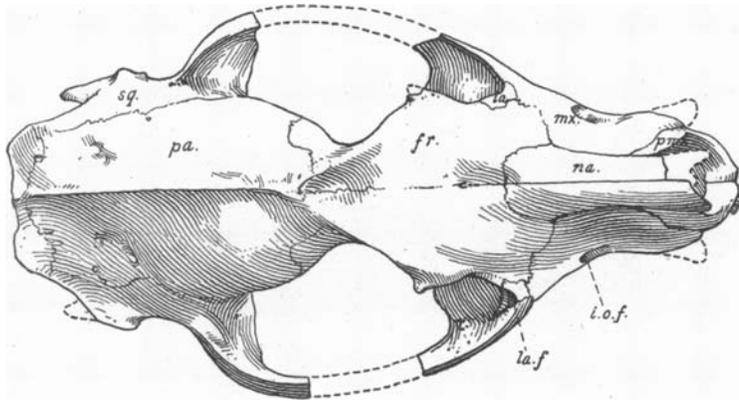


Fig. 24. *Vulpavus profectus*, top view of skull, natural size, type specimen.

rotunda. The fenestra rotunda lies close in front of and anterior to the stylomastoid foramen; the fenestra ovalis is more anterior and external, lying deep within the fossa. The grooves for the tympanic and stapedial branches of the internal carotid artery are distinctly shown; beginning just anterior to the

fenestra rotunda the former passes forward on the outer slope of the auditory prominence to the foramen lacerum medius while the latter descends to the fenestra ovalis. The inner branch of the entocarotid artery is not so certainly recognizable but appears to pass into the otic depression over the lip of the basioccipital a little in front of the foramen lacerum posterius.

The glenoid fossa is limited internally by a strong crest on the external border of the alisphenoid. The foramen ovale is just in advance of this crest, and internal to it, and the posterior opening of the alisphenoid canal is close in front of the foramen ovale, hardly separated from it. The condylar foramen is well separated from the posterior lacerate. The orbitosphenoid foramina cannot be determined.

The superior plate of the alisphenoid is remarkably extensive, reaching half way up on the side of the brain-case, but its pterygoid plate is of moderate size. The pterygoid bones themselves are rather large and prominent, and the post-nareal gutter deep and wide.

The remaining bones call for no especial comment.

Dentition. (Figs. 7 and 8, pp. 344, 347.) The upper incisors are set in a convex row and are of rather small size. The third was the largest, but its crown is not preserved, the first and second have crowns slightly spatulate with internal basal cusps but no lateral cusps. The upper canines are not preserved. The first premolar is a very small one-rooted tooth with pointed crown and minute posterior basal cusp and is set close to the canine. The second premolar is not much larger, but two rooted, and separated from p^1 and p^2 by short diastemata. The third premolar shows an internal root but no trace of internal cusp on the crown; it is simple, except for a slight antero-internal and stronger posterior cingulum. The fourth premolar is triangular with well developed deuterocone, antero-internal in position, and metastyle of about the same size, crested but not so much extended as in the more predaceous *Miacinæ*. A moderately strong basal cingulum surrounds the whole tooth except the internal side of the deuterocone and external side of the protocone.

The first upper molar is considerably larger than p^4 , and nearly symmetrical externally, the antero-external angle not extended into a crested parastyle as in the more carnivorous types. The metastyle is likewise absent. The hypocone is large, postero-internal in position, the protocone is connected with the indistinct paraconule and metaconule by ridges, the former continued around the base of the paracone into the external cingulum. The hypocone is likewise continued into cingular ridges around the antero-internal and the whole posterior side of the tooth. The whole tooth is subquadrate in outline, its outer half not much wider than the inner half, and its transverse diameter is about twice the antero-posterior. The crown of the second molar is not preserved except by a couple of fragments, but it was of much the same construction as m^1 , only not so large, and of less antero-posterior diameter. The external cingulum is wider anteriorly, so that the outer part of the tooth is less symmetrical, but no distinct parastyle or metastyle are present. The third molar is considerably smaller, lacks the conules, and is of less antero-posterior diameter; the hypocone is more internal in position.

The lower incisors are three in number on each side in a very convex row,

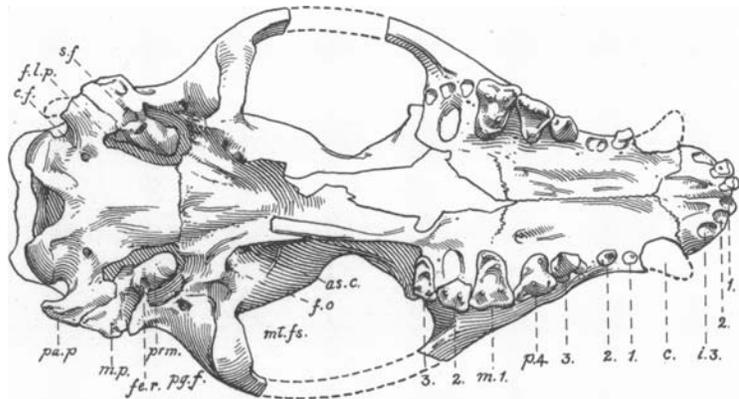


Fig. 25. *Vulpavus profectus*, under view of skull, natural size, type specimen. Lettering as in Fig. 2.

pointed or slightly spatulate, increasing in size from first to third and close to the canine. The canine is like that of *Miacis* and *Uintacyon*, rather small, strongly curved toward the base of the crown, not compressed and without anterior or postero-internal ridges. The first premolar is small, one-rooted, the others two-rooted, increasing regularly in size to the fourth. All have rudimentary heels and the fourth a rudimentary posterior accessory cusp and a small anterior basal cusp. The molars have low trigonids and large basin heels, as wide and as long as the trigonids. The three cusps of the trigonid are about equidistant, and the protoconid overtops the two internal cusps a little, but by no means so much as in the more predaceous genera. The third molar is absent, but was two-rooted and considerably smaller than m_2 , which is as wide as m_1 but only three-fourths as long.

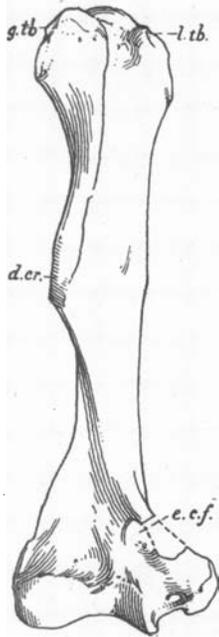


Fig. 26. *Vulpavus profectus*, front view of humerus, natural size, type specimen.

The lower jaw is rather deep anteriorly and moderately stout. Its inferior outline is somewhat convex under the molars and straight under the premolars, lacking the thinning out under the premolar region which is very characteristic of *Uintacyon*. The masseteric fossa is of moderate depth and not sharply defined inferiorly; the coronoid process is wide, blunt and moderately recurved, the angle is prominent, wide and somewhat hooked, not inflected.

The humerus displays the same peculiar characters as in other Miacidæ and Arctocyonidæ, of high compressed deltoid crest most prominent near its distal end about the middle of the shaft, strong supinator ridge, wide entepicondyle with large entepicondylar foramen, convex radial surface antero-internal to the wide shallow ulnar trochlea, greater tuberosity small, lesser tuberosity comparatively large and continued by a ridge along the inner side of the shaft. No modern carnivore has this type of humerus, nor any of the Inadaptive Creodonts, but some of the Insectivora, Rodentia and Marsupialia resemble it rather closely, especially the arboreal types, the Sciuridæ more than any other. It is probably a primitive adaptation to arboreal conditions, affording an exceptionally strong purchase for the pectoral muscles (distal end of the deltoid crest), the rotating muscles of the shoulder (lesser trochanter), and the flexor muscles of the lower limb (entepicondyle).

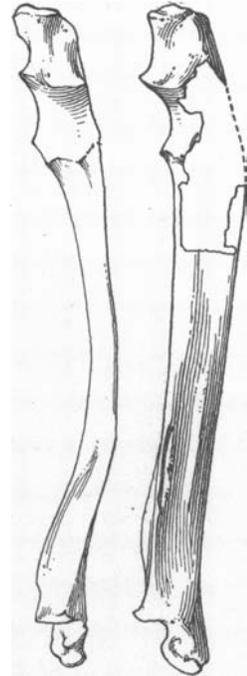


Fig. 27. *Vulpavus profectus*, ulna anterior and internal views, natural size, type specimen.

The ulna and radius are short as compared with modern carnivora with similar length of humerus, the radius being shorter than the humerus and the ulna but slightly longer.

The ulna resembles that of *Cercoleptes*, but the distal part of the shaft is much heavier. The olecranon is short and not expanded posteriorly; the sigmoid cavity is comparatively wide and shallow, the coronoid process less prominent anteriorly, but its lip extended more on the inner border of the sigmoid cavity. The distal half of the shaft is composed of three concave sides, the roughened surface of the anterior border (for attachment of the interosseous membrane) begins abruptly and extends along the penultimate fifth of the length of the shaft as a high prominent crest, while another equally prominent sharp edged crest marks the distal third of the interior border. The space between these two crests gives an attachment to a large part of the pronator quadratus, and is much wider than any modern carnivora, but situate further down on the shaft. This I take to indicate that this muscle was short but powerful. The nearest approach among modern carnivores is seen in *Cercoleptes* and *Genetta*.

The radius corresponds in its adaptive characters to the ulna. The head is round-oval and the ulnar articulation strongly convex, indicating extensive power of pronation and supination.

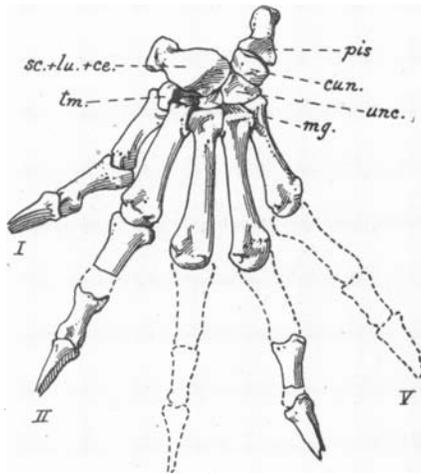


Fig. 29. *Vulpavus profectus*, fore foot, dorsal view, natural size, type specimen. Lettering as in Fig. 4.



Fig. 28. *Vulpavus profectus*, front view of radius, natural size, type specimen.

The shaft is curved, and the pronator and supinator ridges strongly developed, so that it has little of the round or oval section usual in the modern carnivora. The bicipital tubercle, on the outer posterior surface, is strong, and just below it is a strong crest on the postero-internal border, which appears to be designed to increase the area of attachment of the supinator?. The rugosity for attachment of the supinator longus is situate about three-fifths of the distance from the proximal end, and is strongly marked on the inner border of the bone; below and behind it is a sharp crest extending down to the styloid process and expanding the area of insertion of the pronator quadratus. On the inner border of the shaft is the rugose attachment for the interosseous membrane, situate on the penultimate fifth of the shaft; behind and below it is a moderately strong crest expanding the pronator quadratus insertion

On the inner border of the shaft is the rugose attachment for the interosseous membrane, situate on the penultimate fifth of the shaft; behind and below it is a moderately strong crest expanding the pronator quadratus insertion

on this side. The distal end of the bone is trihedral, the styloid process not very prominent, the scapholunar facet cup-shaped, the grooves for the extensor tendons shallow, the ulnar articulation large, concave.

Fore-foot. (See Fig. 29.) The carpus and metacarpus are complete, except that the trapezoid is missing, and two proximal, two penultimate and three distal phalanges are preserved. The scaphoid, lunar and centrale are consolidated into a single bone as in all the True Carnivora of Oligocene and later time,— a character not known to occur in any other Primitive Carnivora, or indeed in any contemporary mammals. In this respect therefore *V. profectus* has advanced beyond the Primitive Carnivore or Creodont stage of evolution. Nevertheless its proper place is with the Creodont Miacidæ, as

(1.) It retains several primitive characters of equal importance — the unossified bulla, the small brain, extension of lachrymal on the face, etc.

(2.) It is in all respects closely allied to *Phlaodectes* in which the scaphoid lunar and centrale are separate, and to *Palæarctonyx* in which scaphoid and centrale are united but the lunar distinct.

This group of Miacidæ was evidently precocious in this and to some extent in other characters, but is properly reckoned with the Primitive and not with the True Carnivora.

The carpal bones compare in detail very closely with those of *Cercoleptes*. The hook-like process of the inner side of the scapholunar is stouter, the radial facet broader over the trapezoid and trapezium, and the unciform facet is not so deep. The unciform is wider but not quite as high; the trapezoid retains more of its primitive peg-like proximal articulation.

The five metacarpals present an approximately paraxonic symmetry; as compared with *Cercoleptes* they are somewhat broader throughout, the first digit less reduced, the heads of the fourth and fifth much wider. The third and fourth are the longest, the second is not quite as long but somewhat stouter, the fifth is a little shorter than the second and about as heavy in the shaft as the third and fourth; the first is considerably shorter than the fifth, but nearly as stout as the second, and somewhat more divergent than the others. The proximal phalanx of the first is considerably shorter than that of the second digit; the three claws preserved are of about equal size, shorter than those of *Cercoleptes*, without any reflection of the proximal border into an incipient hood such as the modern genus displays.

Hind Limb. Only the distal end of the femur is preserved in the type, and this corresponds so closely with that of *V. palustris* that no separate description is necessary.

The tibia is about as long as that of *Cercoleptes* but has a somewhat narrower head, strongly compressed shaft expanding into a heavy trihedral distal end. The cnemial crest is long, extending more than half way down the bone, but not as prominent as in many primitive types, although much more so than in *Cerco-*

leptes or most modern Carnivora. The posterior ridge is remarkably high and sharply defined in the upper part of the bone, fading out toward the middle third. The distal facet is very oblique, the malleolus stout and its inner facet fades into the principal astragalar facet. The tuberosity above the malleolus is prominent and heavy, and the groove for the *tibialis posticus* wide and well defined as is also that for the *flexor longus digitorum*. There is no facet for the fibula.

The fibula is considerably stouter than in *Cercoleptes* or any other modern carnivora. Its distal end is expanded postero-externally into a stout process behind which lie the sharply defined grooves for the peroneal muscles. It has no facet for the tibia, and where the two bones are articulated and placed in position on the pes it can be seen that they do not quite touch being separated by the high inner crest of the astragalar trochlea. There is no facet for the calcaneum.

The pes (Fig. 31) is preserved entire, and most of its bones were found articulated in approximately their natural position, so that there can be no question as to their correct determination.

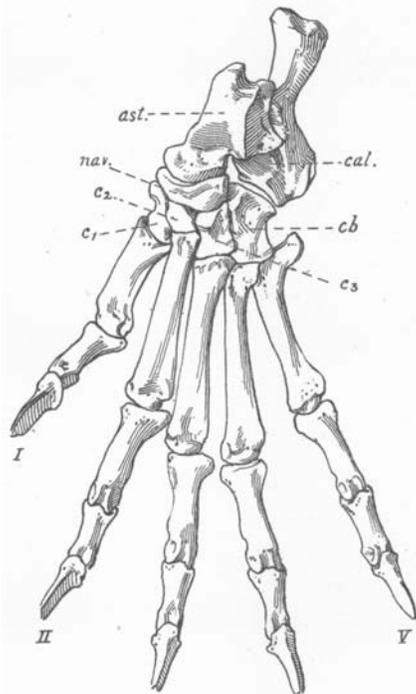


Fig. 31. *Vulpavus profectus*, hind foot, dorsal view, natural size, type specimen.

The astragalus (Pl. XLVII, Fig. 2, b) is much like that of *Cercoleptes*, but the neck is shorter, the head wider, the tibial facet more oblique, the fibular facet less vertical, the crest between them sharper, and the fibular facet more limited postero-externally. The body of the astragalus is considerably deeper, the groove for the flexor tendons better defined, the astragalar foramen is small, situate just in front of the plantar tendinal groove, and in front of it is a considerable triangular space limited anteriorly by the tibial and fibular facets.

The calcaneum has a rather short, slender tuber, expanded at the head, and moderately grooved for the plantaris tendon. The peroneal tubercle is very prominent and its tendinal groove well marked. There is no facet for the fibula. Between the distal portions of the astragalus and calcaneum



Fig. 30. *Vulpavus profectus*, tibia and fibula, anterior views, natural size, type specimen.

lies a broad deep fossa, narrowed above into the groove for the interosseous ligament. This fossa is much larger and deeper than in *Cercoleptes*, and far more so than in other modern carnivora, and imparts a peculiar aspect to the foot. It is doubtless conditioned by the lateral expansion of this region of the tarsus. The cuboid is like that of *Cercoleptes* in having a considerable proximal-internal facet, but the expansion of the external side of the navicular apparently cut this facet off from any contact with the astragalus, whereas in *Cercoleptes* there is a slight astragalo-cuboid articulation. The facet may have been functional for the navicular but could hardly reach the astragalar head.

The ecto- and meso-cuneiforms are much like those of *Cercoleptes*, the meso-cuneiform having the same peculiar obliquity in position and in its navicular articulation. The ecto-cuneiform is larger than in the modern genus and has a well marked facet for the articulation of the "pre-hallux" which is present in the modern genus. It is presumably a sesamoid in the tendon of the tibialis anticus muscle.

The metatarsals, like the metacarpals, are paraxonic in their symmetry, the first being stouter but much shorter than the other four, which decrease slightly in stoutness of shaft from II to V. They are shorter and stouter than in *Cercoleptes*, especially the first, while the fifth is proportionately shorter and its peroneal tubercle less massive, although much more prominent than in most modern carnivora. The phalanges are about as long as in *Cercoleptes*, except the unguis, which are somewhat larger than those of the manus and have the same form. The penultimate phalanges are somewhat bent upward at their extremities, but not asymmetric or excavated on the external dorsal aspect of the shaft, as in carnivora with retractile claws.

From the above description it will be apparent that we have in *Vulpavus* a very primitive member of the Carnivora, with some degree of specialization in the teeth, but very little in the structures of the skull and skeleton. In the organization of the skull and skeleton, especially in the structures of the feet, it is undoubtedly nearer to the Kinkajou than to any other living type, and the evidence for regarding it as ancestral to this animal is far more cogent and complete than that on which many elaborate phylogenies have been based by students of fossil vertebrates (the present writer included). But with the more extensive and complete materials available for study, and a better insight into the causes and courses of the evolution of different races, it is becoming more and more apparent that many of these phyla have been based upon quite inadequate evidence, and should be regarded as merely provisional arrangements awaiting conclusive evidence.

In the present case it is clear that most of the features in which *Cercoleptes* agrees with *Vulpavus* are simply primitive characters retained by the modern genus. These are characters common to all the Miacidæ and for the most part equally well shown in all the Bridger Creodonta. *Cercoleptes* has lost these to a

less degree than any other modern carnivore. Nevertheless there is a certain residuum of resemblances between *Vulpavus* and *Cercoleptes* which cannot reasonably be regarded as primitive characters and which point to a real relationship.

***Vulpavus (Phlaodectes) ovatus* sp. nov.**

Plate XLIII; Fig. 3; Text Figs. 32-41.

An incomplete skeleton including a well preserved skull, represents a species very distinct from *V. palustris* and *profectus* but presenting throughout the same general characters of teeth, skull and skeleton, and referable to the genus *Vulpavus* as a fairly distinct subgenus. It was found on Little Dry Creek, by L. S. Quackenbush.

Specific characters. Dental formula $\frac{3.1.3.3}{2.1.2.3}$. Premolars more reduced than in *Vulpavus* proper, all spaced, except the fourth. P^3 oval in cross-section. Upper molars of sub-ovate outline, with no hypocone, and strong internal cingula around m^1 and m^2 . Paracones and metacones of equal size. M^3 much reduced, without internal cingulum. Canines long, laterally compressed, with strong posterior ridge, the upper canine nearly straight, the lower moderately curved. Lower molars with proto-, para- and meta-conid of approximately equal size and height, third molar much smaller than the others, with two approximated roots. Skeleton

more robust than in the type species, astragalar trochlea flatter, a small calcaneofibular facet.

Skull. The skull is of moderate length, brain-case large for an Eocene carnivore, but much smaller than in modern carnivora. The orbits are wide apart, the postorbital construction hardly greater than in the Canidæ, much less than in the typical Viverrines, but, owing to the small brain-case, it is situated far back on the skull, just in front of the fronto-parietal suture. In *Sinopa* it is behind this suture. The sagittal crest is single but very low, the occipital crest of moderate height and width. The orbits lie above the molars and the lacrymal has a small expansion upon the face. The nasals are much longer than

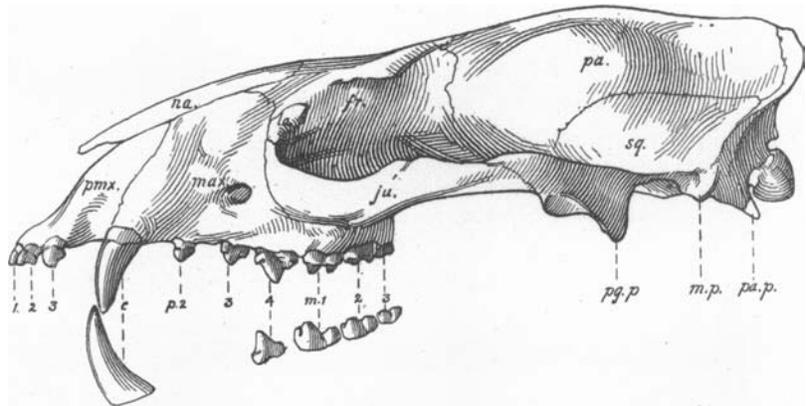


Fig. 32. *Vulpavus ovatus*, skull and lower teeth, side view, natural size. Type specimen, No. 11498; Lower Bridger.

in modern carnivora, not expanded posteriorly, but their width little reduced at the frontal suture. The frontals send small splints forward between the nasals and maxillæ, but do not nearly reach the premaxillæ. The frontals are wide, longer than in *Sinopa*, but much shorter than in modern carnivora; they

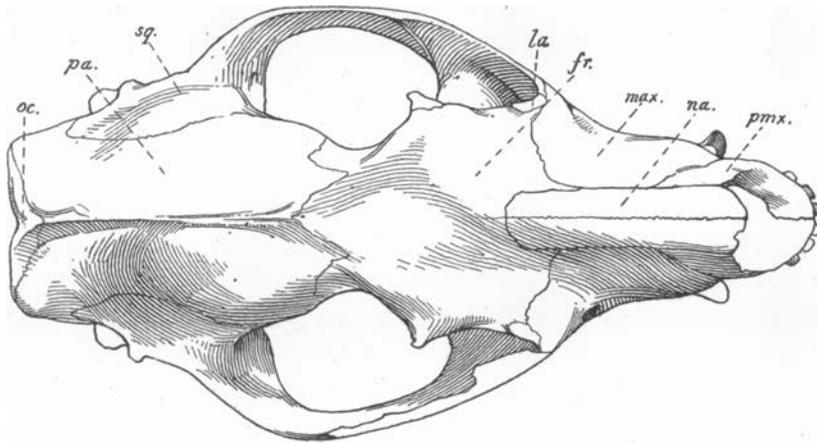


Fig. 33. *Vulpavus ovatus*, top view of skull, natural size, type specimen.

are not inflated over the orbits nor excavated along the median line, but present a nearly plane surface, slightly concave between the low supratemporal ridges. The infra-orbital foramen is small, situate above p^3 , about as far in advance of the orbit as in *Canis*.

Postorbital processes are moderately developed on the frontals, slight on the jugals. The jugal is of moderate depth and reaches back nearly to the glenoid fossa, ending posteriorly in a thin splint. The zygomatic process of the squamosal is short and not heavy. The basicranial region is wide, its proportions more as in *Ursus* and *Arctictis* than in *Canis*, *Viverra* or *Herpestes*. There is no indication of an osseous bulla, and the petrous bone is exposed, as in nearly all Eocene mammalia.

In the low and flattened form of the auditory prominence of the petrosal, *Vulpavus* resembles *Canis* and *Ursus* much more than *Viverra*, but it is not sunken as in the bullate carnivora, and projects somewhat below the inferior surface of the basioccipital. The condylar foramen is well separated from the posterior lacerate foramen, as in

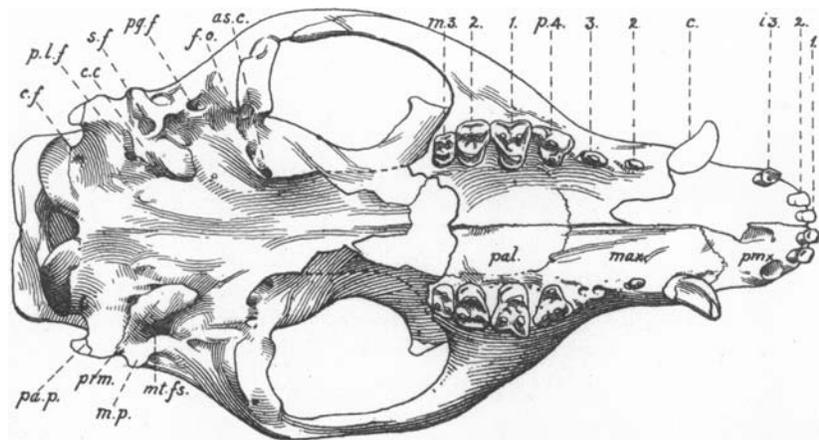


Fig. 34. *Vulpavus ovatus*, under view of skull, natural size, type specimen. Lettering as in Fig. 2.

Arctoidea and Cynoidea; in the Aeluroids they are close together. The paroccipital process is short, stout and round, much as in the bear; in the Aeluroids it is laterally expanded and applied to the posterior face of the bulla; in the Cynoids it is appressed to the bulla but retains more of the primitive form. The foramen lacerum posterius is rather small; a little in advance of it is the clearly defined posterior opening of the carotid canal. The groove for the tympanic branch of the entocarotid is faintly marked on the external slope of the auditory prominence commencing just in advance of the fenestra rotunda and leading forward and downward. The mastoid process is distinct, short and stout and expanded transversely; it is much nearer to the postglenoid process than in *Viverra* or *Herpestes*, and connected with it by a strong lateral crest as in *Ursus*, *Canis* and *Arctictis*. The postglenoid foramen is large as in Arctoidea and Cynoidea; in Aeluroidea it is reduced or lacking. The foramen ovale has its usual position in the alisphenoid bone opposite the posterior border of the glenoid fossa; anterior to it is a rather long alisphenoid canal, present in Bears, Dogs and Viverrines but absent in some other modern groups. The anterior foramina are not exactly determinable.

The palate is short and rather wide, the posterior nareal opening opposite the second molar, as in Canidæ, in *Arctictis*, bears and viverrines the palate is prolonged backward to a varying degree.

The lower jaw is short and deep especially in the symphyseal region, and the depth under the dental series is nearly uniform, slightly greater under the premolars. In some species of *Uintacyon* (*U. vorax*, *major*) the jaw is equally short and deep but the depth under the premolars is less. The posterior part of the jaw does not differ from ordinary short-jawed carnivora.

Teeth. There are three small upper incisors of which the median is the least, its crown is short, spatulate, not expanded. The canine is nearly straight, with a flat postero-internal face bounded by a strong posterior and weaker internal ridge — it is not as straight as in *Arctictis*, and lacks the anterior ridge of that genus. The premolars are much reduced; the first is absent, the second and third are small, two-rooted, simple, oval, without internal cusps or heels; there is a considerable diastema in front of p^2 , a smaller one in front of p^3 , and a short one behind it. P^4 is smaller than the first or second molar, and is not extended into a shearing tooth but has more the form seen in *Arctictis*. The internal cusp is strong but not anterior in position, the postero-external is crested but comparatively short and low, the principal cusp is much higher than the others, conical but with a postero-external ridge, and the antero-external cusp is minute. The molars are broadly rounded internally with lunate protocone, strong internal cingulum, small conules. The paracone and metacone are of equal size and height, well separated, and set well in from the external margin, which is symmetrically developed around them, and bordered by a strong cingulum. The parastyle is not extended antero-externally as in the more carnassi-

form dentition. The second molar is smaller than the first and the third considerably smaller than the second, and its postero-external border reduced, giving it an oval outline.

The lower canine is long and much compressed, with a strong posterior ridge. The lower premolars are comparatively small, and were probably spaced as well as reduced. They are short and high, rather robust, and without accessory cusps, with very small heels and on the fourth a minute anterior basal cusp. The lower molars diminish in size from the first to the third, which is quite small; the trigonid and heel are of about equal size and width, the three cusps of the trigonid of equal size and well separated, the hypoconid and entocoid about equally developed and not much lower than the trigonid cusps.

Skeleton. The vertebral column presents some interesting comparisons with the *Fissipedia* on one hand, the Inadaptive Creodonts on the other. The cervicals and first two dorsals, the last dorsal and the entire lumbar series, sacrum and anterior caudals are fairly complete; the remaining dorsals and caudals are represented only by a few fragments.

Cervical vertebræ. The atlas shows a deep vertebrarterial groove in front of the transverse process, as in *Miacis* and the *Felidæ*, instead of a foramen, as in *Oödictes* and most modern Carnivora. The odontoid process of the axis is much longer than in *Cercoleptes*, the remaining cervical vertebræ are comparatively long, much longer than in *Cercoleptes*, somewhat longer than in *Arcticitis*; the zygapophyseal facets much larger and more horizontal than in either genus; and the neural spines are very rudimentary, even upon the sixth cervical. The vertebrarterial foramen is present upon the fourth, fifth and sixth cervicals, but of smaller size than in *Cercoleptes*; the seventh cervical has no foramen.

Dorsal vertebræ. The first dorsal retains the cervical type of articulation in the posterior zygapophyses. In various modern carnivora with which I have made comparison this articulation is of the usual dorsal type, as it is in *Creodonta* generally. The articulation between D_2 and D_3 has assumed the normal anterior dorsal type. The spines of D_1 and D_2 are also somewhat of the type of posterior cervical spines, thin and flattened laterally and with less slant backward than is usual in these vertebræ; and the rib facets are unusually concave from front to back indicating unusual amount of mobility of these vertebræ on the ribs. It would appear from these data that the flexibility of the neck was extended backward to the first two dorsals, to a greater extent than is usual among modern carnivora, the first dorsal in particular functioning as a cervical. This, in connection with the rather long cervicals and slight development of spines points to a very flexible as well as long neck for a carnivore.

Only a few fragments are preserved of the remaining dorsals except the last. This is nearly complete but somewhat crushed, and I cannot be certain of the presence of a rib-facet, so that it may have been a lumbar; it has no transverse

process however. It is rather long, with strong anapophyses, zygapophyses of the usual anterior lumbar type, neural spine somewhat like that of *Arctictis*, but longer, flatter, and wider at the tip.

Lumbar vertebræ. Six lumbar vertebræ are preserved nearly complete. They are of moderate size and length, comparable in general proportions with *Arctictis* and *Cercoleptes*, but differing materially from either in character of transverse processes and spines. The first lumbar is very similar to the last dorsal but has a small transverse process. The second has a much broader centrum, stronger transverse process, broader zygapophyses and reduced anapophyses. The third lumbar has both spine and transverse processes complete

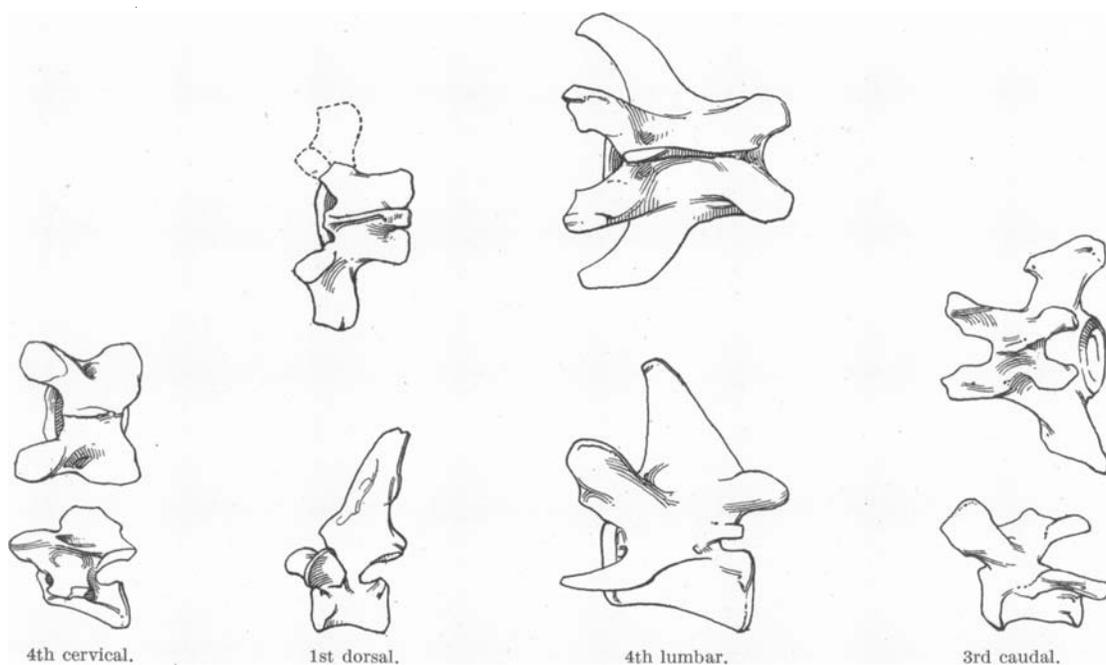


Fig. 35. *Vulpavus ovatus*, lateral and superior views of typical vertebræ. Natural size, type specimen.

and is quite distinctly cynoid in the development of these parts, but differs from the dogs in the larger and relatively flat and widely separated zygapophyses. This type of lumbar spine, thin, flat, wide at the base, slanting forward, and tapering regularly to a slender tip, is not usual among carnivora. The width and flatness of the zygapophyses is common among the more primitive forms. The fourth and fifth lumbar are similar to the third but with decreasing anapophyses, centra progressively broader and flatter, transverse processes successively wider at the base. The sixth lumbar has a shorter and wider centrum than the preceding ones, the spine is not so wide at the base, tapers less, and points nearly upward, approximating the type of the sacral spines.

Sacrum. This is composed of three vertebræ, of moderate width, narrower

transversely in proportion than in *Cercoleptes*, the neural spines narrower antero-posteriorly, higher and more vertical, but otherwise similar.

Caudals. Only a few caudals are preserved, mostly proximal. The first three are probably in series, and are exceptionally large, with short centra, wide transverse processes and large zygapophyses set well apart. The character of the transverse processes in C_1 compares with the corresponding vertebra in *Cercoleptes*; that of C_2 and C_3 is intermediate between C_2 and C_3 in *Cercoleptes*; but the size and width apart of the zygapophyses and shortness of the centra in all three vertebræ compares with C_1 of the modern genus. Behind these three caudals are two with successively longer centra, comparable in proportion with C_2 and C_3 in *Cercoleptes*. The only other complete caudal centrum is from much further back in the column, but it compares fairly in construction with C_8 of *Cercoleptes*. Two chevrons preserved are of exceptionally large size, and belong presumably with the proximal caudals.

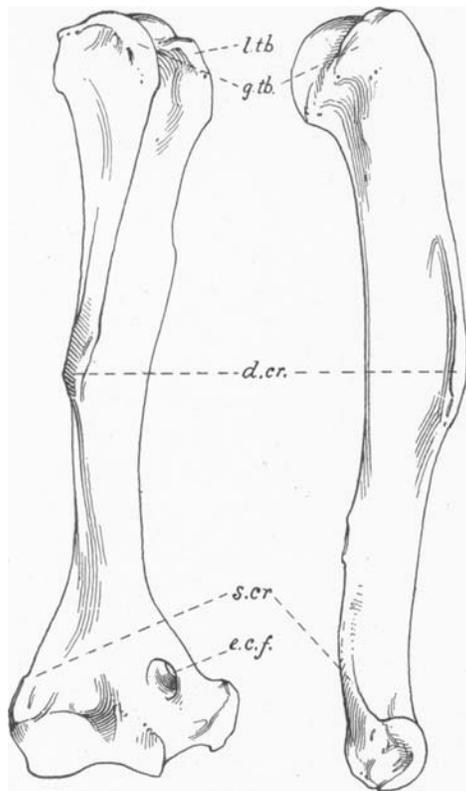


Fig. 36. *Vulpanus ovatus*, humerus, anterior and external views, natural size, type specimen.



Fig. 37. *Vulpanus ovatus*, front view of radius, natural size, type specimen.

So far as preserved, the characters of the caudals indicate a tail of the peculiar type shown in *Sinopa*, *Tritemnodon*, *Oxyæna* and other Creodonta, and probably common to all primitive carnivora. It is very thick and long, relatively stout and inflexible towards the base, probably very strong and flexible toward the distal end, but whether actually prehensile or not I am unable to decide.



Fig. 38. *Vulpanus ovatus*, dorsal view of part of fore foot, natural size, type specimen.

Ribs. A few ribs are preserved more or less complete, but do not afford any very marked peculiarities. The first three were somewhat broader and longer than in *Cercoleptes*.

Fore limb. A considerable part of one *scapula* is preserved, showing a very long overhanging acromion, longer, flatter and broader toward the

tip than in *Cercoleptes*, from which I infer that the clavicle was well developed. The metacromial and coracoid processes are broken off. The postspinous fossa is of moderate width, considerably narrower than in *Cercoleptes*; the anterior and superior borders of the scapula are incomplete. The *humerus*, *radius* and *ulna* are very similar to those of *Vulpavus profectus* already described, but of somewhat larger size and more robust proportions. The head of the radius is rounded, the shaft a little straighter than in *V. profectus*; the deltoid crest of

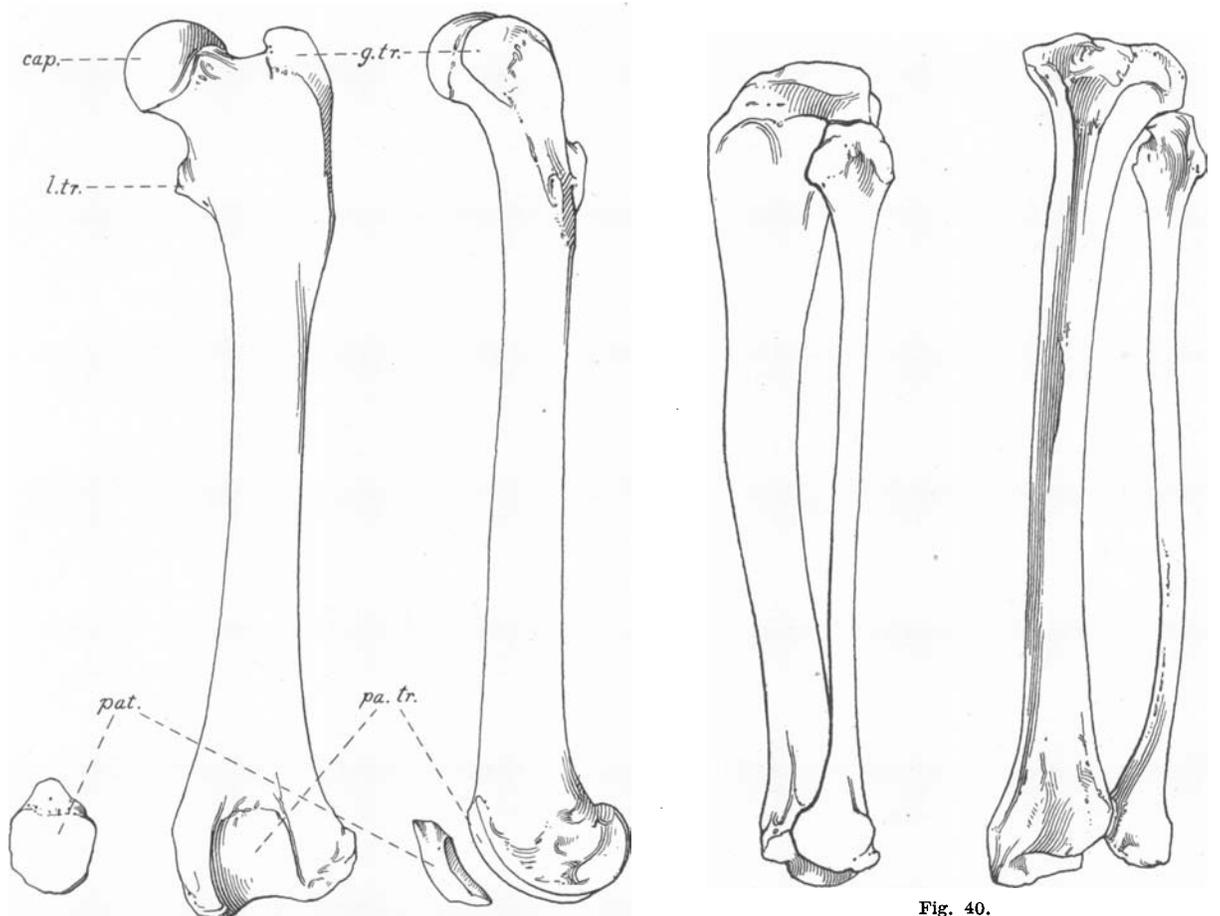


Fig. 39.

Fig. 40.

Fig. 39. *Vulpavus ovatus*, left femur, anterior and external views, natural size, type specimen.

Fig. 40. *Vulpavus ovatus*, left tibia and fibula, external and anterior views, natural size, type specimen.

the humerus is slightly less prominent. Of the *fore-foot* the only bones preserved are the scaphoid, lunar, magnum, and metacarpals III and IV. These are materially larger than in *V. profectus*, the scaphoid and lunar are separate, and the third metacarpal somewhat shorter, smaller and less symmetrical than the fourth, indicating apparently that the external side of the foot was more developed than in the typical species of the genus. The dorsal surface of the

scaphoid is reduced to a narrow line, the distal and proximal facets meeting superiorly at nearly a right angle — this, with other correlated features, may be regarded as indicating a plantigrade manus.

Hind Limb. Part of the *pelvis* is preserved, but not enough to afford any characters of especial interest. The *femur* is perfect and uncrushed. It shows a rudimentary third trochanter, as in *Cercoleptes* but somewhat more prominent; the lesser trochanter is more prominent and more internal in position than in the Kinkajou and the digital fossa merges internally into a broad shallow uniform depression between the greater and lesser trochanters. The greater trochanter is more robust than in the modern genus. The shaft of the femur has a noticeable dorsad curvature towards the proximal end of the bone, but lacks the



Fig. 41. *Vulpavus ovatus*, left astragalus, superior view, natural size, type specimen. a.f., astragalar foramen.

mediad curve prominent in the Hyænodonts; toward the distal end it broadens more uniformly into the epicondyles than in most modern carnivora. The patellar trochlea has the same short broad shallow form as in *Cercoleptes* and *Arctictis*; the condyles are more convex from side to side than in the Kinkajou. The *tibia* and *fibula* agree in most respects with the corresponding bones in *V. profectus*, save for greater size and robustness, and the somewhat longer cnemial crest of the tibia. In the *hind foot*, all the tarsals except the ectocuneiform are preserved, with metatarsals I and IV and parts of others and several phalanges. They agree very nearly with the hind foot bones in *V. profectus*, but differ in a few significant details. The astragalus is somewhat broader with shorter neck and wider head. The peroneal tubercle of the calcaneum is more prominent. The navicular is deeper toward its internal side; the mesocuneiform has the same oblique attachment to the navicular but is proportionately larger and its metatarsal facet more directly distal. The entocuneiform is considerably longer. The first metatarsal is considerably smaller in proportion, while mt. IV is relatively longer and more slender.

It would appear that both manus and pes were more completely plantigrade than in *V. profectus*, and probably associated with this difference is a tendency to lengthening of the external and reduction of the internal digits of manus and pes — as in the bears among modern plantigrade carnivora.

***Vulpavus completus* sp. nov.**

This species is represented principally by lower jaws, distinguishable from the neotype of *V. palustris* and from *V. ovatus* by the number and proportions of the lower teeth.

Specific characters. Dental formula $\frac{\quad}{3.1.4.3}$. Molars of more uniform size than in the two last preceding species, premolars not so high as in *V. palustris*.

Type No. 11506, lower jaws; paratype No. 11503, lower jaws without teeth, parts of skull, etc.; Nos. 12627, 12625 and 11501 are also referred to this species.

Vulpavus is the most primitive of the Miacidæ, and in most respects the most primitive of the Bridger Carnivora. It represents very nearly the central type from which the Adaptive Creodonts and Carnivora are hypothetically derived. The teeth strongly suggest those of the Basal Eocene Oxyclænidæ, and are in some respects more primitive than those of *Oödectes*. The high compressed unfissured claws and other characters of the feet suggest relationship to the Arctocyonidæ; the teeth, while low-cusped, lack the flat crowns of that family. Although the carnassial is undeveloped, the relationship to the Miacidæ is evident in all details of form and proportions of the teeth, and in all the characters of the skeleton, and *Oödectes* furnishes the intermediate stage between *Vulpavus* and the more specialized members of the family.

Palæarctonyx gen. nov.

Molars much as in *Vulpavus* but with lower cusps. Premolars somewhat more reduced, the fourth with broader deuterocone more median in position, and postero-internal cingulum. Scaphoid and centrale united, lunar separate, claws somewhat larger, higher and more compressed than in *Vulpavus*. Skeleton, especially the fore limbs, larger in proportion to size of jaw.

This genus is based upon an upper jaw and various fragments of the skeleton from the upper levels of the Bridger formation. Part of a hind foot from the same level is also referred to the type species, and an upper jaw of a species considerably smaller from the Lower Bridger, is provisionally referred to the genus.

Palæarctonyx is nearly related to *Vulpavus* and especially to the subgenus *Phlaodectes*. The resemblance extends to all the minutiae of construction in teeth and skeleton bones, and I cannot but regard the two genera as closely allied, *Palæarctonyx* being a lineal or approximate descendant of *Phlaodectes*. On the other hand, *Palæarctonyx* is by definition a member of the Arctocyonidæ, and if this family were of later instead of earlier age, *Palæarctonyx* would serve excellently as an ancestral type from which they might be derived. It has the more or less quadrate molars, reduction of the premolars, flattening of the molar crowns, united scapho-centrale with distinct lunar, divergent or partially opposable pollex and hallux and high compressed claw phalanges, which are the distinctive characters of the Arctocyonidæ. The humerus is very like that of *Arctocyon*, with high sharp deltoid crest extending far down on the shaft and ending abruptly. It differs from Arctocyonidæ in the proportions of the molars, $m^1 > m^2$ in *Palæarctonyx*, $m^2 > m^1$ in *Clænodon* and *Arctocyon*, in the less completely quadrate form of molar, and lack of corrugations on the surface of the teeth, all three being in the main due to a lesser grade of specialization, exactly paralleled in any of the phyla which have been proposed for the descent of the Ursidæ, and just what we should expect to find in an ancestor of *Clænodon* and *Arctocyon*. The

Bridger genus is more specialized than *Arctocyon* in some respects, less in others, but the general direction of the specialization is identical throughout.

When, however, we compare in detail the minutiae of construction of teeth and bones in *Clænodon* and *Palæarctonyx*, we do not find them in close agreement. The arrangement of the molar cusps is somewhat different. The form of the scapho-centrale is different. The trapezium is of much smaller size and considerably different form. The shape of the facets for magnum, trapezoid and unciform indicates a somewhat different arrangement of the carpus. The astragalus shows various differences in its proximal facets. In short the correspondence in detail is almost exact with *Phlaodectes*, not very close with *Clænodon*. These facts accord with the geological position of the genera, indicating that the typical Arctocyonidæ represent an early branch of the Adaptive Creodont stem, paralleled by the later specialization seen in the *Oödectes-Vulpavus-Phlaodectes-Palæarctonyx* series. The relation may be seen in the provisional phylogeny, p. 353.

A more thorough exploration of the Wasatch will probably result in the discovery of connecting forms between Miacinæ and Viverravinæ, which on our present data are more easily separable than the Miacinæ and Arctocyonidæ. The absence of Miacinæ from the Torrejon is somewhat remarkable. Some of the Torrejon and Puerco forms referred provisionally to Triisodontidæ and Oxyclænidæ may on better knowledge prove to be closely related to the undiscovered connecting forms at the root of the Miacid phylum.

Palæarctonyx in short is more nearly related to the Miacidæ than to the Arctocyonidæ, and its resemblance to the latter group is due to parallelism. Nevertheless the closeness of this parallelism is the strongest kind of evidence, to my mind, that the two families are nearly related. For similar adaptation in remotely related groups does not result in exact parallelism; the resemblance is always a superficial one, and the degree to which it extends to the details of construction is a fairly accurate measure of the nearness of relationship of the animals compared. This statement is, if analyzed, almost a truism, for we have no other means of judging of the relationships of animals except through their correspondence in structural detail. Yet it is so often asserted that resemblance in structure is not a certain indication of relationship because it may be due to similar adaptation of unrelated groups, that it seems necessary to point out the fallacy of such an argument. The assertion is true only when we make our comparisons and base our classifications upon a few prominent characters, instead of upon the sum total of the resemblances and differences of the animals compared, including in our study minor and apparently unimportant, as well as the more obvious features, and considering with care the interdependence of characters, so that the numerous structural changes entailed by one important difference may not be regarded as independent features of resemblance or difference. The classification itself expresses only a few of the more obvious

and constant features of resemblance and difference, which are selected by the student for distinction of groups; but the studies upon which it is based must include an immensity of observations of detailed characters, which can be only partially set forth in the detailed descriptions and figures. If the study be thorough and the material adequate, parallelism will supply interest but not cause confusion.

In distinguishing *Palæarctonyx* from the Arctocyoniidæ, the following Miacid features may be selected.

- (1) Molars decreasing in size from first to third.
- (2) Proximal facets of scaphoid and lunar more extended towards palmar surface.
- (3) Dorsal surface of centrale reduced by extension of trapezoid over it.

These three features are, in my interpretation, neither primitive characters nor specializations in an Ursoid direction, but the remains of the early stages of specialization of the typical Miacidæ, and indicate that the *Vulpavus-Palæarctonyx* phylum parted from that of the more carnivorous Miacidæ after the latter had advanced further in its typical line of development than when the Arctocyoniid phylum branched off from it. The adaptation to an omnivorous diet would tend to enlarge the molars, and, as far as one can judge, to enlarge the posterior molars relatively to the anterior. The plantigrade foot tends to extend the proximal carpal facets dorsally instead of ventrally, hence the more ventral extension indicates a greater degree of progress towards digitigrade fore foot in the Miacidæ at the time *Palæarctonyx* branched off. The reduced centrale I judge from comparison of known phyla not to be a primitive character but a stage in the disappearance of this element, associated with the evolution in various phyla of a cursorial foot.

As nearly as I am able to judge from a careful survey of the evidence, the Arctocyoniidæ, *Palæarctonyx*, *Cercoleptes*, the Ursidæ, the Procyoniidæ, and the Amphicyonine dogs are all adaptations of a more or less similar character from the main stem of the Cynoid carnivora at various stages of its evolution. The Arctocyoniidæ are the earliest, the Amphicyons the latest — the first branched off after the main phylum had assumed the Adaptive Creodont characters but before the family differentiation had begun; the Amphicyons, Procyoniidæ, etc. branched out after a greater or less cynoid modification had been fixed in the stirp. *Cercoleptes*, although included by most authors in the Procyoniidæ, has but little in common with either *Nasua* or *Procyon*, but in all its skeletal characters shows such marked affinities to *Vulpavus* and *Palæarctonyx* that it may be provisionally regarded as derived from this section of the Miacidæ. The derivation of the other groups, and the independence of their phyla, is not entirely clear, and is not to be solved by study of the teeth alone, or by the other fragmentary specimens upon which we are principally dependent for our knowledge of the European members of the phyla. Arguments and phylogenies based upon

such fragmentary materials are not conclusive, and no amount of learning or intensity of study can make them so. In more than one instance in the Bridger fauna described in this paper, it will be seen how far astray have been the earliest classing of Bridger species known from fragmentary jaws alone, *e. g.*:

<i>Hyopsodus</i>	referred to	Artiodactyla, Primates, Insectivora.
<i>Pantolestes</i>	“	Carnivora, Primates, Artiodactyla, Insectivora.
<i>Notharctus</i>	“	Carnivora, Primates, Lemurs.
<i>Tinoceras</i>	“	Proboscidea, Perissodactyla, Amblypoda.

***Palæarctonyx meadi* sp. nov.**

Figs. 7, 42-46.

The type specimen, No. 12158, is a fragmentary skeleton consisting of the right maxilla, several vertebræ, humerus and parts of other limb bones, scaphoid, lunar and trapezium bones of the wrist, astragalus and ectocuneiform bones of the ankle, and several phalanges. It was found near the base of the exposures at Twin Buttes (Hor C₁), by Mr. Chas. S. Mead of the Museum Expedition of 1904, to whom I have dedicated the species. A second specimen, No. 11551, from Henry's Fork, consists of the calcaneum, metatarsal IV and parts of the others, and several phalanges including four unguals.

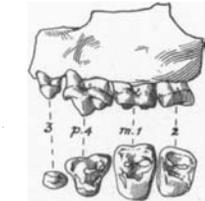


Fig. 42. *Palæarctonyx meadi*, upper jaw, external view, and crown view of upper teeth. Natural size, type specimen, Upper Bridger.

including four unguals.

The upper molars are much worn, so that their exact construction is not shown, but they appear to have been very like those of *Vulpavus ovatus*, with strong internal cingulum, and on *m*¹ a very rudimentary hypocone. The form of *m*¹⁻² is nearly as in *V. ovatus*, but the cusps were lower. *P*⁴ has a wider deutocone, more median in position than in *Vulpavus* and *p*³ is smaller, but still two-rooted. *M*³ is not preserved, but seems to have been small. The humerus compares rather closely with that of *Arctocyon*. It is smaller, but shows the same high compressed deltoid crest, extending far down the shaft and ending abruptly. The crest is somewhat lower in *Vulpavus* and *Oödictes*, and a little more reduced in *Miacis*, *Uintacyon* and *Lycarion* but in all these genera retains the same form.

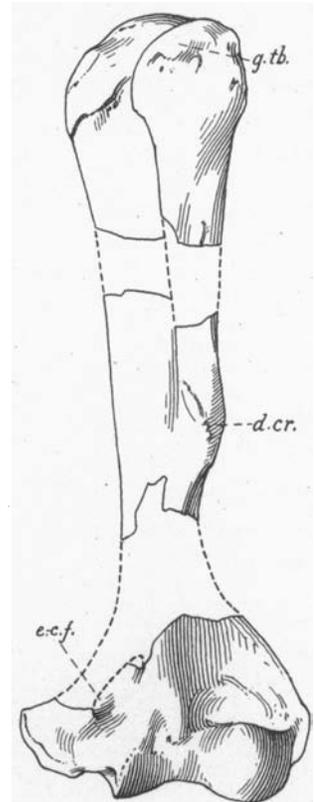


Fig. 43. *Palæarctonyx meadi*, humerus, anterior view, natural size, type specimen.

In *Didymictis* the hu-

merus is more like that of modern carnivora. None of the other Creodonta approach the Miacine-Arctocyonid type of humerus except *Oxyæna* and *Patriofelis*. In *Limnocyon*, *Sinopa*, *Hyænodon*, *Sarcothraustes*, *Dissacus*, *Mesonyx*, as in all modern carnivora, it has departed to a varying extent from this high crested form, which I take to be the primitive one for the Carnivora in general. The high compressed crest is associated with strong supinator ridge, widely expanded condyles and little antero-posterior depth, shallow supra-trochlear fossæ separated by a complete although thin bony plate, ulnar trochlea but little excavated, radial facet convex, antero-external to the ulnar facet, so that the ulna and radius are completely crossed in the prone position of the limb. The tuberosities are small and do not project above the level of the head, which is less convex and faces more proximally than in the more specialized types. *Cercoleptes* retains somewhat more of these features than any other modern carnivore.

The remaining fragments of the limb bones agree on the whole with *Vulpavus*, but exaggerate its peculiar features. The olecranon process of the ulna is short and directed somewhat forward, indicating a sigmoid curve to the shaft as in *Vulpavus*. The distal end of the radius has the usual primitive form, the facet being round, cup-shaped with a strong distal-internal prolongation from the inferior border, to cover the internal end of the scaphoid. This prolongation is very suggestive of the internal malleolus of the tibia, and indicates a greater degree of correspondence in the form and function of the wrist and ankle joint than the later specialization of the two would lead one to suppose.

Carpals. The centrale lies mainly under the scaphoid and is firmly coössified to it; dorsally it projects under the lunar so as to support two-thirds of its width. The scaphoid is not so wide as in *Clænodon*, the internal hook being much reduced. The lunar is supported chiefly by the magnum, except towards the dorsal surface, where the centrale extends beneath it; it has a large unciform facet facing externally and somewhat distally, and a small cuneiform facet proximal-external. Its scaphoid facet lies almost in the same plane as the unciform facet and is slightly roughened, as though approaching coössification. The trapezium is quite small, hardly half the relative size of the *Clænodon* trapezium, and has a somewhat peg-like head, and cup-shaped distal facet, as in that genus and in *Vulpavus* and *Phlaodectes*, indicating a divergent and mobile pollex, more or less opposable.

The distal facet of the tibia is flat in its main portion, but the malleolar portion is broken off; the extension of the astragalar trochlea on its inner side indicates, however, that there was a heavy internal malleolar facet, as in *Vulpavus*, a distinction from Arctocyonidæ, in which the malleolar facet is absent. The astragalus has a slightly grooved trochlea with the external crest high and sharp, the internal crest broad and indistinct as in Miacinæ, the facet extending beyond it on the internal side. The tendinal groove behind the trochlea is deep,



Fig. 44. *P. meadi*, carpals, nat. size, type.

and the bone much less extended in this direction than in *Clænodon*, corresponding closely with *Vulpavus* (*Phlaodectes*). The fibular facet of the astragalus is much more vertical than in *Clænodon* and probably the fibula was more reduced with little or no calcaneal articulation.



Fig. 45. *P. meadi*, astragalus, nat. size, type.

The ectocuneiform is rather large and presents the same facets and shape as in *Vulpavus*, the navicular facet rather oblique and forming an acute angle with that for the cuboid.

The ungual phalanges are large, high and compressed, without hood, and compare with those of the Bears and *Cercoleptes*.

The third metatarsal (No. 11551) is of moderate length, its distal end not symmetrical but forming a pair with the fourth. The head of the first metatarsal is stouter than the third, its proximal facet strongly convex in a dorsal-plantar direction but not convex from side to side. The distal ends of the metatarsals are like those of *Vulpavus*, and the second phalanx is nearly symmetrical, showing that the claws were not retractile. The remaining phalanges show no characters of especial interest.



Fig. 46. *P. meadi*, claw phalanx, nat. size, type.

Four vertebrae are present in the type. A cervical is of remarkably small size — confirming the indications from the upper jaw that the skull was very small in proportion to the skeleton. Two lumbar are present, one large, probably posterior, the other comparatively small, probably anterior. Their transverse processes appear to have been slender; the centra are rather short and slightly keeled medially. Several parts of neural arches which appear to be from the lumbar region, show comparatively flat zygapophyses, as in *Vulpavus* and the *Miacidæ* generally. A middle caudal indicates a long and powerful tail; it is considerably longer than the large lumbar, two and a half times as long as the cervical; the neural canal appears to have been complete and of considerable diameter, but the transverse processes are represented only by small knobs at one end of the centrum.

Summing up the characters derived from the fragmentary type, and interpreting them by the help of the better known and nearly allied *Vulpavus* and *Phlaodectes*, we perceive in *Palæarctonyx meadi* a medium sized carnivore with small head, compact body, short flexible limbs, plantigrade feet and powerful prehensile tail. The feet were five-toed with paraxonic symmetry (in the pes, presumably in the manus) the hallux large, but not much opposable, the pollex semi-opposable but of small size. The claws were large, compressed, bear-like, non-retractile. The teeth were small, the molars low-crowned, tubercular, the premolars much reduced in size. The animal resembled *Cercoleptes* in many respects but was considerably larger, with relatively smaller head,

shorter limbs, more powerful feet and larger claws, and presumably a much smaller brain.

The near resemblance of this animal to the Arctocyoniidæ, while partly due to parallelism, yet indicates a relationship not very remote. It strengthens the position taken by Matthew in 1901 that the Arctocyoniidæ should be reckoned among the Adaptive Creodonta, and not with any of the Inadaptive types, on account of the compressed, unfissured ungual phalanges and the arrangement and form of the carpals, the characters derived from the teeth being inconclusive.

Wortman, following Cope's earlier ideas as to *Clænodon* ("*Mioclænus ferox*") — a view afterward rejected by Professor Cope — has endorsed Cope's statement that "this genus finds its nearest living ally in the *Thylacinus cynocephalus* of Tasmania" and criticizes Matthew's conclusions as follows: "Had he taken the trouble to compare the feet of *Clænodon* with a living Opossum or Dasyure, he would have found such a striking similarity of structure in every detail, with the possible exception of the astragalus, that he would have concluded that the Arctocyoniidæ are much nearer to the Marsupials in these characters than to the Bears."

I can hardly take Dr. Wortman's assertion very seriously, or suppose that he really meant what his language would imply, that the Arctocyoniidæ belong to the Carnivorous Marsupials, and not to the Eutheria, still less that they are more nearly related to the Thylacine than to any of the less specialized Marsupials. The points of resemblance that he alleges, even if they were well founded, would not begin to offset the wide and radical distinctions between the two groups, and indeed Wortman tacitly acknowledges this by inclusion of the family in the Creodonta. But there is not even any resemblance, except in the merely nominal character of union of scaphoid and centrale, which is far from being peculiar to marsupials, and is never accompanied in them by the tendency to coalescence of lunar and scaphoid to which I called attention in describing the *Clænodon* foot. In fact, *Clænodon* differs so widely from the marsupials in the whole organization of manus and pes and the shape and arrangement of every individual bone thereof, that it is superfluous to make any extended comparison. In all marsupials the lunar is remarkably small and the magnum large, the astragalus is of quite peculiar type, very small, low and flat, with the head hardly separate from the body, and the fibular facet facing upward instead of outward. *Clænodon* shows no approach to these peculiarities except to a comparatively slight degree in the astragalus, which, although of distinctly carnivore type, has a less vertical fibular facet, an obviously primitive character. The high compressed claw phalanges are not at all like those of the Thylacine, Dasyure or any other marsupial, but they *are* like those of the bears, of *Cercoleptes*, *Mydaus* and other true carnivora. The partially opposable pollex is likewise not peculiar to marsupials, and remains of it are seen in the Carnivora and many Eutherian groups; and in these, as in *Clænodon*, it is usually the pollex which is principally opposable, whereas in Marsupials it is the hallux.

Dr. Wortman considers it important to insinuate that although my material was much more complete than Cope's¹ my study of it was superficial and my reasoning unsound. To those who know the facts of the case the present instance will appear a singularly unfortunate one to select for the purpose, but I do not desire to discuss personalities in a scientific memoir. I have endeavored in this as in all points where I have occasion to discuss Dr. Wortman's views, to do full justice to the scientific value of his arguments and criticisms, and to the undoubted ability and learning by which they are backed, without regard to the spirit of personal antagonism to co-workers in this field, by which, however carefully disguised, they are very apt to be inspired.

2. FAMILY OXYÆNIDÆ Cope.

This family of Creodonta was based by Cope in 1877 upon "*Stypolophus*, *Oxyæna*, *Pterodon* and perhaps *Patriofelis*," the definition being: "Last superior molar transverse, the preceding ones sectorial; inferior molars sectorial."

In 1884 Cope added *Protopsalis*, but removed *Stypolophus* to the Proviverridæ and placed *Patriofelis* provisionally in the Mesonychidæ.

In 1892 Osborn and Wortman re-defined the family as follows, omitting all the genera except *Oxyæna*:

"Face long. Fourth upper premolar and first upper molar, first and second lower molars developing into sectorials. Dental reduction unlike that in Felidæ (*i. e.*, m_3^1 disappears)."

In 1894 Wortman added *Patriofelis*, defining the family as follows:

"Muzzle short and truncate; interorbital region constricted and elongated; sagittal crest extended well in advance of brain-case. A post-glenoid process and no post-glenoid foramen; an alisphenoid canal and prominent mastoid. Lachrymal bone not extended out upon the face. Two pairs of lower incisors. Trapezium enlarged; pubic symphysis not anchylosed; fibula unreduced; calcaneo-cuboid facet very oblique; cuboid having large contact with astragalus. Fibula not articulating with calcaneum."

In the same year Scott distinguished the Oxyænidæ and Hyænodontidæ as representing diverging lines derived from a common stock (Proviverridæ). "In the Oxyænidæ the face is much shortened with a consequent reduction in the number of teeth. . . . m^1 is much the largest of all the cheek teeth. . . . the fourth upper premolar is a well developed sectorial. . . . in the lower jaw m_1 is large though somewhat smaller than m_2 , which with m^1 forms the principal pair of sectorial teeth. . . . In the Hyænodontidæ the emphasis of development, so to speak, is differently placed, the principal pair of sectorials being m^2 and m_3 ."

¹ In point of fact the description of the feet was almost exclusively based upon the same specimens studied and described by Professor Cope, after I had pieced them together more completely, and identified certain bones which he failed to recognize (scapho-centrale, trapezium, fibula and tibia).

In 1899, Wortman added *Oxyænodon* and *Thereutherium* and defined the Oxyænidæ as:

“Second lower molar enlarged — Oxyænidæ. Includes the genera *Oxyæna*, *Patriofelis*, *Oxyænodon*,”

Osborn in 1900 defined and analyzed very fully the characters of the Oxyænidæ as derived from *Oxyæna* and *Patriofelis*, basing the primary distinction upon the specialized carnassials. Matthew in 1901 also defined the family upon this ground. In 1902 Wortman included *Limnocyon* and *Thereutherium* as a distinct subfamily, identifying *Oxyænodon* with *Limnocyon* and defined the family thus:

“Pm⁴ and m_{1,2}¹ carnassial,¹ of which m₂¹ are largest and most specialized; claws, as far as known, depressed, little curved and fissured.” In a later part of the same article he extends the definition as follows: “Two sub-equal tuberculo-sectorial lower molars in which the internal cusp of the trigon and the tubercular heel progressively decrease in size or disappear in the later forms; second inferior molar slightly larger than first; two superior molars of which the last is transverse when present, but becomes small or disappears in advanced stages of evolution; most highly developed sectorial tooth consisting of first molar above and second molar below, but fourth premolar above and first molar also sectorial; two external cusps of first superior molar tending to unite and internal cusp becoming reduced or disappearing in advanced forms, as in Hyænodontidæ.”

The earlier definitions are conflicting and inapplicable to the group as now understood.

Cope regarded the family as including Creodonta with sectorial teeth (*Hyænodon* being excluded from the Creodonta as having scaphoid and lunar united) and this arrangement was adopted by Schlosser (1888) and Von Zittel (1893). Osborn and Wortman in 1892 distinguished them from Palæonictidæ as inadaptable in the dentition, while Wortman's definition of 1894 is intended to connect them with the Pinnipedia, and takes no regard of the teeth.² In 1894 Scott first recognized the essential distinctive character of the group in the dentition, and the more complete knowledge of the various species shows that this primary distinction in the teeth is supported by various common characters in skull and skeleton peculiar to the Oxyænidæ. On our present knowledge the family may be defined as follows:

The carnassials or principal shearing teeth are m₂¹, instead of m₂² as in Hyænodontidæ or $\frac{P_4}{m_1}$ as in Miacidæ. In all the known genera m₃² are absent, the paracone and metacone of m¹ are connate,

¹ Wortman apparently means by “carnassial” any tooth that possesses any shearing function. As I have observed in an earlier section of this paper, the term as applied to modern carnivora denotes the principal but not necessarily the sole shearing tooth, enlarged and specialized for the function of flesh-cutting.

² This definition is in several respects incorrect as applied to any Oxyænidæ, in other respects applicable only to *Patriofelis*, or to *Patriofelis* and *Oxyæna*, while the remainder of the characters are common to other families of Creodonta as well, as may be seen by comparison with the present definition.

m² is transverse, reduced, or absent. The basicranial region is broad, the occiput wide; the mastoid has a slight lateral exposure, the post-tympanic process of the squamosal embracing the mastoid process superiorly and anteriorly. The lachrymal has a semicircular expansion upon the face and the foramen is within the orbital rim. The nasals are long and sometimes slightly expanded posteriorly. The jaws are stout and the symphysis peculiarly heavy and solid. The manus and pes are mesaxonic, pentadactyl, plantigrade or sub-plantigrade, with digits rather widely spreading. The humerus has an entepicondylar but no supratrochlear foramen. The fibula articulates with the calcaneum (very slightly in *Patriofelis*), the astragalus with the cuboid, the astragalar trochlea is flat or slightly grooved, and the ungual phalanges are fissured. The brain is low and wide and in *Limnocyon* displays a single indistinct sulcus on the cerebral lobe. In *Patriofelis*, according to Wortman, there are two longitudinal sulci.

As in the Creodonta generally the brain is small, the tympanic bulla not ossified, the condylar foramen well separated from the foramen lacerum posterius, the postglenoid foramen is present, the paroccipital process projects backward, the tail is long and powerful, the scaphoid, lunar and centrale are separate.

In the large *Patriofelis* the mastoid and paroccipital processes are prominent, massive and truncate; in the small *Thinocyon* they are small, flattened or spatulate; in *Oxyæna*, *Limnocyon* and *Oxyænodon* they are intermediate, varying with the size. A large post-mastoid foramen is present in *Patriofelis*, absent in *Limnocyon*. The dorsolumbar formula in *Oxyæna* and probably in *Patriofelis* is 20; in the remaining genera it is not known. The course of the main carotid artery in *Patriofelis* corresponds with that in the Arctoidea; it is less clearly traceable in the smaller genera, and in these, as in the Creodonts generally, and probably in most primitive mammals, an external branch of the carotid enters the tympanic fossa, and after giving off a stapedial branch which enters the *fenestra ovalis*, proceeds forward across the external slope of the periotic to the median lacerate foramen.

Wortman has divided the family into Oxyæninæ and Limnocyoninæ, on the following characters:

“Lower jaw of considerable vertical depth and especially thickened from side to side; symphysis not particularly enlarged; fibula not articulating with calcaneum, and trochlear surface of astragalus ungrooved with head very oblique *Oxyæninæ*.”

“Lower jaw shallow and relatively thick from side to side; symphysis much enlarged; fibula articulating with calcaneum (*Limnocyon*); astragalus considerably grooved and head with comparatively little obliquity *Limnocyoninæ*.”

Oxyæna and *Patriofelis* are placed in the first subfamily, *Limnocyon* and *Thereutherium* in the second.

As a matter of fact, however, there is no material difference in depth of jaw between *Limnocyon* and *Patriofelis* or *Oxyæna*. *Thinocyon* and *Thereutherium* are much shallower, *Oxyænodon* is intermediate. The jaw of *Patriofelis* is fully as thick as that of the Limnocyons, and the symphysis as heavy. The fibula articulates with the calcaneum in the Oxyænas; the trochlear surface of the

astragalus is very slightly grooved in *Limnocyon*, flat in *Thinocyon*, and I can discover no difference in the obliquity of the head. All the distinctions cited by Wortman therefore appear to be invalid. The geological occurrence of the different genera make it very obvious, however, that there are two distinct phyla, one (*Oxyæninæ*) including large powerful predaceous animals with precociously specialized dentition, ranging from Lower to Middle Eocene, the other (*Limnocyoninæ*) smaller types with persistently primitive teeth, ranging from Middle Eocene to Oligocene. The two phyla are not very satisfactorily definable on adaptive characters, since the ancestral types of the older phylum must have been structurally almost like the later appearing but more conservative group. The following definitions may serve to distinguish them as far as at present known.

Oxyæninæ: Internal cusps on P^{3-4} and rudimentary on p^2 . Medium to large predaceous types early specialized with shorter muzzle, reduction of premolars and loss of m^2 , and sectorial dentition.

Limnocyoninæ: Internal cusp on p^4 only. Small to medium creodonta, persistently primitive, with longer muzzle, unreduced teeth and tuberculo-sectorial molars.

The genera may be distinguished as follows:

OXYÆNINÆ.

Oxyæna: Dentition $I_3^2 C_1^1 P_4^1 M_2^2$. I^{1-2} small, i^3 larger. P_1^1 one-rooted, p^{3-4} with distinct deuterococones, rudimentary on p^2 . M^4 with well developed protocone, m^2 transverse, m_{1-2} with small heels and low metaconid internal to protoconid. Muzzle deep and heavy, lower jaws deep but not very thick, occiput wide, mastoid and paroccipital processes moderately stout, the latter pointed, spatulate. Limbs and feet of moderate length.

Patriofelis: Dentition $I_3^2 C_1^1 P_3^2 M_2^1$. P_1^1 absent; p^{3-4} with successively larger deuterococones, rudimentary on p^2 . Protocone of m^1 vestigial or absent, m^2 absent. M_1^1 with small heel and posteriorly placed metaconid, but functional only in juvenile stages, shearing against dp^4 ; the premolars developing as imperfect shearing function in the adult. M_2^2 large, completely sectorial with vestigial metaconid and heel. Muzzle very short and heavy, jaw massive, arches very wide and deep, occiput broad and of moderate height, sagittal crest very heavy. Mastoid and paroccipital processes massive, prominent and truncate. Limbs and feet very short and heavy, digits spreading, phalanges short.

Palæonictis: Dentition, $I_3^2 C_1^1 P_4^1 M_2^2$. P^{3-4} with deuterococones; m^1 with well separated pa and me , large pr and small conules. M^2 vestigial. Lower molars with large well separated me^d and pa^d and large basin heels. M_2^2 smaller than m_1 .

Ambloctonus: Dentition $I_7^2 C_1^1 P_4^1 M_2^1$. Second upper molar absent, m_1 and m_2 sub-equal, otherwise as in *Palæonictis*.

LIMNOCYONINÆ.

Limnocyon: Dentition $I_3^{3-2} C_1^1 P_4^1 M_2^2$. I^1 small, i^2 enlarged, i^3 reduced or absent. P_1^1 = two-rooted. Deuterocone on p^4 only. M^1 with well developed protocone. M^2 transverse, the metacone reduced. M_{1-2} tuberculo-sectorial with well developed metaconids and basin heels. Skull low and broad with moderately heavy and long muzzle, strong sagittal crest, broad semicircular overhanging

occiput and rather slender arches. Mastoid and paroccipital processes moderate, the former flattened, the latter short, spatulate. Petrosal crested. Posterior opening of alisphenoid canal at some distance in front of foramen ovale. Jaw deep and massive. Limbs short and curved, feet of moderate length, phalanges rather long.

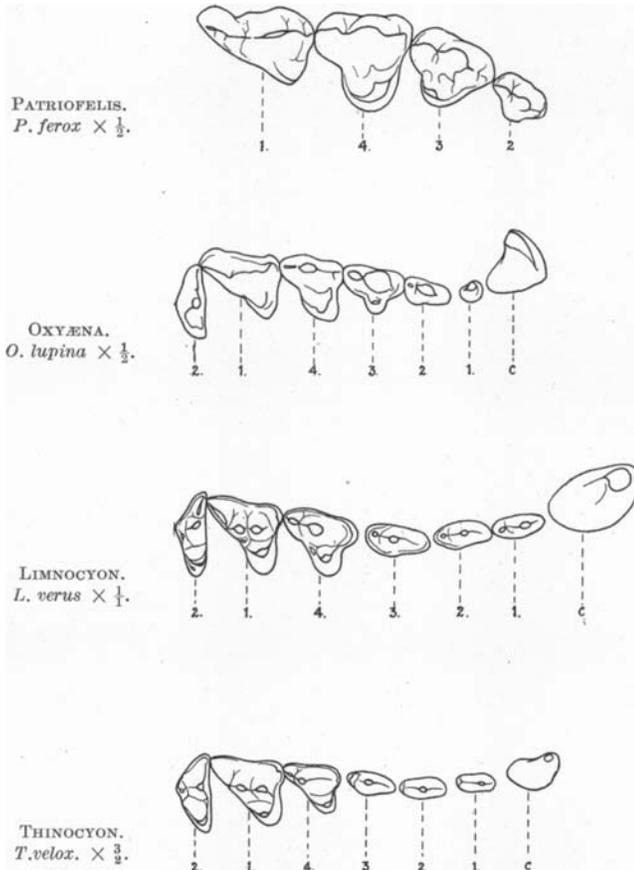


Fig. 47. Upper teeth of Oxyænidae.

compressed, molars with reduced heels and metaconids. M_2 not larger than m_1 , as in all the preceding genera.

Relationships of the Palæonictidæ.— This group has been regarded as ancestral to the Felidæ, through *Ælurotherium*. It will appear, however, that *Ælurotherium* is based upon the milk dentition of *Patriofelis*, and a re-examination of *Palæonictis* and *Ambloctonus* leads me to conclude that these genera are quite closely related to *Oxyæna* and *Patriofelis* and are not ancestral or in any way nearly related to the Felidæ.

The face in *Palæonictis* is short, but not more so than in *Patriofelis*; the first lower molar is larger than the second, but in *Limnocyon* the two teeth are sub-equal in size, and in some species of *Sinopa* m_2 is larger than m_3 , so that the proportionate size of the lower molars is not decisive of family relationship.

Thinocyon: Dentition $I_2^2 C_1^1 P_4^4 M_3^3$. P_1^1 mostly two-rooted, remaining teeth as in *Limnocyon* but less robust. Jaw shallow but thick, skull low and flattened with slight sagittal crest, occiput nearly vertical, broad and semi-circular, and arches very slender. Mastoid process small, flattened, paroccipital process very small, long, spatulate. Petrosal low crested. Posterior opening of alisphenoid canal close to foramen ovale. Limbs long and slender, feet slender, spreading with long phalanges.

Oxyænodon: Dentition $I_3^3 C_1^1 P_4^4 M_3^3$. I_1^{1-3} small, of equal size. Premolars reduced and crowded, heels small, molars much as in *Limnocyon*. Skull similar, jaws stout but not so deep. Palate extended posteriorly; petrosal prominent, sharply crested. Posterior opening of alisphenoid canal close to foramen ovale.

Thereutherium: Dentition $I_2^2 C_1^1 P_4^4 M_3^3$. P_1^1 one-rooted, m^2 vestigial, m_{1-2} with reduced heels and vestigial metaconids.

Machæroides: Dentition $\overline{2.1.4.2}$. Jaw with flange at symphysis as in Machairodonts. Teeth much

(See p. 321.) On the other hand, the upper dentition agrees much more closely with the Oxyænidaë than with the Miacidaë or the primitive Fissipedia. The carnassial specialization is very rudimentary, but we observe that m^1 has the *postero-external* angle extended, as in Oxyænidaë, while in Miacidaë and Fissipedia it is the *antero-external* angle that is extended; that the principal pit for reception of the lower carnassial is behind m^1 as in Oxyænidaë, not behind p^4 as in Miacidaë and Fissipedia; that the angle of the outer tooth row is behind m^1 as in Oxyænidaë, not behind p^4 as in Miacidaë and Fissipedia; that the details of construction of both molar and premolar cusps corresponds quite closely throughout with *Oxyæna* and *Patriofelis*, and are widely different from the Miacidaë, the Felidæ or any true carnivora. The principal difference from *Oxyæna* and *Patriofelis* lies in the wider separation of the paracone and metacone, and of the protoconid and metaconid in the lower molars; and this is partly bridged over by *Limnocyon*.

So far as any carnassial specialization is present in *Palæonictis*, it is *unmistakably* m^1 and not p^4 that is assuming the principal shearing function. It would appear proper, therefore, to place *Palæonictis* and *Ambloctonus* provisionally in the Oxyæninaë, and to set aside as impossible the supposed derivation of the Felidæ from this group.

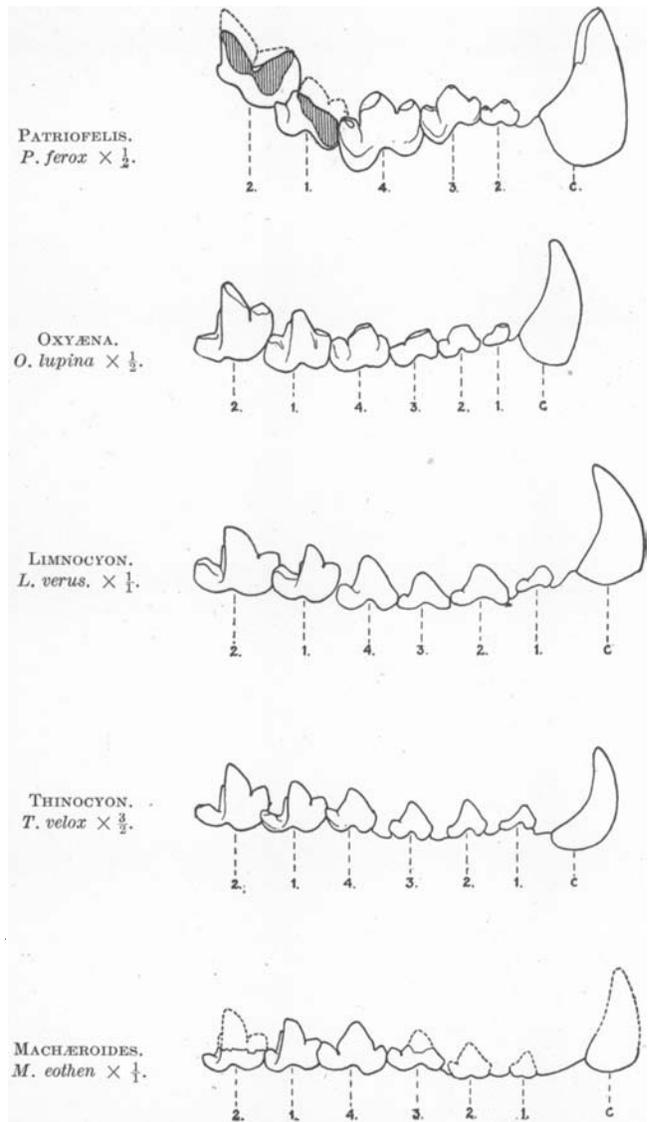


Fig. 48. Lower Teeth of Oxyænidaë.

It would appear proper, therefore, to place *Palæonictis* and *Ambloctonus* provisionally in the Oxyæninaë, and to set aside as impossible the supposed derivation of the Felidæ from this group.

Geological Distribution of Oxyænidaë and "Palæonictidaë."

	EOCENE											OLIGOCENE			
	Basal		Lower			Middle			Upper			Phosphorites	White River		
	Puerco	Torréjon	Suessonian	Wasatch	Wind River	Lower Huertano	Upper Huertano	Lower Bridger	Upper Bridger	Lower Washakie	Upper Washakie			Lower Uinta	Upper Uinta
"Palæonictidaë"															
Palæonictis gigantea			×												
" occidentalis				×											
Ambloctonus sinosus				×											
Oxyænidaë															
Oxyæna lupina															
" forcipata				×											
" morsitans				×											
" huerfanensis				×											
Patriofelis tigrinus					×										
" coloradensis							×								
" ulta								×							
" ferox								×	×						
Limnocyon verus								×	×						
" potens									×			×			
Thinocyon sp.															
" minimus					×				×						
" velox									×						
" medius									×						
" cledensis										×					
Oxyænodon dysodus													×		
" dysclerus													×		
Thereutherium thylacodes															×
Machæroides eothen									×						

Adaptation. The Oxyænidaë appear to correspond in the Eocene fauna to the Mustelinaë among modern carnivora. They are a strictly carnivorous group with powerful jaws, short limbs, and more or less plantigrade feet. They include large powerful predaceous types with shortened jaw (*cf. Gulo* and the Miocene *Megalictis*) and smaller more vermiform genera with more primitive dentition, possibly semi-aquatic (*cf. Mustela, Putorius, etc.*). In the low, broad occiput, wide basicranial region with backwardly directed paroccipital, and the arrangement of the basicranial foramina, they are considerably like the Mustelidæ, and as in this family, and various other groups, the large, robust species have very prominent and massive mastoid and paroccipital processes, while in the small species these processes are inconspicuous. The resemblance of the dentition in

the more primitive Oxyænidæ to that of the Oligocene Mustelidæ is equally striking; but the corresponding teeth are not homologous. The angle of the outer line of the upper dentition in the Oxyænidæ is between the sectorial m^1 and the transverse m^2 ; in the Mustelidæ it is between the sectorial p^4 and the transverse m^1 . The jaws are relatively shorter and the orbits further forward in the Mustelidæ. The resemblance is due to parallel adaptation, and the Mustelidæ, as shown in a previous section of this memoir, are derivable from the Miacidæ, while the Oxyænidæ left no descendants. In the *Oxyæna-Patriofelis* phylum the dental reduction is carried considerably further than in Mustelidæ, paralleling more nearly the cats and hyænas.

Relationship to the Pinnipedia. Wortman regards this family as ancestral to the Pinnipedia, but has failed to adduce any very convincing arguments in support of this view, which has not been generally accepted. The arguments adduced in its favor are as follows:

1. The astragalus in both presents the primitive ungrooved trochlea and an astragalar foramen is present.

2. The seals are descended from a comparatively short-muzzled type in which there was great reduction of the true molars and comparatively little of the premolars.

3. The seals are descended from a type in which the incisors of the lower jaws were reduced to two pairs.

4. Their ancestors possessed in addition the following important characters: "(a) Skull with inter-orbital region constricted and long between post-orbitals and the anterior termination of the brain-case; (b) an alisphenoid canal; (c) an anterior or preglenoid process; (d) a prominent mastoid; (e) a metacromion process of the scapula; (f) an entepicondylar foramen of the humerus, and a prominent deltoid crest; (g) a long and powerful olecranon; (h) an enlarged trapezium; (i) a free scaphoid lunar and centrale; (j) a short unanchylosed pubic symphysis; (k) a femur with a digital fossa; (l) an unreduced fibula; (m) an astragalar foramen; (n) a cuboid with a very oblique facet for the calcaneum and a very large contact with the astragalus; (o) a calcaneum with a relatively short tuber; (p) and ungual phalanges with well developed and large perforated subungual processes.

"5. Their ancestors were, judging from these characters, not exclusively but semi-aquatic in habits, with limbs fitted for progression upon the land."

6. (a). Absence of postglenoid foramen; (b) tongue-and-groove lumbar zygapophyses; (c) broad and spreading feet; (d) lachrymal reduced, not spreading upon the face.

7. In all of these characters the Oxyænidæ correspond with the hypothetical ancestors of the seals.

The above list of characters may appear very convincing at first sight. On analysis, we find that the characters common to Oxyænidæ and Pinnipedia fall into three groups:

1. Characters common to the Creodonta, Adaptive and Inadaptive, and to many of the Arctoid Fissipedia — Nos. 1; 2; 4*a, b, f, h, i, j, k, l, m, n*; 6, *c*.

2. Characters common to the larger genera of Creodonta and the larger Arctoid Fissipedia, but not found in the smaller Oxyænidaë or in small genera of Carnivora — Nos. 4 *c, d, e, g, o*, and *p*; 6 *b*.

3. Characters erroneously ascribed to the Oxyænidaë, not present in any of the genera as far as known.— Nos. 3; 6*a, d*.

The first group of characters are simply primitive and do not connect the Pinnipedia with the Oxyænidaë any more than with the other Creodont families. The second group are related merely to the size of the animal, and have no bearing upon the family relationship. The third group are due to errors of observation. The accuracy of the above analysis may readily be verified by comparison with the general observations upon the Creodonta and the detailed descriptions and figures in this memoir. It does not appear, therefore, that they afford any evidence for deriving the seals from the Oxyænidaë, or from Inadaptive Creodonts. Against this derivation and in favor of their derivation from Adaptive Creodonta or from Arctoid Fissipedia may be noted the following:

1. The lachrymal is large and broadly expanded upon the face in both the Inadaptive Creodont groups. In the Adaptive Creodonta it is smaller, in the Fissipedia still further reduced, especially in Ursidaë and some Mustelidaë. In the Pinnipedia it has entirely disappeared.

2. The mode of molar reduction indicated in the Pinnipedia corresponds well with that generally indicated in the Adaptive Creodonta and Fissipedia, and disagrees fundamentally with the Oxyænidaë and Hyænodontidaë. In the Pinnipedia m_1^1 are always present and of large size; a small m^2 is occasionally present, but never any trace of m_2 . Their more generalized ancestors must therefore have had $m_{2,3}^{2,3}$ small, early reduced and lost. This agrees with the Adaptive Creodonts and Fissipedia, in particular with Mustelidaë and Ursidaë. In the Oxyænidaë $m_{2,3}^{2,3}$ are early reduced and lost, but m_2 is the largest of the lower teeth, and progressively increased and specialized. If the seals were descended from Oxyænidaë their formula might vary from $m_{1,2}^{-1}$ to $m_{1,2}^{-1,2}$ but not from m_1^1 to $m_{1,2}^{-1,2}$. In the Hyænodontidaë $m_{1,2,3}^{1,2}$ or $m_{1,2,3}^{1,2,3}$ would be the molars likely to be preserved.

3. The ungual phalanges in Pinnipedia are unfissured, as in Adaptive Creodonts and Fissipedia. In both groups of Inadaptive Creodonts the claws are fissured.

4. The seals possess a tympanic bulla very similar to that of the Ursidaë and larger Mustelidaë. In the Creodonta the tympanic is not usually expanded into a bulla; in the later Mesonychidaë a substantially similar bulla is present, and in certain species of *Hyænodon* a bulla of rather different type. In the Oxyænidaë, as far as known, there is no tendency to form a tympanic bulla, and in the latest survivor (*Oxyænodon*) an incipient *petrosal* bulla takes its place.

5. The united scapho-lunar of the Pinnipedia is a character which must

have preceded their aquatic adaptation, as in aquatic vertebrata generally the carpals tend to become reduced and imperfectly ossified but not to become fused. In the Inadaptive Creodonts there is little or no tendency to fusion of the scaphoid and lunar; the Adaptive Creodonts on the contrary early manifest a tendency in this direction, and it has become complete and universal in the Fissipedia, and in the Pinnipedia as well.

6. In the form of the petrosal the Pinnipedia agree better with the Adaptive Carnivora and Fissipedia than any of the Inadaptive groups, and differ most from the Oxyænidæ.

7. There are a number of points of resemblance to the Ursidæ and to a less extent to the Arctoidea generally in the soft anatomy of the Pinnipedia. These are pointed out by Weber (Säugethiere, pp. 543-551).

The very considerable resemblance to the Pinnipedia among large primitive Arctoid Fissipedia may be illustrated by comparison of the large Miocene Musteline *Megalictis* recently described by Matthew. In this genus we find the skull broad and massive with long constricted postorbital region, wide basicranial region, short, robust, and prominent mastoid and paroccipital processes, a very similar type of bulla, a similar arrangement of the basicranial foramina with few exceptions, an alisphenoid canal, a reduced lachrymal, the molars much reduced, and on similar lines with the pinnipede reduction, the humerus with entepicondylar foramen and prominent deltoid crest, the ulna large with powerful olecranon, the trapezium comparatively wide, scapho-lunar united, astragalus with flat trochlea and astragalar foramen, digits 5-5, the first relatively little reduced, the anterior lumbar zygapophyses with tongue and groove articulation, etc. These are all characters which might be displayed by any large and primitive Arctoid Fissiped, and they are throughout the precise characters which we should expect to find in a terrestrial ancestor of the Pinnipedia.

As far as I am able to judge, the palæontological evidence, therefore, is in entire accord, so far as it goes, with the indications from the comparative morphology of the modern Pinnipeds, and indicates that they are derivable from the Arctoid Fissipedia, with especial affinities to the Ursidæ, as pointed out by Mivart and Huxley. This is substantially the view expressed by Weber.

In a more recent contribution Dr. Wortman regards¹ as conclusive against this view, the fact that the seals were substantially in their present stage of specialization as early as the Miocene, while "the bears have been pretty thoroughly proven by Schlosser to be derived from the Amphicyons" of contemporary age; hence the seals are a much older specialization and could not have originated from the comparatively late specialized bears.

He re-asserts his belief in the Oxyænid ancestry of the Pinnipedia, basing his argument mainly on the following assertions:

1st. That the Creodonta are distinguished from true Carnivora by excep-

¹ Science, July, 1906.

tionally robust mastoid and paroccipital processes, the latter directed backward, and by the opening of the stylomastoid foramen on the posterior surface of the skull.

2d. That the same is the case with the Pinnipedia and they are therefore of Creodont derivation.

3d. That the Creodont ancestors of the seals were distinguished by considerable reduction of the molars, and as the Oxyænidæ are the only known Creodonts with reduced molars the seals must be derived from them.

4th. That the reduction of the lower incisors is another important character common to Oxyænidæ and Pinnipedia.

By the Creodonts Wortman here means the Inadaptive families only.

I readily acquit Dr. Schlosser of responsibility either for the origin or maintenance of the supposed derivation of the bears from *Amphicyon*, which his thorough studies of the Ursoid carnivora of the European Tertiary have pretty thoroughly *disproved* (Schlosser, 1899). But this does not affect the question of the affinity of the seals to the Arctoidea, and if we derive the bears from either Miocene or Oligocene Canidæ, their morphologic resemblance to the seals may be explained by regarding the latter as an independent but closely related phylum, specialized at an earlier date from the Adaptive Creodonts.

As to the further argument, it will be sufficient to observe that:

1. The large robust mastoid and paroccipital processes are neither peculiar to Inadaptive Creodonts nor characteristic of the majority of the genera. They are found only in certain of the large powerful forms and equally in many of the larger Fissipedia. Nor are they found in the smaller seals. The backward direction of the paroccipital processes is characteristic of all Creodonts, Adaptive and Inadaptive, of most primitive Fissipedia, and of the Arctoidea generally.

2. The foramen identified by Wortman as stylomastoid in *Mesonyx* and *Patriofelis*, is, I believe, correctly identified by Osborn (1900, p. 274) as the post-mastoid, and is not present in any other Creodonta, Adaptive or Inadaptive, so far as I have been able to examine, but is present in some of the larger Fissipedia and Pinnipedia, as also in Perissodactyla, etc. The stylomastoid foramen in the seals has its normal position, and as far as I am able to judge, it is perfectly normal in all Creodonta.

3. The reduction of the molars, as already observed, corresponds better with the Arctoidea than with the Oxyænidæ.

4. In *Thinocyon* i_{1-3} are small and subequal; in *Patriofelis* one lower incisor is larger, the two others vestigial. In the remaining Oxyænidæ they are not certainly known. The incisor reduction in this family, therefore, as far as known, tends to disappearance of two pair or all of the lower incisors but not towards the disappearance of one pair as in Pinnipedia.

It is but fair to Dr. Wortman to observe that at the time of writing this last communication he was apparently out of reach of comparative material

and probably of adequate literature, and unable to verify his recollections by reference to specimens and figures and the publications of other writers.

Patriofelis Leidy.

Syn., *Limnofelis* MARSH, *Oreocyon* MARSH, *Ælurotherium* ADAMS, *Protopsalis* COPE.

The genus *Patriofelis* was described by Leidy in 1870 from a lower jaw with teeth much broken. Marsh in 1872 based the genus *Limnofelis* upon a part of the lower jaw with the last molar preserved and some fragments of the skeleton, and referred to it other fragmentary material, part of which he subsequently distinguished under the name of *Oreocyon*. Cope in 1880 based the genus *Protopsalis* upon part of a lower jaw with the last two teeth preserved, and some fragments of the skeleton. Osborn and Wortman in 1892 placed *Patriofelis* in the Palæonictidæ, and based a much smaller species, *P. leidymanus*, upon a jaw fragment with three unworn teeth (supposed to be permanent premolars and molar) regarding the genus and this species in particular as a connecting link between *Palæonictis* and the Felidæ. The discovery of two well preserved skeletons of *Patriofelis* by the American Museum Expeditions enabled Wortman in 1894 to determine the true affinities of the genus and to place it in the Oxyænidæ. He regarded it as an aquatic Creodont ancestral to the Pinnipedia, and placed "*P.*" *leidymanus* in an entirely separate phylum connecting *Palæonictis* with the Felidæ. Adams in 1896 accepted Wortman's view of the position of *Patriofelis leidymanus* and gave it the generic name *Ælurotherium*. In 1897 Osborn referred to *Patriofelis ulta* Leidy a lower jaw from the upper Huerfano beds of Colorado. In 1900 Osborn questioned the aquatic habitat of *Patriofelis* and its relations to the Pinnipedia, regarding it as terrestrial or partly arboreal, and described some additional specimens of the dentition. In 1902 Wortman united the type of *Oreocyon latidens* Marsh with *Patriofelis ferox* (Marsh), but distinguished a referred specimen as the type of "*Ælurotherium latidens* Marsh" referring *Æ. leidymanum* to it as a synonym. This specimen consisted of an immature lower jaw with milk premolars, the canine and first true molar preformed in the jaw but not yet erupted. He also added a second species, *Æ. bicuspis*, based upon a separate unworn tooth identified as M_1 . He appears to have recognized at this time that the supposed permanent premolars and first molar which formed the type of *Æ. leidymanum*, were really the three milk molars, for he implies that the permanent premolars are unknown. He defends the aquatic habitat and pinniped relationship of *Patriofelis*, and regards *Ælurotherium* as a "not only possible but extremely probable ancestor of the Felidæ."

We may summarize the knowledge of these genera to date by saying that *Patriofelis* (including *Limnofelis* and *Oreocyon*) is known from the nearly entire skeleton, but our knowledge of the skull and especially the dentition has been incomplete; in the lower jaw the canines, permanent premolars and second molar,

in the upper the molar and one premolar have been described. It is a member

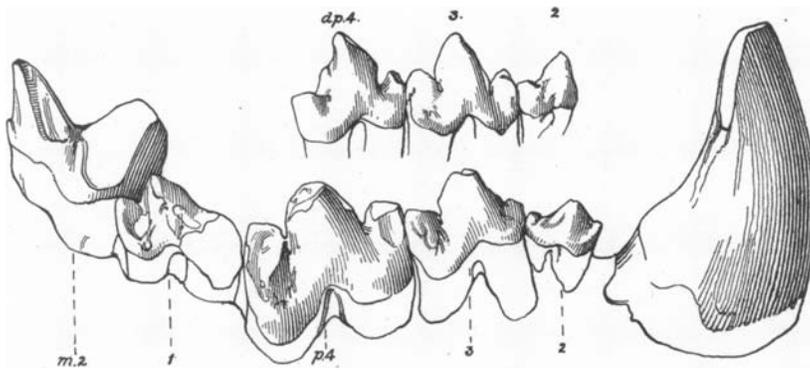


Fig. 49. *Patriofelis ferox*, lower dentition, temporary and permanent. The temporary teeth are the type of *Ælurotherium leidyannum*, the permanent from No. 12078. Natural size.

of the Oxyænidæ and its habitat and relationship to the seals are in dispute. *Ælurotherium* is known only from the canine, milk premolars and first true molar, nothing being known of upper teeth, skull or skeleton. It is regarded as a mem-

ber of the Palæonictidæ and a probable ancestor of the Felidæ.

No corresponding parts of the two genera have been known hitherto (save the canines); but the specimens collected for the American Museum in 1903-4, show that they are identical, based in the one case upon the mature, in the other upon the juvenile dentition of the same species.

Five additional specimens of the lower dentition were obtained by our party, as follows:

- No. 12078, lower jaws complete with good dentition, not much worn.
- No. 12163, right lower jaw with the permanent premolars unworn.
- No. 12162, left lower jaw with teeth more or less broken.
- No. 12074, lower teeth, unworn, i_{1-3} , p_4 and m_1 (or dp_4).
- No. 11522, first lower molar unworn.

The type specimens of *Patriofelis*, *Limnofelis*, *Oreocyon* and *Ælurotherium* are preserved in the National, Yale and Princeton Museums. Through the courtesy of the curators of these museums I have been able to make a careful comparison of all the typical specimens with the new material listed, and with other specimens in the American Museum which have been referred to *Patriofelis*. The comparison brings out the following facts:

In No. 12078 the first molar, although considerably worn, appears to have been identical in form and size with that of *Ælurotherium* "*latidens*" figured by Wortman. The premolars and second molar agree entirely with *Patriofelis ferox*.

In No. 12074 the p_4 agrees with that of *Patriofelis ferox* while the m_1 (or dp_4) agrees with the dp_4 of *Ælurotherium leidyannum*, and less closely with the m_1 of *Æ. "latidens."*

No. 11522, an unworn m_1 agrees with the m_1 of *Æ. "latidens"* and with the same tooth in No. 12078.

The three premolars which form the type of *Æ. leidymanum* agree, as far as comparison can be made, with the milk premolars of *Æ. "latidens,"* and the last of them agrees fairly with the type of *Æ. bicuspis*, described as m_1 , but which may hence be considered as more probably dp_4 .

It appears therefore that *Ælurotherium* is the juvenile dentition (dp_{2-4}, m_1) and *Patriofelis* the mature dentition (p_{2-4}, m_2) of one and the same animal. The only evidence against this view is Wortman's statement that in *Æ. "latidens"* the chamber for formation of m_2 is present in the jaw and indicates a smaller tooth than m_1 . If *Ælurotherium* is *Patriofelis* the chamber would have to accommodate a tooth considerably larger than the m_1 . But it would appear very unlikely that in so immature an individual the chamber would be completely formed and of full size, and examination of the specimen referred to shows that if present at all the chamber was quite incompletely preserved, and does not furnish any good grounds for the assertion that m_2 was of small size. So small a part of the chamber is shown on the specimen that the identification of it as such is open to serious question. Moreover, in *Patriofelis*, as in *Hyænodon*, the first molar is functional with the milk series of premolars and is worn to a stump or drops out by the time the permanent premolars and second molar come into full use. In the *Æ. "latidens"* jaw the first molar is preformed but not yet erupted from the gum, and the milk premolars are unworn, so that it is unlikely that the second molar was already preformed or that its chamber was completed, if it was to be of the *Patriofelis* type.

Since *Ælurotherium* is the milk dentition of *Patriofelis* it has nothing to do with *Palæonictis* or the Felidæ, but belongs in the Oxyæninæ. On the other hand the jaw from the Huerfano, Middle Eocene, referred by Osborn to *Patriofelis ulta* does not belong to that species, and appears to be almost as nearly related to *Palæonictis* and *Ambloctonus* as it is to *Patriofelis*. This species shows no characters intermediate between *Palæonictis* and Felidæ, but suggests a rather close connection between Palæonictidæ and Oxyænidæ. The premolars are very like those of *Palæonictis*, but the second molar has no heel and is as large as the first, if not larger, as nearly as can be judged from the alveolus of m_1 and the much worn m_2 . In *Palæonictis* and *Ambloctonus* m_2 is considerably reduced and in the former genus has a basin heel. I distinguish the Huerfano species as *Patriofelis coloradensis*, leaving it provisionally in the genus to which it is referred.

The exact relationship of the "Palæonictidæ" is uncertain, as we know nothing of the skeleton. They seem to be nearer to the Oxyænidæ than any other group, as the construction of the premolars is very similar, especially to *Patriofelis*, and of the molars not widely different from *Oxyæna*. I do not think that they can be regarded as even possibly ancestral to the Felidæ, for reasons summarized on p. 410 of this memoir.

Protopsalis tigrinus Cope is certainly identical generically with *Patriofelis*

and is closely allied to *P. ferox*. It appears to be distinguishable from that species by the larger heel on m_2 and larger size of m_1 . *P. ferox* and *P. ulta* are at present distinguishable only by the size and robustness of jaw and teeth. It is probable, however, that better specimens would enable us to distinguish them by more satisfactory characters.

Patriofelis ferox (Marsh).

Syn. *Limnofelis ferox* MARSH, 1872.

Limnofelis latidens MARSH, 1872; *Oreocyon latidens* MARSH, 1872.

Patriofelis leidymanus O. & W., 1892; *Elurotherium leidymanum* ADAMS, 1896.

Elurotherium latidens ("Marsh") WORTMAN, 1902.

" *bicuspis* WORTMAN, 1902.

The principal specimens referred to this species are:

Type, lower jaw fragment with m_2 much worn, and a few fragments of the skeleton. Figured by Wortman, 1902. Yale Museum.

Part of lower jaw, $c-p_4$ upper premolar p^3 and part of humerus, type of *Oreocyon latidens* Marsh. Figured by Wortman, 1902. Yale Museum.

Lower jaw fragment with dp_{2-4} , type of *Elurotherium leidymanum*. Figured by Osborn and Wortman, 1892. Princeton Museum.

Immature jaw with dp_{3-4} , m_1 and c_1 emerging from the jaw. Type of *Elurotherium latidens* "Marsh," Wortman. Figured in 1902. Yale Museum.

Unworn tooth probably dp_4 , type of *Elurotherium bicuspis* Wortman. Figured in 1902. Yale Museum.

No. 1507. Parts of skull and jaws and the greater part of the skeleton, teeth weathered or broken away. Amer. Mus. Exped., 1893. This and the following specimen were combined to make the mounted skeleton described and figured by Wortman in 1894 and by Osborn in 1900.

No. 1508. Parts of lower jaw with premolars, separate upper molar and large part of skeleton. Amer. Mus. Exped., 1893. Teeth figured by Osborn, 1900.

No. 2303. Upper carnassial. Washakie Basin, Exped. 1895.

No. 13145. Under side of skull. Washakie Basin, Exped. 1906.

No. 12078. Lower jaws, complete except incisors. Exped. 1904.

Nos. 12162, 12163. Lower jaws incomplete. Exped. 1904.

No. 11522. Unworn m_1 . Exped. 1903.

No. 12074. Teeth found together, 3 incisors, p_4 and dp_4 (or m_1).

No. 13146. Hind limb nearly complete. Washakie Basin, Exped. 1906.

All the American Museum specimens are from the Upper Bridger beds except those noted as from the Washakie Basin. The type specimens are all from the Bridger Basin, from the upper beds or level unrecorded.

The skull from the Washakie Basin has the post-canine teeth well preserved, and the under side of the skull, especially the basicranial region, is much more complete and perfect than in the fragmentary skull of No. 1507, upon which Dr. Wortman's description was based. The permanent lower teeth are now completely known, principally from No. 12078, and the temporary lower premolars.

It will be advisable, therefore, to give a somewhat detailed description of the teeth and of the base of the skull, and a more condensed summary of the principal characters of the skeleton as understood by the present writer.

Upper teeth. The canine and incisors are unknown. The second, third and fourth premolars are preserved in No. 13145; whether p^1 was present cannot be

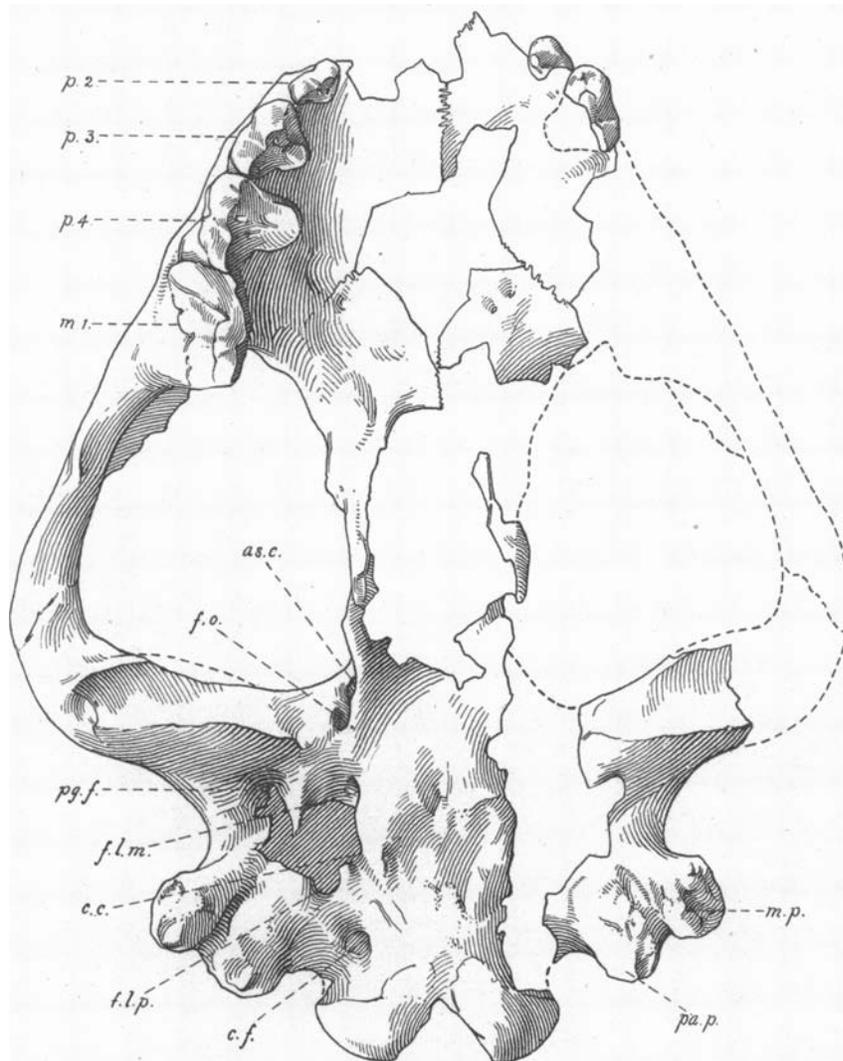


Fig. 50. *Patriofelis ferox*, skull, under view, half natural size. No. 13145, Washakie Basin, Wyoming. Lettering as in Fig. 2.; *m.p.*, mastoid process of the periotic bone; *pa.p.*, paroccipital process of the exoccipital.

certainly determined, but from the close approximation of the canine alveolus to that of p^2 I judge that it was absent, as it is said to be by Wortman in No. 1507. P^2 has two roots, the posterior one expanded inwards; it is relatively smaller than in *Oxyæna*, the protocone lower and more robust, with an internal heel but no distinct deuterocone, and a large triticocone. The third and fourth pre-

molars are three-rooted, the construction similar to p^2 but the deuterocone successively larger and more anterior in position, and the triticocone (metastyle) more developed. In p^4 the deuterocone is antero-internal and composed of a broad curving crest the convexity antero-internal, with a broad shallow basin behind it. The transverse diameter of this tooth is a little greater than the antero-posterior. In p^3 the deuterocone is smaller and nearly median in position. The proportions of the premolars and arrangement of the cusps correspond fairly well with those of *Oxyæna*, except that they are more robust throughout. The first molar has a small internal root but the protocone is absent or destroyed through wear. The metastyle is less extended than in *Oxyæna* and the shear is antero-posterior. The second molar is absent.

The third premolar agrees with the type of *Oreocyon latidens* Marsh as figured by Wortman. Wortman supposed this tooth to be p^4 and describes it as a "carnassial" tooth (*i. e.*, having a certain degree of shearing function) on account of the oblique wear of the outer cusps. This oblique wear is equally seen in p^4 and to some extent in p^2 ; the worn surface of the outer cusps of these teeth faces partly inward, lying in nearly the same plane as the worn surface of the carnassial. The lower premolars show a corresponding obliquity of wear, their worn surfaces facing externally, so that an imperfect shearing function appears to have been performed by the premolars in this genus. In *Oxyæna* the posterior part of p^4 has some shearing function, but otherwise in all the specimens I have seen, the premolars wear horizontally, as they do usually in modern carnivora. But in *Patriofelis*, as in all the Oxyænidæ, the principal shearing teeth, enlarged and specialized for this purpose, are m_1 . Coördinated with the oblique wear is the prominence and inward pitch of the upper premolar-molar series as seen from below, and corresponding outward pitch of the lower series, so that the shearing surfaces, oblique in the crown view of the teeth, are brought into a vertical plane with respect to the skull. The palate also is strongly concave, and the anterior end of the zygomatic arch very deep.

Lower teeth. In the type of *Oreocyon latidens* Wortman found evidence of but two incisors. In the more perfectly preserved jaw No. 12078 there certainly were three on each side. Two of them are very small, the third much larger. The roots are set in an antero-posterior row, owing to the crowding occasioned by the approximation of the large canine roots. The crowns (No. 12074) are short, pointed, not expanded into spatulate form, and have strong posterior basal cingula. One of them is very much larger, both in crown and alveolus, than the two others. The canine is very large, short and stout with semi-obsolete internal and postero-external ridges. The roots of the canines are especially massive, and quite closely approximate in the jaw. There are three premolars, all very massive, broad, stout and low-crowned. P_2 is comparatively small, two-rooted, and set partly transverse in the jaw, with a slight space between it and the canine; it has a strong internal cingulum and rudimentary heel-cusp. P_3 and

p_4 are much larger, the latter equalling or exceeding m_2 in size. Each has a broad heel-cusp separated by a deep transverse valley from the principal cusp, and an anterior basal cusp, small in p_3 but very large in p_4 .

The molars are of sectorial type but the first is so worn in No. 12078 that it has ceased to be effectively functional, and the much larger m_2 which is but little worn is the carnassial in the adult animal, while m_1 probably performed that function in the young, shearing against dp^4 . When unworn, m_1 has a small trenchant heel, large protoconid-paraconid blades and a posteriorly placed metaconid of moderate size. In No. 12078 the blades are

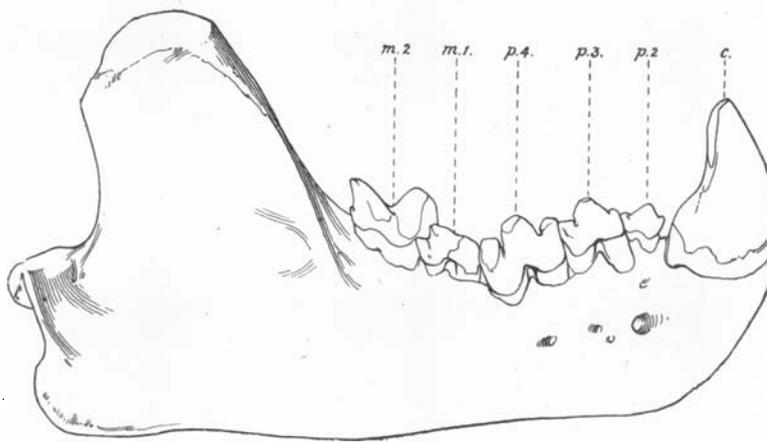


Fig. 51. *Patriofelis ferox*, lower jaw, external view, half natural size. No. 12078, Upper Bridger.

worn down to the roots of the tooth, but the heel and metaconid are not much worn, so that it can be compared with the unworn m_1 of "*Ælurotherium latidens*" figured by Wortman, and with No. 11522. The last is a somewhat larger individual but agrees otherwise in the characters of the tooth. The metaconid is postero-internal to the protoconid, and as high as the paraconid although much smaller, the protoconid overtopping both considerably; protoconid and

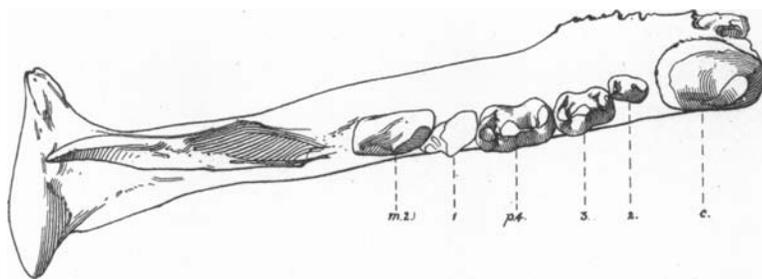


Fig. 52. *Patriofelis ferox*, lower jaw, superior view, $\times \frac{1}{2}$. No. 12078.

paraconid are compressed into strong shearing blades nearly antero-posterior in direction, of equal size but unequal height and separated by a deep notch expanding internally into an open valley.

The anterior end of the paraconid and posterior end of the protoconid blades bend inward, the latter coming into line with the less compressed metaconid. A small accessory cusp appears on the external side of the heel near its base.

The second molar consists simply of the large paraconid and protoconid blades of nearly equal height and size, with deep notch between, expanding internally into a valley much broader than that in m_1 . The heel (or possibly

the metaconid) is represented by a minute vestigial cusp; and a still more minute cusp in front of it on the inner side may represent the metaconid.

The milk premolars (type of *Ælurotherium leidyannum* and "*Æ. latidens*" jaw) are like the first and third permanent premolars and first true molar respectively, but smaller and less broad and massive. The heel of dp_4 is narrower than that of m_1 and basin-shaped instead of trenchant; the paraconid blade is less developed. If the type of *Ælurotherium bicuspis* be correctly interpreted as dp_4 of *Patriofelis*, which it resembles more nearly than it does m_1 , it either belongs to a distinct species from *P. ferox* or indicates some variability in the heel of this tooth, composed in this instance of two distinct cusps instead of a crescentic border with the two cusps imperfectly defined.

Base of skull. The mastoid and paroccipital processes are robust, prominent, and closely conjoined, resembling those of *Pterodon*, and to a less degree the larger Arctoidea. The mastoid process is completely embraced anteriorly by the post-tympanic process of the squamosal, and the mastoid bone between the mastoid and paroccipital processes is deeply grooved above and below, the inferior groove being apparently continuous anteriorly with the stylomastoid foramen at the postero-external angle of the otic fossa, the superior groove passing upward into a very large postmastoid foramen on the posterior aspect of the skull, which I take to be homologous with the postmastoid foramen of *Perissodactyla*, *Amblypoda*, etc., and with a correspondingly situate foramen in *Mesonyx*. Wortman identifies this foramen as the stylomastoid, and regards its posterior position as characteristic of the Creodonta. Even if this identification were admitted, it is certainly not characteristic of the Creodonta or even of the Oxyænidae. As far as I can discover it is not known to be present in any of them except *Patriofelis*, and the larger Mesonychidae. In *Limnocyon*, *Thinocyon*, *Sinopa*, *Vulpavus* and *Viverravus* the stylomastoid foramen appears to have the usual position, as in the Fissipedia and most other mammals, at the postero-external margin of the otic fossa, and there is no foramen on the posterior aspect of the mastoid. Its presence in the larger genera of Creodonta and absence in the smaller ones is natural enough if it be a nutritive foramen, as the postmastoid is.

The condylar foramen is large and well separated from the foramen lacerum posterius. The post-glenoid foramen is large; the foramen ovale lies opposite the glenoid fossæ, and a little in advance of it is the posterior opening of the rather long alisphenoid canal. The foramen lacerum posterius is of moderate size. The course of the entocarotid artery can be traced by a well marked groove on the basioccipital beginning near the median line at a point opposite the condylar foramina, passing outward and forward and entering the otic fossa at a point a little anterior to the f. l. p. and more median, thence grooving the side of the basioccipital forward to the foramen lacerum medius where it enters the cranial cavity. This is the normal course in the Arctoid Carnivora, and in such Creodonta as it has been determined.

The petrosal was destroyed in this specimen and the form and position of the auditory prominence and the position of the stylomastoid foramen cannot be certainly determined. There is no indication of a tympanic bulla and the auditory meatus is rather widely open.

The processes for attachment of the recti capitis muscles on the basioccipital are very prominent in *Patriofelis*.

The postglenoid and preglenoid processes are well developed. The nareal canal is wide and deep, the pterygoid alæ very slightly approximate below. The palate does not extend further back than the tooth-row, and is not thickened to any extent at its posterior margin. The zygomatic arch is very wide and deep; the jugal ends posteriorly in a short splint which does not reach backward to the preglenoid process.

Lower Jaw. The lower jaw is very deep and massive, the symphysis stout and heavy but not coössified, obliquely oval in outline and extending backward nearly to the anterior end of p_4 . The chin is abruptly rounded, without any indication of flange. The coronoid process is very wide and little recurved; the condyles are very broad and heavy. The inferior border of the ramus is nearly straight and does not curve upward behind the tooth line as in nearly all modern and most fossil carnivores, but is continued backward to a very deep and massive angle. The angular process is broad and flat and projects but little backward; the interior margin of the angle is thick, flat and somewhat inflected. The masseteric fossa is of moderate depth and its lower border lies a little below the condyles and tooth line, but the scar for attachment of the masseter muscle extends down to the lower border of the jaw, the great depth of the angular region affording large additional space for its attachment.

The characters of the skeleton as here given are derived from a re-examination of the specimens in the collection principally Nos. 1507, 1508 and 13146, and comparison with other Carnivore and primitive Ungulate skeletons, supplemented and checked from the descriptions given by Wortman and Osborn.

Vertebrae and Ribs. The vertebral formula is C, 7; D, 13+; L, 6; S, 3; C, 28+. The vertebrae are in general short, robust, with stout short processes and massive spines. The cervicals are all more or less fragmentary, so that many of their characters are unknown. The atlas is low and broad with wide transverse processes not greatly expanded antero-posteriorly. The axis is short, with deep centrum and short, thick odontoid peg. The remaining cervicals have short centra and in the sixth at least, the neural spine is unusually high. The dorsals are of moderate size, their neural spines short and heavy, the transverse processes massive and rather short. Their number is uncertain; thirteen ribs of one side, according to Wortman, are preserved in No. 1507, but it is probable that there were 14 dorsals, making the number of dorso-lumbar vertebrae 20, as in *Oxyaena* and in the Carnivora generally. This is also the number in *Amblypoda* and *Condylarthra*. The posterior dorsals and lumbar are short and high, with

deep centra, broad, short massive spines, short heavy transverse processes and revolute zygapophyses (provided with a double tongue-and-groove articulation). The backbone is strongly arched, especially between the lumbar and dorsal regions. The ribs are exceptionally long, not at all flattened, the sternebrae short, wide and massive. The proportions of the dorsals, lumbar and ribs compare most nearly with those of the Ursidæ and Amphicyonine dogs. (*Amphicyon* likewise exhibits the revolute zygapophyses¹ which are more generally characteristic of the Artiodactyla and are approximated but not quite attained in *Mesonyx*.) *Smilodon* and *Odobenus*, *Mellivora* and some other genera also approach the proportions of *Patriofelis* in vertebrae and ribs, but in the remaining Machærodonts, Pinnipedia and the Carnivora generally, the lumbar are much larger and more elongate, their centra more flattened, spines more slender and zygapophyses nearly flat, the ribs shorter and sternebrae more slender and elongate.

The posterior sacral and proximal caudal vertebrae are large and massive; the distal caudals are heavy but not so long as in the majority of Creodonta. The neural spines of the proximal caudals are large and heavy, the transverse processes stout and short. In the middle caudals the spines and arches are rapidly reduced, the arches being incomplete beyond the 9th caudal; and the transverse processes become rudimentary, and are not expanded into flat plates as they are in *Tritemnodon*, *Sinopa*, *Hoplophoneus* and most other Creodonts and Carnivora with long, heavy tails. In *Oxyæna* and *Limnocyon* the tail is longer and less massive, but too imperfectly known for detailed comparison. In *Hyænodon* the tail is much smaller and shorter.

Fore-limb. The scapula is short and wide, most like that of *Ursus* in proportions, but lacking the accessory plate at the posterior upper angle; the neck is short, the prespinous and postspinous fossæ subequal, the spine is a high crest extending far out nearly to the upper border, but the acromion is only moderately developed.

The humerus is of moderate length, stout and massive in all its parts, with very long, heavy prominent deltoid crest curving inward at its distal end, much higher than in *Ursus* but otherwise very like it, also like that of *Coryphodon* and *Pantolambda* but not so high. The crest differs considerably from the narrow, straight, high, abruptly ending deltoid crest of the Arctocyonidæ and Miacinæ. The proportions of the proximal end of the humerus are much like those in *Ursus*; the shaft is nearly straight, the supinator crest stout and prominent, the condyles broad and massive with heavy entepicondylar bridge. The radius and ulna are relatively short, the ulna about as long as the humerus, the radius one fourth shorter. The olecranon is thick, deep and massive, but for a Creodont rather short, although much longer than in *Ursus*; the shafts of ulna and radius are of

¹ See Blainville's *Osteographie*, *Subursus*, Pl. XV, *Amphicyon major*. A large *Amphicyon* from the Colorado Miocene, probably *A. sinapius*, also shows the double tongue and groove on the zygapophyses of certain lumbar vertebrae.

about equal size, the ulnar shaft heavier proximally, the radial shaft heavier distally. The head of the radius is considerably flattened, limiting the rotation of the fore-arm.

The carpus is short and wide, the centrale, lunar and scaphoid separate as in Creodonta generally, the lunar-unciform facet narrow and less lateral¹ than in Adaptive Creodonts and Fissipedia, much as in *Limnocyon*, *Oxyæna* and Hyænodontidæ. The magnum is of moderate size, its dorsal surface considerably larger than in *Limnocyon* or *Sinopa*; the *trapezium* is very large and broad, as in all Hyænodontidæ and Oxyænidæ. The manus is approximately mesaxonic, the median digit being nearly symmetrical, the second and fourth paired, and the first and fifth less exactly paired. The fifth metacarpal is longer than the first, but the projecting trapezium helps to equalize the length of the digits. The phalanges are short, wide and flat, most like those of *Synoplotherium* among the Creodonta, and of some Eocene Perissodactyls (cf. *Hyrachyus*), but very different from the usual Carnivore type. They approach *Phenacodus* and *Pantolambda*, but are not so wide and flat as in these genera. The unguals are short, wide, and deeply fissured, intermediate in type between those of *Hyænodon* and of *Mesonyx* or *Synoplotherium*; they are more robust and shorter than in *Limnocyon* or *Oxyæna*, but otherwise very similar, and broader and more deeply fissured than in *Hyænodon*.

In many respects *Patriofelis* compares quite nearly with the Ursidæ and Amphicyons in the construction of the fore limb. The form and proportions of the scapula and head of the humerus are very similar; the shaft of the humerus is shorter and the deltoid crest prominent but otherwise very like; the ulnar and radial shafts are considerably like those of *Ursus*, but much shorter, and the reduction in length of the olecranon is not carried so far. The symmetry, proportions and construction of the manus are more widely different; the foot is comparatively short and spreading and more or less plantigrade, but shows clearly the relationship to the other Oxyænidæ and the Hyænodontidæ in its more essential and less directly adaptive characters.

Hind limb. The pelvis is large, short, deep and heavy compared with the usual Carnivore type. The ilium is considerably expanded into a concave plate above the primitive bar, and the distal end of the bar everted to a greater extent than in other Creodonts, less than in primitive Ungulates except *Euprotogonia* and *Meniscotherium*. The ischium is short, wide and flattened in comparison with other Creodonts; the pubis is deep and the ischio-pubic symphysis much shorter than in *Sinopa* and other Creodonta.

The femur is of moderate length with heavy somewhat flattened shaft, the greater trochanter massive, well separated, somewhat higher than the head, the lesser trochanter internal, prominent, the third trochanter situate one third from the proximal end of the bone, indicated by a powerful muscular attachment

¹ I. e., facing more nearly proximal on the unciform, distal on the lunar.

but no very distinct process. The shaft has a lateral bend inwards at the proximal third, as in *Limnocyon*, *Oxyæna* and Hyænodontidæ but very slight antero-posterior curvature. The patellar trochlea is rather wide and short, and well excavated, the condyles massive, moderately deep antero-posteriorly. The patella is rather large, and of obovate outline, not unlike that of *Coryphodon*. The tibia is short, with cnemial crest heavy and extending far down upon the shaft, nearly to the distal end, so that the distal part of the shaft does not assume the round-oval outline usually seen. The crest is not as long and prominent as in *Pantolambda*, more so than in *Phenacodus*, much more than in *Sinopa*, *Hyænodon*, *Mesonyx* or Fissipedia generally, although the tibia of *Hoplophoneus* is not unlike this type. The fibula is straight-shafted, unusually stout, and has at its distal end a large facet facing internally and a little distally for the astragalus, and a small distal calcaneal facet.

The pes is short, wide, and like the manus is approximately mesaxonic, with the third digit symmetrical, the second and fourth paired, the first and fifth nearly paired. The astragalus is wide and short with very broad flattened head, wide, very slightly grooved tibial facet extended very slightly upon the neck and limited in its backward extension, and large astragalar foramen, behind which is the usual tendinal notch of the Carnivora. The fibular facet is broad and slopes outward somewhat toward its plantar border in the horizontal position of the pes. The calcaneum is rather short, with short, heavy tuber calcis, a small fibular facet, a stout and deeply grooved peroneal process, and the very oblique cuboid facet which is usually present among Creodonta. The cuboid is very short and wide with a broad astragalar facet, present also in *Oxyæna*, smaller in *Limnocyon*, small to absent in Hyænodonts, well developed in Mesonychidæ (where it articulates in the later genera with a distinct facet on the astragalus), and of moderate size and less proximal position in *Vulpavus* and some other Miacidæ. It is not usually present in Fissipedia. The navicular is of rather small transverse diameter considering the breadth of the tarsus as a whole. The cuneiforms are all very short and the entocuneiform very large and broad (as in Amblypoda) corresponding with the development of the first digit, much greater than in other Carnivora except the Pinnipedia. The metatarsals are like the metacarpals, short and wide and but little interlocking, the lateral digits are less reduced than in the manus. The phalanges are very similar to those of the manus.

Interpretation of Skeleton Characters. *Patriofelis* shows a very considerable general resemblance to the bears and to other large heavily proportioned carnivora, and a less exact resemblance to primitive ungulates and pseudungulates of similar size. These resemblances are all more or less superficial and adaptive, indicating similarity in proportions and habits. On the other hand many details of construction of the skeleton, especially in the manus and pes, indicate relationship to the Hyænodontidæ, and this is in spite of a considerable diver-

gence in adaptation of the limbs and feet. The closer relationship to *Oxyæna* and *Limnocyon* is of course obvious, and entirely confirms Wortman's association of the three genera in a single family, as determined upon characters of the teeth.

There appears to be a rude adaptive parallelism, principally in limb and foot-structure, between the three families of Inadaptive Creodonts, Oxyænidæ, Hyænodontidæ and Mesonychidæ, and the early stages of development in the Amblypoda, Condylarthra and Artiodactyla respectively, as follows:

1. Mesaxonic, heavy-bodied, becoming short-footed (rectigrade) and pentadactyl.
Oxyænidæ (*Patriofelis*); Amblypoda (*Pantolambda*).
2. Mesaxonic, lighter-bodies, becoming cursorial and functionally tridactyl.
Hyænodontidæ (*Hyænodon*); Condylarthra (*Phenacodus*).
3. Paraxonic, lighter bodies, becoming cursorial and functionally tetradactyl.
Mesonychidæ: primitive Suidæ, etc.

Adaptation of Patriofelis.—Wortman in 1894 regarded *Patriofelis* as an aquatic animal on account of the "broad flat plantigrade feet with spreading toes . . . the eversion of the feet and general clumsiness of the limbs." Osborn in a later study shows that the adaptation of the teeth is analogous to that in the cats (the hyæna would perhaps offer a closer parallel) and considers *Oxyæna* and *Patriofelis* as "terrestrial or partly arboreal carnivores analogous to the cats in habits of feeding." In 1902 Wortman maintains his former view, asserting that the chief osteological distinctions of aquatic carnivora in the hind limbs are:

1. Eversion of the pes.
2. Plantigrade gait.
3. Short metatarsals, little interlocking.
4. Spreading toes and elongate phalanges.

Patriofelis, he states, exhibits all these characters except the elongate phalanges.

With respect to the first character noted by Dr. Wortman, while it is a very characteristic and significant feature of the Pinnipedia, I am unable to detect any evidence of its existence in *Patriofelis*. After carefully articulating several well preserved specimens I can find no indications of eversion, and the tibia lacks that peculiar twist by which it is principally accomplished in the seals, the sea-otter, and in the Bridger genus *Pantolestes* to be described on a later page. The second of Wortman's characters is common to all primitive carnivora, and lost only in cursorial adaptation. The third appears to be an error of observation, as the metatarsals in all aquatic carnivora, and in aquatic mammals generally, are exceptionally long instead of unusually short. The spreading toes are also a primitive character, lost only in cursorial types, and the phalanges of *Patriofelis* are exceptionally short.

In his valuable discussion of aquatic adaptation among mammals, R. C. Osburn (1903), points out that the principal changes in the limbs are the shortening of the proximal and elongation of the distal elements, and the progressive limitation of the flexibility at the joints, and final disappearance of the articulations. This change in proportion may be illustrated among the aquatic Carnivora by the following series, showing the proportions of the elements of the hind limb, the femur being taken as 100. The series begins with *Galictis* as an unspecialized terrestrial Musteline, and ends with the most specialized of the Pinnipedia.¹

	Femur	Tibia	Metatarsal	1st Phalanx
<i>Galictis</i> (Galera)	100	94	33	14
<i>Lutra</i>	100	121	54	25
<i>Enhydra</i> (Latax)	100			
<i>Odobenus</i>	100	150	75	58
<i>Phoca</i>	100	183	92	75
<i>Zalophus</i>	100	207	97	87

These changes in proportion are coördinated with progressive eversion of the pes (indicated especially by twisting of the tibia), limitation of the articular motion (the ball and socket joints of the toes being converted into hinge joints), and a relative increase in the size of the internal (anterior) side of the foot.

In the Oxyænidæ on the other hand, the proximal segments of the limbs are long, and the distal segments progressively shorter in the series from *Limnocyon* through *Oxyæna* to *Patriofelis* (regarding the first as a generalized type), as follows.²

	Femur	Tibia	Metatarsal	1st Phalanx
<i>Limnocyon</i>	100	95	35	18
<i>Oxyæna</i>	100	76	23	12
<i>Patriofelis</i>	100	76	22	11

It will be observed that the proportions in *Limnocyon* agree very nearly with those in *Galictis*. In *Oxyæna* there is a marked shortening of the distal segments, carried somewhat farther in *Patriofelis* in company with a greater robustness of the bones, increase in size and massiveness of the skeleton. There is no eversion of the pes, the axis of the ankle joint being in the same plane with that of the knee joint, and the internal digits are not elongate nor relatively enlarged. The reduction of the distal elements of the limb is quite the reverse of what should occur in an aquatic adaptation, but agrees very well with the changes in the hind limbs of heavy bodied terrestrial animals of ambulatory type tending towards the short-footed or *rectigrade* modification of the extremities as Professor Gaudry has recently (1906) named it. The Amblypoda afford

¹ Measurements of skeletons in the American Museum collections.

² Measurements from skeletons in the American Museum collections.

a very good illustration of this progressive shortening of the distal segments, as follows:¹

	Femur	Tibia	Metatarsal	1st Phalanx
<i>Periptychus</i>	100	97	34	16
<i>Pantolambda</i>	100	83	23	8
<i>Coryphodon</i>	100	58	13	7
<i>Uintatherium</i>	100	67	10	3

Corresponding changes in proportions are seen in the progressive evolution of the Proboscidea, Arsinoitheria, Pyrotheria, Astrapotheria, the Titanotheres and Rhinoceroses among Perissodactyls, the Hippopotami among Artiodactyls, the Diprotodons among Marsupials; but in these cases the phylogenetic series is less completely known. The progressive shortening of the foot is correlated with the increase in size and weight of the body and the use of the limbs more exclusively for support and slow locomotion on land.² It is associated with progressively stiffer and less flexible joints, a limitation of the articular facets, which tend in the pes to become nearly plane surfaces permitting of very little motion at the joint. There is no tendency to eversion of the foot, and the symmetry and proportionate size of the digits remain much the same as in the ancestral type of each race. The astragalar trochlea remains flat or tends to become so.

So far, therefore, as may be judged from the proportions of limbs and feet, *Patriofelis* was not an aquatic carnivore, but a large, heavy-bodied, slow-moving terrestrial type. In proportions of the limb segments, as in size, it is intermediate between *Pantolambda* and *Coryphodon*. The feet, however, remain more or less plantigrade, as in *Ursus* or in the Marsupial *Diprotodon*, and retain a greater flexibility than in the Amblypoda, although much less than in *Ursus*. The claws are broadened and probably functioned to some extent in supporting the weight; the phalangeal facets are more limited than in *Oxyæna* and *Limnocyon*, and the whole foot much stiffer and less flexible, and probably heavily padded. The head of the femur is more nearly in line with the axis of the shaft, and the knee-joint is slightly less flexed than in *Limnocyon*, again paralleling the early stages of rectigrade evolution among the ungulata.

The various features which led Osborn to suggest a partly arboreal habit for this genus are better explained as primitive characters handed down from a remote arboreal ancestry, for the stiff and clumsy limbs, short inflexible feet, and broad, blunt claws, are quite unsuited to arboreal life.

The short heavy jaw, robust premolars and powerful shearing teeth, may be compared most nearly with the hyaena among living carnivora, and indicate a flesh-eating type, as opposed to the fish-eating adaptations in the teeth of the

¹ Measurements from skeletons in the American Museum collections.

² Or in shallow water in the case of the Hippopotamus.

otter, sea-otter and pinnipedia, in which the shearing action degenerates or disappears and the cheek teeth are used for crushing or for prehension. The great massiveness and rapid wear of the teeth, and the peculiar shearing action of the premolars, would seem to indicate gross feeding habits, bone-crushing or perhaps, as Wortman has suggested, that the animal fed largely upon turtles or alligators (land tortoises were abundant as well as aquatic turtles in the Bridger). But it is hardly safe to infer more than that the prey of *Patriofelis* consisted of comparatively slow moving, clumsy animals, and that he was probably an indiscriminate and voracious feeder like the modern hyaenas, gluttons, etc. The cats are much daintier eaters, and their teeth correspondingly delicate and usually little worn by use.

***Patriofelis ulta* LEIDY.**

This species is somewhat smaller than *P. ferox*, and distinguished from it by a less massive construction of teeth and jaws. The worn and broken character of the teeth in the type preclude exact comparison with the teeth described above, and I am by no means certain that the species are distinct, as there seems to be a considerable degree of variation in the different specimens of *P. ferox*. In *P. ulta* the second premolar is not transverse but set straight in the jaw; in *P. ferox* it is transverse to an extent varying with the size and robustness of the jaw. *P. ulta* comes from the Lower Bridger; all our specimens of *P. ferox* come from the Upper Bridger, and the most robust are from the highest levels. I think that the two species should be held distinct on these grounds.

***Patriofelis coloradensis* Matthew, 1909.**

The type and only known specimen is No. 2691, lower jaws, figured by Osborn in 1897, from the upper beds of the Huerfano Basin, supposed to be equivalent in age to the Bridger. It is decidedly smaller than *P. ulta*, p_2 is considerably less reduced, and m_1 and m_2 of more nearly equal size, as far as can be judged from the alveolus of the first and the complete but worn second molar. There is no heel nor metaconid on the second molar.

***Patriofelis tigrinus* Cope.**

This species, from the Wind River, is considerably larger than the largest *P. ferox* and distinguished from all the preceding species by a small but distinct heel on m_2 , and the large basin-shaped heel of m_1 . These features are intermediate between *Patriofelis* and *Oxyæna*; in the latter genus m_2 has a well developed metaconid and basin heel like that of m_1 .

***Limnocyon* Marsh.**

This interesting genus, briefly indicated by Marsh in 1872, was first adequately described and figured by Wortman in 1902. The material at Dr. Wortman's command consisted of a large part of the skull and jaws and a few skeleton bones of one or other of the two species *L. verus* Marsh and *L.* (= *Thinocyon*) *velox* Marsh, and various fragmentary jaws, among which he distinguished a third species *L. medius*. Except for the dentition, however, the osteology was very incompletely known. We have now in the American Museum a fine series of skulls and jaws with incomplete skeletons associated, and are able to give a

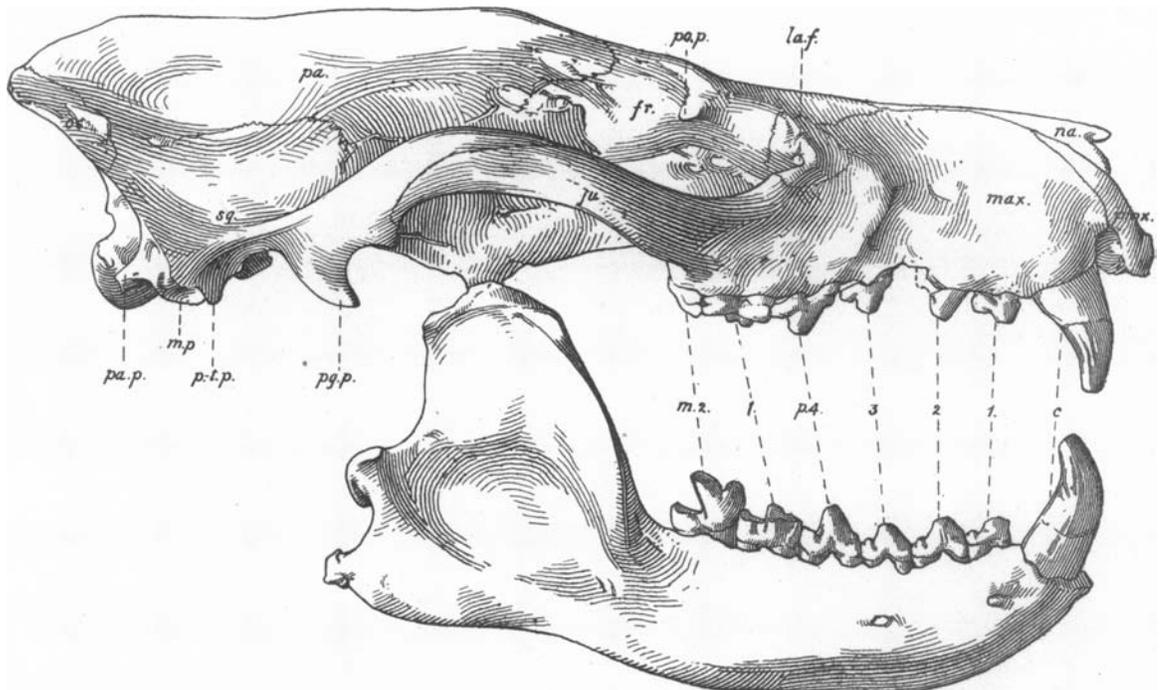


Fig. 53. *Limnocyon verus*; skull and jaw, natural size, No. 12155, Upper Bridger, *fr.* frontal bone; *ju.* jugal, *la. f.*, lachrymal foramen; *max.*, maxillary bone; *m. p.*, mastoid process of periotic; *na.*, nasal bone; *oc.*, occipital bone; *pa.*, parietal bone; *pa.p.*, paroccipital process of occipital; *pg.p.*, postglenoid process of squamosal; *pm.x.*, premaxillary bone; *pa.p.*, postorbital process of frontal; *p.t.p.*, post-tympanic process of squamosal; *sq.*, squamosal bone.

complete account of the osteology of skull and limbs in each of these species, and to determine more clearly their relationships.

Wortman has united with *Limnocyon* the genera *Thinocyon* Marsh and *Oxyænodon* Wortman. The teeth are very much alike in the three, but the skulls and limbs show more considerable distinctions, which would generally be regarded as generic. I retain them therefore as distinct, although very nearly allied genera, and place in *Limnocyon* the type species *L. verus* from the Bridger,

and a larger, more specialized species *L. potens* from the Washakie. Of *L. verus* we have a complete skull and jaws, with fore and hind limbs associated, and various more fragmentary specimens. Those from the Upper Bridger show certain constant differences which for the present may be regarded as varietal. The Washakie species is likewise represented by a nearly complete skull and jaws with various parts of the skeleton.

The principal characters of the genus as thus limited are:

Dentition I_{1-2}^{3-2} C_1 P_1^4 M_2^3 . Second upper incisor enlarged, median incisor small, lateral incisor reduced or absent. Lower incisors minute, crowded. Teeth robust, canines and premolars with vertical grooving. P_{1-3} two-rooted without deuterocone, p_4 three-rooted with strong deuterocone. M_1^4 large, triangular, with moderate metastyle and paracone and metacone connate. M_2^3 transverse, large, paracone median, metacone vestigial, parastyle long. P_{1-4} two-rooted with successively larger heels; m_{1-2} tuberculo-sectorial with basin heels and triangular three-cusped trigonids, the protoconid much higher on m_2 and the whole tooth a little larger.

Skull low and broad, with heavy rather long muzzle, stout deep jaws, long and very solid symphysis, broad basicranial region, semicircular much overhanging occiput, and high sagittal crest. Mastoid process rather prominent, wide, flattened, embraced superiorly by the post-tympanic, mastoid exposure very slight laterally but considerable inferiorly. Paroccipital process stout, projecting backward. Petrosal prominence low-crested. Nasals long, somewhat expanded posteriorly. Frontals short, truncate anteriorly. Parietals long and wide. Lachrymal with semicircular expansion upon the face, prominent tubercle and submarginal foramen. Lower jaws stout and deep with massive symphysis.

Limb bones short and curved. Feet moderately short, sub-plantigrade, astragalar trochlea somewhat excavated, phalanges relatively long. Ungual phalanges rather long, not compressed, fissured at the tips. Lumbar vertebræ with tongue-and-groove zygapophyses. Tail very long and heavy.

***Limnocyon verus* Marsh 1872.**

Plate XLIV, Fig. 1; Text Figs. 53-58.

Syn., *L. riparius* MARSH 1872; *Telmatocyon riparius* MARSH 1899.

This species is represented in our collections by about ten specimens, principally jaws, some with fragments of the skeleton. No. 12155, found near Lone Tree (Hor. C₄) by Mr. Granger, consists of the skull and jaws complete and in fine preservation, with fore and hind limbs and feet.

The type, consisting of upper teeth, was figured by Wortman in 1902; *L. riparius* is founded on the lower teeth of a somewhat smaller individual. The skull here described is intermediate in size and robustness; No. 11541 is larger and more robust than the type of *verus*; but there is less evidence of individual variation in size in this species than in the smaller *Thinocyons*. In the specimens from Horizons C and D (Upper Bridger) p_2 and p_3 are of equal size, in the typical form from Horizon B (Lower Bridger) p_2 is of smaller size than p_3 . I am unable to determine other constant distinctions on the material at hand although I suspect that more complete specimens would show the Upper Bridger species to be distinct.

Description of the Skull: As in most Creodonta the skull is large in comparison with the size of the skeleton. The arches are wide but not very deep, the muzzle heavy, the postorbital constriction long and narrow, the brain small, the sagittal and occipital crests high. The occipital crest is remarkably broad and overhangs the condyles considerably.

The proportions of the basioccipital and basisphenoid are about as in *Arcticitis* or *Vulpavus*. The condylar foramen is well separated from the posterior lacerate. The paroccipital processes are short, stout, and as far apart as the post-glenoid processes, and project backward; the mastoid processes are prominent, project outward and somewhat downward, and are well behind the post-

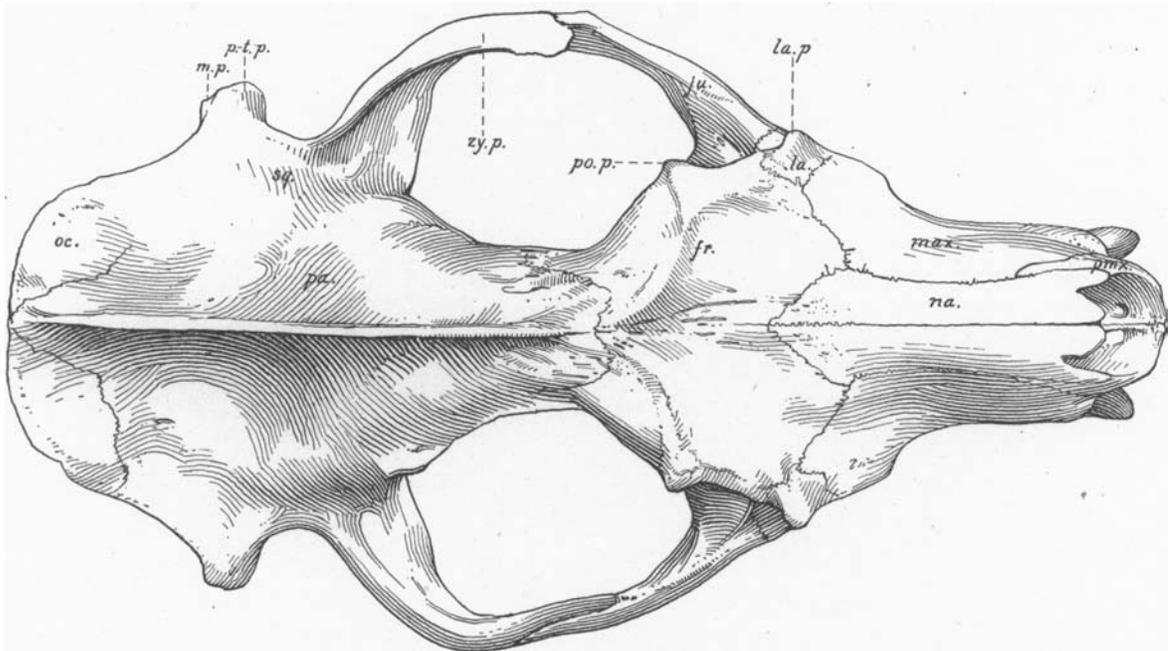


Fig. 54. *Limnocyon verus*, top view of skull, natural size, No. 12155. Lettering as in Fig. 53, and in addition; *la.*, lachrymal; *la.p.*, lachrymal crest; *zy.p.*, zygomatic process of squamosal.

glenoid and considerably exterior to them in position. There are no tympanic bullæ, and the auditory prominence projects above the basieranial surface with a strong oblique crest. The petrosals are considerably damaged in No. 12155, but a fragmentary skull and jaws, No. 11541, enables us to supply the deficiency in the description of this important region. The form of the prominence is peculiar to the Oxyænidæ so far as I know; it is widest and most prominent postero-externally; a strong crest runs from its most prominent part, just in front of the *fenestra rotunda*, obliquely forward and inward to the anterior internal corner. Internal to the crest is a more or less vertical surface descending to the basioccipital, external to it a convex slope descending to the meso-tympanic fossa, which lies external and antero-external to the prominence, and lodges the

bones of the middle ear. The posterior surface of the prominence is rounded and pierced by the large *fenestra rotunda*; antero-external to this and deep within the meso-tympanic fossa lies the *fenestra ovalis*, which lodges the plate of the stapes; and more exteriorly, at the bottom of the fossa, lies the Fallopian canal for the facial nerve, which appears at the surface of the skull at the posterior end of the fossa (postero-external corner of the otic depression) in the stylo-mastoid foramen. Following the Fallopian canal inwards in No. 11541 it circles around the outer base of the petrosal prominence, becomes buried between mastoid and petrosal and finally pierces the petrosal and appears upon its upper surface in the cranial chamber, in a distinct foramen just lateral to the internal auditory meatus. In general these two openings are united or semi-separate among the Fissipedia. This course, except for the distinct internal opening, appears to be the normal mode of exit of the facial nerve, in the Carnivora at least; where the tympanic bulla is present, the stylo-mastoid foramen lies on the posterior border of the bulla, between tympanic and mastoid. In the Creodont genera *Vulpavus*, *Viverravus*, *Uintacyon*, *Thinocyon*, *Tritemnodon* and *Sinopa*, the course of the facial nerve and position of the stylomastoid foramen appear to be the same as in *Limnocyon*; the same is true of *Patriofelis* so far as our material permits us to judge. In *Mesonyx* it is more deeply buried in the mastoid in the middle part of its course and opens internally in the internal auditory meatus; the external opening (stylomastoid foramen) has the usual position in this genus and in *Harpagolestes*. The foramen on the posterior exposure of the mastoid in the Mesonychidæ and in *Patriofelis*, identified by Wortman as stylomastoid, I take to be the post-mastoid foramen; it does not appear to be represented in any of the smaller Creodonta, nor in *Hyænodon*.

The petrosal of *Limnocyon* is grooved upon the outer slope by the stapedia artery passing into the *fenestra ovalis* and by the tympanic branch of the entocarotid artery passing forward to the foramen lacerum medius; the two grooves starting from a common point just in advance of the *fenestra rotunda*. These grooves indicate that besides the small stapedia branch, the main entocarotid or a branch of it entered the tympanic chamber and passed forward along the side of the meso-tympanic fossa, external to the crest of the auditory prominence, to the foramen lacerum medius. The more internal branch of the entocarotid, the principal or only branch in the Fissiped Carnivora, is not certainly indicated, but it may nevertheless have been the principal branch, as it certainly is in *Patriofelis*, *Mesonyx*, *Sinopa* and *Viverravus*, less certainly in *Vulpavus* and *Uintacyon*. It does not enter the tympanic chamber, but lies between the bulla and the basioccipital, passing forward over the margin of the latter bone at or in front of the foramen lacerum posterius, and grooving the side of the basioccipital forward to the foramen lacerum medius, where it enters the skull.

So far as it appears from present evidence, both these main branches of the entocarotid, besides the stapedia one, were present in the primitive Insectivora-

Creodont ancestral type, and were retained in most or all of the Eocene Carnivora. In the Insectivora the internal branch became vestigial or disappeared; in the Fissipede Carnivora the external branch became vestigial, while the internal carried the principal blood supply, in the Arctoidea at least. But the evidence on this subject in fossil mammals is necessarily so incomplete that it cannot well be satisfactorily interpreted.

The postglenoid processes are large, stout and prominent; preglenoid processes are absent. The postglenoid foramina are well developed. The alisphenoid canal is long but begins some distance in front of the foramen ovale. The post-nareal gutter is broad and deep, and almost closed in by the overarching pterygoids; its lateral walls, formed by palatines, pterygoids and alisphenoids, are very

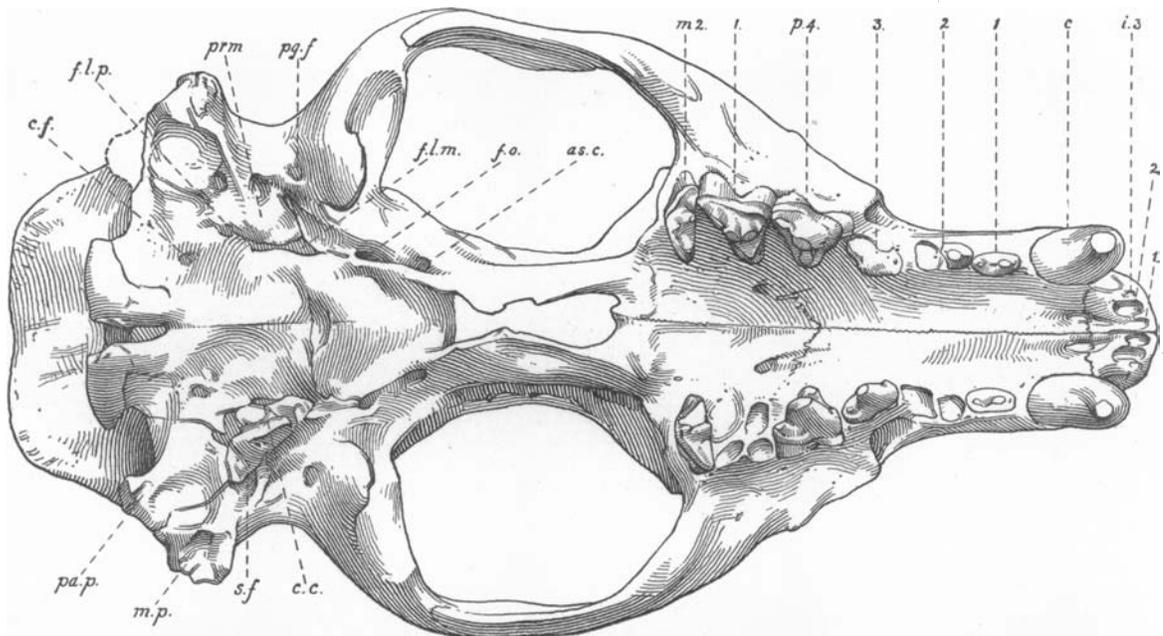


Fig. 55. *Limnocyon verus*, skull, under view, natural size, No. 12155. Lettering as in Fig. 2.

strongly convex. A well marked ridge appears on the palate just posterior to the tooth-rows; the posterior nares are roofed over for a short distance behind this ridge, so that it does not form the posterior boundary of the palate as it does in *Sinopa*, *Thinocyon*, etc. The palate is wide and strongly concave; the anterior palatine foramina are rather small.

The *premaxillæ* are of moderate size, their ascending processes short and small as compared with modern Carnivora; the body of the premaxilla is excavated in a well marked recess in front of the canine, for the reception of the lower canine. The *nasals* are wide and long, slightly expanded posteriorly and considerably expanded anteriorly. Their anterior border bears a broad deep notch, much more marked than in modern carnivora, more as in *Pantolestes*. The

maxillæ are of moderate size and their ascending processes do not closely approach the orbits nor are they extended backward above them. The *frontals* are wide anteriorly, much narrower posteriorly, short, and very wide from side to side; the anterior process which in modern carnivora is splinted in between nasals and maxillæ, is absent. They are not excavated along the median line as in *Sinopa*; the temporal crests are low but distinct, and unite to a sagittal crest at the fronto-parietal suture. The *lachrymals* have a considerable facial expansion of semicircular form, very like that in *Sinopa* and *Hyænodon* but less extensive. The lachrymal tubercle is prominent, and the foramen almost marginal, the anterior border of the orbit being less defined than in most of the Creodonta. The *jugals* have a rather slender superior branch, which abuts superiorly against the lower border of the lachrymal; the lower (anterior) branch is not developed, and the posterior branch extends backward to a short distance from the glenoid fossa, ending in a slender splint. The *parietals* are exceptionally long and narrow; the distance from the fronto-parietal suture to the occipital crest is more than half the entire length of the skull. In *Sinopa* it is somewhat less than half, in *Oxyæna* and *Patriofelis* about half; in *Hyænodon* and all modern carnivora it is much less, ranging from a third to a quarter of the total length. This is partly due to the great development and posterior overhang of the occipital crests. The squamosals are exceptionally large, and expand laterally so as to give great width to the posterior part of the skull; their zygomatic processes extend forward nearly to the posterior boundary of the orbit.

Dentition. Upper incisors three, the second largest, the lateral much reduced. Canines stout, moderately curved and vertically striated; they are shorter but much larger than in *Sinopa*, especially at the roots. Premolars stout and of moderate size, with a more or less obsolete vertical striation. P¹ two-rooted with well developed heel; p² similar but larger; p³ two-rooted, broadened posteriorly but without internal cusp, with minute anterior basal cusp and well developed heel-cusp. P⁴ triangular, three-rooted, with large internal cusp (deuterocone) somewhat anterior in position, well developed and slightly crested postero-external cusp, minute antero-external cusp, and a more or less obsolete cingulum except around the deuterocone. M¹ triangular with an anterior, an external, and an elongate postero-internal border, paracone and metacone moderately connate (more than in *Sinopa*, less than in *Tritemnodon*), metastyle extended into a shearing blade, protocone subcrescentic and moderately compressed, conules small, parastyle minute, strong external and distinct anterior cingula. M² extended transversely, width equal to or exceeding m¹, metacone vestigial, parastyle extended into a shearing blade, conules small, protocone subcrescentic, anterior and postero-external cingula and a rudimentary hypocone.

Lower incisors (three in number according to Wortman) very small and much compressed by the approximation of the lower canine roots. Lower canines large, with stout, rather short, recurved crown, striated longitudinally.

The lower premolars are similarly striated, all are two-rooted with robust crowns, strong and somewhat crested heel-cusps, and no anterior basal cusp except a minute rudiment on p_4 ; the principal cusp is stout, strong, not much compressed, inclined forward in p_1 and backward in p_4 . The molars have moderately high triangular trigonids and rather large basin heels, bounded by an external and a curving internal and posterior crest. The cusps of the trigonids are well separated, the protoconid overtops the others a little on m_1 and is much larger on m_2 , which is a little larger throughout than m_1 .

Lower jaw. The jaw is unusually thick and massive, deep anteriorly, with long and strong symphysis which reaches back beneath p_3 . The mental foramina have their usual position beneath p_1 and p_3 . The coronoid process is very wide, the masseteric fossa of moderate depth and the angular portion of the jaw beneath it is unusually deep, the angular process being wide but not projecting beyond the condyle. The jaw characters show a very considerable degree of resemblance to *Oxyæna* and *Patriofelis*.

Limb-Bones. The limb-bones compare in general proportions and size with those of *Lutra* and *Taxidea*, while the skull is much larger and widely different in shape.

The *humerus* (Fig. 57) is considerably curved, as in the otter. The greater tuberosity is much larger and more prominent than the lesser, as in *Sinopa*, and most modern Carnivora. In Miacidæ they are more nearly equal in size, as in Rodents and Insectivora. The deltoid crest is strong and heavy, extending two thirds down the shaft, much flattened at the top. It is much more prominent than in *Sinopa*, but of the same general form, and differs widely from the high, compressed, sharply crested and abruptly ending deltoid crest of the Miacidæ and Arctocyoniidæ and is very like the corresponding parts in *Lutra*. The supinator crest is high and strong, much larger than in *Sinopa*, the ulnar part of the trochlea more oblique and strongly keeled, the radial part more limited internally and posteriorly, and somewhat more convex anteriorly. The trochlea is considerably narrower and deeper than in the Miacidæ the end much more oblique. In the obliquity of the trochlea *L. verus* resembles *Taxidea* more than it does *Lutra*, but it lacks the massive internal condyle of the badger.

The *ulna* and *radius* are comparatively short, as in the otter or badger, considerably shorter than in *Sinopa*, and much more curved. The ulnar shaft is somewhat convex anteriorly, the olecranon is long and large, bent considerably forward and inward, moderately expanded antero-posteriorly.

In *Sinopa* the olecranon is shorter, more expanded antero-posteriorly, and



Fig. 56. *Limnocyon verus*, ulna and radius, natural size, No. 12155.

projects almost in line with the shaft, being bent a little inward but not at all forward. In the Miacidæ it is much shorter, less expanded antero-posteriorly, but its direction is about the same. In the otter it is rather short but much expanded antero-posteriorly and internally, in *Taxidea* longer but less expanded. The shaft of the ulna is flattened and expanded as in *Sinopa*, but the internal expansion much thicker, especially towards the distal end. The facet for the head of the radius has much less transverse expansion than in *Sinopa*, permitting a greater rotation of this bone; the distal facets are very much the same as in *Sinopa*, the styloid process not being well separated. The radius is rather short, with strongly curved shaft and massive distal end. The head is flattened oval as in *Sinopa*, the humeral facet somewhat more excavated, the ulnar facet less extended. The bicipital tubercle is large and prominent, while in *Sinopa* it is small and weak. The carpal facets are much deeper dorso-ventrally than in *Sinopa*, the ulnar facet looser and more concave. As compared with the Miacidæ, the curvature of the shaft is greater, the distal end more massive, carpal facets deeper, internal hook less prominent.

The femur is comparatively short and massive. The shaft is not so straight

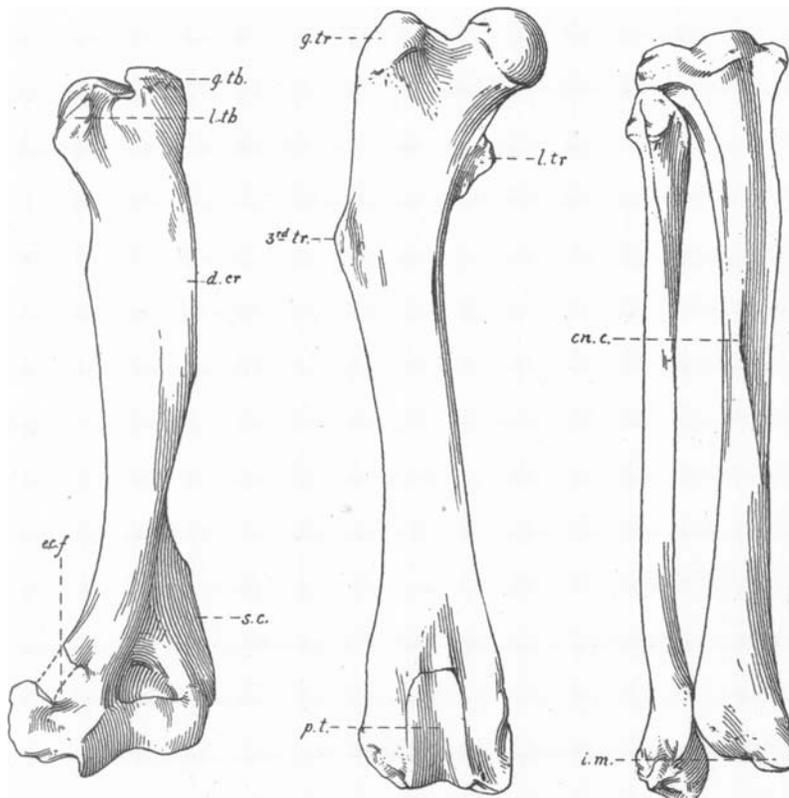


Fig. 57. *Limnocyon verus*, limb bones, natural size, No. 12155.

as in the Miacidæ, but, as in *Sinopa*, the upper part is bent over toward the internal side, so that the axis of the shaft is in line with the great trochanter instead of with the notch between it and the head. The lesser and third trochanters are prominent as in *Sinopa*, the third trochanter being much more prominent than in Miacidæ and situate further down on the shaft. The lesser trochanter is internal, as in *Creodonts* generally. In modern carnivora the third trochanter

is absent, the lesser trochanter posterior. The distal end of the femur is deeper

than in Miacidæ and the patellar trochlea narrower; in both these respects *Limnocyon* is intermediate between Miacidæ and *Sinopa*. The shaft is not bowed out on the dorsal surface, as it is in Canidæ and to a slight extent in *Lycarion* and *Oödectes*, but straight, as in *Vulpavus*, *Miacis* or *Sinopa*, and in the Viveridæ and many other Fissipedia.

The *tibia* is rather short and stout and the shaft considerably bowed. The cnemial crest is nearly obsolete except along the middle of the shaft (cf. *Pantolestes*). The astragalar facet is nearly flat except for the internal malleolus which is broken off in our specimen, and is moderately oblique, hardly more than in the badger and much less than in the otter but much flatter than in either.

The *fibula* is about as long as in *Sinopa*, larger than in *Lutra*, *Taxidea* or other modern carnivores, and resembles that of *Sinopa* in general form. The proximal end is considerably flattened and its tibial facet irregular and somewhat concave. The distal end is rather massive; the astragalar facet faces almost directly internal, the tibial facet is small, facing internally, anteriorly and proximally, while the small flat calcaneal facet faces distally and is smaller and simpler than in *Sinopa* in which genus it takes on somewhat of the form characteristic of the Artiodactyla.

Fore and Hind Feet. The fore foot is incompletely known, while the hind foot is nearly complete. In the *carpus*, the scaphoid, lunar and centrale are separate. The scaphoid and lunar have but small vertical height and the radial facet is extended over nearly all of their dorsal surfaces. This indicates a plantigrade or semi-plantigrade manus. The *scaphoid* has a short but heavy internal hook, a large, flat or somewhat saddle-shaped quadrate facet for trapezium, a somewhat concave facet of the same size for centrale, at the dorsal-internal corner of which is a very small facet where the trapezoid just reaches the scaphoid. The *lunar* is rather small and its dorsal surface much reduced by the extension over it of the radial facet; the centrale facet is triangular, wide dorsally and extending down to the ventral surface; the magnum facet is very narrow dorsally, wider ventrally and moderately concave; the unciform facet is of moderate width and strongly concave dorso-plantar; and the ridge between unciform and magnum facets is comparatively low and broad. The cuneiform facet is quite small, and limited to the plantar part of the external face of the lunar. The *cuneiform* is of small proximo-distal diameter, and has a short but stout inferior hook. Its ulnar facet is rather large and moderately concave in a dorso-plantar direction; the pisiform facet is also of good size and slightly concave. The unciform facet is broad and nearly flat, somewhat saddle-shaped, and there is a well marked facet of smaller size for mc. V. The *magnum* is much compressed, with very small dorsal surface and narrow proximal keel fitting between lunar and centrale; it is much expanded towards its plantar and distal surfaces, so that the facet for mc. III faces at right angles to the proximal facets of the carpus; this facet is not very wide and strongly convex, and its position places the meta-

carpus in a normal position at right angles to the ulna and radius, as in the plantigrade manus. The trapezoid facet is narrow and mc. II appears to have barely touched the magnum; the unciform facet is wide and flat. The *centrale* has the usual form and position, the greater part lies under the scaphoid but the dorsal-external end is beneath the lunar. The dorsal surface is reduced to a narrow border; the scaphoid facet is broad, moderately convex, facing proximad; the lunar facet is about half as wide dorsally and thins out to nothing towards the plantar side forming a flat, triangular surface facing toward the proximal-internal side. The magnum facet is very narrow and lies on the internal end of the centrale; the trapezoid facet is broad, convex in a dorso-plantar direction, and faces nearly distal. The *trapezium* is a large broad, irregularly triangular bone, with a blunt process projecting proximal-externally beneath the scaphoid and trapezoid, and a strongly convex distal-internal facet for mc. I, facing partly plantad; on the internal side of the trapezium are flat, vertical facets for trapezoid and mc. II, and on the proximal side a saddle-shaped facet for the scaphoid. The trapezoid and unciform are not preserved.

The *metacarpals* are incompletely known, but were short, stout and spreading. The fifth is a little longer than the first and of about the same thickness of shaft. The second is nearly one half longer than the fifth; of the third and fourth only the proximal ends are preserved. The contacts between mc. II and the magnum and mc. III and the unciform are limited, but wider than in *Vulpavus*; mc. V has a broad facet for the unciform. The phalanges are very like those of the hind foot but more slender, and the unguals longer and less curved. They will be described more in detail in connection with the description of the pes.

In comparison with *Vulpavus* and the Fissipedia on the one hand, and with *Sinopa* and *Tritemnodon* on the other, the fore foot of *Limnocyon* shows a much closer agreement with the latter group. The first and fifth digits are more nearly equal in length, and associated with this difference in the symmetry of the foot are considerable differences in the arrangement and relations of the carpal bones from any of the Adaptive Creodonts or Fissipedia. The trapezium is much larger and its metacarpal facets more distal. The head of mc. II is less oblique. The magnum is narrower, the lunar-unciform facet smaller and less lateral. In all these features *Limnocyon* agrees with *Sinopa* and *Tritemnodon*. It differs from *Sinopa* in the broader and more spreading manus, greater relative width of most of the carpal bones, shorter and stouter metacarpals, the slighter overlap of the heads of the second and third metacarpals upon the third and fourth; (this overlap, resulting in a contact between magnum and mc. II, unciform and mc. III, is very considerable in *Sinopa* and *Tritemnodon*, small in *Limnocyon* and very slight in *Vulpavus* and the less specialized Fissipedia). The *Limnocyon* manus differs from the other three in the somewhat flatter, more limited and apparently less perfect facets between all the bones. In almost all points of comparison except size, the *Tritemnodon* manus is intermediate between *Limnocyon* and *Sinopa* although much nearer the latter.

The above data indicate that *Limnocyon* is much nearer to the Hyænodonts than to the Miacidæ in the characters of the manus, sharing with them two independent characters, the mesaxonic symmetry and the blunt-pointed claws resting upon the ground. The other characters cited appear to depend upon these two primary distinctions. The shifting of the weight of the foot towards the external side in *Vulpavus* makes necessary a stronger connection of the radius with the external metacarpals through the lunar and unciform, the expansion of the magnum and reduction of the trapezoid setting over the scaphoid and lunar, so that they rest more directly over metacarpals II and III, and the reduced mc. I is freed from their support. The broader and less angulate phalanges transmit a part of the weight of the body to the unguals, thus affording a distinct approximation to the conditions among unguulate mammals. This is more clearly seen in the larger and more specialized genera of Inadaptive Creodonts in *Hyænodon* and *Patriofelis* and especially in *Mesonyx* but it is quite perceptible in any of them on a careful study of the relations of the phalanges.

I am not certain whether the limitation of the facets, indicating a stiffer and less flexible foot in *Limnocyon* than in either Hyænodonts or Miacidæ, should be regarded as an initial stage of aquatic adaptation, or merely as the retention of the primitive insectivore-like foot; it is in any event a comparatively slight distinction.

The *hind foot* is in general proportions and most details of construction very like that of *Sinopa*, only with shorter and more spreading digits and various indications of a more plantigrade gait. It is of about the same size as *S. rapax*. The astragalus (Pl. XLVII, fig. 2, *d*) is so much like those of *Sinopa* and *Tritemnodon* that it might readily belong to the same or a closely related genus. The chief difference is in the more constricted neck and flatter, laterally expanded head. The trochlea is shallow, its inner crest a little more developed than in

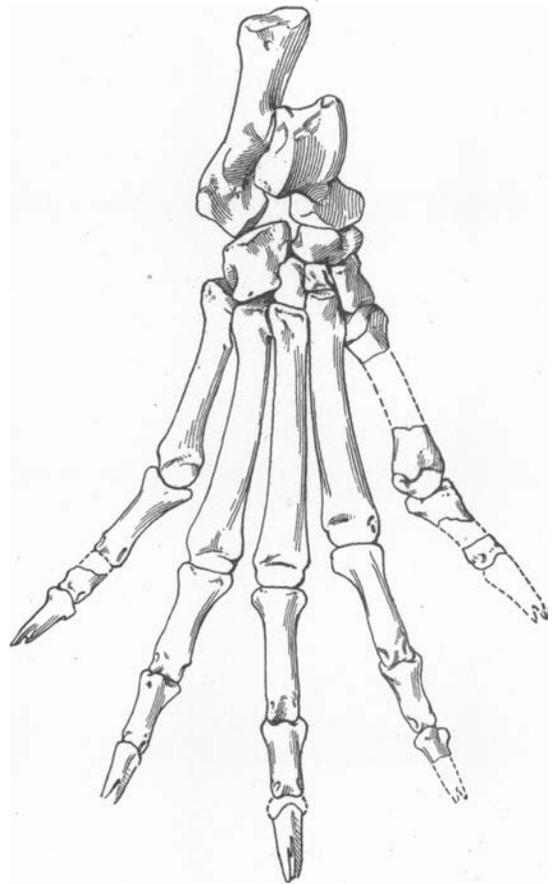


Fig. 58. *Limnocyon verus*, hind foot, dorsal view, natural size. No. 12155.

Sinopa, much more than in the Miacinæ. The trochlear faceted surface extends down on the neck only towards its external side, while in *Vulpavus* and to a less extent in other Miacinæ it extends on the internal side of the neck. The head of the astragalus in Miacidæ is also expanded toward the internal side, but the facet extends more over the superior dorsal surface than in *Limnocyon*. On the whole the astragalus is that of a semi-plantigrade animal.

The *calcaneum* differs from *Sinopa* and resembles the Miacinæ in the large size of the peroneal tubercle — an indication of plantigrade gait — but the groove for the tendon of the peroneus longus is imperfect as in *Sinopa*, while in the Miacinæ it is very well marked. The obliquity of the calcaneo-cuboidal facet is about the same in *Limnocyon*, *Sinopa* or *Vulpavus* — it is a primitive character common to most of the Creodonta and many other unspecialized animals. The fibular facet is of moderate size, about the same as in *Sinopa* or *Didymictis*. In the Miacinæ it is absent and slight in the Oxyæninæ. The *cuboid* has a rather small astragalar facet, less than in the Oxyæninæ, Miacinæ or Mesonychidæ, more than in Hyænodontidæ. The navicular is not so wide as in *Vulpavus*, and the first and second *cuneiforms* very different in shape with much less transverse width, and agreeing much more nearly with *Sinopa* and *Tritemnodon*, although more compressed laterally than in these genera. The *metapodials* differ very much in proportions from those of *Vulpavus* and are much more like those of *Sinopa* and *Tritemnodon*. (Cf. Fig. 4, p. 325.) The third is the largest, the second and fourth somewhat shorter but a little more robust, the first and fifth shorter and more slender, of about equal length and stoutness. In *Vulpavus* mt. I is considerably shorter and stouter than the rest, and strongly divergent with a considerable freedom of lateral motion, so as to be semi-opposable. In *Limnocyon*, as in *Sinopa* and *Tritemnodon* mt. I is paired with mt. V, and is very slightly divergent with but little lateral motion and not at all opposable. The different proportions of the internal and middle cuneiforms is dependent upon this adaptation of the digits. The *phalanges* are as long as in *Sinopa* while the metapodials are shorter and more spreading. The angulation between the first and second row is slight, as in *Sinopa*, *Tritemnodon*, and the Mesonychidæ; in *Vulpavus* it is very marked — less so in the Oxyæninæ. The phalanges of the second row are shorter and much broader and flatter than in *Vulpavus*; their distal facets are flatter than in the Hyænodonts and more limited than in either *Sinopa*, *Tritemnodon* or *Vulpavus*, much less reflected over the superior and inferior surfaces of the bone than in any of these genera. The unguals are not compressed and are very slightly curved, rather stout, and rounded in section, very different from those of *Vulpavus* or any of the Adaptive Creodonta, and rather deeply fissured. In *Sinopa* they are somewhat compressed and not so deeply fissured.

The pes in *Patriofelis* and *Oxyæna* is intermediate in proportions of the digits between *Limnocyon* and *Vulpavus*, but nearer the former. The peroneal tubercle is not so prominent, the astragalar trochlea is flat, the fibulo-calcaneal

articulation slight, the phalanges relatively shorter, especially in *Patriofelis*, the astragalo-cuboid articulation broader, exceeding *Vulpavus* in this respect. The unguals are broader and shorter and about as deeply fissured as in *Limnocyon*.

On the whole *Limnocyon* comes nearer to *Sinopa* in the characters of the pes than it does to the Oxyæninae. The resemblance is no doubt partly due to conservatism, and partly to similar adaptation and size. But it emphasizes the comparatively near relationship between Oxyænidæ and Hyænodontidæ illustrated in many characters of the skull and skeleton. The more spreading pes with relatively long phalanges, the heavy peroneal tubercle, and some minor characters, may be taken to indicate a more plantigrade foot than in *Sinopa* or *Tritemnodon*, but in the absence of skull and limbs they would be distinguished with difficulty.

Habitat and Relationship. The indications of habitat obtainable are not very clear. The carpus indicates a plantigrade fore foot, and the hind foot would appear to be more or less plantigrade, if we may judge from the posterior limitation and anterior extension of the astragalar trochlea, the width and flatness of the tarsus, lack of trochlear groove, prominence of peroneal tubercle, etc. The relatively short and curved limb bones, the somewhat stiff and inflexible wrist and ankle, the broad spreading foot with long phalanges, and rather long, rounded and slightly curved claws may indicate some degree of aquatic adaptation. The resemblance of the basicranial region, and of the humerus, to the corresponding parts of the otter, is obvious, but can hardly be taken as evidence of adaptation, for it is equally marked in comparison with terrestrial or fossorial Mustelines, such as the skunk and the badger. On the whole I incline to regard *Limnocyon* as of somewhat generalized habits, lacking the cursorial specializations apparent in *Sinopa* and *Tritemnodon*, or the arboreal adaptations of *Vulpavus*.

The resemblance to the Mustelidæ is superficial and does not indicate any near relationship. The affinity to *Patriofelis* and *Oxyæna* is obvious and is seen in all parts of the skull and skeleton as well as in the dentition. The differences are principally associated with the larger size of these genera and their greater specialization. The long, wide and low cranial region, broad occiput, and rather short face with heavy muzzle, stout jaw with long solid symphysis, distinguish the group from the Hyænodonts.

Measurements of L. verus, No. 12155.

Skull, total length, nasals to occipital crest	148.2
“ “ incisors to occipital condyles	143.
“ width across zygomata	84.
“ width of muzzle in front of infraorbital foramina	30.
“ “ between orbits	41.
“ “ at postorbital constriction	20.5
“ “ of occiput	44.5

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Skull, width across mastoid processes	67.5
" slant height of occiput	36.
Upper dentition, total length	67.5
Length of molar-premolar series	48.
" premolar series	33.6
Transverse width across incisors (6)	12.5
Diameters of upper canine, antero-posterior 9. ; transverse	6.5
" " p ⁴ , antero-posterior 8.4; "	8.2
" " m ¹ , " 10. ; "	9.3
" " m ² , " 4.4; "	12.
Lower jaw, total length	100.5
" " height at coronoid process (from angle)	47.5
" " depth beneath p ₃	18.3
" " " " m _I	18.
" " thickness beneath m _I	10.
Lower dentition, total length	58.
Length of molar-premolar series	45.2
" " premolar series	28.
Diameters of canine, antero-posterior 8.5; transverse	6.1
" " p _I , " 6.3; "	2.9
" " p ₄ , " 8. ; "	4.1
" " m _I , " 8.5; "	5.4
" " m ₂ , " 9.8; "	5.7
Humerus, total length	94.
" " antero-posterior diameter of proximal end	22.
" " transverse diameter of distal end	26.5
Ulna, total length	95.8
" " major diameter of shaft	8.6
Radius, total length	67.2
" " major diameter of shaft	6.9
Femur, total length	103.2
" " transverse diameter of proximal end	25.
" " antero-posterior diameter of shaft	8.8
Tibia, total length	99.4
" " transverse diameter of shaft	8.1
Fibula, total length	95.5
" " transverse diameter of shaft	4.6
Hind foot, total length	120.
" " length of astragalus	19.6
" " width of body of astragalus	12.
" " " " head " "	10.5
" " length of calcaneum	31.
" " width of tarsus at distal end	18.
" " length of third metatarsal	40.
" " diameter of shaft of third metatarsal (transverse)	4.4
" " length of proximal phalanx, third digit	18.
" " " " second " "	12.
" " " " metatarsal II	34.
" " " " " IV	36.

Hind foot, length of metatarsal V	28.
Fore foot, width of scaphoid	8.3
“ “ height “ “	4.2
“ “ width of lunar	4.2
“ “ height “ “	5.0
“ “ width of magnum	3.5
“ “ height “ “	4.9
“ “ width of cuneiform	8.7
“ “ height “ “	4.5
“ “ diameter of trapezium	8.2
“ “ length of metacarpal II	26.1
“ “ “ “ “ V	19.

Limnocyon potens sp. nov.

Type, No. 13138, a complete skull and jaws, with nearly all the presacral vertebræ, pelvis and hind limb from the Upper Washakie beds, found by Walter Granger of the American Museum Expedition of 1906.

This species appears to be a more advanced stage in the evolution of the *L. verus* phylum. It is larger and more robust than its Bridger predecessor, the lateral upper incisor has disappeared, and the second upper incisor is very large. The teeth are very similar but somewhat more robust. The upper molars and p^4 are more extended transversely, the protocone of m^1 and deutocone of p^4 more distinct. P^3 is relatively larger, broadened postero-internally. P^3 has a rudimentary and p^4 a distinct anterior basal cusp. The nasals are less expanded than in *L. verus* at the posterior end, but extend further backwards to a point opposite the middle of the orbit. The astragalus has a somewhat deeper trochlea, extending further forward upon the neck. The cervicals are of moderate length with large plane zygapophyses. The lumbar are five in number, rather large and long with flattened keeled centra and strongly convex zygapophyses.

Besides the type, I refer to this genus a fragmentary and weathered skeleton No. 13139, from the same horizon and locality. Most of the vertebræ are preserved in this skeleton, but not enough to determine the dorso-lumbar formula. The caudals are very long and large, indicating a stout and powerful tail; their zygapophyses are moderately convex, and the neural arches are complete on ten of the long caudals, indicating that the spinal chord was enclosed in bone much further posteriorly than in *Patriofelis* (to the 14th caudal at least). This is probably a primitive feature retained by *Limnocyon* in accord with its general conservatism.

Measurements.

Skull, length from nasals to occiput, not less than	165.
“ width of muzzle in front of infraorbital foramen	34.
“ width between orbits	51.
“ “ at postorbital constriction	22.5

Length from tip of nasals to anterior end of sagittal crest	81.
Upper dentition, total length	72.7
Width across incisors	14.
Length of molar-premolar series	53.
Length of four premolars	36.
Diameters of i^1 , antero-posterior 4.5; transverse	2.
“ “ i^2 “ 7.3; “	4.
“ “ canine “ 12.3; “	8.2
“ “ p^4 “ 11. ; “	11.8
“ “ m^1 “ 12.3; “	12.
“ “ m^2 “ 5.4; “	13.2
Lower jaw, total length	122.5
“ “ height at coronoid process (including angle)	58.
“ “ depth beneath p^3	24.5
“ “ “ “ m^1	22.
Lower jaw, thickness beneath m^1	12.
Symphysis, length 42.; depth	17.
Lower dentition, total length	69.
Diameters of c, at base, antero-posterior 12; transverse	8.5
Length of four premolars	35.5
Diameters of m^1 , antero-posterior 11; transverse	6.

Thinocyon Marsh.

Under this genus I include besides the type *T. velox* Marsh, *Limnocyon medius* Wortman, and two undescribed species, one from the Lower Bridger, the other from the Washakie formation. The genus is nearly allied to *Limnocyon* but includes animals of much smaller size and slenderer proportions, comparable with the minks and weasels, while the *Limnocyons* were of about the size and proportions of the otter. The teeth are less robust but otherwise very similar.

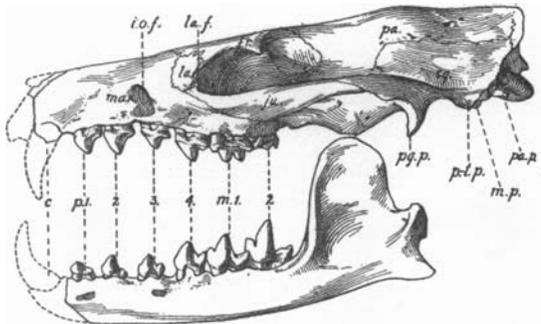


Fig. 59. *Thinocyon velox*, skull and jaws of No. 13081, natural size. Lower Bridger. Lettering as in Fig. 53, and in addition *i. o. f.*, infraorbital foramen, *la.*, lachrymal bone.

Thinocyon was the most abundant of the Bridger carnivora, so far as can be estimated from our collections. The specimens from the Lower Bridger differ very considerably in size, but with a single exception all are referable to *T. velox*. The specimens from the Upper Bridger also

vary a great deal in size, but average somewhat larger, and in all of them p^4 has a distinct anterior basal cusp, which is never present in specimens from the lower beds. This cusp is shown in the type of *L. medius* Wortman, to which species I refer the specimens from the upper beds.

The teeth are higher, sharper and the cusps more angulate and less massive than in *Limnocyon*. The incisors are not known. The canines and premolars display the same vertical grooving as in the larger genus. The sagittal crest is low, and the occiput vertical or but slightly overhanging. The zygomata are slender and the mastoid and paroccipital processes small. The peculiar jaw, thick but very shallow, and with stout massive symphysis, is very characteristic of the genus. The limbs are much longer and slenderer than in *Limnocyon*, the metapodials and especially the phalanges elongate. The ungual phalanges are long, little curved, not compressed, and rather deeply fissured. The astragalar trochlea is flat.

The species are distinguished as follows:

$P_1-m_2 = 30.5$ mm.; p_1 two-rooted; p_4 without anterior basal cusp	<i>T. velox</i> Marsh.
$P_1-m_2 = 35$ mm.; p_1 two-rooted; p_4 with distinct anterior basal cusp	<i>T. medius</i> Wortman.
$P_1-m_2 = 30$ mm.; p_1 one-rooted; p_4 without anterior basal cusp	<i>T. cledensis</i> sp. nov.
$P_2-m_2 = 21.9$ mm.; p_1 unknown; p_4 without anterior basal cusp; teeth more compressed than in the preceding species	<i>T. mustelinus</i> sp. nov.

***Thinocyon velox* Marsh.**

Plate XLIV, Fig. 2 and 3, Text Figs. 59-61.

Thinocyon velox MARSH, Amer. Jour. Sci., 1872, Vol. IV, p. 204. Separata published August 7.

Limnocyon velox WORTMAN, Amer. Jour. Sci., 1902, Vol. XIII, p. 118, figs. 76-80 excepting fig. 77.

The type of the genus and species is a lower jaw in the Yale Museum. Wortman has described the lower jaws and some fragments of the skull and skeleton in the Marsh collection. The upper teeth which he attributes to this species (fig. 77, above citation) are wrongly associated; they may belong to a small species of *Sinopa* (cf. *S. minor* Wortman, described on a later page of this memoir), but are certainly not *Thinocyon*.

The species is represented in the American Museum collections by several well preserved skulls and jaws with large parts of the skeleton associated; and by a number of more fragmentary specimens. The principal specimens are:

- No. 13081. Skull and jaws nearly complete, with a large part of the skeleton, all in excellent preservation. Horizon B₃. Found by Paul Miller.
- No. 12631. Skull, jaws, cervical vertebræ, etc. Superior surface of skull weathered so as to expose the brain-case, otherwise very complete. Horizon B₁. Miller.
- No. 11525. Skull crushed, lower jaws, several vertebræ, pelvis, etc.
- No. 11524. Lower jaws, facial part of skull, most of the limb bones, forefoot and many vertebræ, all uncrushed and well preserved. Horizon B₂. Granger.
- No. 11526. Skull, crushed and incomplete.
- No. 11527. Parts of jaws and fragments of skeleton.
- No. 13082. Skull, jaws and a large part of skeleton. Horizon B₃. Granger.

There appears to be a rather wide variation in size, which may be sexual, comparable to the variation in modern species of Mustelines. The specimens give an almost complete knowledge of the skull, jaws, limbs and feet, but the rest of the skeleton remains incompletely known, as in *Limnocyon*. All the specimens are from the lower beds, and it is probable that the specimens from the Lower Bridger referred by Wortman to *L. medius* are large individuals of *L. velox*. The variation in the teeth is much less than in the size and depth of the lower jaw.

Dr. Wortman (1902) has given a brief but clear diagnosis of the principal characters of this species, based on the fragmentary material at his command. He was impressed with the Insectivore resemblances in basicranial and other characters, and with the adaptive resemblances to "certain of the otters, notably *Potamotherium*"; and suggests that the group (*Limnocyoninae*) may belong rather to the Insectivora than to the Carnivora, and that this species was aquatic or partially so. According to our present knowledge the Insectivore resemblances are common to all primitive Creodonts, whether adaptive or otherwise, and the resemblances to *Potamotherium* are mostly resemblances to the Mustelidae generally.

The description of the skull in *Limnocyon verus* applies in most respects to this species, but with many points of difference mostly associated with the much smaller size of *T. velox*. The lineal dimensions are from two fifths to one half those of *L. verus*. The top of the skull is nearly flat, with no postorbital crests, and a very slight sagittal crest which does not extend much if at all in advance of the tentorium. The occipital crest does not project backward as far as the

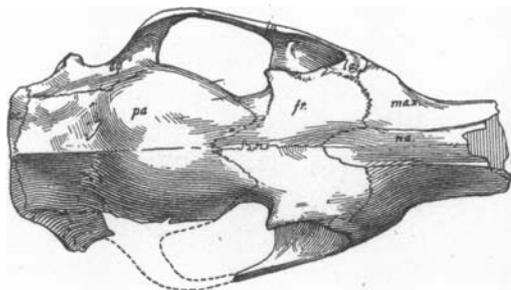


Fig. 60. *Thinocyon velox*, top view of skull of No. 13081, natural size.

condyles. The zygomatic arches are slender and lack the upward curve behind the orbits characteristic of *Limnocyon*. The nasals are narrower and are not expanded posteriorly. The frontals are longer extending on the median line and at the sides behind the postorbital constriction, which is not so narrow as in *L. verus*. The lacrymals have about the same facial expansion, but the tubercle is not so prominent, and the foramen is more completely internal. The

orbits are larger and their anterior border more uniform and defined. Prominent postorbital processes are present on the frontals; on the jugals they are entirely absent. The anterior border of the orbit is above the middle of p^4 , and the infraorbital foramen above p^3 , as in *Limnocyon*. In *Viverravus* the orbit is further forward, in *Vulpavus* further backward, while the infra-orbital foramen is slightly further backward in both the Miacid genera. The parietals are long,

but differ widely in form from those of *L. verus*, on account of the absence of sagittal crest, prominence of the cerebral fossæ, and the low, broad occiput. They extend a considerable distance behind the swellings which mark the position of the cerebral lobes, with nearly flat surfaces meeting in the median line at an obtuse angle slightly crested. The postparietal foramen is represented by a small oblique slit just behind the cerebral lobes. The squamosal is much smaller than in *L. verus*, the superior plate is nearly vertical, the zygomatic process short and slight, extending but little in advance of the glenoid fossa, while in *Limnocyon* it extends nearly to the posterior boundary of the orbit. The post-tympanic process is much less prominent, the lateral exposure of the mastoid is very small, and faces less posteriorly. The occiput is low and wide; the condyles are large and widely separated; the paroccipital processes are small, with spatulate tips directed backward.

The basicranial region is wide and flat. The auditory prominence of the petrosal is prominent and crested obliquely near the median side, the crest descending to the median lacerate foramen. This form is quite different from that in the Miacinæ or in *Hyænodon*, where the prominence ends anteriorly in a rounded surface, but is more nearly approached in *Viverravus* and *Sinopa*. The deep meso-tympanic fossa lies external and anterior to the prominence, separating it from the squamosal and mastoid which bound the otic depression. The post-tympanic process of the squamosal sends a small spur inward across the posterior end of this fossa, nearly reaching the petrosal, as in *Vulpavus* and *Viverravus* and apparently in all the smaller Creodonta; this spur defines anteriorly the outer opening of the fallopian aqueduct, or stylomastoid foramen.

The *fenestra rotunda* is large and situate on the prominent posterior end of the auditory prominence. The *fenestra ovalis* is small, and situate on its external side, just in advance of the spur from the post-tympanic process. The external slope of the petrosal shows a groove for the stapedial branch of the internal carotid artery, and another groove for a branch passing directly forward to the *foramen lacerum medium*; both grooves start from a common point just in front of the *fenestra rotunda*. These grooves are similar to those of *Limnocyon* and of the Miacidæ, and are likewise present in the small Eocene Artiodactyls *Homacodon* and *Helohyus*. In each case they doubtless conserve a common primitive type of carotid circulation which has since been variously modified. The more median branch of the internal carotid, which passes between basioccipital and petrosal forward to the foramen lacerum medium, and is the entocarotid of

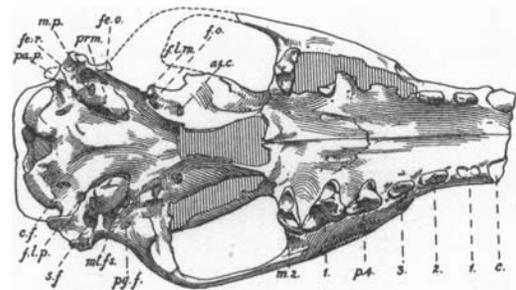


Fig. 61. *Thinocyon velox*, under view of skull of No. 13081, natural size. Lettering as in Fig. 2.

modern carnivora, is not indicated by a groove on any of our specimens of *T. velox*. But since it appears to have been present in *T. medius* and was certainly well developed in *Patriofelis*, I presume that the median branch was generally present in the Oxyænidæ, as in the other Creodont families.

The posterior lacerate foramen is rather small, and lies behind the middle of the auditory prominence as in the Creodonta generally. In *Fissipedia* it is more internal, in *Insectivora* more external in position. The condylar foramen is of moderate size situate about half way between the *for. lac. post.* and the inner end of the occipital condyle. The mastoid appears on the under surface of the skull as an irregular surface enclosed between the paroccipital and post-tympanic processes, but can scarcely be said to form any process. The postglenoid foramina are rather small and in the usual position; the foramina ovalia are wide apart in consequence of the breadth of the basicranial region. The pterygoid plates are somewhat less closely approximated at their inferior borders than in *Limnocyon*, but extend further backward, and the posterior opening of the alisphenoid canal is nearer to the foramen ovale. As in *Limnocyon*, there is no trace of a preglenoid process of the squamosal such as is present in *Patriofelis*. The posterior border of the palate is slightly thickened and is opposite the posterior end of m^2 .

The brain-case shown in No. 12631 is of much interest. The cerebrum was broad and low, its surface marked by a single broad but shallow longitudinal depression in the position of the lateral sulcus. The preservation of the specimen does not allow the absence of other sulci to be proven beyond question, but there is no indication of their presence. As far as appears from the specimen the brain was intermediate between the lissencephalous type without cerebral convolutions, and the simple convolutions shown in the brain of *Cynohyænodon* and *Cynodictis*. The shallow depression would seem to indicate a less definitely marked sulcus than in *Cynohyænodon*. The cerebellum was broad and low, contrasting with its high, compressed form in *Cynohyænodon* and *Cynodictis*, and completely uncovered, as in most primitive brains. The olfactory lobes, of which the cast is well preserved in No. 11524, were unusually large. In *Cynodictis* they are exceptionally small, in *Cynohyænodon* comparatively small.

The brain-case of *Patriofelis*, according to Wortman, shows two cerebral convolutions.

Skeleton. The limbs and feet are almost completely known in this species, the vertebræ and other parts only partially represented in our collections. The limbs and feet are longer and much more slender than in *Limnocyon verus* but show throughout the near relationship to that species. The size and proportions of limbs and feet compare quite closely with those of the mink (*Putorius vison*) but the backbone is much shorter, smaller and less vermiform, the tail much longer, comparing in these respects more nearly with some of the smaller viverrines. The description is from No. 13081, except as noted.

Vertebræ. The cervicals are about two thirds as long and five sixths as wide as in *P. vison*. The atlas has a much smaller transverse process, separated from the cotylar process by an open notch which represents the groove or foramen for the anterior course of the vertebral artery and for the inferior branch of the spinal nerve at the side of the atlas. In this respect *Thinocyon* agrees with *Sinopa*, *Tritemnodon* and *Synoplotherium*; probably with all Inadaptive Creodonts. In the Dogs, Cats, *Procyon* and *Nasua*, and in *Miacis* this part of the course of the vertebral artery is marked by a deep, narrow groove. In the Bears, Mustelines, Viverrines, Hyænas, *Cercoleptes* and in *Oödetes*, the groove is bridged over, forming a foramen continuous with the vertebrarterial foramen proper in the posterior part of the axis, except for the inferior outlet for the spinal nerve which opens on the under surface of the transverse process. The posterior opening of the vertebrarterial foramen is upon the upper surface of the base of the transverse process as in Canidæ, instead of upon its posterior border as in most Carnivora. In Marsupials the notch in front of the transverse processes is much as in these Inadaptive Creodonts, but the vertebrarterial foramen is absent in the posterior part of the atlas. In Insectivora and most other Placentals the conditions appear to be as in the Mustelines and Viverrines. It is not clear, therefore, which, if either, condition should be regarded as primitive. The remaining cervicals have rather short centra, rather flat and very strongly keeled, slender arches of very small antero-posterior extent, weak transverse processes, narrow zygapophyses, and the neural spines vestigial or absent. The fourth cervical has no spine. The superior lamina of the transverse process is absent upon the sixth and weak or absent upon the fourth; it is usually developed into a strong hooked process in Carnivora. The seventh cervical has no vertebrarterial canal, agreeing with all Placentals and differing from all Marsupials in this important character.

The dorsal vertebræ, so far as they are known, correspond fairly well with those of the genet, and are considerably shorter in the centra than in *Putorius*, the spines longer and directed more uniformly backward. In the anterior part of the series the centra are rather strongly keeled; in the posterior part they are semi-cylindrical. The number of dorsals and lumbar cannot be stated. The lumbar (best preserved in No. 12630) are of moderate length, the centra rather deep, with a strong median ridge beneath in the anterior part of the series. The zygapophyses are strongly convex and concave as in *Mesonyx* and the Hyænodonts, not revolute as in *Patriofelis*.

The sacrum (No. 13081) is relatively large, long and narrow, the transverse processes being but little expanded. The pelvic articulation is almost entirely

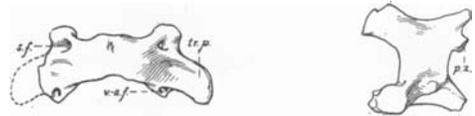


Fig. 62. *Thinocyon medius*. Atlas and axis of No. 12154, natural size. *P. z.*, posterior zygapophysis; *s. f.*, foramen for exit of the spinal nerve; *tr. p.*, transverse process; *v.-a. f.*, vertebrarterial foramen.

with the first sacral, and is extended anteriorly in a long point, as in *Sinopa* and other Creodonts, and in the Viverridæ but not in Mustelidæ. The posterior sacrals are large and longer than in Mustelines, their transverse processes less expanded than in Viverrines. Except in the last character the sacrum is much like that of *Sinopa*. The limitation of the pelvic articulation to the first sacral is presumably a primitive character, approximating the condition in the less specialized Carnivorous Marsupials.¹ The number of sacral vertebræ is three, as in Carnivora generally; in Marsupials the normal number of true sacrals appears to be two. The proximal caudals are nearly as large in proportion to the body as in the Genet, but their transverse processes smaller and much shorter, and the centra keeled inferiorly. The elongation of the caudals does not begin until the sixth or seventh, as in *Patriofelis*. In other Creodonts and Carnivora it begins at the fourth or fifth vertebra. As far as the evidence goes this feature is a family character of the Oxyænidæ. It does not appear in Marsupials or in the Insectivora generally² and is most nearly approximated in some of the long tailed Viverridæ, *Herpestes* especially. The middle caudals in *Thinocyon* resemble those of *Sinopa* and *Tritemnodon* and differ from those of *Patriofelis*, in the expansion of the transverse processes into lateral plates extending the whole

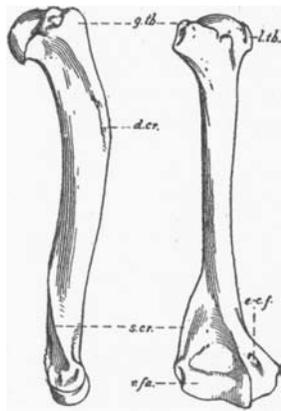


Fig. 63. *Thinocyon medius*. Humerus of No. 12154, anterior and external views, natural size. *D.cr.*, deltoid crest; *e.-c. f.*, entepicondylar foramen; *g.t.b.*, greater tuberosity; *l.tb.*, lesser tuberosity; *r.fa.*, radial facet; *s.cr.*, supinator crest.

length of the caudal. This character appears in *Hoplophoneus*, in two or three of the middle caudals of *Didelphys*, also in *Potamogale*³ and *Pantolestes*, but the correspondence in general form and proportions is not close with any of these genera. The distal caudals are long and slender and of the usual type. The entire number of caudals is not known, but the tail was evidently very long and of moderate thickness, comparing most nearly with the long tailed Viverridæ.

Fore limb. The scapula is rather narrow and elongate, more so than in the Genet, much more than in Mustelidæ. It has a moderately slender neck; the prespinous fossa is narrow and deeply excavated, the postspinous fossa is not as wide as in *Genetta* or *Mustela americana*, the spine a little higher than in *Mustela* but not as prominent as in *Putorius vison*, the form of the acromial process cannot be stated; the coracoid process is longer than in any modern carnivora, but quite slender, unlike Marsupials.

The humerus has the same strongly curved shaft, low deltoid crest and mod-

¹ Not true of the Diprotodonts generally nor of all the Polyprotodonts. It is equally characteristic of some primitive Artiodactyls.

² But in *Potamogale* the elongation of the caudals begins more distally, about the 9th or 10th.

³ As far as I can judge from Allman's figure.

erate distal expansion as in *Limnocyon*, but the shaft is comparatively slim and round, the tuberosities smaller, the supinator crest lower, the epicondyles less massive; the entepicondylar foramen is present and the supratrochlear vacuity absent. In comparison with *P. vison* the principal difference appears in the distal end, the epicondyles being less massive, the articulation of less depth antero-posteriorly, the radial articular surface much less convex and more limited postero-internally, retaining more of the arboreal type. The ulna and radius are much more slender and somewhat straighter in the shafts than in *Limnocyon*, the olecranon is very much shorter, the head of the radius is much less flattened, the distal part of the ulnar shaft is sharply trihedral, owing to the development of the postero-internal border into a sharp crest, as in Mustelidæ and Viverridæ; compared with the mink, the shafts of ulna and radius are a little longer in proportion to the humerus, the ulnar shaft much straighter, the postero-external border lacking the considerable expansion seen in *P. vison*; the postero-internal crest in the distal part of the shaft of *Thinocyon* is lacking in Mustelidæ, but present in Viverridæ; the styloid process is much larger in *P. vison*. The head of the radius lacks the stout process and articular extension seen in the corresponding part of the mink; the shaft is somewhat straighter, the distal articulation has considerably greater depth towards the posterior or plantar surface. Most of these characters are present in Mustelidæ and Viverridæ and may be regarded as primitive.

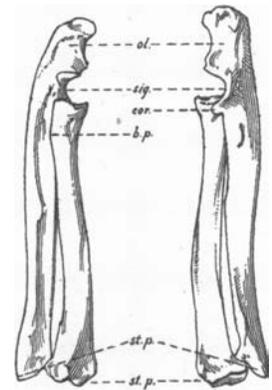


Fig. 64. *Thinocyon medius*. Radius and ulna of No. 12154, anterior and posterior views, natural size. B.p., bicipital process; cor., coronoid process; ol., olecranon; sig., sigmoid cavity; st. p., styloid processes of radius and ulna.

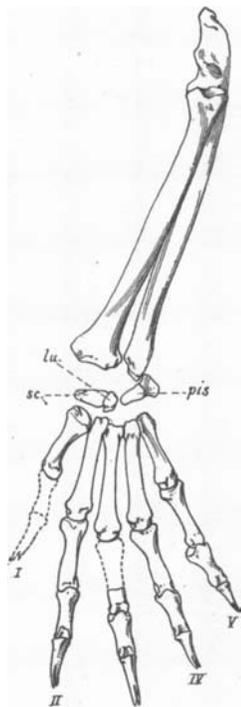


Fig. 65. *Thinocyon medius*. Radius ulna and fore foot of No. 12154, natural size. Lu., lunar; pis., pisiform; sc., scaphoid bones of the carpus.

A large part of both fore and hind foot is present in No. 13081, and in No. 11524 the five metacarpals are preserved in position with most of the carpus and the distal ends of ulna and radius; this specimen also has a considerable part of the hind foot. The description is based upon these two specimens.

Fore foot. The carpus as a whole is remarkably low and broad, as in *Limnocyon* more so than in *Sinopa*, much more than in *Vulpavus*. The scaphoid is separate from lunar and from centrale; the lunar is rather small; the magnum small and narrow with dorsal surface much reduced; the unciform has a narrower lunar contact than in *Sinopa* or *Vulpavus*. In details of construction the carpals agree quite closely with *Limnocyon*.

The five metacarpals are all well developed and functional; the fifth is somewhat smaller in the shaft than the other four. The fourth is incomplete, but the third is considerably longer, and the fifth much shorter than the second, so that the symmetry of the foot was apparently mesaxonic, mc. IV paired with mc. II and mc. V with mc. I. The first metacarpal has a somewhat saddle-shaped proximal facet covering the head as in *Sinopa*; the proximal facet of the second metacarpal is narrower than in *Sinopa*, less oblique than in *Vulpavus*; the unciform facets of metacarpals IV and V are of about equal width. In general the form and relations of the metacarpals agree with those in *Limnocyon* except for much smaller size and greater slenderness, and correspond much more nearly with *Sinopa* than with *Vulpavus*; the shafts of the metacarpals are much less spreading than in the latter genus. The extremely narrow magnum with greatly reduced dorsal surface differs from either and is approached only in *Limnocyon*.

The phalanges are unusually long and slender for a Creodont; the proximal and median series compare in proportions and construction with *Putorius vison*; the unguals are much longer, less compressed, and fissured at the tips. These very long, uncompressed, fissured unguals are quite characteristic of the genus. (Cf. Fig. 3, p. 324.)

Pelvis and Hind Limb. The *pelvis* (No. 13081), is of the same type as in the Hyænodonts, and differs from that of the Eucrodi and Fissipedia in several important features. The ilium is considerably everted at the tip, but not de-curved as in *Sinopa*, and the upper border is expanded into a rather narrow flange above the primitive bar. The flange is not extended as far back toward the acetabulum as in *Sinopa*, and rises less sharply, but gives the same strongly convex sharp edged superior border to the ilium, very different from the straight thick edged upper border of *Miacis* or the smaller Fissipedia. The ischium is long and its tuberosity moderately expanded and not very thick, the spine rather prominent and situate half way down its length, as in *Sinopa*, instead of near the proximal end as in *Miacis* and small modern Mustelines, etc. The obturator foramen is much wider and the pelvis deeper than in the Hyænodonts.

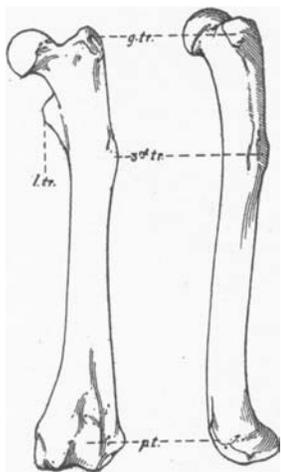


Fig. 66. *Thinocyon medius*. Femur of No. 12154, anterior and external views, natural size. *G.tr.*, greater trochanter; *l.tr.* lesser trochanter; *3rd tr.*, third trochanter; *p.t.*, patellar trochlea.

The *femur* is intermediate in proportions between those of the mink and marten. It is considerably shorter than in *Miacis parvivorus*, the shaft is more slender and not so straight, the head projects more inward and the neck is longer. Like *Miacis* and *Sinopa*, *Thinocyon* retains the third trochanter and the primitive internal

position of the lesser trochanter of the femur, but the third trochanter is placed further down upon the shaft than in *Miacis*, again agreeing with small Hyænodonts. The patellar trochlea is narrow and long, the depth of the distal end of the femur is not great.

The tibia is slightly longer than the femur, with slender and somewhat compressed shaft, the cnemial crest reduced to an obscure process situate a third of the way down the shaft, the trochlear facet ungrooved and very oblique, scarcely separated from the malleolar facet, but more concave anteroposteriorly than in *Miacis*. The malleolar process is much wider anteroposteriorly than in *Miacis*, less prominent and distinct, and ends in a pit distally as in *Sinopa* instead of a convex surface as in *Miacis*. It is straighter and much slenderer in the shaft than in *Limnocyon*, the trochlear facet much more oblique and less grooved.

Hind Foot. The pes is long and slender in comparison with that of *Limnocyon*, agreeing in proportions with *Putorius vison*. The astragalar trochlea is ungrooved and very oblique, the astragalar foramen vestigial, the neck wide and moderately long, the head much flattened. The groove behind the astragalar foramen is narrow, long and deep, instead of comparatively shallow as in *Limnocyon*. The calcaneum has a prominent but ungrooved peroneal process, and its cuboid facet is much less oblique than in *Limnocyon*. The cuboid is comparatively short and wide, as in the larger genus, but its astragalar contact is much more reduced and at the dorsal surface has completely disappeared. As in *Limnocyon*, there is no appreciable overlap of the head of mc. III over the head of mc. IV, and it barely touches the cuboid. Metatarsal I is shorter and slenderer than mt. V; the second, third and fourth metatarsals are sub-equal, the median one slightly longer than the others; but the foot is less clearly mesaxonic than that of *Limnocyon* or *Sinopa*, and approaches the paraxonic type. The styliform process of the fifth metatarsal is less prominent than in either of these genera, much less than in *Vulpavus*. In the remaining details of construction the metatarsals agree with those of *Limnocyon* save that they are much more slender and less spreading; the proportions being nearly those of the mink. The phalanges are like those of the fore foot, but somewhat larger, and the unguals less elongate.



Fig. 67. *Thinocyon medius*. Astragalus of No. 12154, natural size, top view.

Measurements of Thinocyon velox.

	No. 13081	No. 12631	No. 11524
Skull, length from nasals to occipital crest	63.8		
“ “ “ premaxillæ to occipital condyles		72.	
“ width across zygomata	38.	37.2	
“ “ in front of infraorbital foramen	14.	15.2	14.2
“ “ between orbits	19.8	23.	22.2
“ “ of postorbital constriction	13.8	14.1	
“ “ across post-tympanic (mastoid) processes	21.3	27.3	

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	No. 13081	No. 12631	No. 11524
Skull, height of occiput	13.6		
“ width of occipital condyles	16.	17.	
“ occipital condyles to postglenoid processes (incl.)	17.	18.	
“ width between inner borders of glenoid fossæ	14.		
“ “ across pterygoid plates	8.2		9.6
“ “ “ palate at m ²	24.	23.8	28.
“ “ “ “ “ canines	12.6	13.	
Upper dentition, c-m ²	32.5	34.	
“ “ premolar-molar series	27.6	26.5	
“ “ premolars	18.2	18.	
“ “ true molars	9.	8.8	8.8
P ⁴ antero-posterior dimension	5.1	5.8	5.7
M ¹ “ “	6.4	5.9	6.3
“ transverse “	5.8		5.3
M ² antero-posterior “	3.		3.2
“ transverse “	6.8		7.4
Lower jaw, total length (estimated) except on 12631	53.	57.	55.
Lower jaw, depth beneath m ₂	6.3	6.	8.8
“ “ height from angle to top of coronid process	21.		
“ “ thickness beneath p ₄	4.2	4.5	5.2
Lower dentition c-m ₂		35.5	37.6
“ “ premolar-molar series	29.2	28.	29.5
“ “ premolars	17.9	18.	18.5
“ “ true molars	12.		11.5
M ₁ , antero-posterior diameter	5.6		5.0
“ transverse “	3.1		3.1
M ₂ , antero-posterior “	6.7		6.8
“ transverse “	3.9		3.9
Atlas width across transverse processes	18.3	22.	
“ “ of occipital cotyli	13.9	16.	
“ antero-posterior dimension	9.7	10.3	
Axis length of centrum and odontoid process			
“ width across atlanteal facets	10.		
Humerus length			53.
“ greatest diameter of proximal end	9.1		
“ “ “ shaft	3.5		
“ transverse “ of distal end	11.		
Ulna, length including olecranon	42.		
“ width of shaft near proximal end	3.8		
“ “ “ “ “ distal end	3.		
Radius, length	31.2		
“ width of head	5.		6.
“ “ “ distal end	5.6		
“ depth “ “ “	5.		
Width of five metacarpals in position at proximal end			11.6

	No. 13081	No. 11524
Metacarpal II, length	13.3	
“ IV, “	16.5	
“ V, “	10.	
Proximal phalanx of 3rd digit, length	8.3	
Middle “ “ “ “ “	5.2	
Ungual “ “ “ “ “	6.1	
Pelvis, length	47.	
“ width of acetabulum	6.3	
“ length of ischium, from acetabular border	16.	
“ long diameter of obturator foramen	13.2	
Femur, length	47.	60.5
“ width of proximal end	11.	14.4
“ “ “ shaft	4.	5.7
“ “ “ distal end		12.
“ depth of “ “	10.	11.1
Tibia, length	est.50.	63.7
“ width of shaft	3.2	3.8
“ “ “ distal end		7.9
Astragalus, length	10.	
“ transverse diameter of body	6.9	7.4
“ depth of body	4.8	5.2
“ width of head	4.3	
“ thickness of head	2.7	
Calcaneum, length, including tuber	13.9	
“ width across peroneal process and sustentaculum	8.	
Cuboid, length	5.1	6.1
“ width	4.4	4.9
Metatarsal I, length	14.7	17.8
“ III, “	23.2	
“ IV, “	22.6	26.8
“ V, “	18.	

Thinocyon medius Wortman.

Text figures 62-70.

Dr. Wortman distinguished this species from *T. velox* Marsh by size and the characters of the superior teeth, based upon incorrect association of upper teeth with Marsh's species. None of the characters assigned are valid. There are, however, certain constant differences between the *Thinocyons* in the Lower Bridger and those in the upper beds, and some of these are indicated in his drawings of the type specimens of the two species, that of *T. velox* coming from the lower, and *T. medius* from the upper horizon.

The principal distinction in the dentition is in the fourth premolar, which in *T. medius* carries a distinct anterior basal cusp, absent in *T. velox*. The size is not a constant distinction, although the teeth are usually larger and more

robust in *T. medius*. There are numerous small differences throughout the skull and skeleton, all in the direction of greater size and more robust proportions, in the later species, but the constancy of these characters is doubtful without comparison of a larger series of specimens than is at present accessible. To this species I refer the following specimens, all from the Upper Bridger:

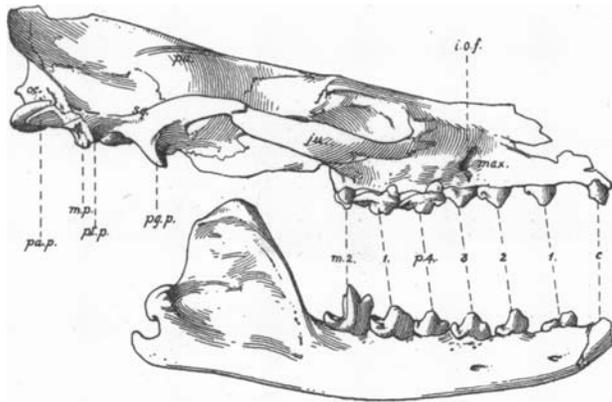


Fig. 68. *Thinocyon medius*, skull and jaws of No. 12154, natural size. Upper Bridger. Lettering as in Fig. 53.

- No. 12075. Lower jaw.
- No. 12077. Front part of skull, teeth broken off.
- No. ?11553-4. Lower jaws.

- No. 12154. Skull, jaws, a few vertebræ, several limb bones, fore feet, calcaneum and astragalus. Paul Miller.
- No. 11529. Lower jaw and fragments of skeleton.

The sagittal crest is higher than in *T. velox* and extends further forward. The skeleton otherwise closely resembles that of *T. velox*. The fore feet are mesaxonic, the 1st and 5th digit having approximately the same length and weight; both are somewhat divergent and the head of mt I has but little lateral convexity. The claws are long, not much compressed, and rather deeply fissured, and the phalanges are disproportionately long as compared with the metacarpals.

***Thinocyon cledensis* sp. nov.**

This species is based upon a lower jaw from La Clede Meadows in the Washakie Badlands, No. 1742. It is about the size of *T. velox*, but with more slender jaw and smaller canines, and the first premolar is single-rooted. The dentition is otherwise similar to that of *T. velox*, and the fourth premolar has no anterior basal cusp. The chief interest of the species is its approximation to *Oxyænodon*.

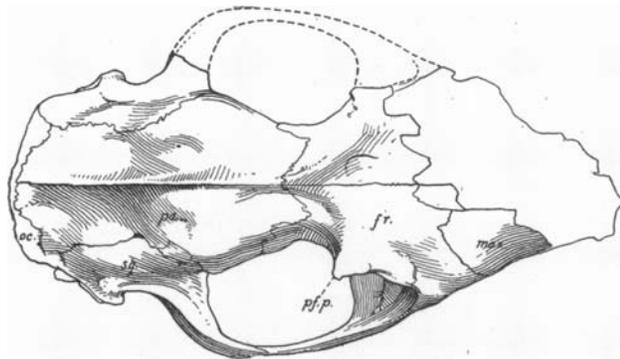


Fig. 69. *Thinocyon medius*, skull of No. 12154, top view, natural size.

Thinocyon mustelinus sp. nov.

The type, No. 12635, consists of parts of the upper and lower jaws and various fragments of the skeleton. It is one fifth smaller (linear) than the smallest specimens of *T. velox*.

The teeth are more compressed, the oblique shear of the carnassials more antero-posterior. The protocone of M^1 is smaller and the parastyle more angulate, and more external in position; the jaw is somewhat more slender. The form and proportions of the limb bones are very much the same as in *T. velox*, except for the smaller size and less development of the muscular attachments. The astragalar trochlea is flat and the calcaneum has a small fibular facet.

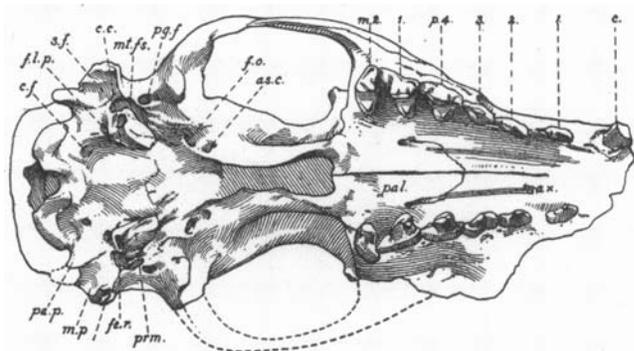


Fig. 70. *Thinocyon medius*, skull of No. 12154, under view, natural size. Lettering as in Fig. 2.

Length of p_2 - m_2	21.9, of m_{1-2}	10.0
Diameters of m^1 , antero-posterior	4.7	transverse 5.0
“ “ m_1	5.1	“ 2.9
“ “ m_2	5.2	“ 2.8
Length of calcaneum		12.3
Diameter of head of humerus, antero-posterior		6.8

Machæroides gen. nov.

This remarkable little genus is known only from the lower jaw, but appears to indicate a branch of Oxyænidae which in some respects paralleled the sabretoothed cats. The anterior end of the lower jaw is flanged, and in proportions and appearance remarkably similar to *Dinictis* or *Nimravus*. The lower premolar and molar teeth are highly compressed, and tend not a little toward the type of the more primitive Machærodonts. The dentition is, however, that of an Oxyænid, with four two-rooted premolars, and two molars of equal size, and the form of the symphysis likewise indicates Oxyænid affinities. With a better knowledge of the genus it would probably be necessary to place it in a distinct sub-family of equal rank with Oxyæninae and Limnocyoninae, but for the present I refer it to the latter group. The generic characters are:

Dentition $I_{\frac{7}{3}}$, C_1 , P_4 , M_2 . Lateral incisor large, one or two small incisors median to it. Lower canine rather small, compressed oval in section, obliquely set, resembling that of *Dinictis*. Lower premolars two-rooted, compressed,

the third and fourth with trenchant anterior and posterior basal cusps. Lower molars of equal size, with vestigial metaconid, small trenchant heel, and somewhat compressed and blade-like paraconid and protoconid, with nearly antero-posterior shear. Lower jaw angulate and slightly flanged anteriorly, the symphysis obovate in form, wide postero-inferiorly as in Oxyænidæ; in Machærodonts and Felidæ it is wide antero-superiorly. Mental foramina beneath postcanine diastema and p_2 .

Machæroides eothen sp. nov.

Based upon two lower jaws from the Lower Bridger beds, No. 12644, type, and No. 11523 paratype. A single first lower molar from the Upper Bridger agrees with the species from the lower beds.

Species characters: Size less than *Limnocyon verus*, smaller than any true Machærodonts. P_1 with a short diastema in front and a shorter one behind it; remaining teeth close set. Heel of p_4 somewhat bifid. Lower jaw deep and laterally compressed, depth nearly uniform.

Relationship: If our inferences from the characters of the lower jaw and teeth are correct, this genus offers a remarkable case of parallelism with the Machærodontidæ. Indeed, if we should disregard the relationship with the more completely known Oxyænidæ, *Machæroides* might very well be considered as a primitive type from which the Machærodonts and Felidæ were derivable, by reduction of the last molar and the anterior premolars and by further specialization of the posterior premolars and first molar. In view, however, of its very

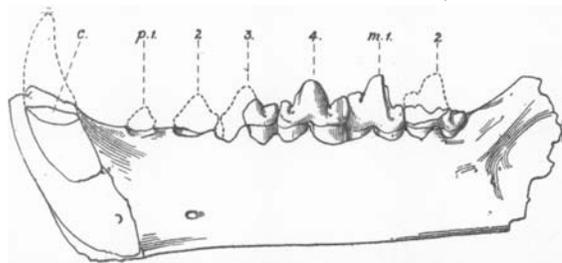


Fig. 71. *Machæroides eothen*, lower jaw, natural size, external view. Type specimen No. 11523.

evident and comparatively close relations with *Limnocyon* and *Thinocyon*, of the identity in type of symphyseal suture with this group of Creodonts, and the correspondence of the teeth in proportions and structure, I think we are obliged to assume a correspondingly near relationship in skull and skeleton. If this assumption be correct *Machæroides* cannot stand in any ancestral relationship to the

Felidæ, for in skull and skeleton this family is not derivable from Oxyænid ancestry, but along with all the Fissipede Carnivora, from Adaptive Creodonts. If *Machæroides* be an Oxyænid we must ascribe to it not only the differently placed carnassial (less specialized in this than in some of the other genera) but also the peculiarities of the occipital and basiscranial regions, the mesaxonic foot and fissured claws, which are distinctive of this family. The hypothetical ancestor of the Felidæ should not only have the carnassial placed as in the Adaptive Creo-

donta, but should share with them the peculiarities of occipital and basicranial regions, paraxonic foot and unfissured claws which are common to all Fissipedes and their Eocene ancestors. It should hold the same relations to *Viverravus* that *Machæroides* does to *Limnocyon*.

It may be observed in support of this view that the angle of the symphysea, plane to the tooth line is considerably less than in *Dinictis*, indicating that the jaws did not spread so widely at the back, and hence that the facial part of the skull was by no means so wide as in *Dinictis* and the cats generally.

3. Measurements.

	Type	11523
Dentition, length from i_3 to m_2 (canine from 11523)	58.5	
Premolar series p_{1-4} including diastemata	29.5	27.5
True molars, m_{1-2}	16.	
P_4 , antero-posterior diameter	8.7	8.5
“ transverse	4.	
M_1 , antero-posterior	8.	8.3
“ transverse	3.3	
M_2 , antero-posterior diameter	8.2	
“ transverse	4.	
Lower jaw, depth at post-canine diastema		18.3
“ “ “ behind p_4	14.5	16.
Symphysis, width on inferior border		14.3
“ “ on superior “ (approximate)		4.
“ depth on anterior border “		23.

3. Family HYÆNODONTIDÆ Leidy.

The typical Hyænodonts are a rather highly specialized group of the Creodonta of the Oligocene and uppermost Eocene in Europe and America. They have a marked cursorial adaptation in the limbs and feet, and a highly specialized predaceous adaptation of the teeth, with the molars completely converted into shearing blades, m_2^3 being the carnassials. In consequence of the mesaxonic symmetry of the feet, the podials show a considerable degree of parallelism with the more digitigrade perissodactyls, just as in the Mesonychidæ the paraxonic foot develops in the cursorial adaptation more or less parallel to the more digitigrade artiodactyls. In either case the podials tend to become more quadrate and compact, their lateral mobility reduced, the metapodials appressed and their distal ends more or less converted into hinge joints, the phalanges short, the unguis broadened and assisting in the support of the foot. In *Hyænodon* the lateral digits are much reduced in the hind foot, less so in the fore foot. The astragalar trochlea is deepened, the head reduced laterally and extended vertically.

Sinopa and *Tritemnodon* from the Lower and Middle Eocene appear to

represent the early stages of the Hyænodont phylum, as was pointed out by Wortman in 1894, and confirmed by the extended study of the entire skeleton (Matthew, 1906). Scott has regarded this group as morphologically ancestral to both Oxyænidæ and Hyænodontidæ, which is true in a broad sense so far as the

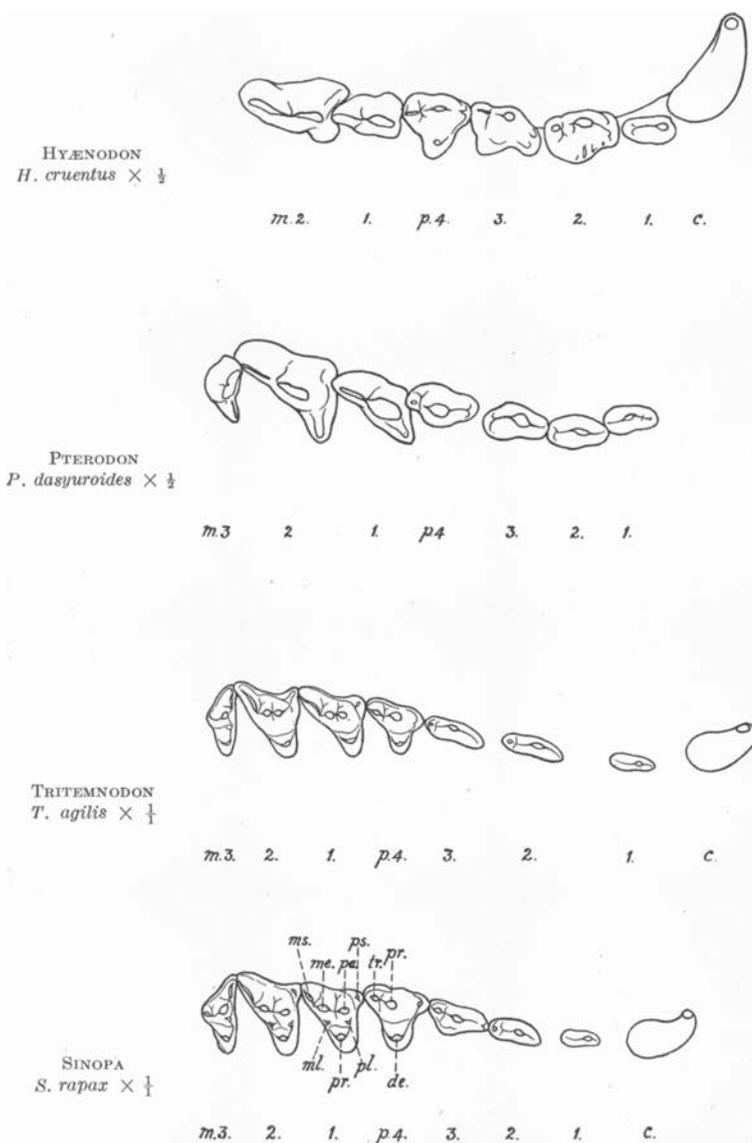


Fig. 72. Upper Teeth of Hyænodontidæ. Lettering: *de*, deuterocoene; *me*, metacone; *ml*, metaconule; *ms*, metastyle; *pa*, paracone; *pl.*, paraconule; *pr.*, protocone; *ps.*, parastyle; *tr.*, triticoene.

dentition is concerned, and on this ground retains (1894) the arrangement of Cope and Schlosser in placing them in a distinct family (Proviverridæ Schl., Leptictidæ Div. II, Cope). The characters of the skull and skeleton, however, enable us to place them definitely in the Hyænodont series and exclude them from any morphologic ancestry to the Oxyænidæ, and on this account it is better to include them as a primitive subfamily of Hyænodontidæ. *Proviverra*, *Quercytherium*, *Galethylax* and *Prorhyzæna* although less completely known, appear to be related to *Sinopa*, and *Cynohyænodon* is certainly a near relative. These genera with *Sinopa* and *Tritemnodon* constitute the typical group of Proviverridæ (Schlosser, 1886) and the family name is therefore applicable in a subfamily

sense to these primitive Hyænodonts. The remaining genera which have been placed under the Proviverridæ are referable to other groups; *Deltatherium* to the Oxyclænidæ, *Hyænodictis* to the Mesonychidæ, *Palæosinopa* to the Pantoles-

tidæ (Insectivora), *Didelphodus* probably to the Insectivora but of uncertain relationship; *Thylacomorphus* to the Artiodactyla (it is probably identical with *Diplobune*).

Classification.

Hyænodontidæ: Molars $\frac{3-2}{3}$. Carnassial teeth m_3^2 , anterior molars and p_4^1 with a subordinate shear. Skull elongate, narrow. Lachrymal with a considerable facial expansion, orbit well defined anteriorly and lachrymal foramen internal. Basi-cranial region narrow, occiput high and narrow. Frontals deeply concave between the orbits. Limbs and feet exhibiting various stages in cursorial adaptation; feet mesaxonic; a fibulo-calcaneal facet and reduced or vestigial astragalocuboid contact. Unguals fissured, non-retractile. Centrale, lunar and scaphoid separate (except in certain species of *Hyænodon*); tympanic bulla usually incomplete or absent (said to be complete in certain species of *Hyænodon*).

Proviverrinæ: Molars tritubercular above, tuberculo-sectorial below, metaconids present, carnassial specialization less advanced. Body vermiform, limbs and feet specialized.

A. Premolars long, spaced anteriorly.

Sinopa. Paracone and metacone well separated. Heels of lower molars basin-shaped.

Tritemnodon. Paracone and metacone closely connate. Heels of lower molars reduced, trenchant.

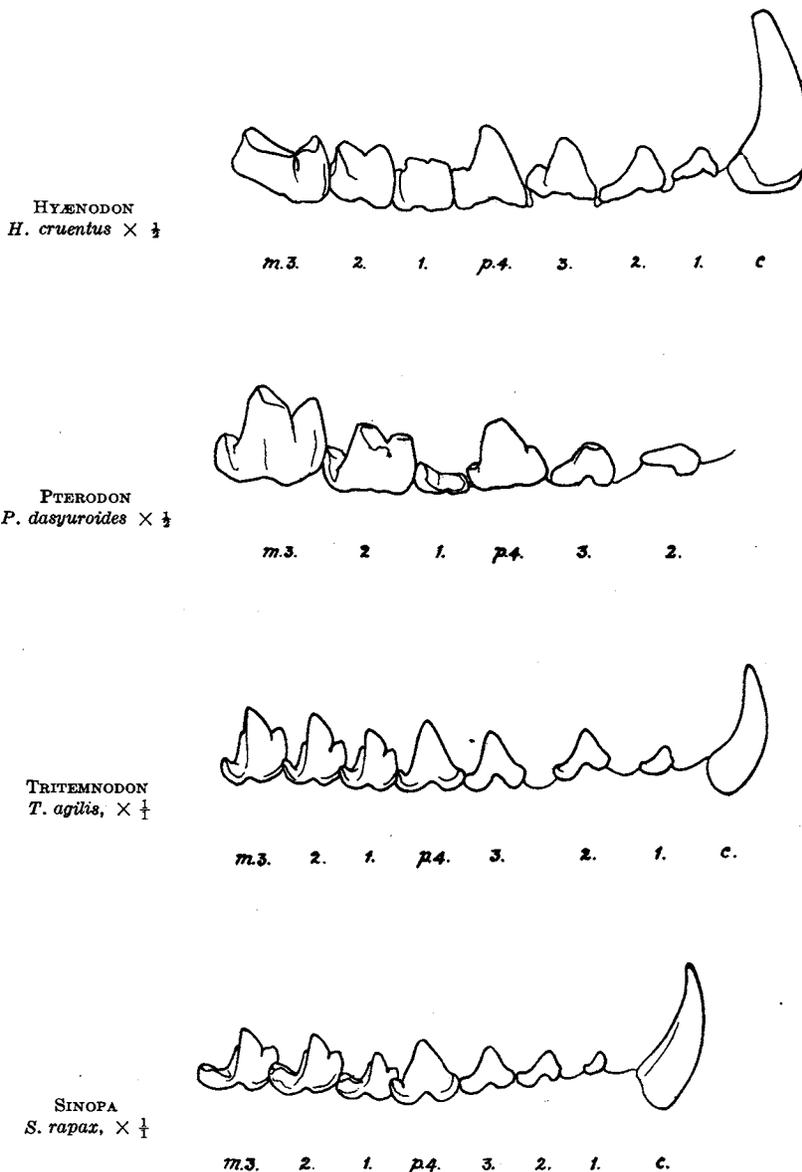


Fig. 73. Lower Teeth of Hyænodontidæ.

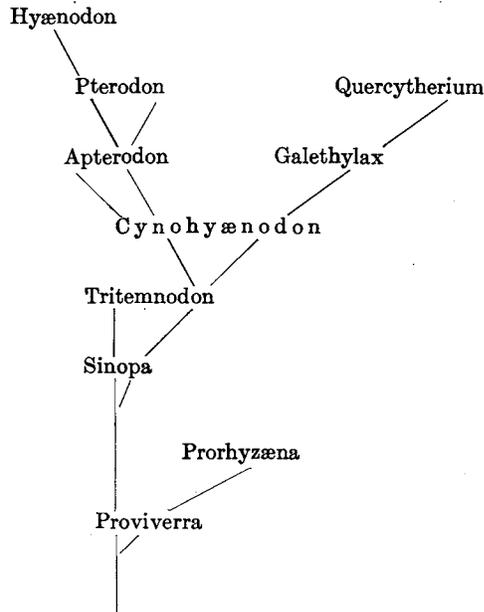
- B. Premolars short and high.
Proviverra. Paracone and metacone well separate.
Cynohyænodon. Paracone and metacone closely connate.
- C. Anterior premolars robust, enlarged.
Galethylax, *Quercytherium*.
- D. Premolars much reduced and crowded, jaw short.
Prorhyzæna.
- Hyænodontinæ*. Molars sectorial, metaconids absent, carnassials more specialized. Body more compact, limbs and feet cursorial.
- A. Molars $\frac{3}{3}$, last molar transverse. Protocones small. Premolars comparatively short and high. Talonid small, trenchant.
Apterodon. Paraconid smaller, heel larger.
Pterodon. Paraconid larger, heel smaller.
- B. Molars $\frac{3}{3}$. Protocones and talonids absent.
Hyænodon.

The Hyænodonts have no very close analogues among modern Carnivora. The Proviverrinæ correspond more or less in adaptation with the civets; the Hyænodontinæ are more nearly comparable in adaptation with the Thylacines than with any of the true carnivora, although in certain respects they parallel the hyænas and dogs. The relative position of the typical Hyænodonts is sufficiently clear — they were the cursorial group of carnivora in that epoch, just as the Canidæ and Hyænidæ are now among the true carnivora, and the Thylacine among the carnivorous marsupials. But the specialization of the Bridger genera is much less advanced, not more than in *Viverra* among the modern Civets.

Geological and Geographical Distribution of the Hyænodontidæ.

		N. AMERICA	EUROPE	AFRICA
Oligocene	Middle	Hyænodon	Hyænodon	
	Lower	Hyænodon Pterodon ?Pseudopteron	Hyænodon Pterodon ?Pseudopteron Apterodon Cynohyænodon Galethylax Quercytherium	
Eocene	Upper			Pterodon Apterodon "Sinopa"
	Middle	Tritemnodon Sinopa	Sinopa Proviverra Prorhyzæna	
	Lower			
	Basal			

The approximate relationship of the genera is represented in the following diagram.



The diagram indicates six branches which culminate successively in *Prorhyzæna*, *Tritemnodon*, *Quercytherium*, *Apterodon*, *Pterodon* and *Hyænodon*. *Prorhyzæna* has molars of very little carnassial specialization and a very short high premolar, a crowded tooth row and a short face, as the comparison with *Rhyzæna* (= *Suricata*) indicates. *Tritemnodon* has three shearing molars of more specialized type, and elongate premolar region as in the dogs. *Quercytherium* is distinguished by the heavy, robust premolars and moderately short face. In African species of *Apterodon* the teeth show a marked tendency to lose their trenchant and sectorial character and acquire round, blunted cusps; but this is not obvious in the typical European species. In *Pterodon* the shear of the molars is more developed, and the carnassial specialization concentrated upon $\frac{m^2}{m^3}$, the jaw robust and short with stout high premolars. *Hyænodon* carries the shearing and carnassial specialization to an extreme, but with a long slender jaw, especially in the American species. The remaining genera show earlier stages of these specializations and are more or less exactly intermediate. The main line of descent of *Hyænodon* may be regarded as passing through the genera *Proviverra*, *Sinopa*, *Tritemnodon*, *Cynohyænodon*, *Apterodon* and *Pterodon*, but in each case through hypothetical marginal species, not through any of the typical or known species. The same is more or less clearly evident with the side branches above noted. It would appear from this fact, and from the known distribution of the genera, as shown in the preceding table, that the evolutionary centre of the family was not in Europe, North America or Africa, at least not in

	EOCENE						OLIGOCENE				
	Lower		Middle			Lower		Lower	Middle		
	Wasatch	Wind River	Lower Huertano	Upper Huertano	Lower Bridger	Upper Bridger	Lower Washakie	Middle Uinta	Upper Uinta	Lower White River (Titanotherium beds)	Middle White River (Oreodon beds)
(<i>Sinopa</i> or <i>Tritemnodon</i>) <i>whitæ</i> (Cope) 1882		×									
<i>Sinopa rapax</i> Leidy 1871					×	?	×				
“ <i>pungens</i> (Cope) 1872					×	?					
“ <i>major</i> Wortman 1902					?	×					
“ <i>minor</i> Wortman 1902					×						
“ <i>grangeri</i> Matthew 1906					×						
<i>Tritemnodon agilis</i> (Marsh) 1872					×						
HYÆNODONTINÆ.											
? <i>Pseudopteron</i> <i>minutus</i> (Douglass)										×	
<i>Hemipsalodon</i> (= <i>Pterodon</i>) <i>grandis</i> Cope 1885										×	
<i>Hyænodon</i> sp.										×	
<i>Hyænodon horridus</i> Leidy											×
“ <i>cruentus</i> Leidy											×
“ <i>crucians</i> Leidy											×
“ <i>leptocephalus</i> S. & O.											×
“ <i>paucidens</i> O. & W.											×
“ <i>mustelinus</i> Scott											×
“ <i>montanus</i> Douglass											×

Sinopa Leidy 1871.

Syn. *Stypolophus* COPE 1872; *Prototomus* COPE 1874; *Limnocyon* MARSH 1872, in part.

This genus was established by Dr. Leidy in 1871 on the species *S. rapax*. *Stypolophus* Cope 1872 was regarded by its author as distinct from *Sinopa* although closely allied, and a number of Middle and Lower Eocene species were referred to it and fully described and figured in "Tertiary Vertebrata." *Prototomus* Cope 1874 was founded on an erroneous association of upper and lower dentition and subsequently referred by its describer to *Stypolophus*. Scott in 1892 united *Stypolophus* with *Sinopa* and this identification has been accepted by subsequent authors. Wortman and Matthew in 1899 referred *Limnocyon* to the same genus, but in 1902 Wortman removed *Limnocyon*, except *L. agilis*, to the Oxyænida. Matthew in 1906 separated *L. agilis* as the type of *Tritemnodon*, nearly related to *Sinopa* but generically distinguishable.

As thus limited, *Sinopa* includes a number of species from the Wasatch, Wind River, Bridger and Washakie formations. Four or five valid species may be distinguished in the Bridger and five or six in the Lower Eocene; the latter may with more complete material be found generically distinct from the Middle Eocene

Sinopas, as Cope has already noted (Tertiary Vertebrata, p. 290), and the genus *Prototomus* revived. In dentition some of the lower Eocene species are more or less intermediate between *Sinopa* and *Tritemnodon*, others are aberrant.

The genus is defined as follows:

Dentition $\frac{3.1.4.3}{3.1.4.3}$. Upper molars $1-2$ triangular with metacone and paracone well separated, metastyle extended into a postero-external shearing blade; lower molars tuberculo-sectorial, with basin heels of moderate size, and well developed metaconids. M_{2-3} subequal, m_1 smaller. M^3 transverse, triangular, unreduced, with distinct metacone and strong parastyle. Premolars elongate, compressed, moderately high, jaw symphysis loose, long and shallow. Anterior premolars spaced, P_1 one-rooted, P^1 two-rooted.

Skull elongate, both in facial and cranial regions, muzzle slender, zygomatic arches rather light and not much expanded. Tympanic bulla absent. Occiput narrow and rather low. Vertebral formula C_7, D_{13}, L_7, S_3 , caudals numerous.

Neck of moderate length, trunk rather slender, tail long and heavy. Limbs moderately long, feet functionally pentadactyl, mesaxonic, semi-digitigrade, claws moderately compressed, fissured at the tips. Astragalar trochlea slightly grooved, astragalar foramen vestigial. Calcaneum with distinct fibular facet and well developed peroneal tubercle.

The characters of the genus are given at length and its affinities more fully discussed in an article by the writer published in Bull. U. S. Nat. Mus., 1906.

The species may be distinguished as follows:

A. Middle Eocene species:

S. rapax Leidy. $C_1-m_3 = 64$ mm.; $m_{1-3} = 25$ mm. Lower canines with thin compressed laniary posterior edge. No diastema between p_2 and p_3 . M_{2-3} subequal. Protocone of p_4 compressed, blade-like, posterior accessory cusp rudimentary.

S. granjeri Matthew. $C_1-m_3 = 74$ mm.; $m_{1-3} = 26$ mm. Lower canines somewhat compressed on posterior border. A diastema between p_2 and p_3 . M_3 smaller than m_2 . Protocone of p_4 less compressed, with rounded tip, posterior accessory cusp distinct. Teeth more robust, skull and skeleton larger than the preceding.

S. pungens (Cope). M_{1-3} (est.) = 20 mm. m_{2-3} sub-equal.

S. minor Wortman. $M_{1-3} = 18.7$ mm.; m_{2-3} sub-equal or m_3 smaller.

S. major Wortman. $M_{1-3} = 29$ mm.; m_{2-3} subequal. Teeth more robust than in any of the preceding, heels of molars larger and broader, trigonids lower and cusps of more nearly equal size. Protocone of P_4 less compressed, tip rounded, posterior accessory cusp distinct. Diastema between p_3 and p_4 slight or none.

B. Lower Eocene species:

Sinopa opisthotoma Matthew. $C_1-m_3 = 80$ mm. (est.): $m_{1-3} = 31$. Third lower molar enlarged, protoconid-paraconid shear more antero-posterior, reduced metaconid and small compressed heel. P^a and m^e of upper molars well separated, m^3 unreduced.

Sinopa hians (Cope). $C_1-m_3 = 68$ mm.; $m_{1-3} = 25$. M_2 and m_3 subequal, shear normal (half-way between transverse and antero-posterior axes). P^a and m^e of upper molars rather closely connate; m^3 reduced with vestigial m^e .

Sinopa strenua (Cope). $m_{1-3} = 23$. m_3 smaller than m_2 , shear more antero-posterior ($55^\circ-60^\circ$ from transverse).

Sinopa viverrina (Cope). $m_{1-3} = 13.5$. P^4 less molariform than in the larger species.

Sinopa multicuspis and *secundaria* are of doubtful validity.

Sinopa whitie of the Wind River is intermediate between *Sinopa* and *Tritemnodon* but nearer to the latter genus.

Some of the Bridger species show considerable variability and it is not at all certain that their number should not be increased. *S. rapax* is the most abundant, and is fairly constant in characters; the complete skeleton is known in this species and in *S. grangeri*. The remaining species are known only from jaws and fragmentary skeletons. *S. pungens* is clearly distinguishable from *S. rapax* with which Wortman united it, but it is very doubtful whether it is distinct from *S. minor* which appears to be very variable in size and proportions. *S. major* is well distinguished from the remaining species, and includes two well marked varieties in size.

Sinopa rapax Leidy 1871.

Plate XLV, Figs. 1 and 2; Plate XLVI, Fig. 2.

Proc. Acad. Nat. Sci. Phila., 1871, p. 115, July 11.

The type is part of a lower jaw with p_4 - m_3 , the trigonid of the second and the entire crown of the third molar broken off. It was found at Grizzly Buttes, Horizon B₂. I refer to this species four specimens from the Lower Bridger the first three found by Mr. Granger, the last by Mr. Thomson.

No. 11535. Skull, jaws, many vertebræ and most of the limbs and feet. Hor. B₂, Grizzly Buttes.

No. 11530. Skeleton without skull including all the presacral vertebræ and many caudals, ribs and most of limbs and feet. From Horizon B₃, Cottonwood Creek.

No. 11534. Skull and jaws, crushed flat. Horizon B₂, Millersville.

No. 11542. Lower jaws, good dentition. Horizon B₂. Grizzly Buttes.

Other more fragmentary specimens are probably referable. I have not seen any specimens from the Upper Bridger which are properly referable to *S. rapax*, but a specimen from the top of the Lower Washakie apparently represents a more advanced variety.

The species is of medium size and characters, but distinguished by a marked tendency in the lower canine and p_4 to assume a trenchant blade-like form. This is more developed in the Washakie specimen than in those from the Lower Bridger. It is smaller than *S. grangeri*, the skull less elongate, the teeth less robust and the jaws more slender anteriorly. The absence of diastema between p_2 and p_3 appears to be a constant character, and the subequal size of m_2 and m_3 , the longer and more trenchant p^3 , smaller deuterocone on p^4 and greater transverse extension of m^3 , further serve to distinguish it from *S. grangeri*. The skull is smaller, the limbs and feet less robust, but in the other characters the skeleton closely resembles that of *S. grangeri* as described and figured by the author in 1906.

***Sinopa rapax* mutation *lania*.**

Plate XLV, Fig. 3; Plate XLVII, Fig. 1.

No. 13142 from the Lower Washakie, found by Walter Granger in 1906, consists of the skull and jaws, fore and hind limbs and feet and about 16 vertebrae, of a *Sinopa* which is very closely allied to the typical *S. rapax* of the Lower Bridger, but shows in a more marked degree the trenchant laniary canines characteristic of that species. As there is but one of the Bridger specimens in which these teeth are perfectly preserved and the Washakie specimen agrees very nearly with those from the Bridger in most respects, I do not think that the evidence warrants its being regarded as a distinct species, although from a considerably later horizon.

The teeth in this specimen are unworn and very perfectly preserved, the animal having not quite reached maturity. The upper incisors are small, pointed, with large external and small internal cuspules, and slight posterior heels. The lower incisors have no posterior heels but are otherwise like the upper ones. The upper canine is of trihedral section, with posterior ridge and flattened anterior face. The lower canine is compressed and its posterior border is produced into a thin knife-like ridge. The remaining teeth are much like those of the Bridger specimens but more compressed, and the metacone of m^3 and metaconid of m_3 reduced. The skull is somewhat smaller, the sagittal crest lower, the limb bones and foot a little smaller and more slender; but these characters are probably associated with the immaturity of the specimen.

***Sinopa grangeri* Matthew, 1906.**

The type, Nat. Mus. No. 5341, consists of a nearly complete skeleton in excellent preservation and was described in the Proc. U. S. Nat. Mus., Vol. XXX, pp. 203-233, pl. XVI, and text figs. 1-20. There are no additional specimens in our collection which can be certainly referred to it.

***Sinopa pungens* (Cope, 1872).**

Stypolophus pungens COPE, Pal. Bull. No. 2, Aug. 3; Tert. Vert., p. 291, pl. xxiv, fig. 8.

Sinopa pungens SCOTT, 1892; MATTHEW 1899A, p. 40, 1901A, p. 24; 1906, p. 209, fig. 2b.

= *Sinopa rapax* WORTMAN, 1902; p. 436.

?*Sinopa minor* WORTMAN, 1902; p. 17, in part at least.

Dr. Wortman has identified this species with *S. rapax* on the ground that a specimen in the Marsh collection agrees equally well with both types. The type of *S. pungens*, however, is about a fifth smaller than the type of *S. rapax*, or any of the referred specimens, including the one figured by Wortman. It is more difficultly separable from *S. minor* Wortman, with which it agrees rather nearly

in size, in depth of jaw and character of the heel of m_2 , the only comparable portion of the dentition.

There are thirteen fragmentary specimens in the American Museum collections of 1903-6 representing one or more species of *Sinopa* considerably smaller than *S. rapax*. They vary from 18 to 20 mm. in length of m_{1-3} , and m_3 is equal to or smaller than m_2 . The teeth are more compressed in the smaller specimens, the jaw more slender anteriorly. The latter agree best with Wortman's type of *S. minor*, the larger specimens with the type of *S. pungens* and presumably the large variety of *S. minor* mentioned by Wortman. I provisionally retain the two species as distinct and refer only the larger individuals above mentioned to *S. pungens*. One specimen, No. 12637, from Church Buttes, Horizon B₂, is more or less intermediate between *S. pungens* and *S. rapax*; m_3 is of the size of *S. pungens*, m_2 considerably larger, and the jaw much deeper; the spacing of p_1 is much less than in *S. rapax* or *S. minor* and the teeth decidedly smaller throughout than in Leidy's species. It may represent another species or an aberrant individual of *S. rapax* or *pungens*. Two fragmentary specimens from the Upper Bridger indicate a species comparable with *S. pungens* in size but the teeth are too much broken for any exact comparison.

***Sinopa minor* Wortman 1902.**

This species (or variety of *S. pungens*) is distinguished from *S. rapax* by the size, one-fourth smaller, the more compressed teeth, jaw shallower especially anteriorly, m_3 one-tenth to one-sixth smaller than m_2 . Nos. 11532, 11546, 12639, 11540, 11539 and several uncatalogued specimens agree fairly well with Wortman's types. The characters of the canine and fourth premolar are unknown, and the various fragments of limb bones and vertebrae do not show any distinctions from the larger species except in smaller size and more slender proportions.

The above specimens are from the lower beds.

***Sinopa major* Wortman.**

Plate XLV, Fig. 4.

This large and well distinguished species is represented in our collections by four specimens from the Upper Bridger. The type is stated to be from Church Buttes, in the lower beds. Two of the specimens, No. 11538, lower jaw and p^4 , and 12079, a complete lower jaw, agree in size with the type, the others, No. 12080, upper jaw, and No. 12081, lower jaw with teeth broken off are about one-fifth smaller linear, and better material would probably show them to be distinct species, but for the present I refer them to *S. major*.

The lower molars have larger, broader heels, lower trigonids and smaller protoconids than in *S. rapax*, *grangeri*, *pungens* or *minor*. The fourth premolar is much like that of *grangeri*. There is no diastema between p_2 and p_3 . The

upper molars in No. 12080 have the paracone and metacone more widely separated, and the connules more distinct, the protocone less compressed than in any of the smaller species.

INDETERMINATE SPECIES.

“*Stypolophus*” *aculeatus* Cope.

Triacodon aculeatus COPE, Pal. Bull. No. 1, dated July 29, 1872; Tert. Vert., pl. xxiv, figs. 6, 7. Not *Stypolophus aculeatus* Cope, Tert. Vert., p. 299, pl. xxvi, figs. 1-2.

Type the trigonid of a lower molar described and figured by Cope, but subsequently mislaid.

From Cope's figure this specimen apparently belongs either to *Sinopa*, *Limnocyon* or one of the Miacidæ. In size and proportions it agrees approximately with *Uintacyon major*, *Limnocyon verus* and *Sinopa grangeri* among known species, but as it is impossible to identify it with certainty I have elsewhere (1901A) suggested that the species must be set aside as indeterminate. The Wasatch specimen in the Princeton Museum referred to the species by Cope and described in Tertiary Vertebrata, cannot be regarded as a neotype, since it comes from a different locality and horizon, the Wasatch and Bridger carnivora being specifically distinct throughout.

“*Stypolophus*” *insectivorus* Cope.

Stypolophus insectivorus COPE, Pal. Bull. No. 3, dated Aug. 7, 1872; Tert. Vert., p. 290, pl. xxiv, figs. 10-11.

Type a lower molar and part of a premolar described and figured by Cope; the molar has been lost.

This species does not belong to *Sinopa* or *Tritemnodon* but is probably Insectivore. It is not further identifiable.

***Tritemnodon* Matthew 1906.**

The type of this genus is *Limnocyon agilis* Marsh 1872. This species was transferred by Wortman in 1902 to *Sinopa*; but our more complete knowledge of the several species of Leidy's genus shows that although closely allied, *L. agilis* is sufficiently distinct for generic separation. The dentition is somewhat more special-

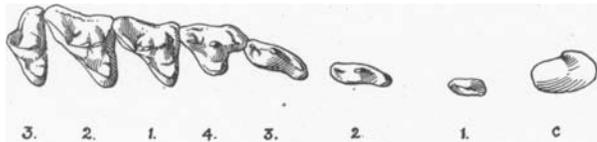


Fig. 74. *Tritemnodon agilis*, upper dentition, crown view, natural size. From No. 11536. Lower Bridger.

ized in the direction of *Hyænodon*, the outer cusps of the upper molars being

closely connate, the protocone small, the third molar reduced, and corresponding changes in the lower teeth appear in the reduction of the metaconid and the small trenchant heel. The premolars are considerably more compressed, the skull more slender and elongate, especially in the facial region. The posterior mental foramen is larger and situate further forward, beneath the anterior root of p_3 instead of the posterior root as in *Sinopa*.

Sinopa aethiopica Andrews, based upon a lower jaw from the Eocene of the Fayûm district in Egypt, appears to be related to *Tritemnodon* by the reduced and trenchant heels of the molars, but the premolars are less elongate. In *Pterodon* and *Apterodon* the metaconids of the molars are absent and the premolars are short and high, teeth more robust and jaw heavier. The limbs are comparatively short and robust, the feet unknown. *Apterodon*, according to Dr. Andrews, shows distinct indications in the limb bones of adaptation to aquatic or semi-aquatic life.

***Tritemnodon agilis* (Marsh 1872).**

Plate XLVI, Fig. 1, and Text Figures 74-90.

Limnocyon agilis MARSH, Am. Jour. Sci., Vol. IV, p. 202; separata dated August 7, 1872.

Stypolophus brevicealcaratus COPE, Palæont. Bull. No. 3, dated Aug. 7, 1872.

Sinopa agilis MATTHEW, 1899A, p. 40; 1901A, p. 24.

Sinopa agilis WORTMAN, 1902. (Type figured.)

Tritemnodon agilis MATTHEW, 1906.

This species is represented by a number of excellently preserved specimens in the Yale and American Museum collections as follows:

Type (Yale Museum). "Parts of skull and a large part of the skeleton of a young individual, somewhat crushed" (Wortman).

No.— (Yale Museum). "Skull and fragmentary skeleton."

No. 12636 (American Museum). Skeleton nearly complete — skull and jaws fragmentary, one hind limb and distal half of tail missing, the remainder of the skeleton perfect and in exceptionally fine preservation. Found by W. J. Sinclair, Expedition of 1905.

No. 11536 (American Museum). Palate, jaws, 28 complete vertebræ and most of the limbs and feet.

No. 11544 (American Museum). Lower jaws, basicranial region, cervical vertebræ, most of fore limb and one half of pelvis.

No. 11543 (American Museum). Upper and lower jaws.

No. 11545 (American Museum). Lower jaws and fragmentary skeleton.

These specimens vary somewhat in size, in robustness of the teeth and various minor characters, but may be retained under the single species. The range in size amounts to about eight percent (linear). The species has been described by Dr. Wortman in considerable detail, but our more complete knowledge of the skeleton enables us to summarize the characters more completely as follows:

Skull and jaws about as large as in *Sinopa grangeri*, but more slender and elongate in both cranial and facial regions. Skeleton somewhat larger and more robust.

Dentition $\frac{3.1.4.3}{3.1.4.3}$. Incisors small, subequal, with pointed cusps and strong accessory cuspules on the external side, smaller ones on the internal. Canines slender, moderately long, oval in section, without the posterior ridge which is so prominent in *S. rapax*. Premolars and molars decidedly higher and more compressed than in any species of *Sinopa*. P^{1-2} two-rooted, spaced, much compressed, without internal heel; p^3 with rudimentary internal heel; p^4 three-rooted, with strong antero-internal heel. M^{1-2} subequal, and protocone compressed, paracone and metacone closely connate; m^3 transverse, reduced,

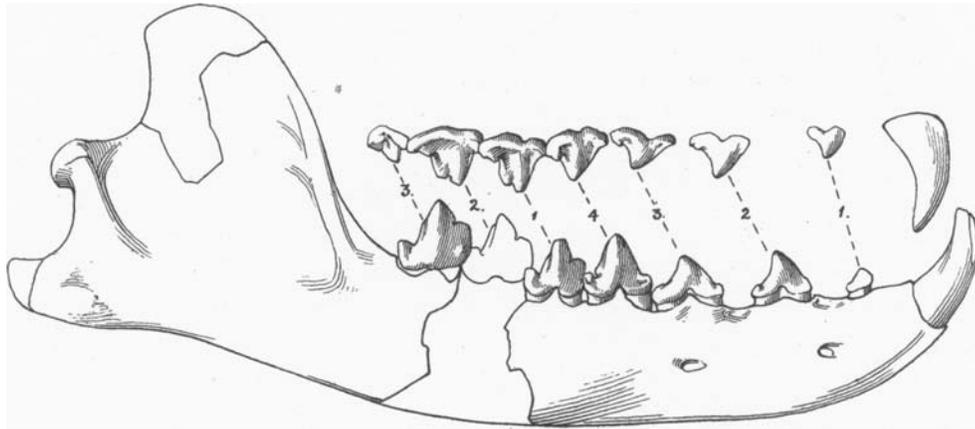


Fig. 75. *Tritemnodon agilis*, lower jaw and upper teeth, external view, natural size. From No. 11536.

metacone absent. P_1 one-rooted, p_2 two-rooted, much compressed, considerably spaced; p_3 in series with the molars, p_4 with anterior basal cusp and heel, and high principal cusp overtopping the adjoining teeth. Molars successively increasing in size and in height of trigonid, with high protoconids, paraconids strong but not so high, metaconids very small, almost vestigial, heels very small, low and trenchant. Coronoid process broad, moderately recurved, condyle nearly on a level with the tooth row, angular process prominent and moderately hooked.

Muzzle slender, nasals long, slightly expanded posteriorly, lachrymal with a semicircular facial expansion, lachrymal foramen internal. Postorbital process rudimentary on frontals, absent on jugal. Infraorbital foramen considerably in advance of orbit. Zygomatic arch more slender than in *Sinopa*. Postorbital constriction long and narrow, frontals concave along the median line, parietals long and narrow, with low sagittal crest. Occiput narrow and not very high, occipital and lambdoidal crests prominent and a deep cavity lying between the lambdoid crest and the paroccipital process and the condyle. Basicranial region much as in *Sinopa*, tympanic not ossified, paroccipital process spatulate, directed

backward, mastoid short and stout, rather prominent, condylar foramen close to anterior margin of occipital condyle, and, according to Wortman, an accessory condylar foramen in advance of it (not demonstrable on our specimens). Petrosal prominence oval, somewhat damaged in our specimens so that the characters of the fenestræ cannot be seen; a slight groove is doubtfully identifiable as the trace of a small tympanic branch of the entocarotid; the course of the main branch of this artery is probably indicated by a groove which leads forward between the petrosal and basi-occipital in the position normal to modern carnivora. This at least is Dr. Wortman's interpretation of this groove, which is recognizable on No. 11544 as well as on the Yale specimen. The postnareal gutter is deep but not overarched, the posterior border of the palate is slightly thickened.

The skeleton is very similar to that of *Sinopa grangeri* and *rapax* except for its greater size and robustness. In

No. 12636 the bones are remarkably perfect and uncrushed. The axis is longer than in *S. grangeri*, the spine projects considerably more posteriorly. The spine of C₆ is higher, the superior lamina of the transverse process projects more posteriorly. The spines of the anterior dorsals are somewhat shorter but their arches more robust.

There are 20 dorso-lumbar vertebræ, of which 14 were rib-bearing; the transverse process of the first lumbar is small, and the processes increase in size to the sixth, are long, flat, thin, moderately wide and directed forward in the usual manner. Strong anapophyses are developed on the last four dorsals and first two lumbar, and decrease in size to the fifth lumbar. The neural spines of the dorsals and lumbar are like those of *Sinopa*. The spines of the first ten dorsals are rather long, and slope strongly backward; the eleventh dorsal has no spine; the last three dorsals have spines of the usual lumbar type, short, wide, thin, and directed somewhat forward; and their centra have decidedly oblique facets. When articulated, these three vertebræ show a very sharp curvature in this part of the vertebral column. The lumbar and anterior dorsal regions of the backbone are nearly straight.

The sacrum is composed of the usual three vertebræ, the first and the anterior end of the second transverse plate taking part in the pelvic articulation.

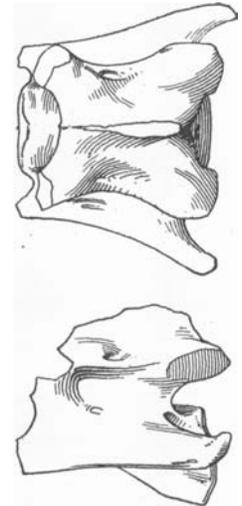


Fig. 76. *Truennodon agilis*, fourth cervical vertebra, top and side views, natural size. No. 12636, Lower Bridger.

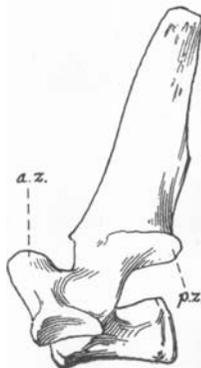


Fig. 77. *Truennodon agilis*, first dorsal vertebra, top and side views, natural size. No. 12636.

The tail is long and stout, the first 13 vertebræ being preserved in series in No. 12636. The first four caudals are short, with long, stout transverse processes, behind this the caudals rapidly increase in length, the transverse processes are converted into flat plates and then reduced until at the twelfth only the anterior and posterior ends are left.

The neural arch is vestigial on the twelfth and absent on the thirteenth.

Ribs and Sternum. The ribs of both sides are preserved nearly all complete. The first rib is very short, stout and strongly curved, the second longer with much straighter shaft, the remaining ribs increase in length and decrease in size to the sixth; the last three ribs decrease rapidly in length and in size of shaft, the last two are single-headed, and the fourteenth (absent in *Sinopa*) was apparently a floating rib. The first two ribs are somewhat flattened in the shaft, the rest are round-oval or quadrate in cross section, the anterior ones not as much flattened as in *Sinopa*, and much less than in *Hyænodon*. The curvature of the ribs is moderate, inter-

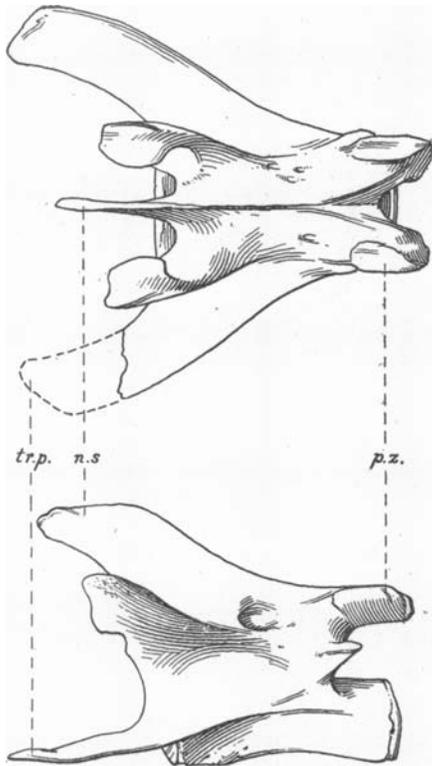


Fig. 78. *Tritemnodon agilis*, fourth lumbar vertebra, top and side views, natural size. No. 12636.

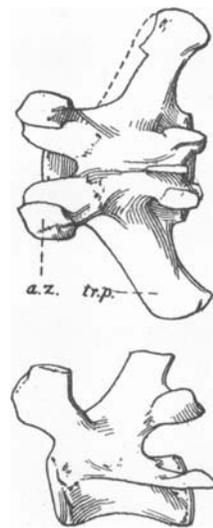


Fig. 79. *Tritemnodon agilis*, third caudal vertebra, top and side views, natural size. No. 12636.

mediate between *Canis* and the smaller Felidæ.

The sternal bones are of the usual Carnivore type except for the presternum, which is exceptionally long, and expanded in front of the rib articulation into a

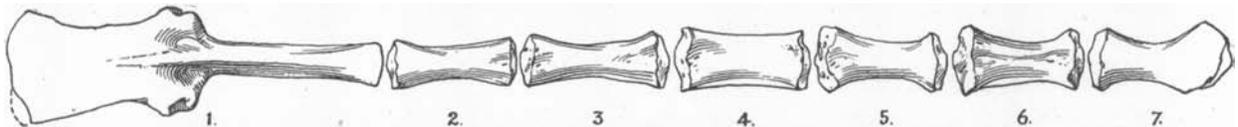


Fig. 80. *Tritemnodon agilis*, sternobræ, superior view, natural size, No. 12636.

broad, flat, quadrate plate equalling in length the narrow compressed posterior portion of the segment and about half as wide as long, flat superiorly, crested inferiorly, the lateral margins thin, the anterior border prolonged apparently in a cartilaginous plate uniting it with the clavicles.¹ The succeeding sternal

¹The presternum in *Limnocyon potens* is very like this, but broader.

segments increase regularly in width and decrease in length, the last being slightly wider than long and about a third as long as the presternal.

Fore Limb. The *scapula* is comparatively broad and short with irregular superior border; this, however, is due partly to the animal not being fully adult, so that the ossification of the superior border is not yet complete. With due allowance for this circumstance, it is still considerably broader than in *Sinopa* and *Hyænodon*, especially the latter. The spine is high, the acromion rather slender and projecting somewhat below the level of the glenoid border, the metacromion a broad, flat plate longer than in modern carnivora but comparable with *Patriofelis*. The coracoid process is exceptionally long, much more developed than in any modern carnivora, or in most Creodonts. In

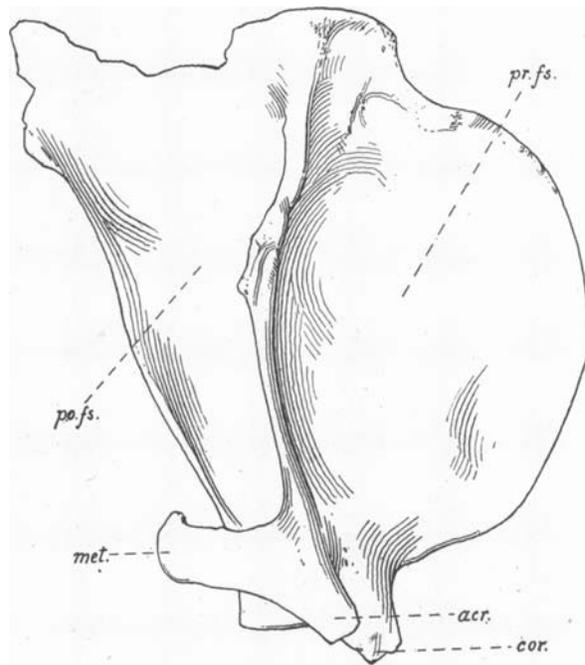


Fig. 81. *Tritemnodon agilis*, scapula, external view, natural size. No. 12636. Lettering: *acr.*, acromion; *cor.*, coracoid process; *met.*, metacromion; *po. fs.*, postspinous fossa; *pr. fs.*, prespinous fossa.

Sinopa this process is somewhat reduced; in *Hyænodon* it has disappeared.

One *clavicle* is complete and about half of the other is preserved. This bone is less reduced than in any modern Carnivora, but it is of distinctly Carnivore type, unlike any Primate, Insectivore or Rodent clavicles with which I have compared it. The larger Felidæ compare most nearly. It is a nearly straight, slender rod strongly recurved and broadened at the sternal end, and incompletely ossified at the scapular end. The union with the presternum was apparently through a flat cartilaginous strap, whose attachments are indicated on the end of the clavicle and the anterior border of the presternum. This is the only Creodont in which the clavicle has been certainly recognized, but it was probably generally present (except in the Mesonychidæ). It is present also in the Oreodontidæ (*Oreodon*, *Mesoreodon*) among primitive Ungulates.

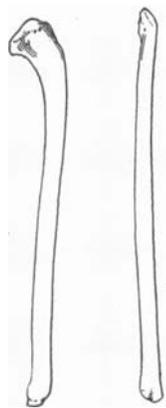


Fig. 82. *T. agilis*, clavicle, natural size, No. 12636.

The *humerus* is in general like that of *Sinopa*, differing slightly in greater size and robustness, higher deltoid and supinator crests and broader entepicondylar process. The supratrochlear

foramen is very small. The *ulna* and *radius* also resemble those of *Sinopa* in all important features. The olecranon is a little longer, the head of the radius less flattened; the posterior (internal) border of the ulna rises to a sharp crest to-

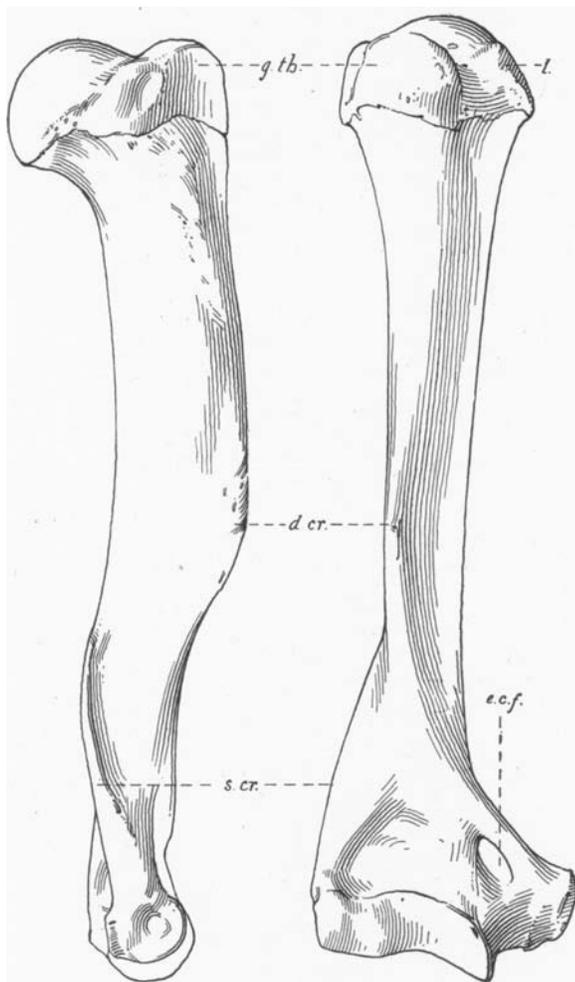


Fig. 83.

Fig. 83. *Tritemnodon agilis*, humerus, external and anterior views, natural size. No. 12636. Lettering as in Fig. 66.

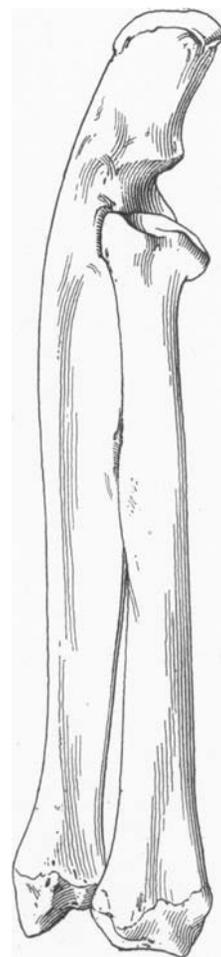


Fig. 84.

Fig. 84. *Tritemnodon agilis*, Radius and ulna, front view, natural size, No. 12636.

ward the distal end, as in some *Viverridæ*, but not in *Sinopa* or *Hyænodon*; the distal end of the ulna is stout, the styloid process, short, the cuneiform facet faces about equally distal and internal.

The *fore-foot* agrees in most respects with that of *Sinopa*, except that the metapodials are somewhat shorter and more robust, the asymmetry of the penultimate phalanges decidedly more marked, the unciform less quadrate. The trapezium retains to a considerable extent the primitive form observable in the

Miacidæ and especially in Arctocyoniidæ, but the opposability of the first digit is more completely lost than in these families. The mesaxonic symmetry of the manus is clear; the first digit is nearly as long as the fifth, and considerably stouter in the shaft.

Hind Limb. The *pelvis* is very different from that of any modern carnivora; in some respects it approximates that of *Hoplophoneus*, but its nearest analogues are *Phenacodus wortmani* of the Lower Eocene and *Hyænodon* of the Oligocene. It is very long and narrow, the post- and pre-acetabular portions of nearly equal length. The pubic symphysis is long, but its depth below the sacrum is comparatively small. The ischia are nearly parallel for the whole of their length. The rather prominent ischial spine is half-way between the acetabulum and the distal tuberosity, as in *P. wortmani* and *Hyænodon*. In Carnivora generally it is close behind the acetabulum. In

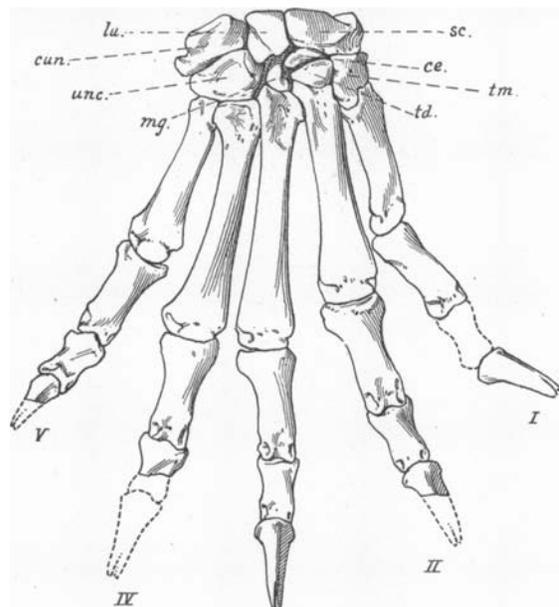


Fig. 85. *Tritemnodon agilis*. Fore foot, dorsal view, natural size. No. 12636. Lettering as in Fig. 4. There should be only two phalanges on the first digit.

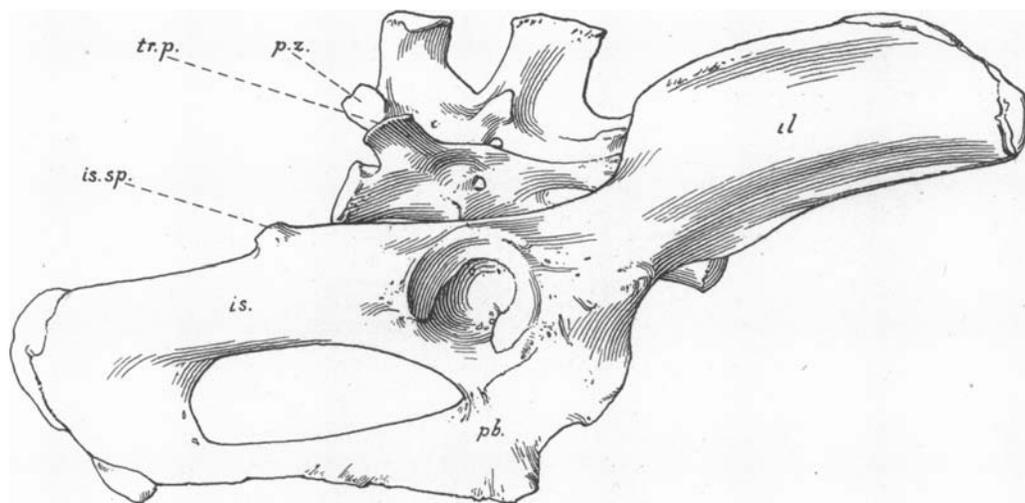


Fig. 86. *Tritemnodon agilis*. Pelvis and sacrum, side view, natural size; No. 12636. Lettering: *il.*, ilium; *is.*, ischium; *is. sp.*, ischial spine; *pb.*, pubis; *p. z.*, posterior zygapophysis; *tr. p.*, transverse process.

P. wortmani the proportions of ischium and pubis are much as in *Tritemnodon*; in *Hyænodon* the post-acetabular portion of the pelvis is much shorter, the

ischia divergent and pubic symphysis shorter; this change appears to be correlated with the reduction of the size and length of the tail. The superior border of the ilium is expanded into a very characteristic, narrow, concave plate, much as in *Hyænodon*; in *P. wortmani* the plate is flatter but otherwise very similar; *Hoplophoneus* affords the nearest analogue among Fissipedia, but in this suborder it is generally the inferior border of the iliac bar that is expanded, the superior border showing little or no expansion. *Dinictis*, *Daphænus* and *Cynodictis* are intermediate in this character, both upper and lower borders of the iliac bar being expanded into narrow plates.

The *femur* in *Tritemnodon agilis* has nearly the same proportions and construction as in *Sinopa grangeri*, but is slightly heavier, with more flattened shaft, third trochanter less prominent, the distal end is not so deep antero-posteriorly,

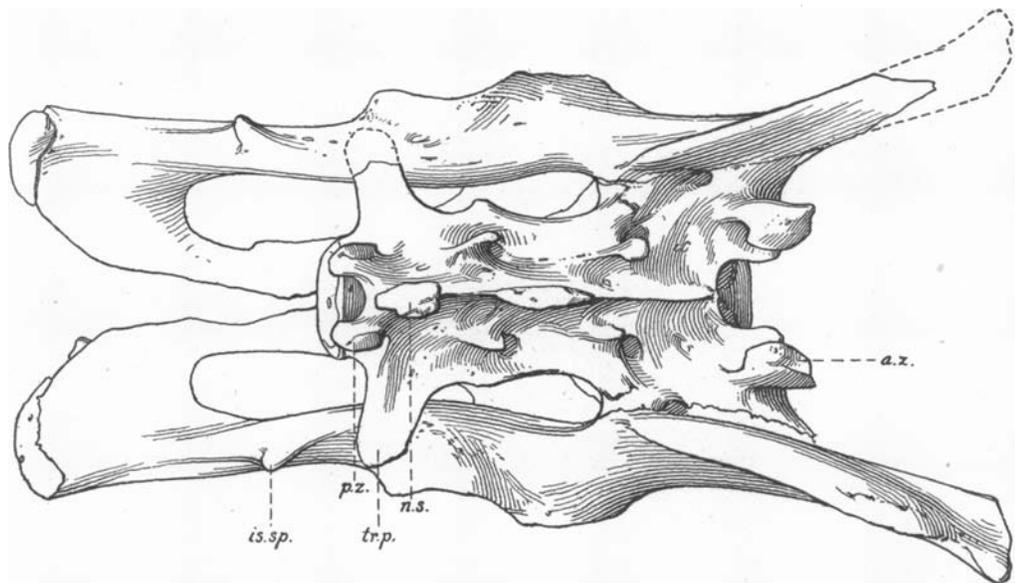


Fig. 87. *Tritemnodon agilis*. Pelvis and sacrum, top view, natural size. No. 12636.

and the rotular trochlea is broader. The shaft shows the same peculiar lateral curvature as in *Sinopa*, *Hyænodon* and the *Oxyænidæ*.

The *tibia* and *fibula* differ little from those of *Sinopa*. The cnemial crest of the tibia is long but not prominent, the distal end very oblique, with very flat trochlear facet indistinctly separated from the malleolar facet. The fibular shaft is about as stout proportionally as in *Sinopa* and *Hyænodon*, heavier than in any modern carnivora; the distal end has a flat internal navicular facet, and a strongly concave saddle-shaped distal calcaneal facet of about the same size.

The *hind foot* agrees very closely with that of *Sinopa*. The astragalar trochlea is more nearly flat, the peroneal tubercle more prominent, the tarsus somewhat broader, the tuber calcis shorter, the proximal phalanges somewhat shorter than in *S. grangeri* and much shorter than in *S. rapax*, the penultimate phalanges

much more asymmetric than in either species. The mesaxonic symmetry is less exact in the hind than in the fore foot, as in all the Hyænodonts.

Interpretation. The characters of the teeth in *Tritemnodon* show a more progressive stage than *Sinopa*, chiefly but not exactly in the direction of *Hyænodon*. The skull characters are more divergent, the long, slender skull being unlike any of the more specialized Hyænodonts, except perhaps *Apterodon*, which is more remote in dental specialization. The skeleton appears to be on the whole more conservative than that of *Sinopa* but is throughout very closely allied. The broader carpus, less quadrate unciform, greater dorsal extension of the radio-scaphoid facet, flatter tibio-tarsal joint, more prominent peroneal tubercle, and many minor features of carpus and tarsus indicate a more plantigrade manus and pes; and the asymmetric penultimate phalanges indicate partially retractile claws. In my description of *Sinopa grangeri* I concluded from comparison with Dr. Wortman's figures and description of *S. (Tritemnodon) agilis* that *Tritemnodon* was more advanced than *Sinopa* in skeletal characters as well as in teeth; but comparison of the skeleton materials of the two genera reverses this conclusion.

Restoration (Pl. XLVI).

Tritemnodon agilis was a long headed, long necked slender bodied and very long tailed carnivore, about the size of the wolverene (*Gulo luscus*) but with much smaller feet, much longer and heavier tail, and slender, elongate skull.

Fig. 89. *Tritemnodon agilis*. Tibia and fibula, natural size, No. 12636.

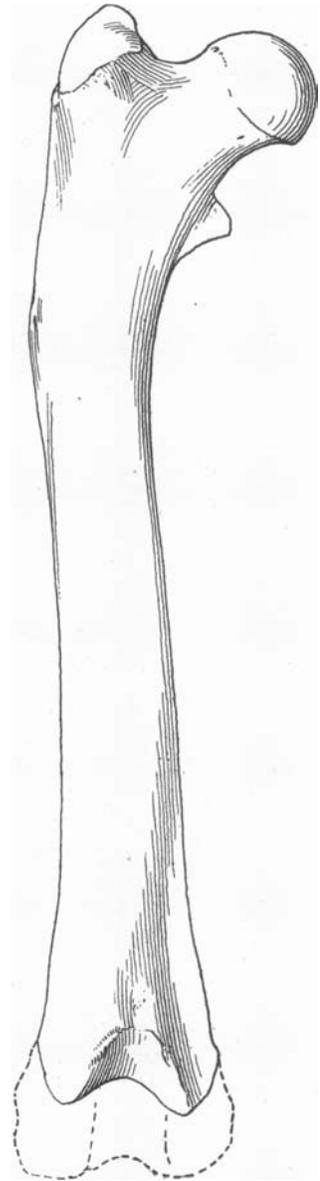
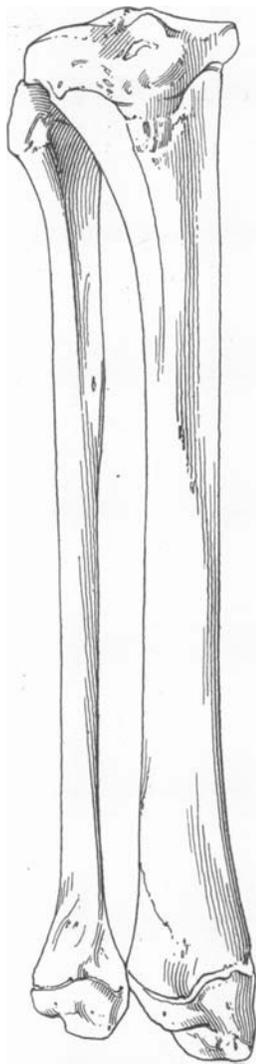


Fig. 88. *Tritemnodon agilis*. Femur, anterior view, natural size. No. 12636.

It was probably semi-plantigrade, the claws somewhat retractile, but not com-

pressed. The organization of the limbs and feet does not indicate the bear-like gait of the wolverene, but may be compared better with the Thylacine, or with some of the more plantigrade civets, in which the knee is strongly flexed in walking and the partial plantigradism is derived from the primitive arboreal

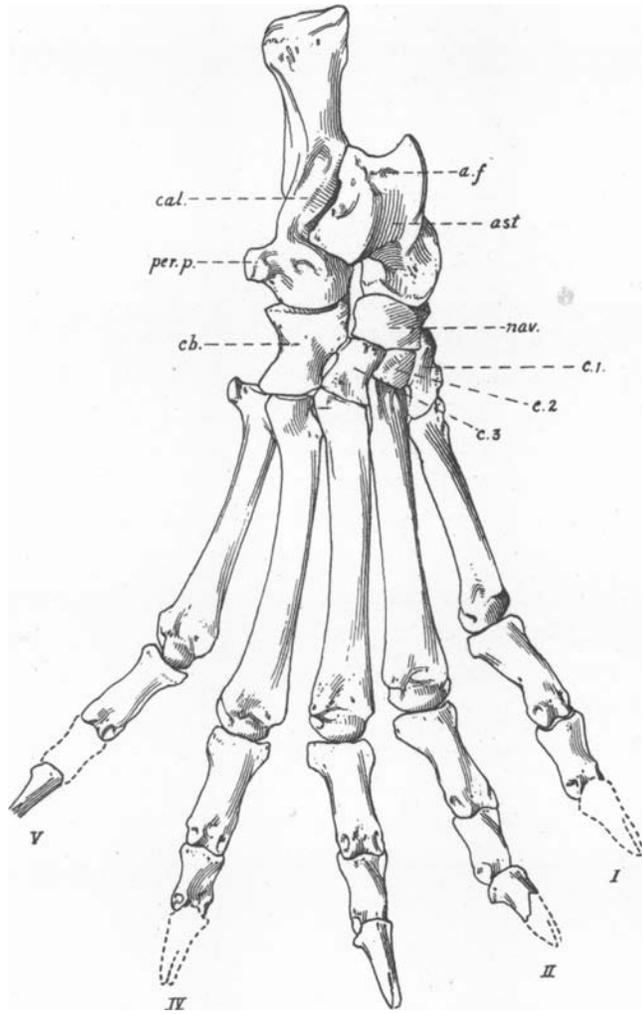


Fig. 90. *Tritemnodon agilis*. Hind foot, dorsal, natural size, No. 12636. Lettering as in Fig. 4. The penultimate phalanx on the first digit should have been placed on the fifth.

closely in the raccoon and some other primitive carnivora. The neck was longer, the tail longer, heavier and less flexible than in the Thylacine, and the feet less digitigrade.

type rather than the terrestrial plantigradism of the bears, wolverenes, etc. I do not know of any satisfactory osteological characters to determine whether the tail was to any extent prehensile.

The skeleton as mounted by Albert Thomson under direction of the writer, shows some very interesting features. The pose is based upon a careful and thorough study of the articulations of the skeleton, in comparison with photographs and skeletons of living Carnivora and carnivorous marsupials, especially of the Coyote, Thylacine, Raccoon, Civet and Wolverine. The animal has on the whole most nearly the general appearance of the Thylacine, especially in the long head and neck, the lank proportions of body and limbs, the long heavy inflexible tail. It differs in one very striking feature, the sharp bend in the backbone, which is paralleled in *Sarcophilus* and certain other marsupials, and less

4. Family MESONYCHIDÆ Cope.

The Mesonychidæ are the most archaic and peculiar of the Creodonta, and least like the typical Carnivora. They include the largest species, equalling the modern bears in size of skull; and the most highly specialized cursorial adaptation of the feet, equalling the modern Canidæ in this respect. The teeth show a unique specialization, with high, conical, blunt-pointed cusps devoid of any shearing function, and with a very suggestive resemblance to the early types of omnivorous Artiodactyla (*Achænodon*, *Elotherium*, *Helohyus*). In other respects the progressive adaptation of the teeth parallels, although imperfectly, that of the predaceous carnivora. The metacone of the upper molars becomes reduced or vestigial and connate with the paracone; the protocone is to some extent reduced; in the lower molars the protoconid becomes high, the paraconid low, the metaconid vestigial, the talonid reduced, low and trenchant. The posterior molars tend to reduction in size or number, the incisors, canines and premolars are enlarged. The adaptive parallelism with the predaceous carnivora is by no means close, but is much nearer than to any omnivorous carnivora. On the other hand the adaptive specialization of the early bunodont Artiodactyla leads in an opposite direction to that in the Mesonychidæ, the molars becoming enlarged, especially m_3 , the crowns quadritubercular or multitubercular, and the premolars and incisors relatively reduced. It would appear from this that the resemblances in the teeth of Mesonychidæ and bunodont Artiodactyla are due to relationship, as they represent divergent, not parallel phyla; and this view is supported by several important points of resemblance in construction of the skull and skeleton, especially the form and relations of the bones of the face, of the astragalus and other tarsal bones, the form of the ungual phalanges, and several features in the arrangement of the basicranial bones and foramina.

The anterior margin of the orbit is well defined, and the lachrymal foramen internal; the lachrymal has a broad *pars facialis* which differs in form and position from the semicircular facial expansion of the earlier Pseudocreodi and is much more like that in certain Artiodactyla, especially *Achænodon*. In Marsupials and Insectivora there is a rather small facial expansion of the lachrymal, less than in the Pseudocreodi, and the lachrymal foramen is marginal or external, the anterior border of the orbit being ill defined. The nasals are also widely expanded posteriorly, as in Condylarthra, Perissodactyla, early types of Artiodactyla, and in Marsupials, and the frontals are excluded, or nearly so, from contact with the maxillæ. The jugal bone is rather small, the antero-inferior branch lacking, the superior branch developed more as in Artiodactyls than any other group, and the posterior branch comparatively short. In Insectivora the jugal is much reduced or lacking, and the superior branch much less extensive; in Marsupials it is a very large bone extending far forwards and backwards and taking part in the glenoid fossa. In the Fissipedia the superior branch is reduced

so that the bone has much less expanse upon the face, and posteriorly it reaches nearly but not quite to the glenoid fossa.

The tympanic ring is expanded in *Mesonyx* and *Synoplotherium* into a small simple bulla. In *Harpagolestes* it is apparently depressed and closely united with the squamosal, as in the Ursidæ, but whether expanded as in all Fissipedia into a complete bulla, cannot be determined.

The dorso-lumbar formula has been determined by Scott as 20 in *Mesonyx*, by Wortman as 19 in *Dromocyon* (= *Synoplotherium*). If the latter number be correct, it would be another point of resemblance to Artiodactyla as well as to Marsupials. It is more probable that a vertebra should have been lost from the series in *Dromocyon* than that a single vertebra of another individual should be accidentally included in the *Mesonyx* skeleton. If therefore the vertebræ determined as belonging to the dorso-lumbar series are all correctly so placed, it would appear more probable that the larger formula is correct. Wortman states, however, that the vertebræ in *Dromocyon* were mostly articulated together when found, so that there may have been no opportunity for one of them to be missing. If both formulæ be correct, there is no evidence as to which was the normal number, except that it was 20 in the six other genera of Inadaptive Creodonts in which the formula is known. It is not known in any other Mesonychidæ. In the Artiodactyla it is 19¹, as also in Marsupialia, many Insectivora and Edentata, most Primates and Rodentia.

The lumbar zygapophyses are strongly concavo-convex in all the Mesonychidæ, as in Pseudocreodi and a few of the Fissipedia. In *Mesonyx* they are slightly revolute, approaching the conditions in *Patriofelis* and the Artiodactyla.

The manus and pes in the later Mesonychidæ was tetradactyl, the first digit a vestigial nodule. In *Dissacus saurognathus* they were probably pentadactyl; the hallux, at all events, was complete, but of reduced size; the manus, as articulated by Osborn and Earle, is pentadactyl with large mc. I and mc. V much reduced. This construction, if correct, would preclude our regarding this species as ancestral to the later Mesonychidæ, and would be a very exceptional character. In *D. navajovius* the digits are unknown, but the foot was evidently much more slender and compressed, to judge from the characters of the tarsals.

The ungual phalanges are broad, hoof-like, and rather deeply fissured, suggesting rather the unguis of Condylarthra, Amblypoda and primitive Perissodactyla than those of the Carnivora. They are a little like those of *Patriofelis*.

It is probable that the various resemblances seen in the skull, teeth and skeleton characters of the Mesonychidæ to the Condylarthra and especially to the early bunodont Artiodactyla are not wholly due to accident or to parallel adaptation. The phylum is certainly of very ancient origin, and may be to a certain extent intermediate between Carnivora and Ungulates in its derivation.

¹ Except in Oreodontidæ.

But the main affinities of the family appear to be with the Creodonta, to which it has been referred by all authorities. The Marsupial affinities appear to be very remote, and such points of resemblance as do occur may all be more nearly paralleled among other Placental orders, especially the early Artiodactyla. Nor does this family show any especial approximation to the Insectivora, except in the teeth of the earliest members, which are of doubtful reference, as they are very incompletely known.

The first representatives of the Mesonychidæ are the Triisodontinæ of the Puerco and Torrejon, which are very closely connected with some, at least, of the Oxyclænidæ, so far as can be judged by comparison of the teeth. The skull and skeleton of this group is very incompletely known, but so far as comparison can be made suggests Mesonychid relationships. The teeth in *Triisodon* and *Goniacodon* are singularly like those of the Insectivore *Pantolestes*; in *Sarcothraustes* they assume a character more like the Mesonychid type, but still much less specialized, and perhaps the resemblance is due to parallelism.

In the Torrejon also appears the more typical genus *Dissacus*, with the peculiar characters of the teeth well advanced, but the feet more primitive, represented by two well distinguished species, *D. navajovius* and *saurognathus*. In the Wasatch are found three distinct species referred to *Pachyæna*, and the very small and slender *Hapalodectes* (*Dissacus leptognathus* O. & W.). The Wind River has not yielded any of the larger Mesonychids¹ but a species of *Hapalodectes* occurs in the formation. In the Lower Bridger are found the large *Harpagolestes* and the smaller and slenderer *Mesonyx*. In the Upper Bridger and Lower Washakie *Synoplotherium* (*Dromocyon*) represents the family; and in the Upper Washakie and the Uinta beds occur large species which I refer to *Harpagolestes*, besides a smaller form referred to *Mesonyx*.

As will appear more in detail in the special descriptions, these species represent at least three sub-phyla, even excluding the Triisodonts. These phyla may have been distinct as early as the Torrejon, and are separable on the following characters:

I. *Dissacus saurognathus* — *Pachyæna gigantea* — *Harpagolestes*.

Metacone vestigial on m². Skull deep and short, limbs and feet short and massive. Tympanic ring extended as a thick irregular mass anchylosed to the squamosal.

II. *Dissacus navajovius* < *Pachyæna ossifraga* — *Synoplotherium*.
Pachyæna intermedia — *Mesonyx*.

Metacone on M² less reduced. Skull more slender, limbs and feet elongate. Tympanic ring expanded into a thin-walled bulla in the later forms, loosely attached to the squamosal.

III. *Hapalodectes*.

Small, very slender jaws, with teeth much compressed.

It is very doubtful whether even these phyla represent direct lines of descent; the relations of the species of *Dissacus* to their successors in the Wasatch being not at all certain.

¹ Dr. Loomis informs me that he found teeth of a large species of *Pachyæna* in the Wind River beds.

The accepted generic distinctions traverse these phyletic lines.
The classification of the family is as follows:

A. *Trisodontinae*.

External cusps of upper molars well separated. Lower molars with basin heel. Teeth moderately wide transversely.

B. *Mesonychinae*.

External cusps of upper molars connate. Lower molars with trenchant heel. Teeth compressed transversely.

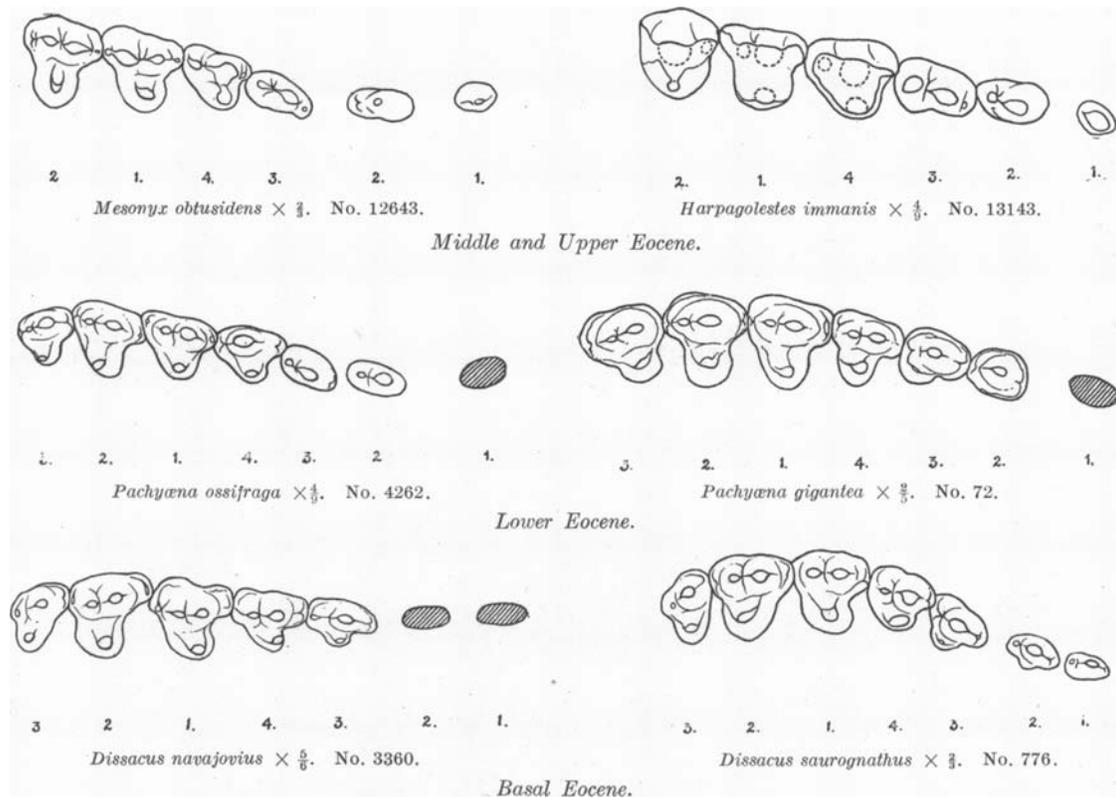


Fig. 91. Upper teeth of Mesonychidae.

- I. Metaconids distinct. Humerus with entepicondylar foramen. Trochlea of astragalus flat. Cuboid facet on astragalus indistinctly defined.
 1. Larger, teeth more robust. Genus *Dissacus*, Basal Eocene.
 - a. Larger, $c-m_3 = 160$ mm.; digits 5-5, feet wide, metacones reduced on m^{2-3}

D. saurognathus Wortman.
 - b. Smaller, $c-m_3 = 85$ mm.; feet compressed, digits unknown, metacones reduced on m^2 only

D. navajovius Cope.
 2. Smaller, teeth highly compressed. Metaconids much reduced. Genus *Hapalodectes*, Lower Eocene.
 - a. $c-m_3 = 45$ mm. (est.)

H. leptognathus (Osborn).
 - b. $c-m_3 = 47$ mm. (canine estimated). Teeth more compressed. *H. compressus* sp. nov.

- II. Metaconids vestigial. Humerus with very small entepicondylar bridge. Astragalus wide with rather shallow trochlea and distinct cuboid facet. Genus *Pachyaena*, Lower Eocene.
- Larger, $p^1-m^3 = 162$ mm.; feet wide, limbs short and stout, metacones reduced on m^{2-3} , skull short and deep, m^3 unreduced. *P. gigantea* Osborn.
 - Medium size, $p^1-m^3 = 135$ mm.; feet more compressed, limbs moderately elongate, metacone reduced on m^3 only, skull longer, jaws not so deep or massive m^3 somewhat reduced. *P. ossifraga* Cope.
 - Smaller, m_3 more reduced, hind limb and astragalus proportioned as in *P. ossifraga* *P. intermedia* Wortman.
 - Size of *P. gigantea*. Distinctions from that species not stated by the author¹ *P. boulei* Trouessart.
- III. Metaconids? absent. Astragalus with deep trochlea and distinct cuboid facet.
- Skull short, deep and wide. Limbs short and stout, feet unknown. Humerus, in one species at least, with entepicondylar bridge. Metacone vestigial on m^2 , m^3 absent. Genus *Harpagolestes*, Middle and Upper Eocene.
 - P^2 absent *H. macrocephalus* Wortman.
 - P^2 present. Premolars crowded; $c-m_3$ (est.) = 226 mm. *H. immanis* sp. nov.
 - P^2 present. Premolars spaced; $c-m_3$ (est.) = 220 mm. *H. uintensis* (Scott).
 - Skull moderately elongate. Limbs comparatively long. Digits 4-4. Humerus without entepicondylar bridge. m^2 present, small. Genus *Synplotherium* (*Dromocyon*), Middle Eocene.
 - $C-M_3 = 160$ mm. *S. lanivus* Cope.
 - $C-m_3 = 150$ mm. *S. vorax* (Marsh).
 - Skull elongate. Limbs and feet long and slender. Digits 4-4. Humerus without entepicondylar bridge. M^2 present, small. Metacones of m^{1-2} well developed. Genus *Mesonyx* Middle and Upper Eocene.
 - $C-M_3 = 127$ mm. Mt. III, 87 mm. *M. obtusidens* Cope.
 - Jaw slightly smaller. Mt III, 80 mm.; pes more slender *M.* sp. (Upper Uinta).

Geological Distribution of the Mesonychidae.

	EOCENE													
	Basal		Lower			Middle			Upper					
	Puercio	Cernaysien (France)	Torfeju	Suessonian (France)	Wasatch	Wind River	Lower Huertano	Upper Huertano	Lower Bridger	Upper Bridger	Lower Washakie	Upper Washakie	Lower Uinta	Upper Uinta
TRISODONTINÆ.														
<i>Trisodon quivirensis</i> Cope	X													
“ <i>heilprinianus</i> Cope	X													
“ <i>gaurianus</i> Cope	X													
<i>Sarcothraustes antiurus</i> Cope			X											
<i>Goniacodon levisanus</i> Cope			X											

¹ Trouessart, Catalogus Mammalium, Suppl. 1904, p. 163; *P. gigantea*, Boule, Mem. Soc. Geol. Pal., 1903, fasc. 4, pl. 1, 2. From the Lower Eocene of Vaugirard, France.

Geological Distribution of the Mesonychidæ. (Continued.)

	Eocene													
	Basal		Lower			Middle			Upper					
	Pierco	Cernajsten (France)	Torrefou	Suessonien (France)	Wasatch	Wind River	Lower Huertano	Upper Huertano	Lower Bridger	Upper Bridger	Lower Washakie	Upper Washakie	Lower Uinta	Upper Uinta
TRIISODONTINÆ.														
<i>Microclænodon assurgens</i> Cope			×											
MESONYCHINÆ.														
<i>Dissacus navajovius</i> Cope			×											
“ <i>saurognathus</i> Wortman			×											
<i>Hyænodictis gaudryi</i> Lemoine		×												
<i>Hapalodectes leptognathus</i> Osborn					×									
“ <i>compressus</i> (infra)						×								
<i>Pachyæna ossifraga</i> Cope					×									
“ <i>gigantea</i> Osborn					×									
“ <i>boulei</i> Trouessart				×										
“ <i>intermedia</i> Wortman					×									
“ sp. (auct. F. B. Loomis)						×								
<i>Mesonyx obtusidens</i> Cope									×					?
<i>Synoplotherium lanius</i> Cope										×	×			
“ <i>vorax</i> Marsh										×				
<i>Harpagolestes macrocephalus</i> Wortman									×					
“ <i>immanis</i> (infra)												×		
“ <i>wintensis</i> Scott													×	×

Dissacus Cope.

The two species of *Dissacus* are known from the upper and lower jaws and parts of the skeleton associated. The larger and more completely known species is *D. saurognathus*, described and figured by Osborn and Earle, under the name of *D. carnifex*. It is quite distinct from *D. carnifex* of Cope which is scarcely separable from the type of the genus, *D. navajovius*. The fore-foot figured by Osborn and Earle, if correctly assembled, indicates a quite different construction from any of the later Mesonychidæ, the pollex being large and the fifth digit much reduced. The pes is pentadactyl with a considerably reduced but still functional hallux, considerably divergent but apparently not at all opposable. In this species the limbs and feet are short and stout and the astragalar trochlea is flat, limited posteriorly but extending anteriorly upon the neck, the astragalar foramen is present and the fibular facet is at a rather broad angle. In *D. navajovius* the limbs are much more elongate, the astragalus is narrow and compressed, the trochlea is flat but extends further backwards and less forwards, and is at a much sharper angle with the fibular facet. The metapodials are not known. The gait of the larger species was probably plantigrade, while in the smaller one it

may have been digitigrade. In *D. navajovius* the paracone and metacone are distinct and of equal size on m^1 and m^2 ; on m^3 the metacone is absent. In *D. saurognathus* the metacone is well developed only upon m^1 ; on m^2 it is much reduced and on m^3 vestigial.

Pachyæna Cope.

The type of *Pachyæna* is *P. ossifraga* Cope, founded on a superior fourth premolar tooth from the New Mexican Wasatch (Nat. Mus. No. 1096). A badly crushed skull and jaws with most of the limb bones and a few foot bones and vertebræ from the Big Horn Basin (Am. Mus. No. 4262) is probably correctly referred to this species, and serves as hypotype. The dentition is $i\frac{3}{5}$, ct , $p\frac{1}{2}$, $m\frac{3}{5}$, the last molar but little reduced, metacone unreduced on m^2 , jaws rather long and slender. The metaconids on the molars are either absent or very slightly developed. The limb bones are as long and slim as in *Mesonyx*, longer and straighter than in *Synoplotherium*, the foot bones indicate a rather slender foot, and the astragalus is much like that of *Synoplotherium* and *Mesonyx* but somewhat wider. The humerus is very like that of *Synoplotherium* except that it has an entepicondylar foramen, but the bridge is very much reduced. (The humerus figured by Cope in 'Tertiary Vertebrata' as that of *Mesonyx ossifragus* really belongs to *Phenacodus nunienus* and *vice versa*. The skeletons of the two species were found together in the field. This confusion led Professor Cope astray in his description of both species in 'Tertiary Vertebrata'.)

The number of digits is not certainly known, but the structure of limb bones and foot bones, as well as of the teeth, is so much more like that of *Mesonyx* than of *Dissacus* that there is little doubt that the feet were tetradactyl and digitigrade. Wortman, following Cope's erroneous determination of the humerus belonging to this species, regards it as pentadactyl.

The second species of *Pachyæna* is *P. gigantea* Osborn¹ described from a series of upper teeth. A fragmentary skeleton and a skull and jaws from the same formation and locality² gives considerable additional data. The metacone on m^2 is much reduced; m^3 is nearly as large as m^2 but has a vestigial metacone. The skull is much higher, shorter and more robust than that of *P. ossifraga* and is proportioned more as in *Harpagolestes*. The limb and foot bones are short and massive, the humerus has a much larger entepicondylar foramen with heavy bridge. The astragalus is like that of *P. ossifraga* but wider, much as in *Harpagolestes*. It differs notably from that of *Dissacus* in the well defined trochlea extending well backward, and without astragalar foramen. It is probable that this species was also tetradactyl and digitigrade, if we may judge from the resemblance of the bones to the later Mesonychidæ and their marked difference from *Dissacus*.

¹ Bull. Amer. Mus. Nat. Hist., 1892, 113.

² Matthew in Bull. Amer. Mus. Nat. Hist., 1901, 32.

A third species, *P. intermedia* Wortman, is known from a part of the upper jaw with m^{2-3} , from the Big Horn Wasatch. I refer to this species part of a hind limb of appropriate size from the same region, Am. Mus. No. 2959a, consisting of femur, tibia, patella and astragalus. The proportions and character are much as in *P. ossifraga*, but m^3 is considerably reduced, and the animal was considerably smaller.

From the above data it will appear that *Pachyæna* is probably tetradactyl and digitigrade and certainly much more closely allied to *Mesonyx* and *Harpagolestes* than to *Dissacus*. It differs from *Mesonyx* or *Synoplotherium* in retaining a more or less vestigial entepicondylar bridge on the humerus. The large species is allied to *Harpagolestes* but retains m^3 ; the two smaller species to *Mesonyx* and *Synoplotherium* (*Dromocyon*) but m^3 is less reduced and a vestigial entepicondylar bridge is present. The metacones are somewhat more reduced than in *Mesonyx*.

Synoplotherium Cope 1872.

Syn. *Dromocyon* MARSH 1876.

The type of *S. lanius* Cope, No. 5022, Am. Mus. Coll., consists of the lower jaws, parts of the skull, and various fragments of the skeleton, including both fore feet, nearly complete. The specimen was an old individual and the teeth much worn. It has been fully figured and described by Professor Cope. The teeth are worn down nearly to the roots, but so far as I am able to judge from a comparison of the type with Wortman's figures of *Dromocyon vorax* they show no distinctions from that species except such as are due to wear. The whole surface of the last lower molar is worn flat, indicating the presence of m^3 . In *Mesonyx* and *Harpagolestes* the posterior part of m_3 is little or not at all worn, owing to absence of m^3 . Professor Cope's description of the anterior teeth (quoted from his field description of 1872 without rectifying certain errors¹) speaks of the lower canines as directed forwards and working against the retrorse crowns of the two external incisors above and laterally against the superior canine, a somewhat inaccurate description of the ordinary conditions in an old individual of a normal Carnivore, as may easily be seen by comparison with his figure, or with the type specimen, which is on exhibition in the American Museum. The fore foot and parts of limb bones preserved agree entirely with Wortman's description and figures of *Dromocyon vorax*. The type of *D. vorax* is from the Upper Bridger (the ash bed on Henry's Fork) and of *S. lanius* from the Lower Washakie. Our recent collections in these horizons show beyond question that the faunæ are equivalent and in large part identical. There appears therefore to be no ground for distinguishing *Dromocyon* from *Synoplotherium* and the latter name has priority. The species may perhaps be distinct, although they differ but little.

¹ When the description was written Professor Cope regarded the animal as allied to *Anchippodus* (order Tillodontia). Hence the description of the teeth is somewhat misleading as applied to a Carnivore.

Mesonyx Cope.

The type of *M. obtusidens* consists of lower teeth and fragments of the skeleton, including parts of the hind limbs, vertebræ, etc. Cope was unable to find adequate characters in the type to maintain the genus as distinct from *Synoplotherium*, over which *Mesonyx* has priority of page, but the fine skeleton of *M. obtusidens* obtained by the Princeton Museum led Professor Scott to conclude that it might be necessary to revive the genus *Synoplotherium*. This view is confirmed by the complete skeleton of *Dromocyon* (= *Synoplotherium*) described by

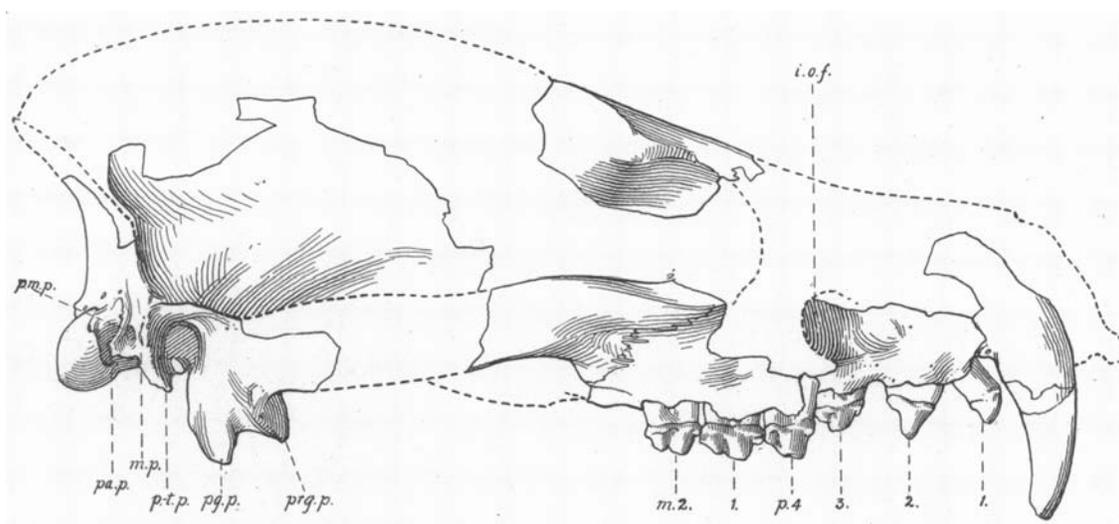


Fig. 92. *Mesonyx obtusidens*, skull, one half natural size. From No. 12643. Lettering as in Fig. 53.

Wortman, and by the skull and hind limbs in the American Museum which I refer to *M. obtusidens*. The distinctions are, however, of hardly more than subgeneric value. In *Mesonyx* m^3 is absent, and the jaws are more slender and elongate, the premolars more compressed, the limbs and feet longer and more slender, and more highly specialized. All the known specimens nevertheless come from the Lower Bridger except a provisionally referred specimen from the Uinta, while *Synoplotherium* is known only from the Upper Bridger and Lower Washakie.

Mesonyx obtusidens Cope.

COPE, Palæontological Bulletin No. 1, July 29, 1872; republished in Proc. Am. Phil. Soc., Vol. XII, p. 460; Proc. Am. Phil. Soc., Vol. XIII, p. 198; Tertiary Vertebrata, p. 355, pl. xxvi, xxvii.
SCOTT, Jour. Phila. Acad. Sci., Vol. IX, pp. 155-168, pll. v-vii.
WORTMAN, Amer. Jour. Sci., 1902, Vol. XIII, p. 39, fig. 1.

The type consists of teeth and numerous fragments of the skeleton, Am. Mus. No. 5021, discovered by Professor Cope in 1872 in the Lower Bridger beds

of Cottonwood Creek. The species is best known from the fine skeleton in the Princeton Museum described and figured by Professor Scott in 1887. A fragmentary skeleton with well preserved hind limb, in the Yale Museum, has been described by Wortman and the foot figured. The principal specimen obtained

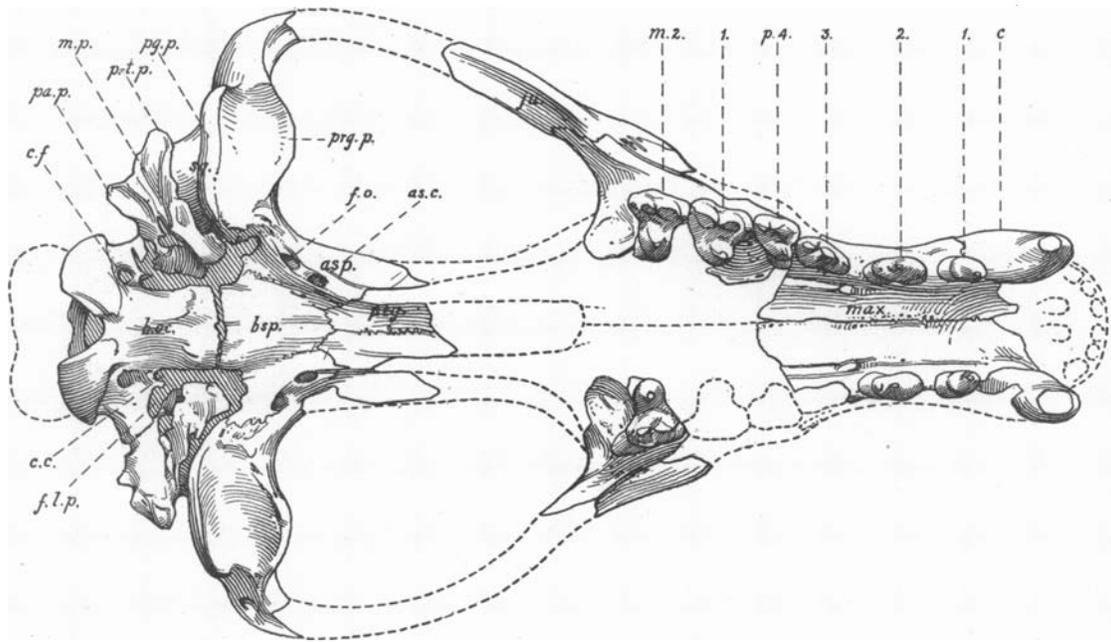


Fig. 93. *Mesonyx obtusidens*, skull, under side, one half natural size. From No. 12643. Lettering as in Fig. 2.

by the American Museum expeditions, No. 12643, found by Mr. Granger, consists of a skull with lumbar vertebræ and hind limbs well preserved; a number of other specimens are provisionally referred to the species or genus, but none of them add much to our knowledge of its structure.

There seems to be a considerable variation in the size and elongation of the

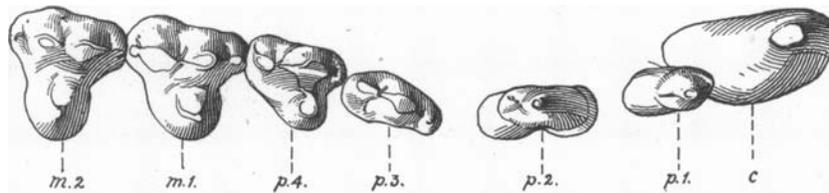


Fig. 94. *Mesonyx obtusidens* Cope. Upper teeth, crown view, natural size. From No. 12643.

pes in the various specimens mentioned above and it is in no wise certain that they all belong to the same species. According to Scott's figure the hind foot of his specimen is nearly as large and robust as that of *Synoplotherium vorax* as figured by Wortman. The specimen referred by Wortman to *Mesonyx obtusidens*

is very much more slender and elongate in the pes. The American Museum specimen is intermediate but nearer to that figured by Scott. The type is too fragmentary for any exact comparison but appears to be smaller than any of the referred specimens and intermediate in proportions between the American Museum specimen and that figured by Wortman.

I have nothing of importance to add to the very excellent description given by Professor Scott. In comparison with *Synoplotherium (Dromocyon) vorax*, the principal points of difference are that the

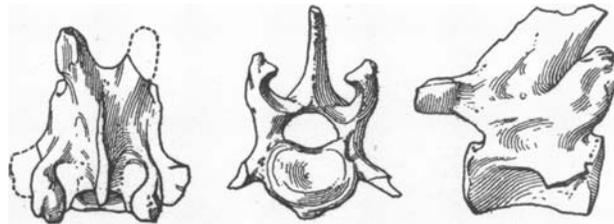


Fig. 95. *Mesonyx obtusidens*, lumbar vertebra, superior, anterior and lateral views, one-half natural size. From No. 12643.

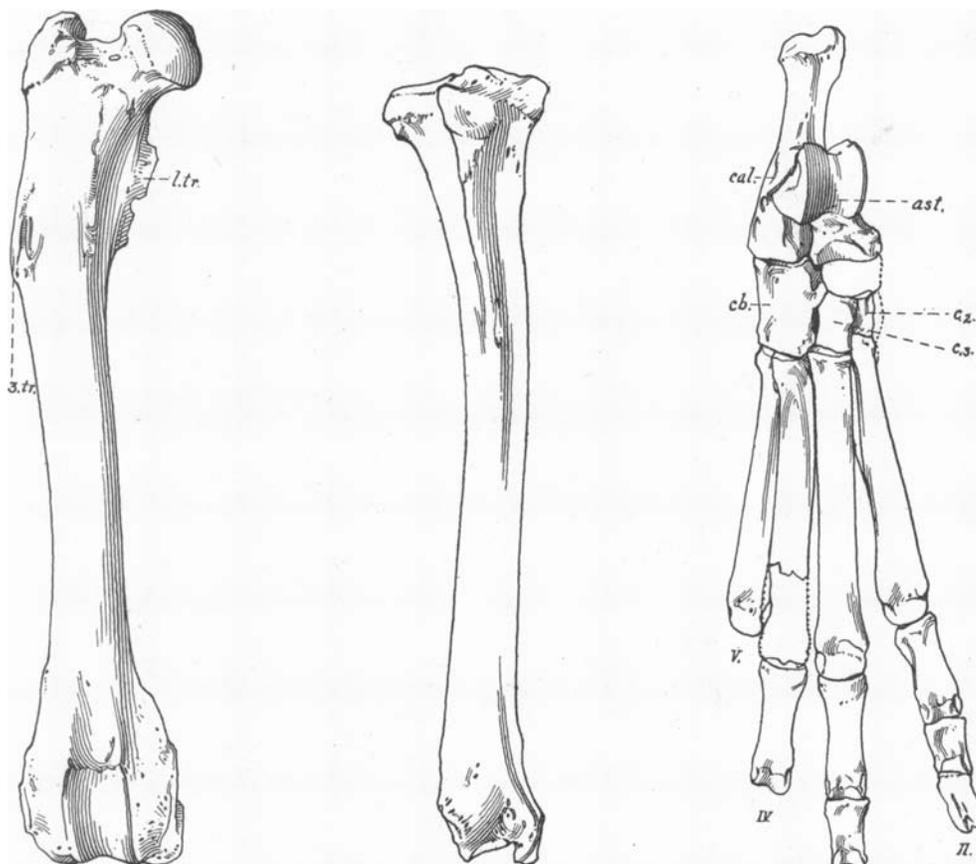


Fig. 96. *Mesonyx obtusidens*, femur, tibia and pes, one half natural size. From No. 12643.

skull is more elongate, the muzzle considerably more slender, the premolars are spaced and more compressed, the third premolar lacks the rudimentary internal

cusps of *Synoplotherium*, the fourth premolar is much smaller and its inner cusp proportionately less, the third molar is absent; the postglenoid process and the occipital condyle are less prominent. The lumbar zygapophyses are strongly convex and concave as in *Synoplotherium*, but, unlike that genus, show a slight development of the revolute or double tongue-and-groove articulation, somewhat less than in *Patriofelis*. The dorso-lumbar formula is 20 in *Mesonyx*, 19 in *Synoplotherium*; this, however, may be individual, as suggested on a preceding page. The limbs and feet are more slender and elongate but to a very variable extent if all the specimens are co-specific.

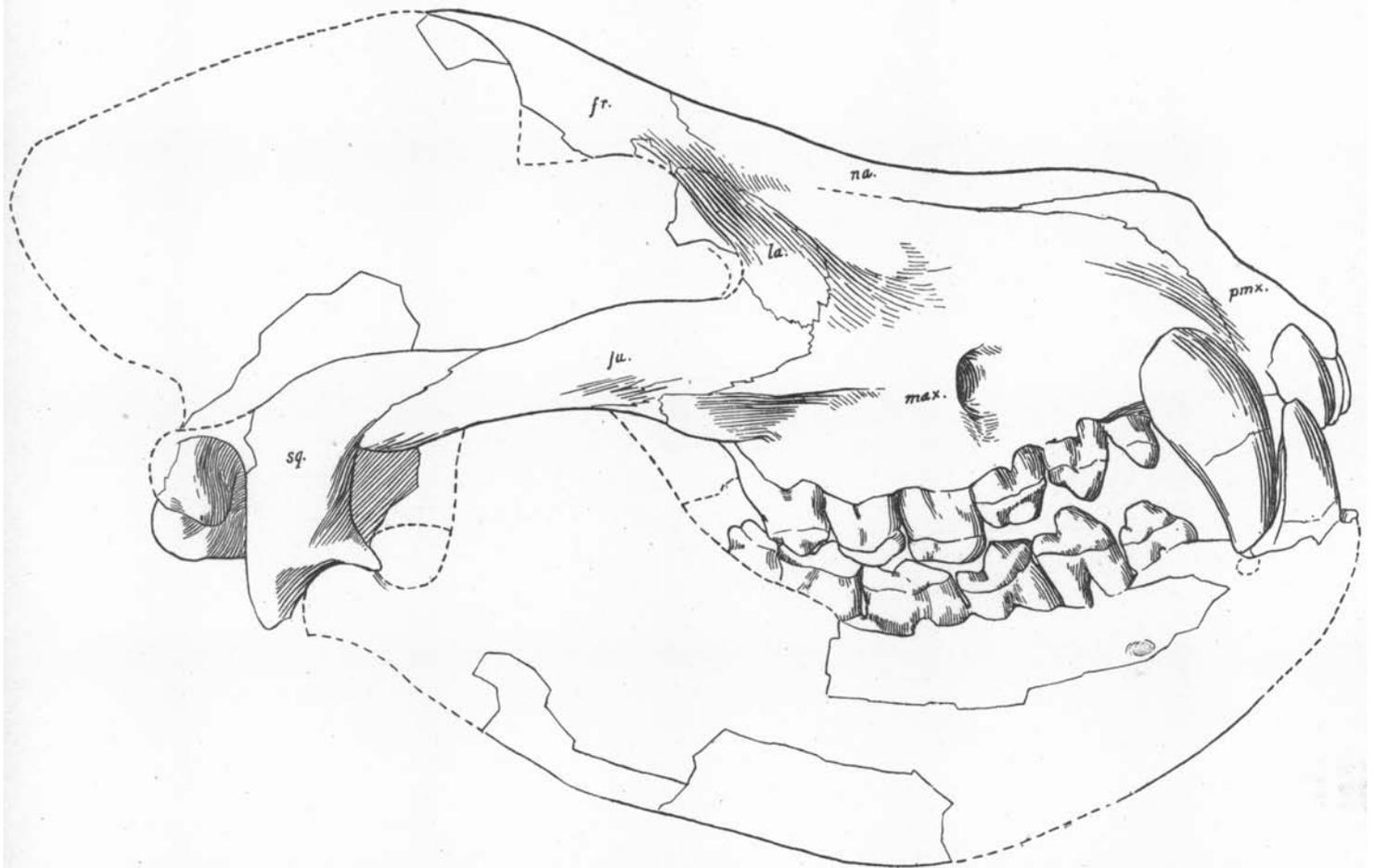


Fig. 97. *Harpagolestes immanis*, skull and jaws, two-fifths natural size. Type specimen, No. 13143, Upper Washakie.

Harpagolestes Wortman.

The type of this genus is *H. macrocephalus* Wortman, founded on an incomplete skull and jaws and humerus from the Lower Bridger beds.

Harpagolestes immanis sp. nov.

This species is founded on an incomplete skull and jaws from the Washakie basin, No. 13143, found by Paul Miller of the American Museum Exp. 1906. The teeth are in fine preservation and moderately worn, and the skull fragmentary but uncrushed. The anterior part of the skull is nearly complete, with one

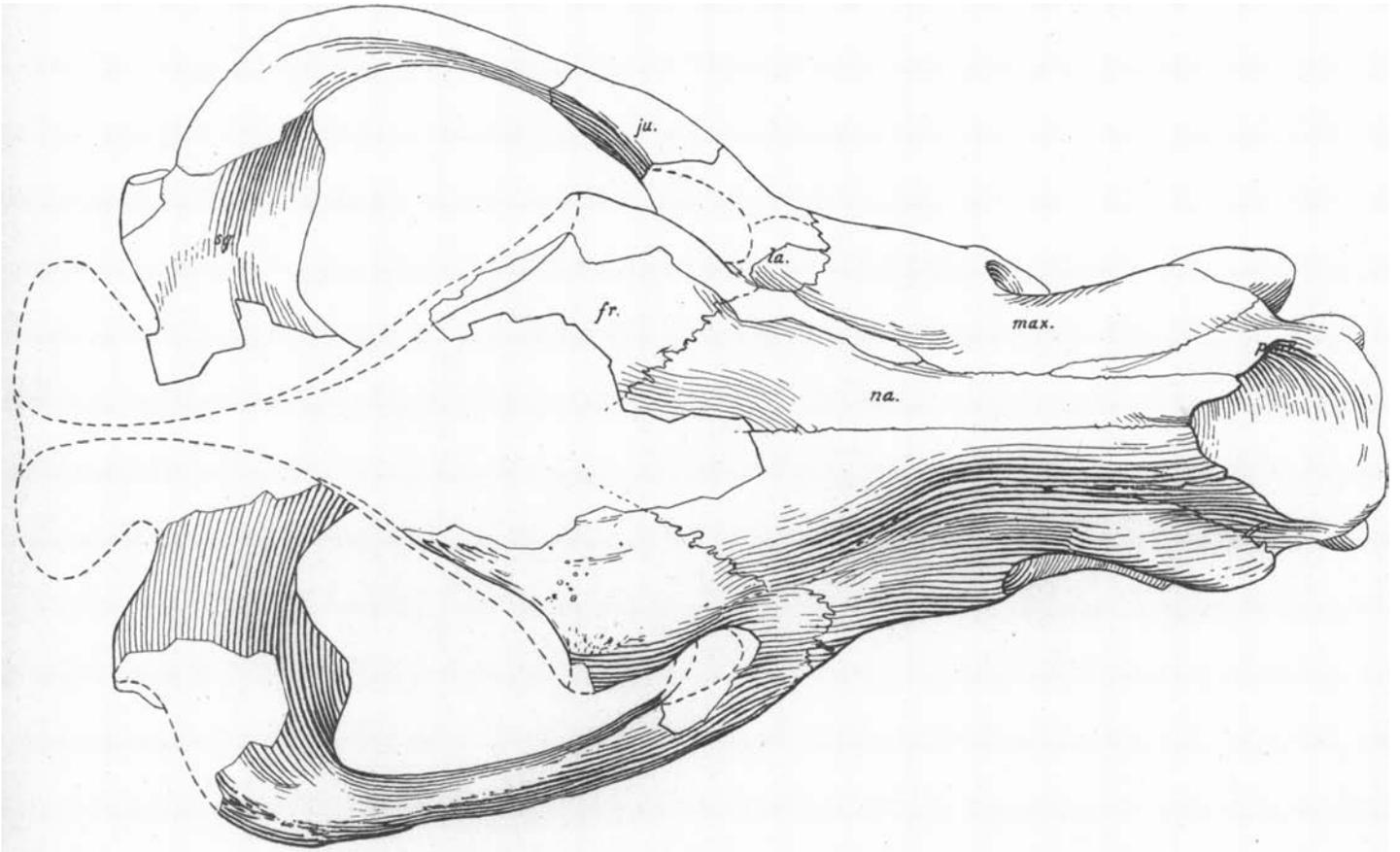


Fig. 98. *Harpagolestes immanis*, top view of skull, two-fifths natural size. No. 13143.

arch and most of the squamosal region and occipital condyles, sufficient to restore the skull with a fair degree of accuracy.

The lower teeth and adjoining parts of the jaws are well preserved, and a few fragments of the skeleton, chiefly of the fore limb.

The species differs from *H. wintensis* hypotype in the deeper, more robust facial region, broader frontals, close-set premolars, absence of prelachrymal fossa, larger glenoid fossæ and various minor characters. The last upper molar is absent, the second is unreduced, but the metaconid was either vestigial or absent, while on the first molar it was apparently well developed. The pre-

molars are more massive than in *Mesonyx*, the first is one-rooted, the second and third two-rooted, but the third has a rudimentary postero-internal heel. The fourth premolar is three-rooted, and apparently constructed much as in *Mesonyx* only the deuterocone is less separated from the outer cusps. The

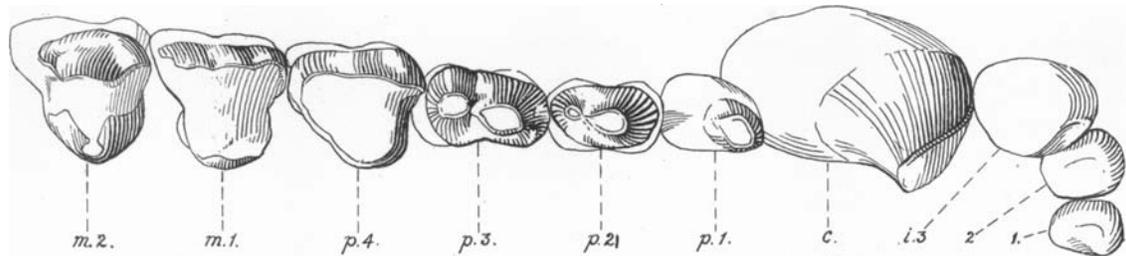


Fig. 99. *Harpagolestes immanis*, upper teeth, crown view, two-thirds natural size. Type, No. 13143.

incisors are stout, much worn, the lateral incisors much the largest. The canines are very large and massive.

The superior branch of the premaxilla is rather short. The nasals are broadly expanded posteriorly and the facial expansion of the lachrymals is remarkably extensive, having a considerable length of suture with the expanded

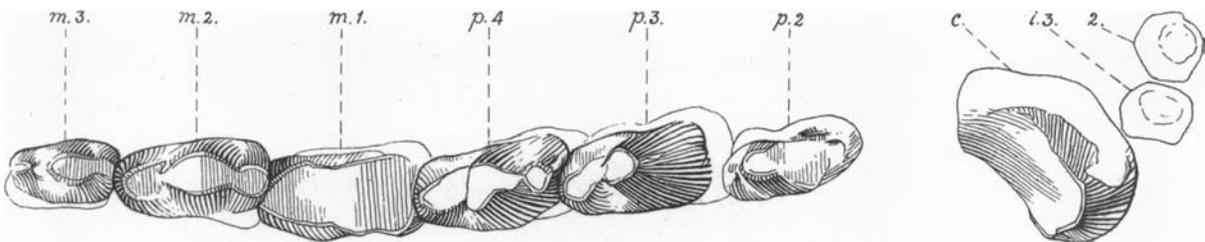


Fig. 100. *Harpagolestes immanis*, lower teeth, crown view, two-thirds natural size. Type.

nasals, so that the frontals do not approach the maxillæ. The jugal is comparatively small; its upper branch extends forward on the face beneath the lachrymals, the lower anterior branch is very slight and posteriorly it does not nearly reach the glenoid fossa.

Hapalodectes¹ gen. nov.

Type *Dissacus (Pachyæna) leptognathus* Osborn, Wasatch. Distinguished from other Mesonychidæ by the highly compressed lower teeth, the cusps converted into narrow trenchant blades.

This curious little genus is known only from lower jaws, which, while they are evidently referable to the Mesonychidæ, differ so widely from any of the described genera as to indicate a phylum of quite different trend. The thin

¹ ἄπαλος delicate, δῆκτης biter, in allusion to the slender and highly compressed teeth.

blade-like protocone has a slight vestigial metacone on its inner side, the paraconid and heel are much lower, the heel very much compressed. There is no indication of any shearing action on any of these sharp crested teeth, and evidently they were simply trenchant as in other Mesonychidæ.

The type from the Wasatch is represented by an incomplete jaw with p_4-m_2 . A closely allied species from the Wind River, with slenderer and somewhat smaller jaw and more compressed teeth, is represented by three jaws, one of which is figured with some of the teeth restored from another. It may be known as *Hapalodectes compressus*. (See also Pl. XLV, Fig. 5.)

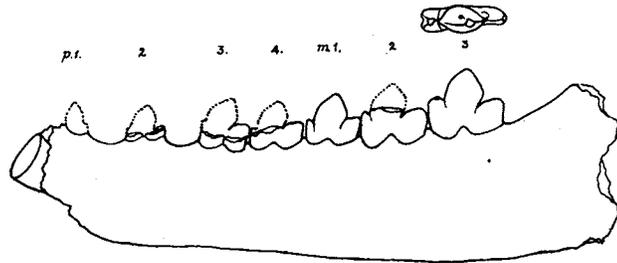


Fig. 101. *Hapalodectes compressus*, lower jaw, external view, $\times \frac{3}{2}$. Type specimen, No. 12781. Wind River Basin, Wyoming.

It may be known as *Hapalodectes compressus*. (See also Pl. XLV, Fig. 5.)

EVIDENCE BEARING UPON THE TRITUBERCULAR THEORY.

Dr. Wortman has cited the supposed course of evolution of the upper molars in Mesonychidæ in disproof of Cope and Osborn's theory of the origin of the tritubercular molar.

According to this theory, the protocone of the mammalian molar is the homologue of the original reptilian cone, and the paracone and metacone have been added as subordinate anterior and posterior denticles, subsequently shifted to the outer side of the trigon in the upper molars, to the inner side in the lower molars, and enlarged to an equality with the protocone; the hypocone of the upper and heel of the lower molars are subsequent additions. In Wortman's view the development of the tritubercular molar was analogous to the development of the molariform premolar, the course of which can be observed in many phyla of mammals. The paracone is the original reptilian cone, the protocone is added on the lingual and the metacone on the posterior side. In the lower jaw the protoconid is the original, the metaconid is added on the lingual and the paraconid on the anterior side.

In support of his opinion, Dr. Wortman cites the supposed evolution of the upper molars in the Mesonychid phylum, and figures the upper teeth of *Dissacus saurognathus* of the Torrejon and *Mesonyx obtusidens* of the Bridger in illustration. In the latter, according to the figure (republished from Scott 1887) the two molars and fourth premolar are typically tritubercular, the third molar being absent. In *D. saurognathus* the fourth premolar and second and third molars are incompletely molariform, the posterior outer cusp being quite small, the

third molar present but of reduced size. Wortman points out the exact correspondence of the successively simpler teeth behind and in front of m^1 in *D. saurognathus* and concludes that both molars and premolars have assumed the tritubercular form in the same manner.

Without entering upon any extended discussion of the origin of the tritubercular molar, it appears necessary to point out several objections to the evidence from the teeth of Mesonychidæ adduced by Dr. Wortman in support of his views, and to present the facts more correctly. The objections are:

1. If Wortman's data and conclusions were correct, the upper molars of the Mesonychidæ would be progressing from the premolar towards the tritubercular molar type, while the lower molars, according to his own statement, are progressing in the opposite direction and "becoming premolariform." This would seem *à priori* more improbable than that the premolars and molars should have complicated in a different manner.

2. The drawing of the upper teeth of *Mesonyx obtusidens* is very far from correct, as may be seen by comparison with the more careful drawings of the upper teeth published in this memoir. The drawing of *Dissacus saurognathus* is only fairly correct and exaggerates the reduction of the metacone on m^2 . There is in fact no such wide difference as the drawings would indicate in the construction of the teeth of these two species.

3. The species selected do not represent the earliest and latest stages of evolution of the family and they belong to two distinct subphyla, in one of which the teeth are more nearly tritubercular than in the other.

The facts appear to be as follows:

In the Creodonta generally, the molars, at first tritubercular above, tuberculo-sectorial below, tend to simplify their structure by loss of cusps and become more like the premolars. Their evolution is thus in an opposite direction to that of the herbivorous orders, in which the molars become further complicated by addition of cusps and the premolars often become molariform. In three of the Creodont families the molars develop shearing edges, but this is not the case among the Mesonychidæ.

The simplification is effected in the upper teeth by the metacone becoming more and more nearly connate with the paracone until it is merged with it (Eucroedi, Pseudocroedi, most Fissipedia) *or* by reduction of the metacone to a cuspule on the side of the paracone (Acreodi). The reduction of the protocone follows or accompanies the reduction of the metacone. In the lower molars the reduction of the metaconid corresponds with the connascence of metacone with paracone, the connascence of the metaconid with protoconid corresponds with the reduction of the metacone, and reduction of the heel corresponds with that of the protocone.

This appears to be the normal course of molar development in flesh-eating animals, and is equally apparent in other groups besides the Carnivora. It is

fairly well shown in the Mesonychidæ although this family was conservative and in certain respects peculiar in its dentition.

In the oldest of the Mesonychidæ, *Triisodon* of the Puerco, the upper molars are typically tritubercular, metacone and paracone of equal size and well separated. The lower molars are tuberculo-sectorial, with metaconids well developed and large basin heels. In *Sarcothraustes* of the Torrejon the metacones of the upper molars are somewhat reduced, the metaconid and protoconid somewhat connate. *Dissacus* of the same formation is considerably more advanced, the metacone being considerably reduced on all the molars, the metaconids and protoconids closely connate, while the protocones of the upper molars and the heels of the lower molars are reduced, and the latter trenchant instead of basin-shaped. The larger species, *D. saurognathus*, is somewhat more advanced than the smaller *D. navajovius*. In *Pachyæna* of the Wasatch the teeth are much as in *Dissacus*, except that the reduction of the metaconid is more advanced. The larger species *P. gigantea* is more progressive and shows a slight advance on *D. saurognathus* while the smaller *P. ossifraga* and *intermedia* are less progressive and scarcely advanced over *D. navajovius*. In the Bridger the small *Mesonyx obtusidens* shows the metacones much as in the smaller *Dissacus* but apparently slightly less reduced. The medium sized *Synoplotherium* and the large *Harpagolestes* have the teeth too much worn to tell much about them. In the Upper Eocene the large *Harpagolestes immanis* has apparently lost the metacone on m^2 but it is still of good size on m^1 although somewhat more connate with the paracone than in the older species. In *H. wintensis* the teeth appear to be about the same as in *H. immanis* as far as can be determined in their worn and broken condition.

From these facts it would appear that the Mesonychidæ exhibit on the whole a progressive simplification in the structure of both upper and lower molars, but that there were two or more phyla and the larger species were — as usual — more progressive than the smaller. The premolars show but little alteration from first to last, but the fourth is of simpler construction in the Triisodontinæ, lacking the postero-external cusp (trittocone or metacone) which is present in the Mesonychinæ although always much smaller than the antero-external cusp (protocone or paracone). Except in this respect the tendency appears to be towards simplification of the premolar as of the molar construction.

It is quite obvious that the history of the degeneration of the tritubercular molar into a simpler, more or less premolariform or haplodont tooth in the Mesonychidæ and other families of Carnivora *may* have followed the method or methods of cusp construction by which the tritubercular molar was previously built up from the primitive cone. But this would not necessarily be so. And the fact that the method of reduction and disappearance of the metacone and metaconid differs among the Creodont families, hints that there may have been more than one method of origin of the tritubercular molar. The direct evidence as to its origin must be obtained from Mesozoic mammals, and at present appears

to the writer quite inadequate to warrant anything beyond speculation. The embryological evidence is open to the objection that the order of calcification of the cusps follows the order of their height and importance and may not necessarily have anything to do with their antiquity. The most probable source of light appears to be in a reconsideration and more careful study of the interaction and correlation of the cusps of the upper and lower teeth, which does not appear to have been correctly interpreted in Cope's original theories of the origin of the teeth and is not yet well understood. Professor Osborn in his recent book on Trituberculy has discussed the evidence at length and in his usual clear and fair-minded manner, and has shown that while the derivation of the various mammalian molar forms from the tritubercular type can hardly now be questioned, the method of origin of the tritubercular molar cannot be regarded as settled. So far as the present writer's observations have extended, two primitive types of molar seem to be indicated among the Eocene mammalia. The principal one, almost universal among Basal Eocene mammals, is the normal tritubercular-tuberculo-sectorial type, with three subequal principal cusps in the upper, and a three-cusped trigonid with large basin heel in the lower molars, the upper molars also provided with paraconule, metaconule and an external cingulum, and the protocone always sub-crescentic. The second primitive type is rare and little known; it shows a large inner and two small outer cusps in the upper molars, and a high trigonid with heel rudimentary or absent in the lower molars. The first or normal tritubercular molar is best preserved among modern mammals in the less specialized Carnivore, Marsupial and Insectivore molars — *e. g.*, *Canis*, *Viverra*, *Didelphys*, *Talpa*. The second is shown in the Zalambdodont Insectivora. There does not appear to be any adequate evidence pointing to the derivation of one of these from the other. Intermediate forms may be found among modern Insectivora but the earliest known Tertiary types are not transitional. These two primary types of molar may quite well be independently derived from the primitive reptilian cone, and examples of both may be found among Jurassic mammals, as well as types which may indicate still other lines of derivation.

III. INSECTIVORA.

1. RELATIONSHIP, CLASSIFICATION AND GEOLOGICAL DISTRIBUTION.

The modern Insectivora have all the characteristics of a group which has passed through its period of evolution and expansion and is well on its way towards extinction. The surviving members are small, few, protected by some unusual adaptation of habitat or limited to remote and out of the way corners of the world, where the competition with higher orders of mammals is less severe.

The several families are distinguished by a high degree of divergent or parallel specialization in certain adaptive features, combined with a generally low grade of organization. Aside from their small size, inferior brain, insectivorous teeth, pentadactyl feet and other primitive features, it is not easy to find common characters by which to distinguish them as an order, and the relationship of the several families is so remote that it is open to serious question whether they are really a single natural order or not. The living forms are apparently the highly specialized survivors of a group or groups of very ancient differentiation, the intermediate and more normal members of which have long since become extinct. We should look therefore to palæontology to supply us with these missing links and clear up the history and relationships of the various families. We should expect to find the Insectivora playing a much more important rôle in the early Tertiary faunæ than they do at present, and to contain larger, more abundant and more central groups, which would serve to unite the scattered survivors in the modern fauna.

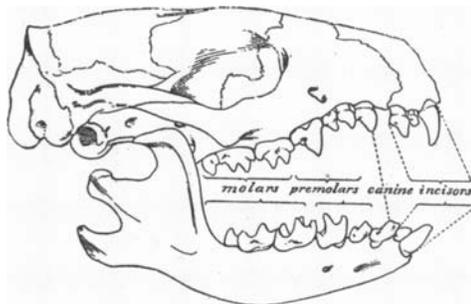


Fig. 102. Skull of the Hedgehog. A surviving type of the Insectivora. Natural size.

In the view of Professor Huxley and other high authorities, the Insectivora represent more nearly than any other order of mammals the central stock from which the various groups of placental mammals have descended. This view has been somewhat discredited in recent years by the unequal development of our knowledge of the past history of different mammalian orders. While our knowledge of fossil insectivores has been up to date extremely fragmentary and incomplete, we have come to know a good deal about the early stages of development of the placental carnivora and ungulate. There has been consequently a tendency, in looking for the primitive type of the Eutheria, to compare the highly specialized modern Insectivora with the primitive and little specialized members of the carnivorous and ungulate orders, with Creodonts and Condylarths of the early Eocene, and in consequence to regard the Insectivora as an aberrant and specialized group or groups, and the Creodonts and Condylarths as more nearly representing the primitive stock. The Eocene Insectivora are therefore of especial interest as affording a better perspective of the relations of the different groups of mammals, and so far as Huxley's view is correct, in presenting a close approximation to the primitive stock of the Eutherian mammals.

A fair measure of the central position of the Insectivora is afforded by the difficulty of defining the order as a whole on other than primitive characters. It is difficult to find any specialized characters common to all members of the order, although there are several peculiarities common to most of the families which may be regarded as specializations, inasmuch as no approximation to them

occurs in the earliest representatives of other orders. But for the most part the characters regarded as definitive of the Insectivora are shared by one or more of the other orders of mammals, especially by rodents, lemurs, creodonts and condylarths, which approach nearest in grade of organization.

Weber gives the following diagnosis of the order:

“Die Insectivora sind unguikulate, plantigrade oder semi-plantigrade, fast stets pentadaktyle animalivore kleine Säuger. Gebiss diphyodont; heterodont, ausschliesslich mit Wurzelzähnen. Ursprünglich $I\frac{3}{1} C\frac{1}{1} P\frac{1}{1} M\frac{3-4}{3-4}$. I können reduziert sein, oben bis auf 2, unten bis auf 1. C entweder caniniform oder, und meist, einem P oder I ähnlich. P und M stets mit spitzen Schmelzhöckern, trikonodont, trigonodont, tritubercular-sektorial mit Neigung quinque-oder quadrituberkular zu werden. Schädelform primitiv. Hirnhöhle klein. Tympanicum meist ringförmig. Clavicula fehlt nur bei *Potamogale*. Foramen entepicondyloideum und Centrale carpi meist vorhanden. Pollex und Hallux nicht opponierbar. Gehirn makrosmatisch. Hemisphären ungefurcht, kurz, lassen Cerebellum, vielfach auch Corpora quadrigemina unbedeckt. Uterus zweihornig. Placenta soweit bekannt, deciduat und diskoidal. Testikel abdominal oder inguinal und präpenial. Meist nächtliche, auf dem Lande, vielfach unterirdisch und grabend lebende Tiere; einzelne arboricole oder im Wasser lebend.”

In general the premaxilla and incisors are well developed, the reduction in number of the incisors being associated with the enlargement and specialization of one pair, $i\frac{1}{1}$. The tubular and overhanging snout, Flower regards as almost characteristic of the order. In most modern Insectivora the canine is two-rooted, an unusual character not present in any of the Eocene Insectivora so far as known (except probably the *Proglires*). The fourth premolar is often molariform and the molars are rarely less than three, their cusps usually sharp and angulate, but not developing any extended shearing edge as in the placental and marsupial carnivora. In the majority of the modern forms, and in two of the Eocene families, the posterior mental foramen is situate under the first molar, instead of under the third premolar as in all other mammals with which I have made comparison. The tympanic ring does not develop into an osseous bulla, but the tympanic chamber is partially enclosed in most of the families by dependent plates from the alisphenoid and basisphenoid, and in the *Tupaiidæ* and *Macroselidæ* a complete bulla is formed, in which, however, according to Weber, the true tympanic remains ringlike, the bulla calcifying from a distinct plate of cartilage which appears to be an outgrowth from the petrosal. In *Ictops* a complete bulla is also formed which corresponds closely to that of *Tupaia* in its relations to the surrounding bones and is probably comparable with it, and not with the true tympanic bulla of Carnivora, Rodentia and Primates. It may therefore be stated that no true tympanic bulla is present in the Insectivora; while a partial or complete false bulla is frequently developed. The course of the entocarotid arteries, according to Wortman, is an important diagnostic feature; the value of this character is further discussed elsewhere. The basicranial region is short and wide, in contrast usually to the elongation of the middle and anterior parts of the skull. The mastoid portion of the periotic has usually a

large posterior exposure, forming a considerable part of the wide and low occiput, as in many Marsupials. In Creodonta and Carnivora, and in most of the Ungulate groups, the basicranial region is comparatively narrow and long, and the exposure of the mastoid lateral instead of posterior, and mostly of small extent. *Limnocyon* and the larger Mustelidæ are exceptional in this respect. The lachrymal foramen is external or marginal, except in Macroscelidæ, Leptictidæ and Hyopsodontidæ. The optic foramen and often the foramen rotundum as well, are confluent with the sphenoidal fissure. The malar bone is usually small and often lacking, in contrast with its large development in Marsupials.

In the skeleton various peculiarities are common to several or the majority of the families, and various primitive features are retained by many or all of them. A clavicle is present except in *Potamogale*; the humerus has a supra-trochlear foramen, as in some Inadaptive Creodonts, Rodents, etc., and the entepicondylar foramen is usually present as in primitive mammalia generally. The centrale is generally present in the carpus, but the scaphoid and lunar are sometimes united; the trapezium is small and the thumb not opposable. The metapodials are short with hinge-joints distally, instead of the ball-and-socket joints of Carnivora and Primates; the median keel of the metapodial is usually extended over the superior surface. The ungual phalanges are clawed, usually small and not compressed, fissured at the tips in certain forms. The feet are nearly always pentadactyl.

The ischia are widely separated in the Insectivora except *Tupaia* and *Macroscelides*, and the pubes are also separated in the fossorial forms. This very unusual condition is perhaps distinctive of the order as a whole. The femur has occasionally a third trochanter. In the Soricidæ, Talpidæ, Erinaceidæ, Macroscelidæ, and Leptictidæ and Pantolestidæ, the distal ends of the tibia and fibula are united. In all Insectivora except *Hyopsodus* the astragalus has a symmetrical trochlea, both keels equally developed, as in Rodentia and Edentata. In *Hyopsodus*, as in Creodonta and Condylarthra, the trochlea is oblique, the inner keel little or not at all developed. The astragalar foramen is sometimes present, in *Erinaceus*, *Hyopsodus*, etc., but is more generally absent.

In the Bridger Eocene the Insectivora play a much more important part than in the later Tertiary or modern faunæ. Three extinct families appear to be referable to this order on the characters of skull and skeleton, the Leptictidæ, Pantolestidæ and Hyopsodontidæ. The first of these has been generally referred to the Insectivora, and is principally known from the Oligocene. The second and third have been referred to other orders, but the characters of the skull and skeleton in the Pantolestidæ show them to be nearer to the Insectivora than to any other recognized order. The relations of the Hyopsodontidæ will be discussed later. There are also numerous small Insectivora known only from jaws or parts of jaws, whose position is provisional, in the lack of more complete knowledge of their osteology. Some resemble the moles and shrews in their teeth, others approach

the Centetidæ and other Zalambdodont families. They are not referable to any of the three better known Eocene families. A third group, which may be considered here, includes a number of small or minute species which might be referred either to Lemuroidea or Insectivora, as they are known only from jaws which mingle characteristic features of both. *Pantolestes* includes species much larger than any other known insectivore; *Hyopsodus* is the most abundant animal in the Bridger fauna; and the total number of genera and species referred to the Insectivora is larger than in any other order, if we include the questionable group above mentioned. It is apparent therefore that the relative importance of the Insectivora was much greater then than now. In fact they almost occupy the dominant position in respect to number and variety of species now taken by the Rodentia. It will also appear in the descriptions that the three principal families are all of an intermediate, unspecialized and extremely primitive structure. They tend to associate the Insectivora with other primitive groups, and emphasize the central position of the order. This is especially true of the Hyopsodontidæ, which are hardly definable or referable to the order except by primitive characters. Relations to the Creodonta are indicated in the dentition of the Pantolestidæ and Leptictidæ, to the Condylarthra in the dentition, skull and skeleton structure of the Hyopsodontidæ. On the whole the Bridger Insectivora entirely confirm the theoretical deductions based upon the modern survivors of the order, and the opinion of Huxley as to the central position of the order among the Eutherian mammals.

The modern Insectivora approximate the less specialized Marsupials in certain important characters of the skull, and in the general construction of the teeth, more nearly than do any other Placental orders. This is especially seen in the construction of the bulla, the relations of the mastoid, the incompletely ossified palate bounded posteriorly by a transverse ridge, marginal or external lachrymal foramen, elongate nasals, posteriorly placed orbits, etc. The tritubercular insectivorous teeth are often remarkably similar, and some Insectivora present approximations to the marsupial dental formula (4 molars sometimes found in *Centetes*, four upper incisors generally in the Shrews). These resemblances are not increased by the study of the Eocene insectivora. The Leptictidæ, Hyopsodontidæ and Pantolestidæ tend to connect Insectivora with other Eutherian orders, but show no especial approximation to either fossil or recent Marsupials, aside from the tritubercular teeth common to all primitive mammals. Their dental formula is typically Eutherian; the skull characters are those of Insectivora but less like Marsupials than some of the modern members of the order. The astragalus is characteristically Insectivore in Leptictidæ and Pantolestidæ; in Hyopsodontidæ it has some resemblance to those of Condylarths, Creodonts and Primates, but makes no approach to the peculiar astragalus of the Marsupials.

The arrangement of the extinct and surviving families of Insectivora is

indicated in the following table. It will probably be necessary in the future to group the minute talpoid and centetoid genera of the Eocene and Oligocene in distinct families from the modern genera, since they cannot be positively referred to one modern family rather than another, and the probabilities are that they would present numerous primitive characters of skull and skeleton, and hold much the same relation to the modern families as the Miacidæ do to the modern carnivora.

	Extinct Families Eocene and Oligocene	Living Families Oligocene to Recent			
Dilambdodonta	Hyopsodontidæ	{ Tupaiidæ { Macroscelidæ { Erinaceidæ { Talpidæ { Soricidæ	Astragalar trochlea oblique	Pubic symphysis short	
	Leptictidæ			Pubic symphysis long. (<i>Menotyphla</i>)	
	? Talpidæ			Astragalar trochlea symmetrical	Pubic symphysis short or none. (<i>Lipotyphla</i>)
	Pantolestidæ				
Zalambdodonta	? Centetidæ	{ Potamogalidæ { Solenodontidæ { Centetidæ { Chrysochloridæ	Astragalar trochlea symmetrical	Pubic symphysis short or none. (<i>Lipotyphla</i>)	

The definitions of the Eocene families will be as follows:

1. *Hyopsodontidæ*. Dentition unreduced, anterior teeth uniformly small, one-rooted, molars sex-tubercular above, quadritubercular below, with round, blunted cusps. Mental foramen beneath p_3 , lachrymal foramen intra-orbital, no post-orbital processes, no bullæ nor false bullæ. Scaphoid and lunar separate, pubic symphysis short, tibia and fibula separate, astragalar trochlea oblique. Digits short, claws small. Eocene of North America. One genus, *Hyopsodus*, Lower to Upper Eocene.

2. *Leptictidæ*. Incisors $\frac{3}{3}$. Canine premolariform, more or less perfectly two-rooted. Molars tritubercular with large heels and angulate cusps. Mental foramen beneath p_3 , lachrymal foramen intra-orbital, false bullæ present. Tibia and fibula united, astragalar trochlea symmetrical. Digits moderately long,

claws small. Eocene and Oligocene, four known genera: *Palæictops* (Eocene), *Ictops*, *Leptictis*, *Mesodectes* (Oligocene); one doubtfully referable, *Phenacops* (Eocene).

3. *Pantolestidæ*. Incisors $\frac{3}{1}$. Canines large, caniniform. Molars with large heels, primitive tritubercular pattern. Mental foramen beneath m_1 , lachrymal foramen extra-orbital, no bullæ (as far as known). Tibia and fibula united, astragalar trochlea symmetric. Phalanges elongate, unguals flattened. Eocene, three genera: *Pantolestes* (Middle Eocene), *Palæosinopa* (Lower Eocene), *?Pentacodon* (Basal Eocene).

4. *Talpidæ*. Incisors unreduced. Molars with high trigonids, large heels, cusps as in *Talpidæ* and *Soricidæ*. Skeleton unknown, but hypothetically as in *Soricidæ*.

The last family cannot at present be sufficiently defined or adequately distinguished from the modern Moles and Shrews to which they are most nearly related, since we know little or nothing beyond the teeth and jaws of any of them. Nevertheless the reference to any modern family of these little Eocene jaws is to my mind misleading. The Eocene talpoid forms are probably related to either moles or shrews, but probably they combined the more primitive dentition of the moles with the more primitive skeleton of the shrews, and may have lacked certain progressive features common to both families. But until we have the skull and skeleton we cannot properly define the extinct groups to which they presumably belong, and I provisionally leave the Eocene genera in the *Talpidæ*, with which they agree fairly well as far as comparisons can be made.

2. Family HYOPSODONTIDÆ.

Lemuravidæ MARSH 1875.

Hyopsodinæ TROUËSSART 1879 (in part).

Adapidæ COPE 1884 (in part).

Hyopsodidæ SCHLOSSER 1887 = Hyopsodontidæ LYDEKKER 1889 (in part).

Hyopsodontidæ OSBORN 1902, WORTMAN 1903, LOOMIS 1905 (in part).

The genus *Hyopsodus* was established by Leidy in 1870 and more fully described and figured in 1873, from upper and lower jaws. The skull and skeleton were completely unknown and the animal was referred by its describer to the Suilline Ungulata in company with *Microsyops*, *Microsus*, *Notharctus* and other Bridger genera no better known. Marsh and Cope in 1873 discovered the Primate characters of the skeleton of *Notharctus* (= *Limnotherium* Marsh, *Tomitherium* Cope) and transferred *Hyopsodus* along with these other small Bridger bunodonts to the primate order. Marsh in 1875 described the fragmentary skeleton of *Lemuravus* which he rightly regarded as closely related to *Hyopsodus* — they appear in fact to be identical — and erected the family Lemuravidæ to contain the two genera. Trouessart in 1879 combined into the family Adapidæ

nearly all the Eocene lemuroids grouped by Filhol as *Pachylemuriens* (*Pseudolemuroides* Schlosser), distinguished *Hyopsodus*, *Lemuravus* and some other American genera as a distinct sub-family, the Hyopsodinæ, and *Notharctus* and *Opisthotomus* as a distinct family Notharctidæ, all being regarded as a primitive suborder (Mesodonta Cope) of Insectivora. Cope in 1883 separated *Anaptomorphus* and *Mixodectes* as types of distinct families, removing them provisionally to the suborder Prosimiæ, and combined the remaining lemuroids under the Adapidæ in the suborder Mesodonta, of Primates. Schlosser in 1887 raised the Hyopsodinæ to family rank, combining under it *Pelycodus*, *Microsyops*, *Hyopsodus* and the remaining genera of the American Eocene. Osborn in 1902 distinguished two families of Mesodonta, Notharctidæ and Hyopsodontidæ, the Mixodectidæ, including *Microsyops*, being placed in the suborder Proglires of Rodentia. Under the Hyopsodontidæ he admitted two valid genera, *Hyopsodus*, with *Lemuravus* and *Microsus* as synonyms, and *Sarcolemur*, with two doubtful genera, *Antiacodon* and *Entomodon*. He described and figured the skull of *Hyopsodus*, confirmed the reference of the family to the Mesodonta, defined as "primitive primates," and pointed out the evolution in the structure of the teeth illustrated by the Lower, Middle and Upper Eocene species. In 1903 Wortman, in revising the Eocene Primates, excluded the Hyopsodontidæ from the order and placed them among the Insectivora. In 1905 Loomis accepted this change and placed the family in the neighborhood of *Erinaceus*. He admitted and defined two valid genera, *Hyopsodus* and *Sarcolemur*.

Species of *Hyopsodus* are the most abundant fossil mammals in the Bridger sediments and are equally common in the Wasatch and Wind River formations. Nevertheless, owing to the small size and generally fragmentary nature of the specimens, the morphology of the genus is not as well known as in many of its larger but less abundant contemporaries. We are now able, however, to give a reasonably full description of its osteology. Besides the skull from the Washakie described by Osborn, we have from the Bridger Basin a complete skull and parts of several others, two fragmentary skeletons and several hundred specimens of upper and lower jaws more or less complete. These specimens, the exact record of level and locality of each one being preserved, enable us to define accurately the vertical range, mutations and mutual relations of the species so far as they are expressed in the teeth, but leave the ordinal position of the family still somewhat obscure and uncertain, since the characters of skull and skeleton are mainly of a negative and generalized kind and do not tend to ally it closely with any recognized mammalian order.

The position of the Mesodonta among the Insectivora advocated by Trouessart in 1879, was based upon Cope's statement that the hallux was not opposable — a statement founded upon the incorrect association of certain skeleton fragments with the teeth of species of *Pelycodus* from New Mexico. In fact, in the Notharctidæ, including *Pelycodus*, the hallux is opposable and the skeleton

characters in all respects approach the Lemurs. Osborn, in his description of the skull of *Hyopsodus*, emphasized the primitive characters of the genus, but did not point out any distinctive Primate characters. The skeleton was not then known save for Marsh's brief statement comparing it with the lemurs and there seemed to be no obvious reason for removing it from the Primates. Wortman in 1903 gives the following reasons for removing it to the Insectivora, based on a study of the skull in the American Museum and upon fragmentary skeletons in the Yale collections: (1) three incisors above and below; (2) no ossified tympanic bulla; (3) the structure of the molars is not like that of the Primates; (4) the enterocarotid circulation is like that of the Insectivora; (5) the limb-bones differ from those of any known Primates [in the presence of a supratrochlear foramen on the humerus]; (6) the metapodials are not Primate [distal ends depressed and strongly keeled]; (7) the phalanges are short; and (8) the hallux is not opposable.

These characters combined with the absence of any positive Primate peculiarities, furnish quite adequate reason for removing the Hyopsodontidæ from the Primates. But with the very doubtful exception of (4), they furnish no good reason for placing the family in the order Insectivora. The first character is common to most orders of mammals, and less generally retained in the Insectivora than in Condylarths, Creodonts, Ungulates, etc. The lack of ossified tympanic bulla is common to nearly all Eocene mammals, Primates alone excepted. The characters ascribed to the metapodials and phalanges, and the non-opposable hallux, are likewise shared by most primitive mammals, and it is quite probable that a more extended research would show that the arrangement of the entocarotid circulation in the Insectivora is an approximation to the primitive type, retained by this order as well as by the Rodents and perhaps by other orders, and modified in various ways in the more specialized mammalia. Dr. Loomis has added two or three more skeletal characters which are equally generalized, and common to Insectivores, Creodonts, Condylarths, etc.; some of them (*e. g.*, the third trochanter of the femur) are also found in the Lemuroidea.

On the other hand the Hyopsodontidæ do *not* exhibit certain distinctive features which are found in many or almost all of the families of Insectivora. There is no trace of the double-rooted canine, caniniform or pincer-like incisors, external lachrymal foramen, reduction of the zygomata, posterior position of the mental foramen, peculiar angle of the jaws, false bulla, and various other features of the skull which, while not common to all Insectivora, are variously developed in most of them. The teeth are widely different in type from those of any known Insectivora, but show a very marked resemblance to those of Condylarthra, especially *Miocænus* and the smaller Phenacodonts. The brain-case indicates a remarkably high type of brain for an Eocene Insectivore. The tibia and fibula are not united distally. The astragalus, a bone which in my experience is of the highest value in determining ordinal affinities, is not at all of the Insectivore

type, with wide trochlea symmetrically developed and bounded by inner and outer keels, but has a flat, oblique trochlea without inner keel, as in Creodonts and primitive Condylarthra. It lacks the peculiar postero-inferior prolongation characteristic of lemurs. (See Pl. XLVII.)

The principal positive arguments for placing the family among the Insectivora appear to me to be the following:

1. The general agreement in proportions of skull, limbs and feet with the least specialized among the Insectivora.

2. The dentition is primitive and little specialized, as it is, relatively speaking, among the Insectivora.

3. The occiput is broad and low with a large posterior exposure of the mastoid (as also in Marsupials) differing from Creodonts and Condylarths.

4. The entocarotid circulation is like that of Insectivores and Rodents (fide Wortman) differing from Creodonts and Primates.

5. The humerus has a supratrochlear and an entepicondylar foramen, as in the majority of Insectivores, Inadaptive Creodonts and some other groups.

6. The pelvic symphysis is short and as far as I can judge from incomplete specimens, formed by the pubes alone, the ischia taking no part. This character is seen in the majority of Insectivora, and is an intermediate between the normal pubic symphysis of pubes and ischia, and the peculiar condition in the fossorial Insectivora, of no pubic symphysis at all. I do not know of its occurrence except among Insectivora and Edentata.

7. The femur has a third trochanter, as in Creodonts, Condylarths, Insectivores, Lemurs, Perissodactyls, etc., but the form and position of the trochanter corresponds more nearly with that of *Erinaceus* than any of the others with which I have compared it.

8. The hinge-like distal joints of the metapodials, permitting of but little lateral motion of the phalanges, are as in many Insectivora, and differ from Carnivora (except Pinnipedia), Creodonta and Primates.

9. The clawed unguals, not compressed nor flattened, agree with Insectivora somewhat better than with Carnivora, Primates or Condylarthra.

On the whole it appears best to place the Hyopsodontidæ in the order Insectivora, as a primitive and unspecialized group with no very close relations to any of the other families despite the superficial resemblance to *Erinaceus*. They differ from the more typical Insectivores in the lack of various peculiarities, nearly all of which, however, may be lacking in one or another of the more typical members of the order. They have a general resemblance to Insectivora in the broader features of size and proportions of skull, teeth and skeleton, and differ from Creodonts in the lack of predaceous specializations in the teeth, in the form of the skull and proportions of limb bones and feet. They differ from Primates in the characters quoted above, and from Condylarths and other ungulates in proportions of skull, characters of the foot-bones, etc.

They appear, however, to be quite closely related to the supposed Condylarth family Mioclænidæ of the Basal Eocene, and in particular to *Mioclænus acolytus*, if I am right in referring to this species a fragmentary skeleton from the Basal Eocene which has been described and figured by Osborn.¹ The limb-bones and especially the astragalus and other tarsals in this specimen are of very similar type to those of *Hyopsodus*. The resemblance in the dentition is also marked; Cope indeed first described this species under the name *Hyopsodus acolytus*; and Matthew has named a closely allied species *Mioclænus lemuroides* in allusion to its resemblance to *Hyopsodus*, then supposed to be a lemur. It is quite possible that a more careful study of the Mioclænidæ would result in merging the whole family in the Hyopsodontidæ. But as we know nothing of their skeleton or skull except in the supposed *M. acolytus*, I do not think it advisable to make the change at present. The resemblance of *Hyopsodus* to the Phenacodontidæ, especially to *Euprotogonia* and the smaller Phenacodi, is very marked in the character of the teeth and form and arrangement of their cusps, so much so as to have misled on several occasions so keen an eye as that of Professor Cope.² There are, however, very wide differences in the occiput and basis cranii, which, together with the clawed unguals, primitive carpus with centrale, hinge-jointed phalanges, etc., make it inadvisable to place *Hyopsodus* in the Condylarthra. Nevertheless I believe that its affinities are in reality closer to the Condylarthra than to the more typical Insectivora. *Euprotogonia* and *Mioclænus* are to a certain extent intermediate, but the relationships of the former are much closer with *Phenacodus*, while *Mioclænus* is of doubtful position.

The family includes but a single valid genus, *Hyopsodus*, with a range from Lower Eocene (Wasatch) to Upper Eocene (Upper Uinta) in the Western Tertiaries. It is not certainly known to occur outside of North America, but I am informed by Professor Ameghino that certain of the interesting forms which he has brought to light from the Eocene or Cretaceous of Patagonia may be referable to this family and quite closely related to *Hyopsodus*. This fact, if confirmed by the further studies of my learned confrère, will be of much interest in correlation and in extending the range of the family. The species described by Rüttimeyer from the Eocene of Switzerland, *Hyopsodus jurensis*, is not related to *Hyopsodus*, as has been observed by Schlosser, Osborn and myself, and recently confirmed by the monographic studies of Professor Stehlin (1907) upon the Egerkingen fauna. The American genus *Sarcolemur* has generally been associated with *Hyopsodus* on evidence of its resemblance in the molars and last premolar; but more complete specimens of this genus from the Bridger Basin show that it is an Artiodactyl, related to *Trigonolestes* and *Homacodon*. The genus *Microsus* Leidy, which has usually been regarded as a synonym of *Hyopsodus*, appears also to be

¹ *Indrodon malaris*, Nos. 823, 829, Osborn & Earle 1895, pp. 16-20. "Supposed primate" Osborn 1902, pp. 170-1. Not *Indrodon malaris* Cope.

² *E. g.*, Cope at first referred *Hyopsodus powellianus* of the Wasatch, to *Phenacodus*.

an Artiodactyl, so far as one can judge from the pattern of the molar teeth as represented in Leidy's figures.¹ The principal cusps of the lower molars are opposite, while in *Hyopsodus* they are partly alternating.

Hyopsodus Leidy, 1870.

Syn. *Lemuravus* MARSH, 1875.

Plate XLVIII, and Text Figures 103-105.

Dentition $\frac{3.1.4.3}{3.1.4.3}$. Incisors, canines and anterior premolars small, one-rooted, with simple, pointed and somewhat spatulate crowns, semi-procumbent below, successively increasing in size, uniformly, except that the median upper incisors are slightly enlarged. Posterior premolars with internal cusps. Upper molars sex-tubercular, cusps round, conical with tritubercular symmetry, styler cusps rudimentary or absent, hypocone outside the primitive triangle, and variably developed on m_2^2 . Lower molars quadritubercular, the cusps partly alternating. Hypoconulid of m_3 variable, partly twinned with metaconid. Lower premolars short, robust, with small heels and subspatulate trigonids, the internal cusp of the trigonid distinct only on p_4 .

The *skull* is rather short and wide, proportioned somewhat as in *Erinaceus* but with longer, slenderer muzzle, deep arches, and marked postorbital constriction. The basicranial region is short and wide, the orbit not enclosed posteriorly but defined by a prominent rim anteriorly and inferiorly. No post-orbital processes. The orbit faces upward and to some extent laterally, but scarcely at all forward. The zygomatic arch is deep anteriorly, the malar bone broad anteriorly but not branched, joining with the lachrymal to exclude the maxilla from the margin of the orbit. The lachrymal has a small facial expansion but its foramen is within the orbit. The nasals are rather long but not expanded posteriorly; they appear to have a short contact with the maxillæ, excluding the frontals from contact with the premaxillæ. The palate is broad and completely ossified; it does not extend further back than the last molar, and lacks the transverse crest at its posterior margin found in most modern Insectivora and in the Marsupials. The glenoid fossa is a rounded pit

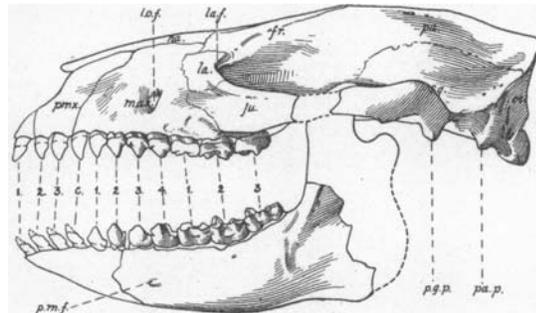


Fig. 103. *Hyopsodus despiciens*, skull and lower jaw, natural size, type specimen, No. 11877. Upper Bridger (Hor. D5).

¹Through the courtesy of Mr. J. W. Gidley, I have recently had opportunity to confirm the correctness of this reference by examination of the type of *Microsus*, preserved in the National Museum.

without transverse expansion; the postglenoid process is low and small, the auditory meatus wide and open, not roofed over by bone, the mastoid process distinct, short and robust. The mastoid exposure is posterior, rather large,

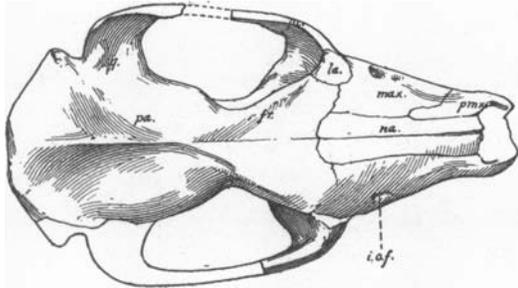


Fig. 104. *Hyopsodus despiciens*, top view of skull, natural size, No. 11877.

forming part of the wide, low occiput. The paroccipital process is well separated from the mastoid process, short, stout, directed downwards. Condyles wide apart. Auditory prominence of the petrosal large, prominent, pear-shaped, the point directed forward and inward. There is no osseous bulla preserved on either of our skulls nor any clear indication of whether true or false bulla was present. If present, the bulla

must have been loosely fastened to the skull, as in *Ictops*, where it is not generally preserved.

Skeleton. The characters are derived from two specimens, both fragmentary and immature. One, No. 11393, consists of upper and lower jaws with permanent dentition but unworn teeth, parts of various limb bones, centra of vertebræ, pelvis, astragalus, navicular and other foot bones. It was found at Grizzly Buttes by Mr. Granger in 1903 and is referred to *H. paulus*. A second more important specimen, No. 11959, was found by Mr. Granger in 1904 on Henry's Fork. It consists of upper and lower jaws with milk dentition, various limb-bones and vertebræ, foot bones, parts of ribs and fragments of skull, belonging to at least three individuals of *Hyopsodus*. In both these specimens the association of skeleton parts with the teeth appears to be certain, as there was no indication of possible admixture of remains of other animals.

The limb-bones, as Dr. Wortman has observed, are short and quite unlike those of any primate. They carry out the general resemblance in proportions to *Erinaceus*, which has already been observed in the skull. The *humerus* has a nearly proximal head, greater tuberosity prominent and nearly as high as the head; lesser tuberosity little developed, deltoid crest moderately high, extending about half-way down the shaft and ending somewhat abruptly, supinator crest moderately developed, entepicondyle a prominent process, pierced by the entepicondylar foramen, but not prolonged upward along the shaft as much as in Creodonts. There is a supratrochlear foramen, as in most Inadaptive Creodonts, Insectivora, Rodentia and some other groups. The distal trochlea is not much expanded laterally, less than in most Insectivora, about as in Creodonts and early Condylarths. The *ulna* is stout and short, the shaft wide but rather thin, the olecranon large and somewhat overhanging the rather wide and shallow sigmoid fossa. The head of the radius is a flattened oval, permitting of but little torsion of the fore limb. The distal end of the radius is round-oval, lacking the trihedral

outline characteristic of Creodonta, is less extended inferiorly than in *Erinaceus*, and has a single, wide concave facet for scaphoid and lunar, without indications of separation between the two. The *carpals* are short and wide, but the scaphoid has a greater vertical depth than in Creodonta, less than in *Erinaceus*, and is not united with the lunar as it is in that genus. Its ventral hook is small and pointed, its two distal facets separated and strongly convex, its proximal facet nearly flat. The cuneiform is short vertically, resembling the scaphoid in size and proportions, its ventral hook equal to the dorsal portion of the bone; the ulnar facet is of moderate size, the pisiform facet quite small, the unciform facet strongly concave. The unciform, like the proximal carpals, is short vertically, and is rather small, with a considerable proximal facet for the lunar and a larger proximal-external facet for the cuneiform; distally it appears to rest equally upon the fourth and fifth metacarpals, with a small vertical facet for the third.

Several *metapodials* and *phalanges* are preserved, but I am unable to distinguish and identify them with certainty. The metapodials correspond with

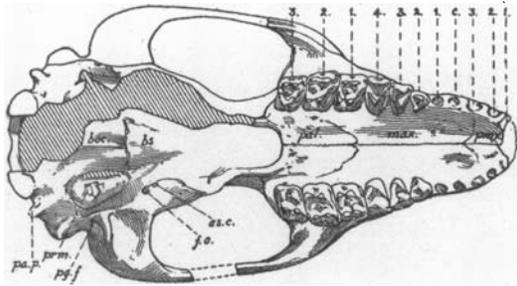


Fig. 105. *Hyopsodus despiciens*, under view of skull, natural size, No. 11877.

those of the middle digits of *Erinaceus*, but are less expanded at the distal end; none of those preserved correspond with the very short, reduced lateral metapodials of the hedgehog, and from these two facts I infer that the lateral digits were probably not reduced. The distal facets are very similar in form to those of *Erinaceus* and the terrestrial Insectivora generally. The proximal phalanges are rather short, the shafts slightly convex superiorly, their shafts

wider than in Creodonta, their proximal facets less concave, and their distal facets not reflected over the superior surface of the bone. The phalanges of the second row are very short, being not much longer than wide, the shafts are as wide as the ends, strongly concave superiorly, and in all respects very similar to those of *Erinaceus*. A single ungual phalanx is preserved. It is short and small, round-pointed, not fissured nor compressed, with a moderate subungual process and no hood. It resembles that of *Myogale*, and is much smaller and less compressed than in *Erinaceus*.

The *pelvis* is moderately long, the iliac bar flattened, trihedral but very little expanded, the ischial and pubic bars of equal size, considerably shorter than the ilium, and the symphysis, as far as I can judge from the collocation of parts of several pelvises, is formed by the pubis alone and resembles that of *Erinaceus* except that the ischium is longer and slenderer. The *femur* has a flattened hemispherical head, short neck, greater trochanter not very high, lesser trochanter postero-internal and rather prominent, and a moderately strong third trochanter

crest much like that of *Erinaceus* but situate farther down on the shaft. The distal end appears to be considerably less expanded than in the hedgehog, but the epiphysis is not preserved. The *tibia* is considerably longer than the femur, and is entirely separate from the fibula; the cnemial crest is prominent, extending about two fifths of the way down the shaft and ending rather abruptly; below this the shaft becomes nearly round, and is moderately expanded at the distal end, which is very oblique, the astragalar facet very moderately concave, the malleolar process scarcely distinct. The *astragalus* has a short, distinct neck, nearly flat and very oblique tibial facet, the fibular facet at about an equal angle with the tibial facet, and separated from it by a prominent crest, while the inner malleolar crest is entirely undeveloped, as is the primitive condition among Primates and Creodonts. In all known Insectivora and rodents on the other hand, the inner and outer crests which bound the trochlea are equally prominent, and the trochlea between is broad and uniformly concave. The *calcaneum* has a short tuber, small fibular facet, and its distal half is quite short. The *navicular* is also short, with moderately developed hook, and the cuneiform facets indistinctly separated. The cuboid is somewhat longer than it is wide, with a distinct astragalar facet facing more internal than proximal, and a larger calcaneal facet facing proximally and partly upward and outward and its distal facet partially divided into a large facet for mt. IV and a small one for me. V.

The numerous fragments of vertebræ, ribs, etc. add nothing of importance to our understanding of the morphology of *Hyopsodus*.

Species of Hyopsodus.

The collections contain several hundred numbered specimens from the Bridger Basin, principally upper and lower jaws, sometimes associated, more generally separate. Very few have parts or fragments of the skeleton preserved. A single complete skull, in addition to the skull from the Washakie Basin already described by Osborn, two anterior halves of skulls, and a fragmentary skeleton, supply the most important evidence as to the ordinal position of the genus. There are also many fragments of jaws not numbered. This abundant material shows considerable difference in size, and a less amount in the form and proportions of the teeth, representing evidently several species, but the limits and range of each species are not easily determined even from a minute study of the teeth. The jaws from the upper beds differ materially from those found in the lowest fossiliferous horizon; while the intermediate levels contain a transition form between the characteristic species of the upper and that of the lower beds, mingled with a larger and a smaller species not found in upper or lower beds. All the species, however, are rather nearly allied; the differences are not so wide either in size or form of teeth, as are the differences between the Wasatch or Wind River

species. Evidently the genus was becoming more and more restricted to a single type through the course of the Eocene, although it is no less abundant in the Bridger than in the Lower Eocene. The teeth of the Bridger species as a whole, show but little advance over those of the Wind River; there is no general increase in size; the premolar crowns are usually somewhat more complicated and the roots more crowded; p_2 is normally one-rooted, excepting in one species, while it is, as far as I have seen, always two-rooted in the Wind River. In the Wasatch the premolars are always considerably more primitive, with simpler, more trenchant crowns, and less crowding in the roots, and the upper molars less completely quadritubercular. In all the formations, however, the larger species are more advanced in tooth-structure.

In the *lower beds*, all the jaws found at Grizzly Buttes, some 150 or more, are referred to *H. paulus* Leidy, and to *H. vicarius* Cope, which appears to be merely a small variety or subspecies of *H. paulus*. *H. minusculus* Leidy appears to be a distinct species, but is represented in our collection only by specimens from a locality south of Granger, and does not appear to occur at Grizzly Buttes. *H. (Lemuravus) distans* Marsh is not known to be distinct from *H. paulus*, with which it agrees in size and, as far as can be told from Marsh's description, in characters.

In the *upper beds* the specimens are nearly all of a single type, closely allied to *H. paulus*, but larger and somewhat more advanced in dentition, described below.

In the *middle beds* there is more variety. Nearly half the jaws are intermediate between the common species of the upper beds and *H. paulus* of the lower beds. Most of the remainder are considerably smaller than *H. paulus* with simpler and more compressed teeth more nearly approaching *H. minusculus*, and a few jaws represent the large and distinct species *H. marshi*.

***Hyopsodus paulus* Leidy.**

Plate XLVIII, Figs. 2, 3, 5 and 7.

Hyopsodus paulus LEIDY, Proc. Acad. Nat. Sci. Phila., 1870, p. 110; Ext. Vert. West. Terrs., p. 75, pl. vi. Not *Hyopsodus paulus* Leidy of Cope, Tert. Vert., p. 237, nor Osborn, Bull. Am. Mus. Nat. Hist., 1902, p. 186, fig. 5.

?*Lemuravus distans* MARSH, Am. Jour. Sci., 1875, Vol. IX, p. 239.

Microsycopos vicarius COPE, Pal. Bull. No. 12, p. 1; Ann. Rep. Hayd. Sur., 1872 (1873), p. 609. Not *Hyopsodus vicarius* of subsequent publications, nor of Osborn, Bull. Am. Mus. Nat. Hist., 1902, p. 187, fig. 12, except for the type specimens, one of which is figured in Tert. Vert., pl. xxiv, figs. 20, 21.

This species was first described from a lower jaw found near Church Buttes, in the Lower Bridger. Dr. Leidy subsequently described and figured a number of upper and lower jaws from Grizzly Buttes. Professor Cope referred to this

species a number of upper and lower jaws from the Wind River and Wasatch, but Osborn has shown that these are specifically distinct and the teeth in an earlier stage of development. The skull and jaws from the Washakie described and figured by Osborn under this name, differs considerably from the rather uniform type presented by the numerous specimens from the Lower Bridger, and must be separated specifically. The types of *Hyopsodus vicarius* Cope, and several other jaws from the Lower Bridger appear to represent a small variety of *H. paulus*, but the Wind River specimens referred to *H. vicarius* by Cope are shown by Osborn to be a distinct species, and the lower jaw figured by Osborn as *H. vicarius*, which comes from the Upper Bridger, is also to be referred to another species, described below.

As thus limited, *Hyopsodus paulus* includes nearly all the specimens (about 150 in our collection) found in the Lower Bridger beds, but is not found in the Upper Bridger nor in any other Eocene formation. About one-fifth of the jaws may be referred to the small variety *vicarius*, which grades into the typical form, but is distinguished by narrow teeth, less robust premolars and narrow heel to the third molar; these differences are, however, slight and not very constant.

Measurements taken on 42 lower jaws show an average length of 12.8 mm. for the three true molars, the range being from 12.3 to 13.3. The type specimen measures 13.0. The smaller variety, *H. paulus vicarius* shows an average length of 12.0 mm., with a range of 11.7 to 12.2 in ten jaws measured. The type specimen has but one molar, m_1 , preserved; this shows a length of 3.6 mm., indicating a length for m_{1-3} , of 11.7.

Lemuravus distans Marsh is recorded as measuring 12.5 mm. for the three true molars, thus agreeing in size with *H. paulus*.

The great majority of the specimens of *H. paulus* come from a rich pocket in Grizzly Buttes, west of the trail from Fort Bridger to Lone Tree. Dr. Leidy's specimens were probably mostly from this pocket as well as many or most of those in the Marsh collection. The type is from Church Buttes, at a horizon probably somewhat lower; the majority of the specimens from that locality are smaller than those from Grizzly Buttes. The types of *H. vicarius* came from Cottonwood Creek at a horizon probably equivalent to Grizzly Buttes or somewhat lower.

Measurements of teeth, typical.

	Average	Range
Length p^1-m^3 on two jaws	21.8	21.4-22.2
“ p^4-m^3 “ ten “	14.1	13.6-14.9
“ m^1-m^3 “ fifteen “	11.3	11.0-11.8
“ p_1-m_3 “ three “	23.5	22.0-24.5
“ p_4-m_3 “ sixteen “	16.0	15.3-16.5
“ m_1-m_3 “ forty-two “	12.8	12.3-13.6

Measurements of teeth, small variety.

	Average	Range
Length p^4-m^3 on five jaws	13.1	12.9-13.4
“ m^1-m^3 “ five “	10.6	10.3-11.0
“ p_4-m_3 “ three “	15.3	15.2-15.5
“ m_1-m_3 “ ten “	12.1	12.0-12.2

Hyopsodus minusculus *Leidy.*

Plate XLVIII, Fig. 8; Plate XLIX, Fig. 3.

Hyopsodus minusculus LEIDY, Ext. Vert. West. Terrs., 1873, p. 81, pl. xxvii, fig. 5.

This species is decidedly smaller than *H. paulus* or its variety *vicarius*, and distinctly smaller than the small species from the Upper Bridger, described below. It is represented in our collections by a single upper jaw in the Cope Collection No. 5005, exact locality unknown, and by a number of specimens found about 6 miles south of Granger. The type is recorded as coming from “Dry Creek” (*i. e.*, Little Dry Creek, ten miles from Fort Bridger¹) hence in the Lower Bridger.

Hyopsodus marshi *Osborn.*

Plate XLVIII, Fig. 1.

This species is distinguished from *H. paulus* by larger size, more robust teeth of greater transverse diameter, especially the premolars, and by a well developed deutocone on p^2 , absent in all other species. The type consists of the upper jaws No. 1706a, from the Upper Bridger, the locality being either Twin Buttes or Henry’s Fork, but probably the former. Three specimens, all from Horizon C_2 at Twin Buttes, are referred to this species. The second upper premolar is not preserved in any of them, but the premolars are exceptionally broad transversely and the teeth agree in size and other characters with the type more nearly than with the species next described.

Measurements.

	P^1-M^3	P^4-M^3	M^1-3	P_4-M_3	M_{1-3}
No. 1706a (type)	24.7	16.1	12.8	—	—
“ 11878	—	15.6	12.8	—	15.0
“ 11879	—	—	—	18.1	14.6
“ 11881	—	—	13.7	—	—

¹ See Leidy, *op. cit.*, p. 18, foot-note.

Hyopsodus despiciens sp. nov.

Text Figures 103-105.

The expedition of 1904 succeeded in obtaining a large number of *Hyopsodus* from the middle and upper levels of the Bridger, which, compared with the numerous specimens obtained in the previous year from the Lower Bridger beds, enable us to trace the common species *H. paulus*, through the intermediate levels into a distinct form characteristic of the upper beds. This species, while separable from *H. paulus* by greater size and somewhat more advanced dentition, is much nearer to it than *H. marshi*, which evidently belongs to a distinct specific phylum, at present known only from the middle beds.

The type of the species is a skull and lower jaw, No. 11877, found by the writer at the top of Horizon D, in the uppermost fossiliferous levels of the Bridger. The distinctions from *H. paulus* lie in the uniformly larger size, the somewhat more quadrate molars and higher molar cusps, and more trenchant premolars. The hypocone on m^3 is in general more developed, but the individual variation in this character is considerable, as in all species of *Hyopsodus*. The second premolar is simple, and the premolars are less robust and more trenchant than in *H. marshi*; the molars are somewhat smaller, especially in their transverse diameters. Some forty specimens of upper and lower jaws from Horizon D are referred to this species. The jaws from Horizon C are intermediate in size and other characters between *H. despiciens* and *H. paulus*.

	Average	Range
Length of m_1 - m_3 in eighteen jaws from Horizon D	14.0	13.1-14.8
“ “ “ “ eight “ “ “ C	13.2	12.9-13.6
“ “ “ “ forty-two “ “ “ B	12.8	12.3-13.3

The skull described and figured by Osborn in 1902 as *H. paulus* agrees more nearly with this species, and is provisionally referred to it. As it comes from a distinct formation, the Washakie, the reference cannot be regarded as certain without a series of specimens to confirm the occurrence of this species in the Washakie beds.

Measurements.

	Average	Range
Length p^1 - m^3 on type skull	23.4	
“ p^4 - m^3 “ six jaws	15.2	14.0-16.2
“ M^{1-3} “ ten “	12.3	11.0-12.8
“ p_1 - m_3 “ six “	25.2	24.1-26.5
“ p_4 - m_3 “ fourteen “	17.6	16.8-18.6
“ m_{1-3} “ eighteen “	14.0	13.1-14.8

Measurement of intermediate forms, from Horizon C, between H. paulus and H. despiciens.

	Average	Range
Length p ⁴ -m ³ on two jaws	14.8	14.5-15.2
“ m ¹⁻³ “ ten “	12.0	11.5-12.6
“ P ₄ -m ₃ “ four “	16.6	16.1-17.0
“ m ₁₋₃ “ eight “	13.2	12.9-13.6

Hyopsodus lepidus sp. nov.

Plate XLVIII, Figs. 4 and 6.

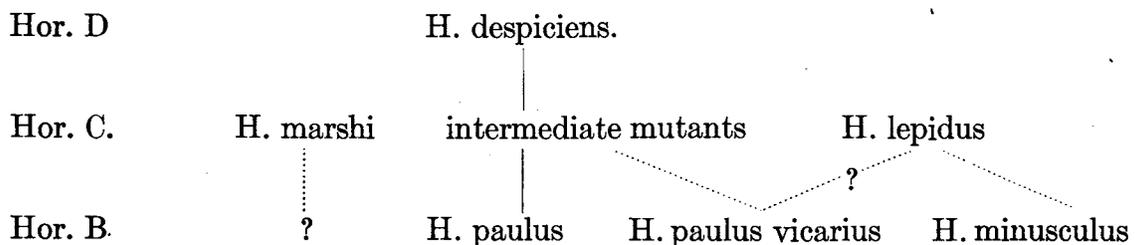
Along with the *Hyopsodus* jaws in Horizon C, intermediate between *H. despiciens* and *H. paulus*, and the few large jaws referred to *H. marshi*, occurs a third group of jaws smaller than *H. paulus* or its variety *H. vicarius* and with narrower, less robust teeth, approaching *H. minusculus* in form and dimensions. Some of them may represent a mutant form descended from the typical *minusculus* of the lower beds, and others may be dwarfed descendants of *H. paulus vicarius*, but from the evidence at hand it seems better to group them together as a single species, to which I give the name of *H. lepidus*.

The type selected is No. 11900, upper and lower jaws. The hypocone on m³ is somewhat better developed than in *H. minusculus*, but considerably less than in the larger species. The teeth are less robust, the cusps higher, and heel of m₃ narrower than in *H. paulus* or *H. despiciens*. The length of three lower molars is 12.0 millimetres, scarcely less than in the smaller variety of *paulus*. The average measurements run somewhat less than in the type, as follows:

Length p ¹ -m ³ in five jaws	Type	Average	Range
	No. 11900		
“ p ⁴ -m ³ “ seven “	21.0	20.2	18.7-21.1
“ m ¹⁻³ “ ten “	13.8	13.1	12.0-13.8
“ p ₁ -m ₃ “ two “	11.4	10.7	9.8-11.5
“ P ₄ -m ₃ “ eight “	21.3	20.7	20.1-21.3
“ m ₁₋₃ “ eleven “	15.2	14.8	14. -15.7
	12.0	11.7	10.9-12.3

Distribution of the Species.

The relations of the above described species appear then to be as follows:



Briefly — *H. marshi* represents a distinct phylum, not yet discovered in the upper or lower beds. *H. paulus* of the lower beds gives rise to *H. despiciens* of the upper beds through intermediate mutants in the middle level, and the nearly allied *H. minusculus* of the lower beds gave rise to *H. lepidus* of the middle beds, although the latter may include descendants of the small variety of *H. paulus*. As far as our present evidence goes, *H. marshi* and *H. lepidus* did not persist into the upper beds, leaving only *H. despiciens*, which is also found in the Washakie.

3. PANTOLESTIDÆ.

The type of this genus and family is *Pantolestes longicaudus* Cope, of which the typical specimen is a lower jaw with badly worn teeth, two caudal vertebræ, and parts of two metapodials, found together in the Bridger Basin by Professor Cope in 1872. Cope referred it at first to Carnivora, then to Primates, and afterwards to the Artiodactyla, the latter reference being based upon the characters of certain small Wasatch species supposed to be related to it. These species he subsequently distinguished generically as *Trigonolestes*, on account of their evident difference from the Bridger Artiodactyl genus *Homacodon* Marsh, which he regarded as identical with *Pantolestes*. This reference of *Pantolestes* to the Artiodactyla and its association with *Homacodon* and *Trigonolestes* has been accepted by all authors except Matthew, who in 1899 questioned it, and suggested that *Pantolestes* should be separated from the Artiodactyla which had been associated with it, and referred to the primates or Creodonts. Its true relationship was still unsuspected,¹ and no additional specimens had been discovered. The Museum parties of 1903–4 were fortunate in discovering a number of specimens of this genus, some referable to the type species, some of much larger size. These include a well preserved skull and jaws, the greater part of a skeleton, and several lower jaws associated with parts of the skeleton, and enable us to describe the osteology of almost all parts of the animal. Their generic identity with the type specimen is certain, as the parts of the lower jaw and of the metapodials preserved in Cope's type are highly characteristic and present a number of peculiar features. *Pantolestes* is neither Artiodactyl, Primate nor Creodont, but an Insectivore of very peculiar and archaic type. The type species is about the size of a hedgehog, but the larger species described below are much beyond any known Insectivora in size.

Definition: Insectivora with teeth like those of primitive Creodonta, and limbs adapted to aquatic life.

Dentition $\frac{3.1.4.3}{2.1.4.3}$. Molars and premolars resembling *Triisodon* teeth, with low, massive cusps, fourth premolar not molariform. Canines large, massive, upper incisors peg-like, spaced. Facial part of skull short, basicranial region broad, middle portion of the skull elongate. Mental foramen

¹ I may observe however that Marsh had recognized in 1872 the Insectivore affinities of *Passalacodon* and *Anisacodon*, which appear to be synonyms of *Pantolestes*.

beneath m_1 ; angle of jaw a short, stout process expanded at the tip. Lumbar zygapophyses flat. Tail long and extraordinarily massive. Humerus with very strong, well separated deltoid and pectoral crests, strong supinator crest, wide distal end. Radius and ulna separate, subequal. Manus and pes with elongate phalanges and flattened claws. Femur with strong third trochanter, short, broad patellar trochlea. Tibia and fibula united distally, tibia much curved, with cnemial crest reduced to a process about the middle of the shaft. Large fibulo-calcaneal articulation. Astragalus with short, wide, shallow trochlea, short neck and convex head. Pes everted.

- I. Paraconid well developed *Palæosinopa*.
- II. Paraconid vestigial *Pantolestes*.

To this family may also be provisionally referred the Basal Eocene genus *Pentacodon* which shows the highly diagnostic Insectivore feature of the position of the mental foramen beneath m_1 . *Pentacodon* is known only from the lower jaw, and the teeth are of peculiar form and proportions, the molars reduced, tritubercular, with large heels, the fourth premolar enlarged, its principal cusp twinned and pointing backward, the third premolar quite small, the second a little larger, both simple and trenchant. *Palæosinopa* was distinguished by Matthew from the Creodont genus *Sinopa*, to which it had previously been referred, by the much more primitive teeth; but its insectivore relations were not suspected. The resemblance of the teeth and jaws to those of *Pantolestes* leaves little doubt as to their near relationship.

***Pantolestes* Cope 1872.¹**

Syn., *Passalacodon* and *Anisacodon* MARSH, 1872.²

Twelve specimens are referred to this genus, and represent at least five species, ranging from the size of the hedgehog to that of the porcupine. The most complete are the skull and jaws and the fragmentary skeleton of the largest species, and it is upon these chiefly that the generic description is based. The smaller species are represented by more fragmentary material, which agrees quite nearly, both in skull and skeletal characters, with the large one. It is surprising that so peculiar and characteristic an animal should have remained unrecognized hitherto; the explanation lies no doubt in the primitive and indifferent character of the teeth, which give no clue to the remarkable features of skull and skeleton.

Teeth. The upper incisors are not known in this genus, but judging from the large size of the premaxillæ they were well developed, and probably were as in the allied genus *Palæosinopa*, "rather large; roots not compressed, the third placed behind and within the second, leaving a deep notch for the lower canine between i^2 and c^1 ." (Matthew 1901, p. 22.) The upper premolars were crowded, the first one-rooted, the second and third two-rooted, the fourth three-rooted.

¹ Palæontological Bulletin No. 2, dated Aug. 3, 1872.

² Preliminary Description of New Tertiary Mammals, Part II, separata dated Aug. 7, 1872.

The molars are tritubercular with rudimentary hypocones; their paracone and metacone equal, conical, with a strong external cingulum which is not developed into a broad shelf as in *Sinopa*. Parastyle minute, metastyle and mesostyle absent; protocone large, internal, the wear of the teeth not permitting us to determine its form or relations with the conules; hypocone postero-internal. Third molar apparently much like the first and second.

The lower incisors are unknown. Canines stout and massive. Premolars crowded, the first one-rooted, the others two-rooted, the crowns trenchant, not compressed, moderately high, somewhat recurved, with rudimentary heels on p_2 and p_3 , low trenchant heel, and rudimentary anterior basal cusp on p_4 . Molars with low trigonid and large, broad basin heels, paraconid vestigial, median in position, protoconid and metaconid subequal, widely separated, hypoconulid strongest on m_3 but well developed on all the molars.

Skull. The skull has a very peculiar appearance. Although presenting

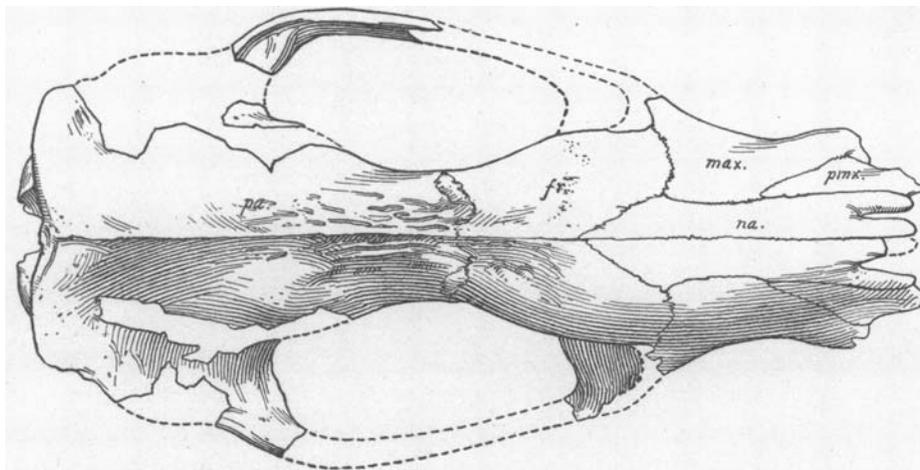


Fig. 106. *Pantolestes natans*, skull, top view, natural size. Type specimen, No. 12153. Upper Bridger.

many features characteristic of Insectivora it shows but distant affinities to any single living type. The face is short, the cranial region elongate. The muzzle is thick and wide, the anterior nares exceptionally large, the infraorbital foramen very large and round. There are no postorbital processes nor temporal crests, the sagittal crest is very low and inconspicuous, the postorbital constriction little defined, the occipital crest high and broad. The ascending processes of the premaxillæ are wide and short; the nasals are wide, rather long, deeply notched on their anterior border, slightly expanded posteriorly. The frontals are short and narrow, truncate anteriorly, and not splinted in between maxillæ and nasals; they are uniformly convex from side to side and slightly convex antero-posteriorly; the sagittal crest extends along their median line nearly as far forward as the posterior end of the nasals. The parietals are very long and ornamented by a series of longitudinal ridges on the surface, parallel to the sagittal crest anteriorly,

but diverging from it posteriorly. The sides of the skull are very incomplete, but the lachrymal appears to have had a considerable expansion on the face, and the orbits to have been very ill defined. The basicranial region unfortunately is imperfectly preserved, and the relation of the condyles to the glenoid and mastoid region is open to question. The glenoid fossa is transverse and much as in

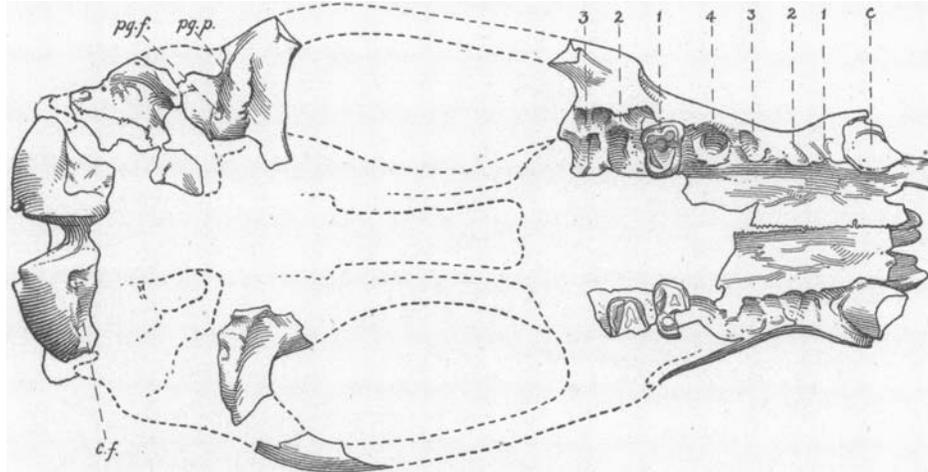


Fig. 107. *Pantolestes natans*, skull, under view, natural size. No. 12153.

Creodonta; the postglenoid foramen moderately developed. The mastoid process is short, projects laterally, and is contained posteriorly in a laterally projecting crest, probably part of the lambdoidal. Inferiorly the mastoid is separated from the paroccipital by a broad, shallow gutter, and from the postglenoid by a similar gutter of less width. The paroccipital process is not preserved.

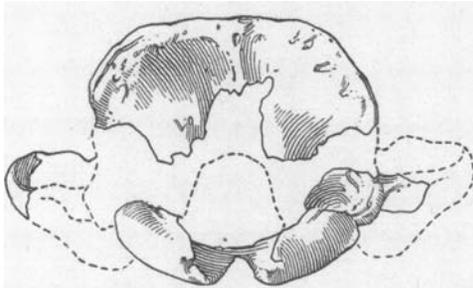


Fig. 108. *Pantolestes natans*, back view of skull, natural size. No. 12153.

There is no indication of an ossified tympanic bulla, but there appears to have been a small descending process at the posterior end of the alisphenoid indicating a rudimentary "false bulla" as in many Insectivora and Marsupials. This process is not present in Creodonta. The condyles are very large and wide; their exact position is uncertain, as no contact could be obtained with the top of the skull or the otic region, but they apparently projected

further back than the occipital crest.

The lower jaw is short and very thick. The symphysis is loose, long, extends back under the third premolar. The depth and thickness near the anterior end is nearly as great as under m_3 . The coronoid process is short and wide and not recurved; the condyle is wide transversely; the angle is a short, straight,

stout process, expanded and thickened at the tip, quite unlike the slender, re-curved, flattened process of the Creodonta and Carnivora. The posterior mental foramen is under m_1 as in most Insectivora (excepting Erinaceidæ, Leptictidæ,

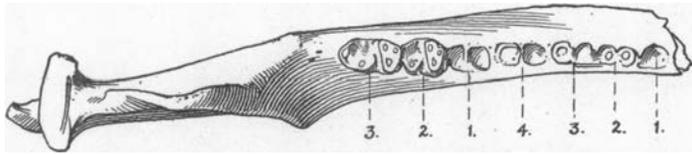


Fig. 109. *Pantolestes natans*, superior view of lower jaw, natural size, No. 12153.

of massive construction throughout. The characters are derived principally from the fragmentary skeleton of a single individual, in which the greater number of the vertebræ, most of the limb bones and parts of the feet are more or less completely preserved, with fragments of the skull and jaws sufficient for identification.

This skeleton had about the size and somewhat the proportions of the Canada Porcupine, but with a much longer and stouter tail. The skeleton material of the smaller species is much less complete, and does not materially add to our knowledge of the genus except in the fore foot.

The most important characters regarded as family distinctions have already been briefly noted.

Vertebræ. The vertebral formula cannot be determined — five lumbar, seven dorsals, two cervicals and eleven large caudals are recognizable, and the sacrum is composed of three vertebræ.

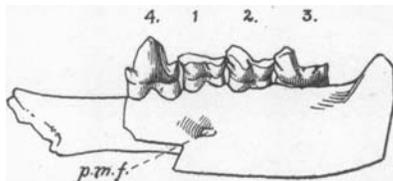


Fig. 111. *Pantolestes phocipes*, lower jaw, side view, natural size. Type specimen, No. 11547. Upper Bridger.

probably to the superior branch of the spinal nerve; the margin of the anterior opening of the vertebrarterial canal is not preserved. A more posterior cervical shows a large, short vertebrarterial canal and the roots of a stout, superior lamella

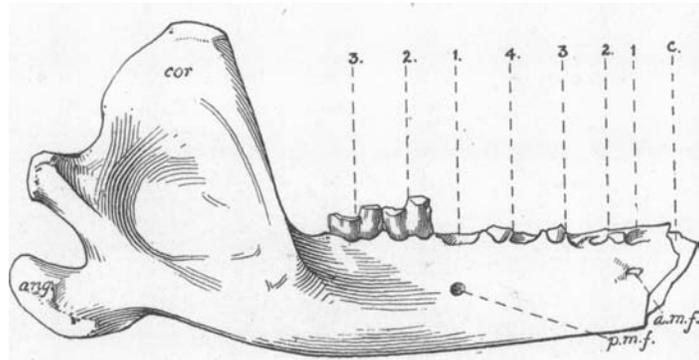


Fig. 110. *Pantolestes natans*, external view of lower jaw, natural size, No. 12153.

Insectivora (excepting Erinaceidæ, Leptictidæ, Tupaiidæ, Chrysochloridæ). In all other animals that I have examined it lies beneath p_3 or sometimes p_2 or p_4 . In the Moles its position varies.

The skeleton is large in proportion to the skull, and

shows a long and large vertebrarterial canal, opening backward on the posterior margin, a small foramen on the inferior root of the transverse process giving exit to the inferior spinal nerve, a large foramen on the superior root of the process near its anterior margin giving exit

and broad plate-like inferior lamella of the transverse process; its centrum is moderately long with a deep median excavation on the superior surface, bridged over by a narrow bony ridge, concave superiorly from side to side; the inferior surface of the centrum is strongly keeled medially and thickened at the posterior end as though for a hypapophysial process. An anterior dorsal, probably the first, has a short, thick arch, and widely separated posterior zygapophyses; the centrum carries a median keel. Four other dorsal centra are preserved, in which the keel has disappeared from the centrum, the arch is preserved on one of these; its zygapophyses are of anterior dorsal type, but placed low down and far apart, as compared with Creodonta, although less so than in modern Insectivora. A spine of moderate length is indicated; and other unplaced spines are longer and comparatively stout. The lumbar vertebræ carry no keels on the inferior surface of the centra, and their zygapophyses are nearly flat; they are larger than the dorsals but the contrast is much less than in most Carnivora or Creodonta.

The sacrum is large, composed of three vertebræ of nearly equal robustness, each longer than any of the lumbar although hardly as stout. The sacral ribs form a continuous lateral flange, very massive anteriorly, and the foramina between them quite small. The proximal caudals equal the lumbar in size, but their zygapophyses are much closer together and the facets nearly vertical instead of horizontal. The median caudals are considerably longer and hardly less in diameter of centra, but the arches are rapidly reduced. The distal caudals are incompletely known, but the tail was clearly very long as well as massive, and Cope's specific name of *longicaudus* applied on account of the association in the type of two distal caudals with the lower jaw, etc., was peculiarly appropriate to the genus.

Fore Limb. The *scapula* is not known. The *humerus* is a very characteristic bone. The head is of rather limited size and faces more posteriorly than superiorly. The greater tuberosity is large, overtopping the head and antero-external in position; the lesser tuberosity is quite small. The shaft is considerably curved, the deltoid crest very strong and high

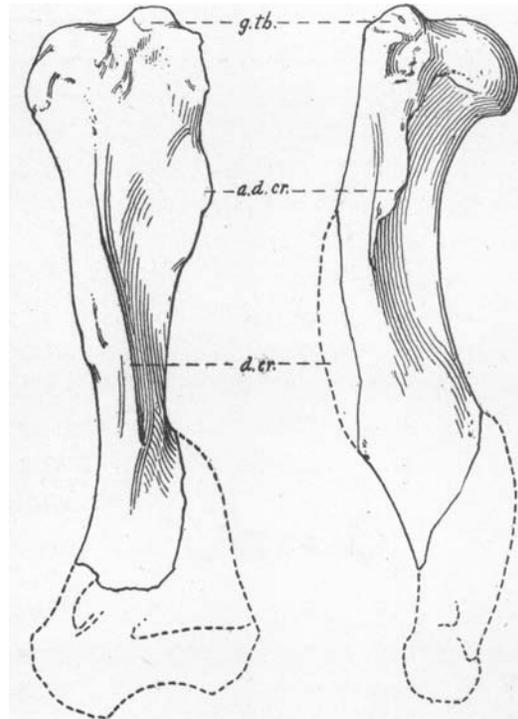


Fig. 112. *Pantolestes natans*, humerus, anterior and external views, natural size. No. 12152. Upper Bridger.

and extends down on the anterior surface of the shaft three fifths of its length.

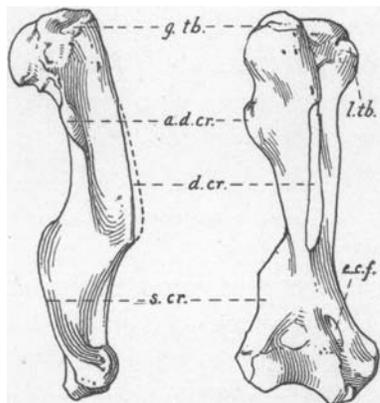


Fig. 113. *Pantolestes intermedius*, humerus, external and anterior views, natural size. Type, No. 11619. Lower Bridger.

On the external side of the shaft is a strong ridge, culminating near the proximal end in a stout process like the third trochanter of the femur. To this the deltoid muscle or part of it was presumably attached, while the pectoralis was attached on the crest on the front of the shaft. The supinator ridge is very high and the distal end of the shaft is wide, with a shallow trochlea and an entepicondylar foramen, the bridge extending rather high up on the shaft as in *Creodonta*. There is no supratrochlear foramen.

The radius and ulna are of nearly equal size, the ulna somewhat more robust. The olecranon is moderately large, expanded transversely as in the badger, not anteroposteriorly as in most Carnivora and especially in aquatic types, the cuneiform facet is rather large, facing distal-internal, with strong, sigmoid curvature.

The number of metacarpals is unknown. Mc. II and III are preserved complete in one specimen, parts of several metacarpals in another. They are moderately long, with shafts exceptionally deep from dorsal to plantar surface, and the distal ends are highly characteristic, the convexity of the facets from side to side being entirely lost, so that they are not ball-and-socket joints as in most unguiculates, but hinge-joints as in most Insectivora, in Ungulata, Pinnipedia and certain cursorial unguiculates (*Mesonyx*, *Canis*). They are peculiar in the presence of a deep ligamentous pit on the middle of the upper border of the facet. The keel is confined to the inferior surface. The head of mc. II is compressed, and

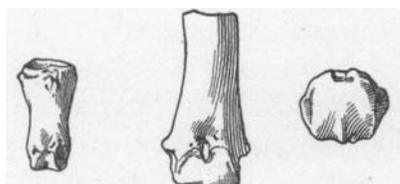


Fig. 114. *Pantolestes natans*, phalanx and distal half of metatarsal, natural size, No. 12152.

The radius and ulna are of nearly equal size, the ulna somewhat more robust. The olecranon is moderately large, expanded transversely as in the badger, not anteroposteriorly as in most Carnivora and especially in aquatic types, the cuneiform facet is rather large, facing distal-internal, with strong, sigmoid curvature.

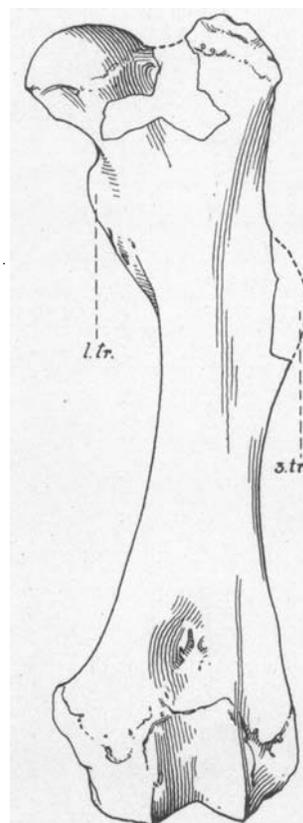


Fig. 115. *Pantolestes natans*, femur, anterior view, natural size. No. 12152.

The number of metacarpals is unknown. Mc. II and III are preserved complete in one specimen, parts of several metacarpals in another. They are moderately long, with shafts exceptionally deep from dorsal to plantar surface, and the distal ends are highly characteristic, the convexity of the facets from side to side being entirely lost, so that they are not ball-and-socket joints as in most unguiculates, but hinge-joints as in most Insectivora, in Ungulata, Pinnipedia and certain cursorial unguiculates (*Mesonyx*, *Canis*). They are peculiar in the presence of a deep ligamentous pit on the middle of the upper border of the facet. The keel is confined to the inferior surface. The head of mc. II is compressed, and

shows a considerable lateral facet for the magnum; the head of mc. III is rather wide, and shows no lateral facet for the unciform. From this and the character of the cuneiform I infer that the unciform was small and the magnum large, as in Marsupials and some Insectivora. The opposite conditions are found in Creodonta and primitive Condylarthra.

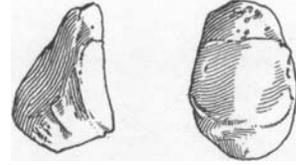


Fig. 116. *Pantolestes natans*, patella, natural size. No. 12152.

The phalanges are long, the proximal ones much elongate with shafts thickened in their dorso-plantar diameter like the metacarpals; the median phalanges are much wider and flatter, the unguals are wide, flattened and decurved, somewhat resembling those of the seal, but more expanded laterally, and more curved.

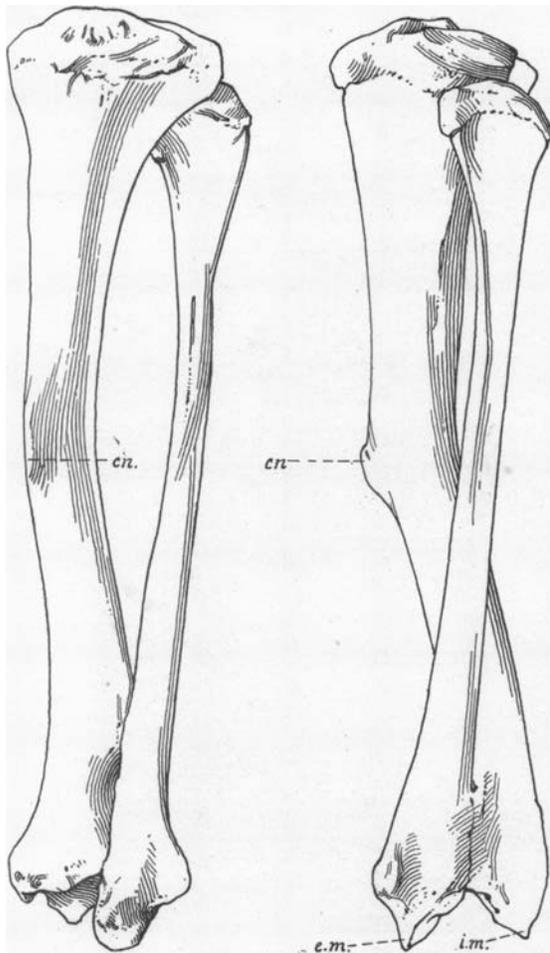


Fig. 117. *Pantolestes natans*, tibia and fibula, anterior and external views, natural size. No. 12152. Lettering: *cn.*, cnemial crest; *e.m.*, external malleolus of fibula; *i.m.*, internal malleolus of tibia.

The above indicates a foot of quite remarkable character, with broad, low carpus, large magnum, small unciform, long pisiform, large contact of cuneiform with mc. V, probably 5 digits, not appressed. The movement of the phalanges was limited to flexion and extension without any lateral motion, the proximal phalanges flattened out and the claws broad and flat.

Hind Limb. The *pelvis* is incompletely known. It appears to be short and massive, the ilium not much expanded, the ischium heavy and as long as in Creodonts. The *femur* is massive, the ball unusually flat, the great trochanter round and prominent, the lesser trochanter prominent and postero-internal in position, the third trochanter strong and situate one-third way down the outside of the shaft. The whole shaft is considerably flattened, the distal end of the bone is wide but not deep, the condyles face posteriorly and the patellar trochlea is wide and short.

The *tibia* is of moderate length, somewhat exceeding the femur. Its shaft

is strongly bowed forward, the cnemial crest absent except for a strong process at the middle of the anterior surface of the shaft. The internal malleolus is little developed, and behind it lies a strong, deep groove for the internal flexor tendons. In addition to the usual facet for the body of the astragalus there is a small antero-distal facet for the astragalar neck.

The *fibula* is rather large, the proximal part of the shaft somewhat bowed backward but the distal part straight. The proximal end is articulated to the back of the tibia, and the distal end is suturally united for about one-fifth the length of the shaft to the outside of the tibia. The proximal end is expanded laterally, the distal end is enlarged and extends down beyond the tibia in a large stout process with a convex, internal facet for the astragalus, and a more posterior facet of about equal size for the calcaneum.

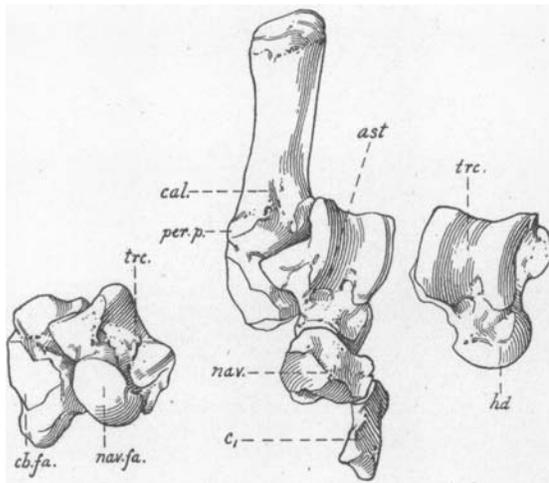


Fig. 118. *Pantolestes natans*, tarsal bones, natural size, No. 12152. Lettering. *ast.*, astragalus; *cal.*, calcaneum; *cb. fa.*, cuboid facet of calcaneum; *c.*, entocuneiform; *hd.*, head of astragalus; *nav.*, navicular; *nav. fa.*, navicular facet of astragalus; *per. p.*, peroneal process; *trc.*, trochlea.

and wide convex head. The trochlea is wide, short, very little oblique and rather limited in its antero-posterior extension; there is no astragalar foramen, and the groove of the tendon is shallow; the fibular facet is strongly concave. The *calcaneum* has a long, stout tuber calcis, thick in the shaft and very little expanded at the end; the inferior end of the bone is short, the facet for the cuboid appears to project very little, if at all, on the dorsal side; the fibular facet is comparatively large and slightly convex.

The *navicular* is wide and low, the *entocuneiform* deep and narrow; the pes was probably wide, and the digits more or less expanded, but the hallux was not large and not at all opposable. The metatarsals and phalanges are little known, but appear to have been like the corresponding fore-foot bones except for larger size.

The shafts of tibia and fibula show a considerable amount of torsion, so that the pes faces *inward* at an angle of about forty-five degrees, when the limb bones and pelvis are articulated with the knee flexed and moderately everted. This inward torsion is just the reverse of the *outward* torsion of the pes characteristic of the Pinnipedia, but a similar inward twist appears to be present in *Potamogale*, judging from Allman's figure of the skeleton. Both are probably natatorial adaptations, the difference being conditioned by the presence or absence of a powerful swimming tail.

The *astragalus* (see Pl. XLVII, Fig. 3, *c*) has a wide body, short neck

Interpretation.

The above characters of skull and skeleton appear to indicate a carnivorous Insectivore of aquatic habits and adaptations.

The Insectivore affinities are seen in:

- (1) Large premaxillæ, as in almost all Insectivora.
- (2) Elongate skull, with postorbital constriction not well defined, no post-orbital processes, and anterior border of orbit not sharply distinguished from the face, large infra-orbital foramen, low sagittal crest, and high, round occipital crest. These features characterize most Insectivora, and are unusual in other mammals.
- (3) Angle of lower jaw short, rounded, projecting downward and expanded at the tip. This appears to be a modification of the Insectivore angle, rather than that of early Carnivora or Ungulata.
- (4) Posterior mental foramen beneath m_1 , as in most Insectivora. In Erinaceidæ, as in all other groups of mammals which I have examined, it lies beneath p_3 or approximately so.
- (5) Dorsal zygapophyses low and wide apart, lumbar zygapophyses flat, as in Insectivora. In Creodonta, Carnivora and Ungulata, the dorsal zygapophyses are higher up and closer together, and in most Creodonta and all Ungulata the lumbar zygapophyses are strongly convex and concave, or in many cases, revolute.
- (6) Tibia united with fibula at distal end, as in the majority of Insectivora, many rodents and some ungulates, but not in Creodonts or Carnivora.
- (7) Astragalus with wide trochlea of little obliquity, shallow, but the lateral ridges well defined, neck short and head wide and convex. This type of astragalus is distinctly Insectivore; the rodents approach it most nearly but have a longer neck; the Creodonta, Carnivora and Condylarthra a more oblique trochlea. The astragalus of the Walrus is of somewhat the same form; that of the other Pinnipedia differs widely.

The teeth do not appear to be adapted for insect-eating as they are in most Insectivora, and the large size of the animal renders it improbable that this was the mode of life. They might be said to be rather omnivorous than carnivorous, the large, stout canines being the principal indication of predatory habits. It may be observed that the teeth, especially the front teeth, are apt to be greatly worn, and this may indicate a special mode of life.

The characters of the feet, in the elongate digits, limited movement of the phalanges, broadened tips of the digits and flattened claws, indicate aquatic adaptation; and the specializations of the limb-bones also accord with this interpretation.

There are many features both of skull and skeleton in which *Pantolestes* agrees with the Pinnipedia, especially the Walruses. Most of these are clearly due to parallel adaptation, but it is by no means certain that all are so. The

flattening of the distal part of the femur, reduction of the cnemial crest and internal malleolus of the tibia, and the facet for the tibia on the neck of the astragalus, the elongate pisiform, elongation of metapodials and especially of proximal phalanges, thickening of the metapodial and proximal phalangeal shafts, flattening of the distal phalangeal shafts and ungues, and above all, the conversion of the ball-and-socket joints of metapodials and phalanges into hinge-joints, all characteristic of the Pinnipedia, are probably adaptive. The deep notching of the anterior border of the nasals, the arrangement of the fronto-nasal maxillary sutures, the large infra-orbital foramen, the arrangement of the upper incisors and canines, the form of the astragalus, etc. compare with the Walrus, and to a less extent with other Pinnipedia, in such a way as to suggest some degree of actual affinity. The form of the skull, teeth and many features of the skeleton preclude any near ancestral connection with the Pinnipedia.

On the whole *Pantolestes* appears to be an aquatic Insectivore of predatory habits, with marked analogy and some degree of affinity to the Pinnipedia. Its food may have been fish or turtles, or, with a closer analogy to the Walrus, fresh water clams; but was more probably an admixture of the three, as far as can be inferred from the characters of the teeth.

Species of Pantolestes.

At least five species are represented by the specimens examined. The distinctions and materials referred are as follows:

P. longicaudus Cope. Syn., *Passalacodon littoralis* Marsh. $M_{1-3} = 13.5$ mm. Teeth less robust, jaw shallower anteriorly, p_1 with semi-double root, canine smaller, anterior mental foramen beneath p_1 .

Type, No. 5142, Cope Collection, lower jaw with p_4-m_3 alveoli of p_{2-3} and part of canine alveolus, a distal caudal vertebra and half of another, a nearly complete metapodial and half of another. Lower Bridger.

No. 11548 lower jaw with c_1 and p_2-m_2 and alveoli of remaining teeth, and a few fragments of the skull. Lower Bridger.

No. 12087, lower jaws with p_4-m_3 of the right side and m_{1-3} of the left, most of humerus and ulna, parts of vertebræ and other limb-bones. Lower Bridger.

Nos. 12085, 12086, 12088 and 12089, provisionally referred either to this species or to *P. elegans* (Marsh), parts of lower jaws with molar and premolar teeth. Upper Bridger.

***P. phocipes* sp. nov.** $M_{1-3} = 21$ mm. Teeth more robust, paraconids more reduced, root of p_1 single, round, jaw deep anteriorly, canines larger, anterior mental foramen beneath anterior root of p_2 .

Type No. 11547, lower jaws with m_{2-3} of the right, p_4-m_3 of the left side, humerus, pisiform, cuneiform, metacarpals II and III, distal end of fibula, and various fragments (Fig. 111). Upper Bridger. Found by W. Granger, Am. Mus. Exp. 1903.

	P. natans		P. phocipes		P. inter- medius		P. longicaudus		
	No. 12153 Type.	No. 12152 Type.	No. 11547 Type.	No. 12090	No. 11619 Type.	No. 11620	No. Type.	No. 11548	No. 12087
Cervical vertebra, length of centrum		15							
“ “ width “ “		15							
Anterior dorsal vertebra, length of centrum		18							
“ “ “ width “ “		19							
“ “ “ “ of zygapophyses		18							
Lumbar vertebra (largest) length of centrum		27							
“ “ “ width “ “		22							
Sacrum, length (of 3 centra)		82							
“ width at anterior end		45							
“ “ of posterior centrum		20							
Proximal caudal, length of centrum		24							
“ “ width “ “		19							
Median “ length “ “		36							
“ “ width “ “		19							
Distal “ length “ “									
Humerus, length (partly estimated except in 11619)		97	72		52				40
Femur, length		109				60			
Tibia “		123				66			
Astragalus, length		21							
“ width		17							
Calcaneum, length		42							
Metacarpal III, length			38						
“ “ width of shaft			5						
“ “ depth “ “			6						
“ II, length			35						
Pisiform, length			16						
“ least diameter of shaft			3.5						
Cuneiform, width (external-internal)			10						
“ height (proximal-distal)			4						
“ depth (dorso-ventral)			6						
Proximal phalanx (estimated) length			20						
Median “ length		15							
“ “ width at proximal end		8							
Ungual “ length		17							
“ “ width near distal end		5.5							
Patella, length		18							
“ width		14							
“ thickness		13							

4. LEPTICTIDÆ.

Insectivora allied to the Hedgehogs and Tree-Shrews but with tritubercular molars. Limbs not fossorial.

Dentition $\frac{2.1.4.3}{2.1.4.3}$. Molars and premolars with high, sharp cusps. Fourth premolar molariform. Replacement of teeth retarded, taking place only after the animal has attained full adult dimensions. Face elongate, basicranial region short, tympanic chamber partially formed by alisphenoid and basisphenoid processes.

Vertebral formula not known. Lumbar zygapophyses simple, flat. Tail reduced.

Humerus with moderately prominent deltoid and supinator crests and an entepicondylar foramen. Radius and ulna separate, subequal. Femur with strong hooked internal trochanter, rudimentary third trochanter, narrow and elongate patellar trochlea. Tibia and fibula completely fused in distal half; no fibulo-calcaneal facet. Astragalus with short, wide trochlea, shallow but sharply defined at edges, distinct neck and wide convex head, with slight contact with cuboid. Cuboid narrow, navicular with strong, stout, inferior hook. Cuneiform separate. Digits of pes five, the laterals reduced, hallux not opposed.

I. Sagittal crest double. Nasals reduced posteriorly. Lachrymals not expanded upon the face. Infra-orbital foramen above anterior end of m^1 .

Third premolar simple *Leptictis*.

Third premolar with internal cusp *Mesodectes*.

Third premolar with internal and postero-external cusps *Ictops*.

II. Sagittal crest simple. Nasals expanded posteriorly.

P^2 with internal and postero-external cusps *Palaeictops*.

A number of little known Insectivores from the Eocene and Oligocene have been referred here by various writers, but quite without warrant. Their position is very doubtful, but it is not in this family.

Fam. indet., ?Leptictidae.

Phenacops gen. nov.

Char. gen. Dentition $I_7 C_1 P_4 M_3$. Jaw short, canine large, premolars very high cusped, short, robust, simple, p_1 one-rooted and very small, the others two-rooted, p_4 apparently molariform. Molars with trigonid and large heel, so worn as to preclude exact description. Jaw short and deep in front, symphysis short and heavy, angle stout and straight, not inflected. Mental foramen beneath anterior end of p_4

Phenacops incerta sp. nov.

Plate XLIX, Fig. 1.

Char. spec. Founded on a lower jaw No. 12091, with the canine, premolars and much worn molars preserved. The crowns of the canine and fourth premolar are mostly broken off. The jaw is smaller than that of a hedgehog, and the teeth proportionately small. Its position is very uncertain — the short premolar region, large canines and high premolar cusps suggest the bats; the molars appear to have the same general character as those of *Pantolestes* and *Palaeosinopa*; but the mental foramen has the normal position beneath the premolars. It may be Chiroptera, Insectivora or Creodonta, as far as can be judged from the lower jaw.

The canine is nearly vertical, round-oval in cross-section at the base, the crown is not preserved. The first premolar is very small, with single root, high protocone, and small postero-internal cingulum. The second premolar is two-rooted, set partly transverse, much higher than wide, with high, round protocone and small postero-internal cingulum. The anterior border of the tooth is almost vertical

from the root up to the tip of the protocone. The third premolar is hardly as high as p_2 , and considerably larger at the base, its anterior border from root to tip of protocone is almost straight but slopes considerably backward; it has a small, posterior heel. Of the fourth premolar only the heel is preserved; it is broad and apparently like that of the molars. The molars are of about equal size but too much worn for description. The jaw is robust and deep anteriorly, with short, heavy symphysis extending back to beneath the posterior end of p_2 , the inferior outline is nearly straight from symphysis to angle, slightly concave beneath the premolars, slightly convex beneath the posterior molar.

Dimensions.

Depth of jaw beneath p_2 6.5, beneath m_1 6.5, beneath m_3 6.6				
Length of jaw from dental foramen to anterior border of canine 30.				
Length of dentition c- m_3 20.6				
" " molar-premolar series 17.6				
" " true molars 8.8				
P_1	length	breadth	height	
P_2	" 1.8	" 1.5	"	3.
P_3	" 2.5	" 1.5	" 2.5	
M_1	" 2.7	" 2.0		
M_2	" 2.6	" 2.0		
M_3	" 2.5			

Owing to the wear of the teeth in the type specimen the measurements of the molars do not represent the original diameters of the teeth; the same applies to the height measurements of the premolars.

5. TALPIDÆ.

It is convenient to group under this name a number of minute Eocene Insectivora with talpid dentition, mostly very incompletely known and of doubtful affinities. They are distinguished from Marsupials by having, so far as known, the placental dental formula, from Chiroptera by the slender, elongate, anterior portion of the jaw, from Primates by the high, sharp and angulate cusps of the cheek teeth. In some of them the posterior mental foramen has the position characteristic of the Moles and of the majority of Insectivora. The anterior teeth are but little specialized. Satisfactory distinctions from the modern Talpidæ are lacking. But in all the numerous fragmentary remains that I have seen in the Bridger formation which from their minute size might be referred to this group, I have failed to find any indications of fossorial adaptation in the limbs. So far as may be judged from these fragments the limbs were shrew-like. If this be correct the Eocene Talpidæ are distinguished from modern Talpidæ by the primitive condition of the skeleton, from Soricidæ by the primitive condition of the teeth.

In this connection it is of interest to point out that there were fossorial Insectivores in North America in the middle and probably in the older Tertiary,

but that they belonged to the Zalambdodont group (*Arctoryctes* and perhaps other genera). Whether the undiscovered Eocene Zalambdodonta were fossorial we do not know, but it is very probable that some of them were, and that the fossorial specialization in the Zalambdodonta preceded that in the Dilambdodonta. This would be in accord with the morphologic and geographic positions of the two groups, the Zalambdodonts being now almost extinct and limited to the outlying portions of the continents, to Madagascar, and Southwest Africa and the West Indies, while they were present in the early Tertiary of North America and later Tertiary of South America. The Dilambdodonts on the other hand, are still relatively abundant and mainly Holarctic in distribution, being a later and higher type which has spread out from a northern center and displaced the earlier group. The oldest true Talpidæ, *Proscalops*, etc., are contemporary with the last Zalambdodonts.

Four well distinguished Eocene genera are provisionally referred to the Talpidæ. Of these, *Nyctitherium* is the most characteristically talpoid in the proportions and construction of the teeth as may be seen by comparison of the figures of the several species with those of the Oligocene mole *Proscalops* (Pl. XLIX, Fig. 5; Pl. LI, Figs. 3 and 4). Even in this genus, however, the teeth much more nearly the primitive tritubercular pattern, especially in the upper molars. The teeth of *Entomacodon* and *Myolestes* are much more like those of certain primitive marsupials, but there are only three true molars, at least in the latter genus, and the angle of the jaw is not inflected. In *Entomolestes* the teeth are partly transitional to the type shown in Apatemyidæ, Proglires, and primitive Lemuroides.

***Nyctitherium* Marsh 1872.**

Syn., *Talpavus* MARSH, *Nyctilestes* MARSH.

Lower molars of four principal cusps, the anterior pair the higher. Cusps high, sharp, well separated, compressed anteroposteriorly. Protoconid and metaconid of equal or subequal height, paraconid much reduced and projecting but little anteriorly. Hypoconid and entoconid of equal height, prominent, well separated; hypoconulid vestigial or absent. Jaw slender and elongate anteriorly, dentition probably not much specialized. Upper molars tritubercular but with broad high-crested hypocone flange; protocone strongly crescentic, paracone and metacone imperfectly crescentic, somewhat connate; cingula well developed. The construction of the molars appear to be transitional between the primitive tritubercular type and that shown in the modern Talpidæ and Soricidæ.

Professor Marsh's reference of *Nyctitherium* to the Chiroptera appears to have been on account of a delusive appearance of a short deep symphyseal region in the jaw which forms the type of *N. priscus*. A more careful examination of

this specimen shows that this appearance is deceptive, and there is no other reason apparent for reference of the genus to Chiroptera, as the teeth are decidedly more like those of the Talpidæ. It was probably the same misconception that led him to regard *Talpavus* as a distinct genus, for in the type of *T. nitidus* (= *Nyctitherium nitidus* infra) the symphyseal region is preserved, and is long and slender; the molars however have the same construction as in *Nyctitherium velox* and differ chiefly in greater breadth. The third genus which I have included here, *Nyctilestes*, differs from *Nyctitherium* only in the more equal height of protoconid and metaconid, which does not appear sufficient for generic separation.

***Nyctitherium velox* Marsh 1872.**

Plate L, Fig. 8.

The type is a jaw fragment in the Yale Museum, with m_{1-3} preserved. Two or three fragments in our collections are probably referable, among which I figure No. 12377, with m_{2-3} perfect. In this species the teeth are narrower, the paraconid more prominent and the metaconid lower than in other species which I refer to *Nyctitherium*, and the basal cingulum is more complete externally. M_2 and M_3 are very similar in size, proportions and construction.

***Nyctitherium nitidus* (Marsh 1872).**

Plate L, Figs. 6 and 7.

Type, two fragments of a lower jaw in the Yale Museum, with a lower molar and part of the symphyseal region. I refer to this species No. 11488-9 a lower and an upper jaw fragment in doubtful association. The molars are of about the same size as in *N. velox*, but M_2 is broader and shorter, the paraconid on m_{2-3} is less prominent, the metaconid more nearly equal to the protoconid in height, the hypoconulid on m_3 is well developed, and the basal cingulum is limited to the anterior border of the molars.

The upper molars are composed of three principal cusps, but the hypocone is a prominent crescentic crest although not as high as the protocone. The protocone is strongly crescentic, the wings extending into basal cingula terminating at the external angles of the molar; there is also a prominent antero-internal basal cingulum and a distinct although not wide external cingulum. The paracone and metacone are about as high as the protocone but are sub-conical imperfectly crescentic sharp pointed cusps, slightly connate at the base. The general outline of the tooth is irregularly quadrate, much broader than long, and strongly concave along the external and lateral borders.

Comparison of these teeth with the upper molars of the Oligocene mole, *Proscalops secundus* (Pl. LI, Figs. 3 and 4) show a very wide difference in structure,

much more indeed than appears on comparison with modern moles and shrews (cf. *Talpa*, *Scalops* and *Blarina*). *Proscalops* is however highly specialized in several features of the skull, on lines divergent from those of either moles or shrews, and suggestive rather of parallelism with the Chrysochloridæ, and it is not surprising that its teeth should fail to be intermediate between *Nyctitherium* and the modern moles or shrews. The fact must nevertheless be regarded as in some degree weakening the evidence — rather slender at best — for the inclusion of *Nyctitherium* and its allies among the Talpidæ.

***Nyctitherium priscum* Marsh 1872.**

Type a part of the lower jaw with m_2 preserved, and roots or alveoli of the remaining molars and p_4 . This species is a little larger than the preceding, the molars shorter and broader. It is not represented in our collections.

***Nyctitherium curticens* sp. nov.**

Plate L, Fig. 5.

Type No. 12055 a fragment of the lower jaw with m_{1-2} and part of m_3 . Nos. 12058 and 12062 are probably also referable. This species agrees in form with *N. priscus* but is of distinctly larger size than Marsh's type specimen although no larger than the measurements given in his description. The teeth are about one fourth larger and proportionately broader than in *N. nitidum*; the basal cingula are limited to the anterior ends of the molars.

***Nyctitherium serotinum* (Marsh 1872).**

This species, the type of *Nyctilestes* Marsh, is represented by a lower jaw with m_{1-3} in the Yale Museum collection. It is somewhat smaller than *N. velox*, and the protoconid and metaconid are of nearly equal height. Unlike the other specimens referred to *Nyctitherium*, this jaw is from the Lower Bridger beds at Grizzly Buttes.

***Entomacodon* Marsh 1872.**

Syn. *Centracodon* MARSH 1872.

Molars with high trigonid and moderately wide basin heel. Protoconid much overtopping metaconid, paraconid somewhat lower than metaconid, well separated; entoconid and hypoconid of equal height; an external basal cingulum. Jaw long and slender anteriorly, premolars compressed, unreduced, incisors and canine unknown, but apparently small and procumbent. Angle of

jaw probably not inflected but much as in *Myolestes* (infra). Premolars four and molars three in number (fide Marsh).

The relationships of this genus are very uncertain. The molar teeth suggest those of some of the more primitive Marsupials, and may be especially compared to those of an undoubted Marsupial from the Bridger which I refer provisionally to *Peratherium* and figure here for comparison. (Pl. L, Fig. 9.) The number of true molars in *Entomacodon* is not positively determinable, unless in the jaw which forms the type of *Centracodon*, concerning which Marsh makes the somewhat enigmatic statement that it had four premolars and three molars and is probably a marsupial. The only evidence that I can discover for the last statement is that the jaw of the type appears, at the point where it is broken off, as though it might be continued into an inflected angle. Comparison with more perfect jaws of *Myolestes* (infra) shows that the form of the jaw is identical in the two genera at this point, and in *Myolestes* the jaw is certainly not inflected; while the *Centracodon* jaw certainly does not agree with the form in the *Peratherium* jaw figured, in which there is a typical marsupial inflection of the angle, nor with other small marsupials with which I have compared it. I conclude therefore that the jaw in *Entomacodon* was probably not inflected.

On the other hand I cannot see any conclusive evidence in the *Centracodon* type that the fourth tooth of the series of seven was a premolar and not a molar. Only the root and a little of the crown is preserved, and it might have been a rather narrow small molar, as in the *Peratherium* figured here (Pl. XLIX, Fig. 4; Pl. L, Fig. 9), rather than a true premolar.

Neither of these characters would be absolutely decisive, since certain Insectivores have a molariform p_4 , and one or two modern marsupials lack the inflected angle. Nor can much weight be placed on the similarity in construction of the molars between *Entomacodon* and *Peratherium*, since a very similar type of molar may be found among both Chiroptera and Insectivora. In the absence of any strong contrary evidence, the probably uninflected angle is sufficient reason for referring *Entomacodon* to the Insectivora, since the long slender symphyseal region is against its reference to Chiroptera (see discussion of relationships of *Entomolestes*, infra).

Centetodon Marsh 1872 is apparently related to *Entomacodon*, but is too incompletely known for satisfactory reference. It is not represented in our collections.

***Entomacodon minutus* Marsh 1872.**

Syn., *Centracodon delicatus* MARSH 1872.

Plate L, Fig. 4.

Type, a jaw fragment in the Yale Museum, with m_3 preserved. The type of *Centracodon delicatus* is a lower jaw with the premolars and molars more or

less broken, p_{1-2} and m_3 being the most nearly complete. The inner side of the heel and the metaconid of m_3 are broken off, which apparently misled Professor Marsh into regarding the specimen as distinct from *Entomacodon*. Allowing for these breaks the construction and proportions of the molar appear to be identical with those in *E. minutus*. A number of jaw fragments in our collections are referable to this genus and probably to the species. No. 12056 is figured here.

Myolestes gen. nov.¹

Molars with high trigonid and deep, broad, basin heel. Protoconid higher than metaconid, paraconid low, hypoconid and entoconid of equal height. Dental formula ? I_3 , C_0 , P_1 or 2 , M_3 , the incisors large with a long diastema behind them.

This genus closely resembles *Entomacodon* in the form and proportions of the molar cusps, but differs in the great reduction of the premolar teeth, and probably in the enlargement of the incisors.

Myolestes dasypelix² sp. nov.

Plate L, Fig. 1.

The two median incisors have large roots, the lateral one is smaller, the premolars are represented by a two-rooted p_4 or by two small one-rooted teeth next in front of the molars, the anterior premolar being certainly absent. The posterior mental foramen is beneath the anterior end of M_1 as in *Talpidæ*. The type, No. 11490, is a nearly complete right ramus of the mandible, which was discovered in extracting from its matrix the little armadillo skeleton *Metacheiromys dasypus*, discovered by Albert Thomson of the Museum expedition of 1903. The specific name alludes to this association.

To the same genus, but of doubtful species, I refer Nos. 12063 and 12054, parts of lower jaws.

Entomolestes³ gen. nov.

Dental formula $\overline{5.1.4.3}$. Teeth in continuous series without diastema. Anterior teeth one-rooted, nearly uniform in size, p_4 two-rooted, with inner cusp and heel. Molars with low trigonid and broad basin heel. Paraconid prominent, projecting well forward. Protoconid higher than metaconid and somewhat posterior to it. Hypoconid lower than entoconid and somewhat posterior to it. Cusps angulate. Antero-external cingulum on trigonid. Posterior mental foramen under p_3 .

This genus appears to be referable to the Insectivora, but its more exact position is entirely uncertain. It resembles *Tupaia* more nearly than any living

¹ Gr. *μῦς* mouse; *ληστής* robber.

² From *dasypus*, a genus of armadillos; *ἡλιξ*, companion.

³ Gr., *ἐντομν*, insect.; *ληστής* robber.

genus. The simplicity of the premolars, low trigonids and minute size distinguish it from the Leptictidæ. The long, slender jaw is a distinction from Primates and Chiroptera, the angulate cusps distinguish it from Primates, the small canine and minute size from Creodonta. Certain jaws from the Oligocene of Langy, France, figured by Schlosser (1887, Pl. I, Figs. 44, 48), are very much like *Entomolestes*. They are referred by Dr. Schlosser to the Chiroptera, genus *Vespertiliavus*. The type of this genus, *V. bourguignati* (Filhol), is, according to Filhol's figures, a widely different animal, with the short, deep jaw, crowded premolars and vertical canine of the Chiroptera, so that it is a little difficult to understand Dr. Schlosser's reference of the two to the same genus, unless Filhol's drawings are very incorrect. Nor is there any evidence, as far as I can understand, that the jaws figured by Schlosser are Chiropteran. It is true that he figures two limb-bones unquestionably of bats, which he refers to one of the species of *Vespertiliavus*. But as he observes in the description that they may well represent another genus, I presume that they were not associated with the jaws as remains of the same individual and therefore prove nothing as to the zoological position of the jaws. As Dr. Schlosser observes, all other bats are distinguished by the short, deep, anterior part of the jaw and he assigns no reason for placing these specimens in the Chiroptera or the genus *Vespertiliavus*. The definition of the genus is drawn from these specimens, but *V. bourguignati* Filhol ("*brongniarti*" Schlosser in error) is the only named species assigned to the genus and must be regarded as the type.

It does not appear therefore that the resemblance to "*Vespertiliavus* sp." affords any ground for placing *Entomolestes* among the bats. Among the numerous unassociated skeleton fragments of appropriate size in our Bridger collections I have seen none that show the characteristic peculiarities of the Chiroptera.

***Entomolestes grangeri* sp. nov.**

Plate L, Fig. 2.

The type specimen, No. 11845, is a lower jaw with p_3 - m_3 and the alveoli of the anterior teeth. It is one of the smallest species from the Bridger, the entire dentition being about 9 millimetres in length, about the size of a shrew. The three incisors are of uniform size, projecting forward; the canine is somewhat larger also projecting forward, the two anterior premolars were apparently much like the canine, but less procumbent. P_3 is set obliquely and has a small heel, and flattened root. P_4 has two well distinguished roots and is sub-molariform, with small paraconid and metaconid, distinct heel, and a strong basal cingulum on the antero-external side of the trigonid. The molars decrease in size from first to third. The jaw is slender and compressed, the masseteric fossa slightly impressed.

The type is from Grizzly Buttes, Horizon B_2 , found by Mr. Granger. Several fragmentary jaws from the lower beds are provisionally referred to this species.

6. ZALAMBDODONTA.

Plate LI, Figs. 1 and 2.

A number of the small Oligocene Insectivora belong to the Zalambdodont division, in which the paracone and metacone of the upper molars, and the heels of the lower molars, are rudimentary. These cannot properly be placed in any near relationship with the Talpidæ, Leptictidæ, etc., and whatever theoretic views may be held as to the ultimate derivation of the dilambdodont from the zalambdodont type of molar or *vice versa*, the fact remains that in Mesozoic as in modern times the two were entirely distinct and that there is no direct evidence for the derivation of any dilambdodont families of insectivora from zalambdodont ancestors. The Oligocene zalambdodonts may or may not be related to the Chrysochloridæ, Centetidæ or Solenodontidæ, but they are not related to the Talpidæ, Soricidæ, Leptictidæ, etc., and should not be placed even provisionally in any of these families.

None of the described Bridger Insectivora belong to this division, and it is not represented by any specimens in our collections from this formation. I had formerly supposed that *Centetodon*, *Centracodon* and *Entomacodon* belonged in this division, judging from Professor Marsh's descriptions of these genera and have so arranged them in faunal lists (1899, 1909). Examination of the types, preserved in the Yale Museum, shows that this conclusion was in error. For comparison I have figured jaws of two Oligocene zalambdodonts, *Apternodus* and *Micropternodus*, showing the difference in type of molars.

The characters of the two Oligocene genera are:

Apternodus. Molars as in *Centetes*. Premolars reduced to three.

Micropternodus. Paraconid and metaconid equal, protoconid overtopping both. Heel simple, trenchant. Premolars 4, molars 3.

7. APATEMYIDÆ fam. nov.

?Insectivora with (1) low-cusped, tritubercular molars, (2) anterior teeth much reduced in number and size except for an enlarged, nearly rootless ? scalpriform incisor, (3) posterior mental foramen beneath molars, (4) size minute.

The molars in this group are unlike Insectivora and singularly resemble those of the Eocene lemuroids. The enlargement of an incisor and reduction of the remaining front teeth, as well as the minute size, are suggestive of the shrews, but as far as can be determined the socket of the incisor is enclosed in bone externally.

The genera of this family may be very doubtfully referred to the Insectivora. They are of minute size, and known only from the lower jaw. The single incisor is enlarged as in most Insectivora but not rootless as in Rodentia. The premolar

and molar teeth are unlike anything known among Insectivora, and are much more of the type of the early lemuroids, a frugivorous adaptation. The posterior mental foramen is even further back than in Insectivora, lying beneath m_2 . The position of this foramen is so constant a character among the mammalia that in the absence of adequate contrary evidence it warrants our placing the group provisionally as frugivorous Insectivores, instead of associating them with the early lemuroids (Anaptomorphidæ) to which the molar and premolar teeth would ally them. (Cf. Pl. LII, Fig. 7.) The enlargement of the incisor, while a highly characteristic Insectivore feature, is seen to a limited extent in some of these lemuroidea as well, as also in the rodentia, tillodontia and other groups — but in all of these the mental foramen has its normal position under p_3 .

The family is probably referable to the Proglires (infra).

Apatemys Marsh 1872.

Dentition $I_1 C_7, P_2, M_3$. Incisor enlarged, rooted, canine minute or absent, premolars simple, much reduced, one-rooted, molars with rather large trigon, paraconid low but well developed, protoconid and metaconid equal, well separated, the latter more posterior, heel basin-shaped with continuous marginal crest, lowest on internal border. Posterior mental foramen beneath m_2 .

This singular little genus is difficult to place with certainty. The enlarged but rooted incisor and reduced premolars suggest *Microsyops* and its allies, and, as in that group, the teeth resemble those of Eocene Primates. The minute size suggests Insectivorous relations, and the enlarged incisor compares with the Soricidæ, but the molars are so totally distinct from those of that group that it seems best to place it with the Proglires. The distinctions from any described genus are well marked. The premolars are more reduced than in *Microsyops* or *Smilodectes*, and the composition of the molars quite distinct.

Apatemys bellulus Marsh 1872.

Plate LII, Figs. 3 and 4.

The type is a lower jaw in the Yale Museum, with m_{1-3} and alveoli of p_{3-4} . I refer to the species, a lower jaw, No. 12048, in which p_{4-m_2} are perfectly preserved, and the roots of the remaining teeth. Another specimen, No. 12060, contains the last premolar and first molar with alveoli of incisor and m_{2-3} . Both are from the Upper Bridger beds, Horizon C. The species compares in size with the short-tailed shrew (*Blarina brevicauda*).

The incisor root is oval, extending back beneath m_2 . The third premolar (or canine) is represented by a very small, round root, very little separated from the incisor. The fourth premolar is very small, close to the third premolar and to the first molar, with broad heel and no anterior basal cusp. The first molar

is curiously like a molariform premolar, the trigon considerably smaller than in m^2 , the metaconid less developed, more posterior in position, nearer to the protoconid and a little lower. The second molar is larger than the first, with trigon and heel of equal size; the third (seen best in the type) is somewhat longer than the second.

The jaw is very short and deep; besides the mental foramen under m_2 , double in this species, the external contour is interrupted by a pit directly under m_1 , above and in front of the mental foramen.

Apatemys bellus Marsh 1872.

Plate LII, Figs. 1 and 2.

This species is the type of the genus and is of somewhat larger size than *A. bellulus*, but in several respects less specialized. It is represented in our collections by a lower jaw, No. 12047, with the molar teeth and alveolus of p_4 . It differs in the larger premolar with semi-double root, molars longer antero-posteriorly, the paraconid better developed, the heel more angulate at the postero-external corner. The last molar is shown in this specimen, the heel is basin-shaped, with a hypoconulid behind and distinct from the basin, and situate on the outer side of the tooth (in *Microsyops* it is internal, in *Smilodectes* median). The mental foramen is single and smaller than in the preceding species, the pit in front of it is further forward, placed under p_{3-4} . No. 11425, a lower jaw with p_4-m_2 and the alveolus of m_3 , is referred with doubt to this species. It is of slightly larger size, with broader m_2 , paraconid more distinct, metaconid and protoconid more separate, the transverse ridge between them being lower p_4 more distinctly two-rooted. In other respects it agrees with *A. bellus*. Both specimens are from the upper part of Horizon D.

Uintasorex gen. nov.

A very small jaw with a supposed fourth premolar of insectivore type, a first molar (or molariform fourth premolar) of *Microsyops* type, enlarged incisor and reduced canine and premolars.

Dentition (provisional determination) I_1, C_1, P_2, M_3 . No diastemata. P_4 two-rooted with broad heel, distinct anterior basal cusp and rudimentary internal cusp. Mental foramina beneath P_4 and $?M_2$. First molar with small tricuspid trigon, pa^d and pr^d of nearly equal height (me^d broken off), heel wide, basin-shaped, angulate, hypoconid and entoconid distinct, hypoconulid semi-separate. Two small, round alveoli in front of p_4 are interpreted as canine and a single-rooted p_3 ; the incisor is enlarged, round oval in section and the external enamel appears to commence above the alveolar border, indicating that it is a rooted tooth. The jaw is by no means so short and deep as that of *Apatemys*, and much resembles that of *Smilodectes*; the P_4 is quite different from either genus, but both teeth are much like those of *Troglemur* (infra).

I place this genus provisionally in the Proglires on account of the type of molar. It is very minute, scarcely exceeding the common shrew in size.

Uintasorex parvulus sp. nov.

Plate LII, Fig. 6.

The type and only known specimen is the right ramus of a lower jaw, No. 12052, in which the fourth premolar, first molar and roots of the remaining teeth are preserved. It was discovered in the upper Bridger Beds, Horizon D.

Trogolemur gen. nov.¹

Dental formula 1.0.3.3. The incisor is enlarged, its root extending under the molars, the crown not preserved. The premolars are crowded, increasing in size uniformly from second to fourth, the last with broad heel and rudimentary metaconid. The molars are broad, short, with wide basin heels, in m_3 the heel is elongate and broad, much as in *Pelycodus*, and quite unlike *Apatemys*. The premolars are much less reduced than in *Apatemys*. The posterior mental foramen is under the posterior end of m_1 .

This genus, from the Lower Bridger, may perhaps be ancestral to the Upper Bridger *Apatemys* and *Uintasorex*, but adequate proof is lacking.

Trogolemur myodes sp. nov.

Plate LII, Fig. 5.

Type, No. 12599, a lower jaw with p_2 - m_3 perfect, and the root of the incisor. Found by Mr. Granger in the lowest fossiliferous beds of the Bridger, Horizon B₁, six miles south of Granger, Wyoming. The species is about the same size as *Apatemys bellulus*.

8. PROGLIRES Osborn 1902.

The family Mixodectidæ was proposed by Cope in 1883 to include *Mixodectes*, *Cynodontomys* and *Microsyops*. It was regarded as allied to *Chiromys* and placed in the "Prosimiæ" (Lemuroidea). In 1897 Matthew observed: "The discovery of some skeleton fragments in good association with a lower jaw of *Mixodectes pungens* makes it probable that this genus should be removed from the Primates and placed as an extremely primitive Rodent. *Microsyops* may perhaps go with it, but this is extremely doubtful, as the type of its lower molars is much more primitive and persistently so, and in several other respects different from *Mixodectes*." The resemblance of the upper molars of *Mixodectes* to those of *Indrodon* was commented upon in the brief description following, but was regarded as illusory on account of the very different characters shown in a fragmentary skeleton ascribed by Osborn and Earle in 1895 to *Indrodon malaris*.

¹Gr. τρογων gnawing, Lemur.

In a subsequent examination the writer discovered that this fragmentary skeleton (Am. Mus. No. 823) was not *Indrodon* but nearly related to *Miocænus acolytus*, and quite probably identical with that species. It was re-figured by Osborn in 1902 and its probable affinities are discussed on p. 512 of this memoir.

In 1902 Osborn proposed the name *Proglires* as a suborder of Rodentia to include the Mixodectidæ, in which he placed *Mixodectes* Cope and *Olbodotes* Osborn from the Torrejon, *Cynodontomys* Cope from the Wasatch, *Microsyops* Leidy from the Bridger (with *Palæacodon* Leidy, *Mesacodon* Marsh and *Bathrodon* Marsh as synonyms) and doubtfully *Indrodon* Cope of the Torrejon and "*Chriacus*" *angulatus* Cope of the Wasatch. The evidence for and against rodent affinities was further discussed, stress being laid upon the apparent lack of adaptation in teeth to orthal motion of the jaw.

Wortman in 1903 returned to the view of Cope that the Mixodectidæ ("Microsyopidæ") were Lemuroidea related to *Chiromys*, which he defended at considerable length. He rejected the evidence from the associated skeleton fragments with *Mixodectes* on the ground that "after long personal experience in collecting in the Torrejon beds . . . in the absence of reasonably conclusive evidence which would tend to preclude the possibility of a mixture I should not feel inclined to attach any very great weight to this association."¹

Wortman adduces additional evidence for the Primate relationship of this group, especially

(1) Its supposed kinship to *Metacheiromys*, which he referred to the primates, and which has a somewhat similar, but much more advanced, dental reduction. This need not be considered, as Osborn has proven *Metacheiromys* to be an edentate related to the Armadillos, and to have nothing to do with the Mixodectidæ.

(2) The molars and posterior premolars in *Microsyops* are unquestionably very much like those of known Eocene Primates and very different from Rodentia. The same is partly true of *Mixodectes*.

¹ As the writer spent over a year in critically examining, piecing together, identifying, labelling, recording and studying the American Museum Collections from the Puerco-Torrejon beds, including all the specimens gathered by Wortman as well as the much larger collections made for Professor Cope, he is reasonably familiar with the probabilities of admixture of individuals in specimens from this locality. It was thought sufficient at the time of writing to state that these fragments were found in "good association"; it is perhaps better, however, to state exactly what the circumstances were.

The specimen in question, Am. Mus. No. 2451, was collected by Mr. Walter Granger of the Expedition of 1896, and bore the field record number 121. It consisted of a part of the lower jaw with roots of the teeth as far back as m_1 , an astragalus, parts of the femur and humerus and other fragments. These were not associated with any fragments which appeared to belong to other individuals or species, and show in common a rather unusual type of weathering. According to Mr. Granger's recollection at the time of cataloguing, they were found by themselves at some distance from any other specimens. While piecing the material together I discovered that field No. 33, part of a lower jaw with m_{2-3} well preserved, fitted on the jaw fragment with No. 121; this made it possible to identify the specimen as *Mixodectes*. Presumably the jaw had been washed or rolled down the slope beyond the rest of the fragments and been picked up separately, and the remainder of the specimen discovered on a subsequent search over the same ground.

Admixture of individuals or species is common enough in the Basal Eocene formations, but I think that the above circumstances fully warrant the statement that the association was good, and are sufficient evidence for the removal of *Mixodectes* from the Primates.

(3) A calcaneum (unassociated), provisionally referred by Wortman to *Microsypops*, is of the very characteristic lemuroid type. The reference, however, is conjectural and probably incorrect; it is probably *Hemiacodon*, on the evidence of various similar specimens, in our collection, one of which includes a considerable part of the skeleton.

(4) The fourth premolar in *Microsypops* differs radically from the Rodents and most other mammals in the course of its cusp complication.

Wortman's arguments (2) and (4) appear to me to be strong evidence against Rodent relationship, especially in *Microsypops*. But it is curious that Osborn, Wortman and the present writer have overlooked the possibility of insectivore relationship of the Mixodectidæ, which may after all be the true solution of this problem. Decisive evidence indeed is lacking, but in one or another of the genera there are several indications that point towards the Insectivora. These are:

(1) The median lower incisors are enlarged, as in Rodents, Insectivores and some other groups.

(2) The enlarged median incisor is rooted and in *Mixodectes* is characteristically Insectivore in the form of the crown, comparing with Soricidæ, etc., and very different from the scalpriform, rootless incisor of Rodents.

(3) The mode of reduction of the remaining anterior teeth is much more suggestive of Insectivores than of Rodents.

(4) The upper canine in *Microsypops* is two-rooted (specimen No. 13041, Am. Mus. Coll.).

(5) The astragalus in *Mixodectes*, while wholly unlike that of any Primate, agrees quite as well with Insectivora as with Rodents; the same may be said of the other fragments of the skeleton. In the remaining genera the skeleton is unknown.

(6) The lack of orthal motion of the jaws, and the apparent manner of complication of the premolars, agree quite well with Insectivora although not with Rodents.

(7) In the Apatemyidæ which I refer provisionally to the Insectivora, the molars are very similar to those of the Mixodectidæ, and to the Anaptomorphidæ which are referred to the Lemuroidea, but the posterior mental foramen is situated under m_1 , a character of the majority of Insectivora, not found outside that order. The skeleton of the Apatemyidæ is unknown.

It is by no means certain that the Torrejon *Mixodectes*, *Olbodotes* and *Indrodon* belong to the same family as the Wasatch, Wind River and Bridger group (*Cynodontomys* and *Microsypops*). The teeth differ very considerably in the form and position of the cusps, and the fourth premolar in the older group is of entirely different and rather specialized type (compare the Insectivore *Pentacodon*, see p. 523, of this memoir). The present evidence, however, seems to favor referring both groups to the Insectivora. If this view be correct we must

admit that the dentition alone does not enable us to certainly distinguish between Insectivora and Primates in the Eocene. For in *Hemiacodon*, which is associated on fairly good evidence with an unquestionably Lemuroid skeleton, the molars are of much the same type as in Mixodectidæ and Apatemyidæ, and in other Anaptomorphidæ the resemblance is even closer; these also show more or less enlargement of the first incisor; nothing is known of their skull and skeleton.

In order to show the general resemblance in teeth, I have figured on Plate LII, Fig. 7, the lower jaw of a small Anaptomorphid, which may be compared with jaws of Apatemyidæ figured on the same plate, and with Osborn's and Wortman's figures of Mixodectidæ.

In view of the uncertainty in regard to the relationships of these small forms, it seems better to postpone any final arrangement of them, provisional or determinate, until the Bridger Primates have been thoroughly restudied with the aid of the materials now in the American Museum. Wortman's elaborate studies of the Bridger Primates in the Marsh collection are unfortunately incomplete, and marred by a very one-sided setting forth of the evidence as to their relationships; and the not less extensive collection of Primates made by our parties of 1903-6 will add considerably to the available data.

IV. ADDENDA, BIBLIOGRAPHY, AND INDEX.

THE VALUE OF THE ASTRAGALUS IN ORDINAL CLASSIFICATION.

Plate XLVII, Figs. 2 and 3.

The characters of the astragalus are of high importance in the estimation of ordinal affinities as well as in determining the nearer relationship of fossil mammals and their functional adaptation. It is intimately associated with the whole machinery of the ankle joint, so that changes in the form and proportions of tibia and fibula on one hand or of tarsals and metatarsals on the other are correlated with modifications in the form of the astragalus.

Its peculiarly irregular form and numerous facets give it more character than any other bone of the skeleton, while its importance in the economy of the ankle joint holds it very rigidly to type, so that it is subject to very little individual variation and displays a remarkable constancy of form among the widely varying functional adaptations of a natural order. Each order of mammals has as a rule its peculiar type of astragalus, usually very readily distinguished from any other, and persistent throughout the order although often with wide variations in proportion, correlated with wide adaptive divergences in the foot-structure. The astragalus of the Perissodactyla, Artiodactyla, Carnivora, Insectivora, Rodentia, Edentata, Primates, Proboscidea, Marsupialia, etc., is

quite unmistakable in any member of the order, and in various extinct orders the astragalus is one of the most important guides in estimating the affinities of the order. The adaptive changes in the structure of the feet may cause wide differences in its proportions, but the fundamental type can usually be clearly seen.

The Carnivore astragalus is distinguished by a distinct neck and round or oval ball-shaped head set very obliquely on the body. The tibial trochlea is rather narrow, the outer side higher, the fibular articulation nearly vertical. Behind and beneath the trochlea the body is deeply notched. In the primary type the trochlea is not grooved, and slopes steeply down from the outer crest, while the fibular facet has considerable obliquity, and an astragalar foramen is present behind the trochlear facet. In the cursorial adaptation of the ankle joint, common to most of the more progressive races, the trochlea becomes deeply grooved and extended backward in digitigrade types to the posterior border of the head, the astragalar foramen closing up and the posterior notch becoming less clearly recognizable. The fibular facet becomes almost vertical with the reduction of the fibula to a slender bone which no longer transmits part of the weight of the animal to the foot.

The Primate astragalus is distinguished by a narrow, flat trochlea, moderately oblique neck with round, convex head, body elongate postero-inferiorly, but without foramen or posterior notch.

The Insectivore astragalus has a broad, shallow trochlea with well defined inner and outer crests of nearly equal height, oblique neck and oval, convex head, no foramen or posterior notch.

The Rodent astragalus is very like that of the Insectivora, but the trochlea extends backward to the posterior margin of the body. The astragalus as a whole varies widely in proportion of width to length but the relative proportions and construction of its parts are fairly constant.

The Perissodactyl astragalus has a saddle-shaped head, and a deeply grooved oblique trochlea. The Artiodactyl astragalus with double ginglymoid facets differs essentially in the straight trochlea and neck as well as in the trochlear joint of the head.

Astragalar foramen. Present in the primitive, unspecialized types of feet in the following groups:

- (1) Insectivora-Carnivora-Creodonta-Condylarthra-Amblypoda group.
- (2) Toxodontia-Typotheria group.
- (3) Litopterna and ? other S. American groups.

It is not found even in the earliest and least specialized members of the following groups:

- (1) Primates.
- (2) Rodentia-Edentata-Tæniodonta-Effodientia group. [Rodents should perhaps be regarded as a distinct group.]
- (3) Perissodactyla-Artiodactyla [?distinct groups].

It disappears when the foot becomes digitigrade owing to the backward extension of the trochlea.

It transmits (fide Ameghino) in modern animals a branch of the peroneal artery. Dr. Ameghino considers that it has also formerly served to transmit the tendon of the *flexor hallucis*. The latter view I regard as improbable and unsupported by any adequate evidence. The position and direction of the foramen, the fact that its disappearance is by closing up, and not by conversion into a notch (in any types I have examined¹), and the fact that in all modern types whether with or without astragalar foramen, the *flexor hallucis* tendon runs in a separate groove close to the *flexor communis digitorum*, are to my mind decisive against it.

On the other hand if it simply transmitted a branch of the peroneal artery, the digitigrade evolution, causing the tibia to pinch it against the astragalus and heel, would naturally constrict the artery, interrupt the flow of blood, and cause abortion of the artery, followed by closing of the foramen exactly in the manner seen in various lines.

The occurrence of the foramen in the Creodonta and allied groups is as follows:

Insectivora. Present in *Hyopsodus*, vestigial in *Pantolestes*, present in *Erinaceus*. I do not observe it in any of the other Insectivora but would not be certain of its absence.

Carnivora (Fissipedia). Present in *Cercoleptes*, absent in *Procyon* and *Nasua*; present in *Meles*, vestigial in *Taxidea*, present in *Megalictis* and ?*Mellivora*. Generally absent in Mustelidæ. Always absent in Æluroidæ except Machærodonts (present in *Smilodon*; vestigial in *Dinictis*). Absent in *Cynodictis* and all the Canidæ (but found by Ameghino in a South American modern species, ?abnormal). Summarily — present in the primitively plantigrade Arctoidea, and in the Machærodonts, but otherwise absent.

Carnivora (Creodonta). Present in Arctocyonidæ and Miacidæ except *Didymictis*. Present in Oxyænidæ, vestigial to absent in Hyænodontidæ (vestigial in *Sinopa* and *Tritemnodon*, absent in *Hyænodon*). Present in *Dissacus* and *Pachyæna*, absent in *Mesonyx* and *Synoplotherium*. Summarily — present except in the more specialized cursorial types.

Condylarthra. Present in *Euprotogonia*, absent in *Phenacodus*, present in *Meniscotherium*. Summarily — as in Creodonta.

Amblypoda. Present in *Pantolambda* and *Coryphodon*, variable (fide Marsh) in *Uintatherium*, present in Periptychidæ.

¹ But see Marsh, Dinocerata Monograph, p. 148.

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EXPLANATION OF PLATES.

PLATE XLII.

Map of the Bridger Basin, showing the exposures of the horizons. Scale 6 miles = 1 inch. Redrawn by L. M. Sterling from draft map by W. D. Matthew and Walter Granger. Published by permission of the United States Geological Survey and by courtesy of Professor H. F. Osborn.

PLATE XLIII.

Skulls of Bridger Miacidæ, etc. Natural size except fig. 1.

Fig. 1. *Viverravus minutus*, superior, lateral and inferior views of skull, magnified three diameters. No. 12621, Lower Bridger. See p. 357.

Fig. 2. *Vulpavus profectus*, skull and lower jaw, natural size, of type specimen, No. 12626, Lower Bridger. See p. 382.

Fig. 3. *Vulpavus (Phlaodectes) ovatus*, skull, natural size, of type specimen, No. 11498, Lower Bridger. See p. 398.

Fig. 4. *Vassacyon promicrodon*, lower jaw, natural size, external and superior views. Type specimen, No. 83, Wasatch of Big Horn Valley, Wyoming. See p. 346.

PLATE XLIV.

Skulls of Bridger Oxyænidæ. Natural size.

Fig. 1. *Limnocyon verus*, skull and lower jaw, of No. 12155 from the middle Bridger beds. See p. 435.

Fig. 2, 2a. *Thinocyon velox*, skull and lower jaw of No. 13081 Lower Bridger. See p. 450.

Fig. 3. *Thinocyon velox*, inferior view of skull and lower jaws, No. 12631. Lower Bridger. See p. 452.

PLATE XLV.

Skulls and jaws of Hyænodontidæ and Mesonychidæ. All natural size.

Fig. 1. *Sinopa rapax*, skull and lower jaw of mounted skeleton, No. 11535., lateral and inferior views. Lower Bridger. See pl. XLVI and p. 471.

Fig. 2. *Sinopa rapax*, lower jaw, external and superior views. No. 11542, Lower Bridger. See p. 471.

Fig. 3. *Sinopa rapax* mut. *lania*. Skull and lower jaw, lateral view. Type specimen, No. 13142, Lower Washakie. See p. 472.

Fig. 4. *Sinopa major*, lower jaw, external view No. 12079. Upper Bridger. See p. 473.

Fig. 5. *Hapalodectus compressus*, lower jaw, external and superior views, type specimen, No. 12781. Wind River Beds, Wyoming. See p. 499.

PLATE XLVI.

Mounted skeletons of Bridger Hyænodontidæ, one fourth natural size.

Fig. 1. *Tritemnodon agilis* (Marsh). No. 12636, Lower Bridger. Found by W. J. Sinclair, 1905. Prepared and mounted by Albert Thomson, 1908. Photo. by Thomson. See p. 475.

Fig. 2. *Sinopa rapax* Leidy. No. 11535, Lower Bridger. Found by Walter Granger, 1903; prepared and mounted by Albert Thomson, 1907. Photo. by Anderson. See pl. XLV and p. 471.

PLATE XLVII.

Fig. 1. *Sinopa rapax*, mut. *lania*. Manus and pes, natural size, type specimen No. 13142. Lower Washakie. See pl. XLV and p. 472.

Fig. 2. Astragali of Carnivora, natural size, superior and internal views: 2a, *Cercoleptes*; 2b, *Vulpavus profectus* (type); 2c, *Umtacyon vorax*, No. 11504; 2d, *Limnocyon verus* No. 12155; 2e, *Sinopa rapax* No. 11531; 2f, *Mesonyx obtusidens*, No. 12643. All except 2a from the Bridger Eocene. See p. 550.

Fig. 3. Astragali of Insectivora, enlarged three diameters except 3c, superior and internal views: 3a, *Hyopsodus paulus* No. 11393 $\times \frac{3}{4}$; 3b, *Erinaceus europæus* $\times \frac{3}{4}$; 3c, *Pantolestes natans* No. 12152, natural size; 3d, *Centetes ecaudatus*, $\times \frac{3}{4}$. Nos. 3a, 3c, from Bridger Eocene; 3b, 3d, modern. See p. 550.

PLATE XLVIII.

Upper and Lower Jaws of Bridger *Hyopsodus*. All magnified three diameters.

Fig. 1. *Hyopsodus marshi*, upper jaw, crown view No. 10878.

Fig. 2. *Hyopsodus paulus*, palate with right upper cheek teeth. No. 10969.

Fig. 3. *Hyopsodus paulus*, upper jaws, showing cheek teeth more worn than in Fig. 2. No. 12945.

Fig. 4. *Hyopsodus lepidus*, upper and lower jaws, crown views. Type specimen, No. 11900.

Fig. 5. *Hyopsodus paulus*, lower jaw, external view. No. 10984.

Fig. 6. *Hyopsodus lepidus*, lower jaw, external view. No. 11897.

Fig. 7. *Hyopsodus paulus*, lower jaw, superior view, No. 11415.

Fig. 8. *Hyopsodus minusculus*, lower jaw, superior view, No. 12496.

PLATE XLIX.

Fig. 1. *Phenacops incerta*, lower jaw, external and superior views, enlarged three diameters. Type specimen, No. 12091, Lower Bridger. See p. 535.

Fig. 2a, 2b. *Pantolestes elegans*, lower jaw, external and superior views, enlarged three diameters. No. 13044, Upper Bridger. See p. 533.

Fig. 3. *Hyopsodus minusculus*, upper jaw, crown view enlarged three diameters. No. 12493, Lower Bridger. See p. 519.

Fig. 4. ?*Peratherium* sp., lower jaw, internal, crown and external views, enlarged six diameters. No. 13046.

Fig. 5. *Proscalops miocænus*, lower jaw, external and superior views, enlarged six diameters. Type, No. 8949a, Upper White River, Colorado. See p. 537.

PLATE L.

Jaws of Bridger Insectivora and Marsupials, enlarged six diameters.

Fig. 1. *Myolestes dasypelix*, lower jaw, external, superior and internal views. Type specimen, No. 11490, Lower Bridger. See p. 541.

Fig. 2. *Entomolestes grangeri*, lower jaw, external, superior and internal views. Type specimen, No. 11445, Lower Bridger. See p. 542.

Fig. 3. *Myolestes* sp., part of lower jaw, external and superior views. No. 12063, Lower Bridger. See p. 541.

Fig. 4. *Entomacodon minutus*, part of lower jaw, external, superior and internal views. No. 12056, Upper Bridger. See p. 540.

Fig. 5. *Nyctitherium curticens*, part of lower jaw, external, superior and internal views. Type, No. 12055, Upper Bridger. See p. 539.

Fig. 6. *Nyctitherium nitidum*, upper jaw fragment, with M^{1-2} , external, obliquely internal and crown views. No. 11489, Upper Bridger. See p. 538.

Fig. 7. *Nyctitherium nitidum*, part of lower jaw doubtfully associated with the preceding, external, superior and internal views. No. 11488. See p. 538.

Fig. 8. *Nyctitherium velox*, part of lower jaw, external superior and internal views. No. 12377, Upper Bridger. See p. 538.

Fig. 9. *Peratherium* sp., lower jaw in matrix, external view. No. 11493, Lower Bridger. See p. 540.

PLATE LI.

Skulls and jaws of Oligocene Insectivora. Enlarged six diameters except Fig. 4.

Fig. 1. *Micropternodus borealis*, lower jaw, external superior and internal views. Type specimen, No. 9602, Pipestone Creek, Montana. See p. 543.

Fig. 2. *Apternodus mediævus*, part of lower jaw, external, superior and internal views. Type specimen, No. 9601, Pipestone Creek, Montana. See p. 543.

Fig. 3. *Proscalops secundus* sp. indesc., anterior half of skull, palatal and oblique views. Type specimen, Lower Rosebud, Pine Ridge Agency, South Dakota. See p. 537.

Fig. 4. *Proscalops secundus*, type skull, enlarged three diameters, lateral and inferior views. See p. 537.

PLATE LII.

Lower Jaws of Bridger Apatemyidæ and Anaptomorphidæ, external, superior and internal views. Enlarged six diameters.

Fig. 1. *Apatemys bellus*, No. 11425, Upper Bridger. See p. 545.

Fig. 2. *Apatemys bellus*, No. 12047, Upper Bridger. See p. 545.

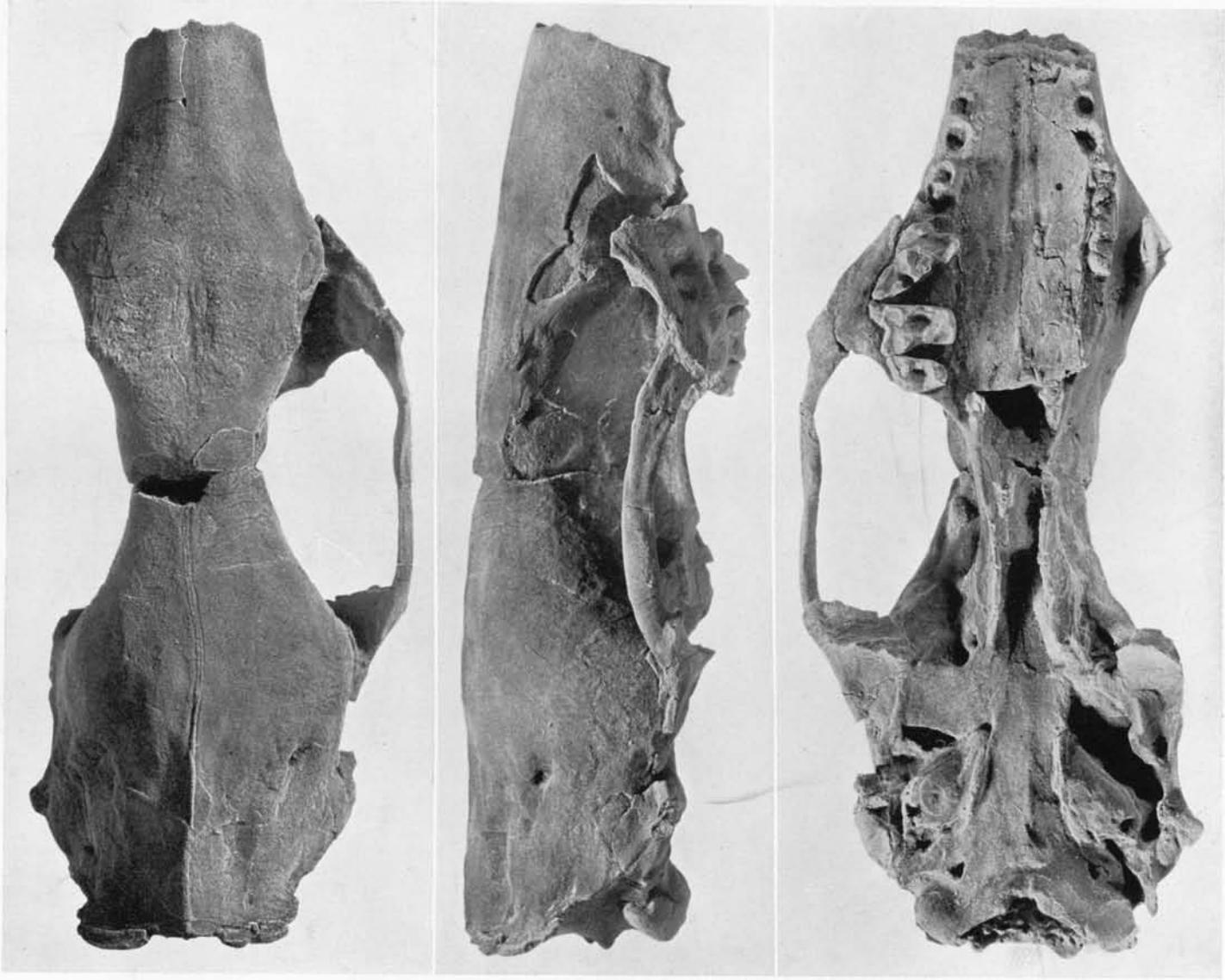
Fig. 3. *Apatemys bellulus*, No. 12048, Upper Bridger. See p. 544.

Fig. 4. *Apatemys bellulus*, No. 12060, Upper Bridger. See p. 544.

Fig. 5. *Trogolemur myodes*. Type, No. 12599, Lower Bridger. See p. 546.

Fig. 6. *Uintasorex parvulus*. Type, No. 12052, Upper Bridger. See p. 546.

Fig. 7. Anaptomorphid, gen indesc. No. 12598, Lower Bridger. See p. 549.



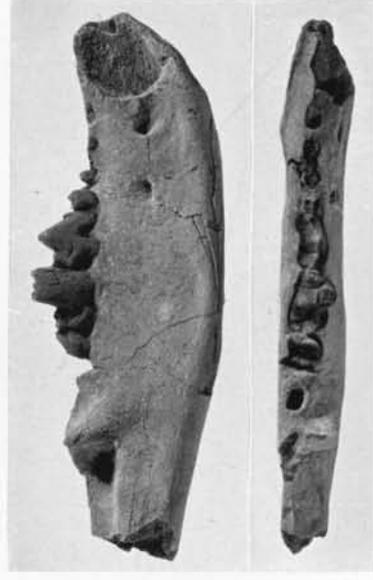
1, *Viverravus minutus*, x $\frac{3}{4}$



2, *Vulpavus profectus*, x $\frac{1}{4}$



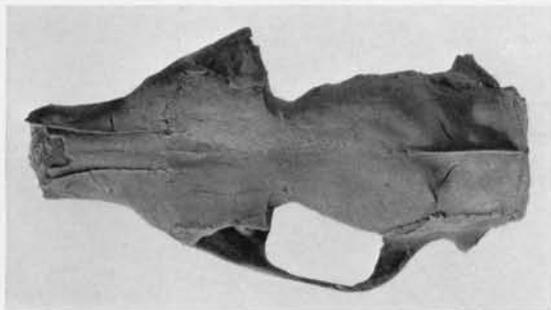
3, *Vulpavus ovatus*, x $\frac{1}{4}$



4, *Vassacyon promicrodon*, x $\frac{1}{4}$



1, *Linnocyon verus*, x $\frac{1}{1}$



2, *Thinocyon velox*, x $\frac{1}{1}$

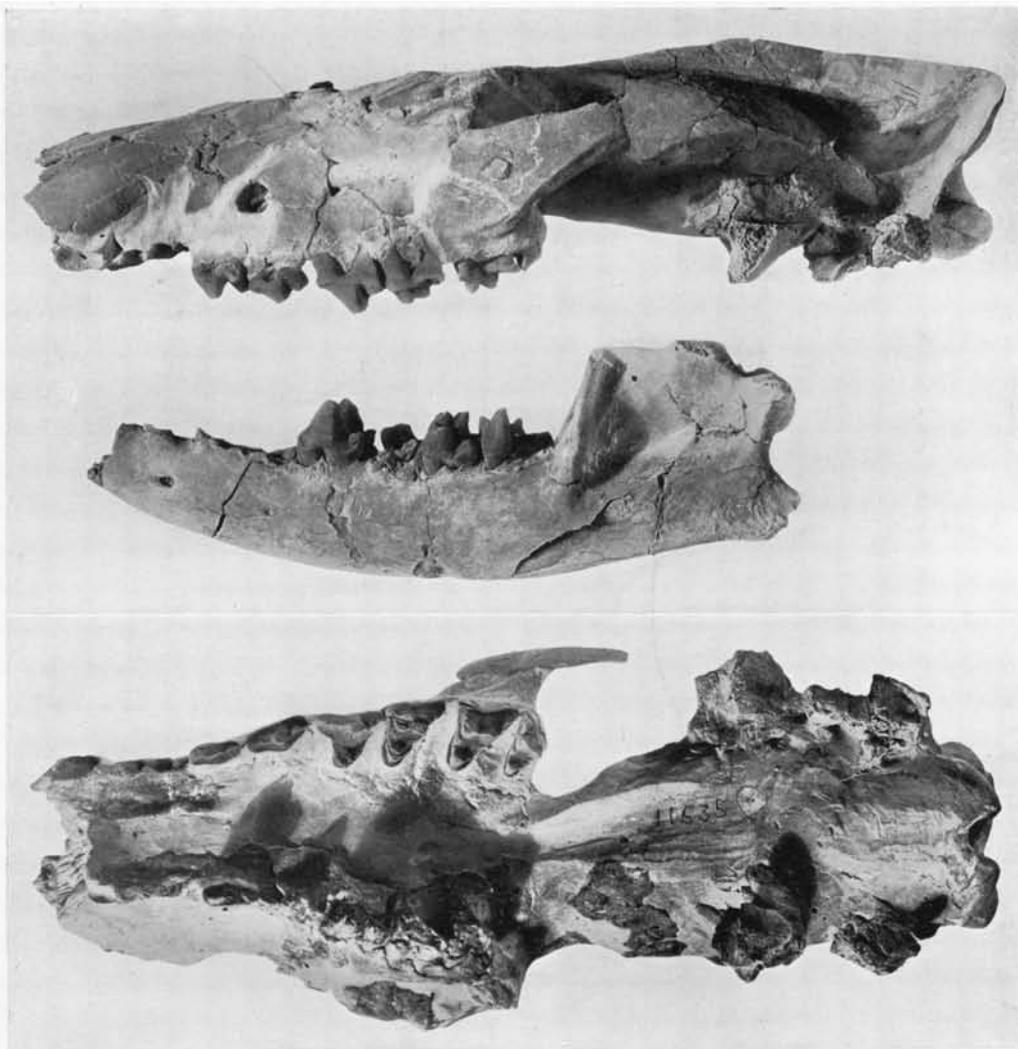


3, *Thinocyon velox*, x $\frac{1}{1}$

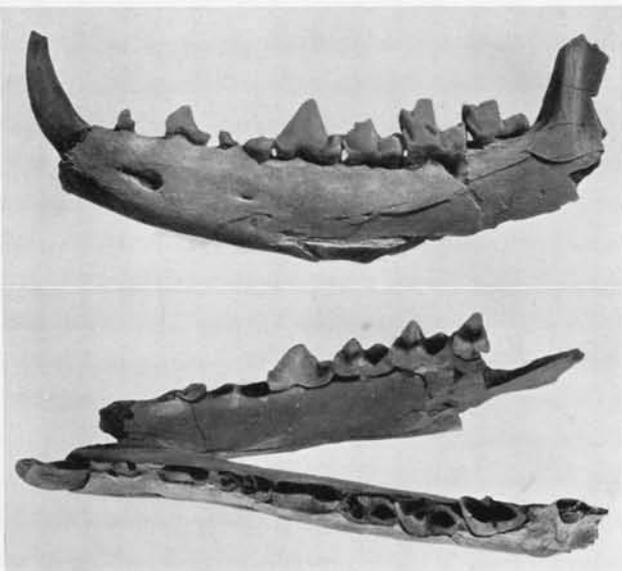


4, *Thinocyon velox*, x $\frac{1}{1}$

SKULLS OF BRIDGER OXYÆNIDÆ.



1, *Sinopa rapax*, x $\frac{1}{1}$



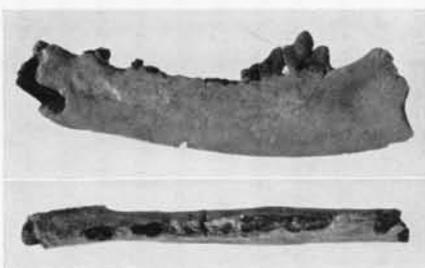
2, *Sinopa rapax*, x $\frac{1}{1}$



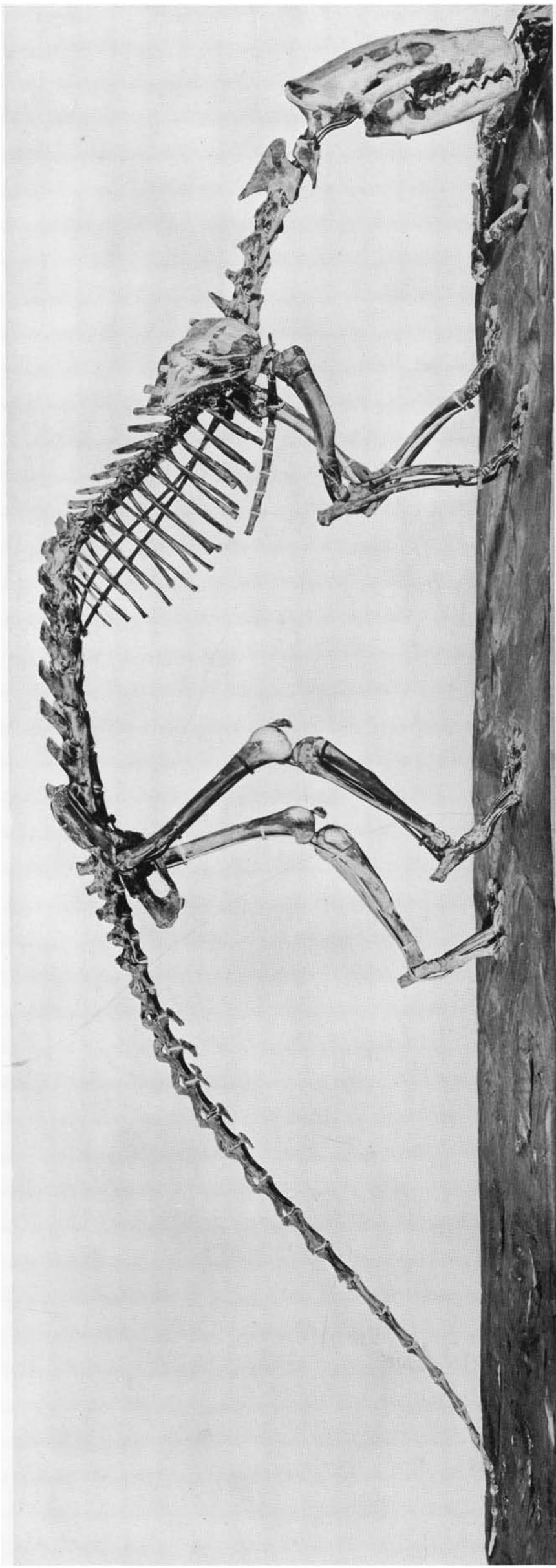
3, *Sinopa rapax lania*, x $\frac{1}{1}$



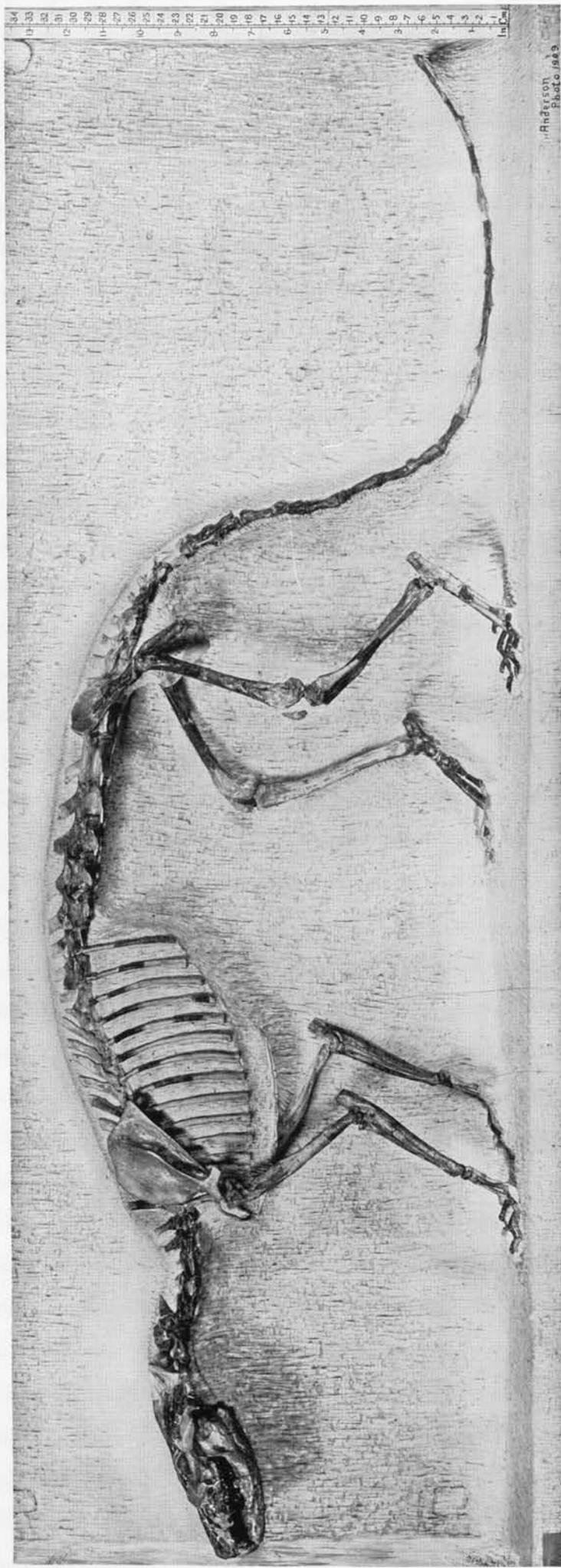
4, *Sinopa major*, x $\frac{1}{1}$



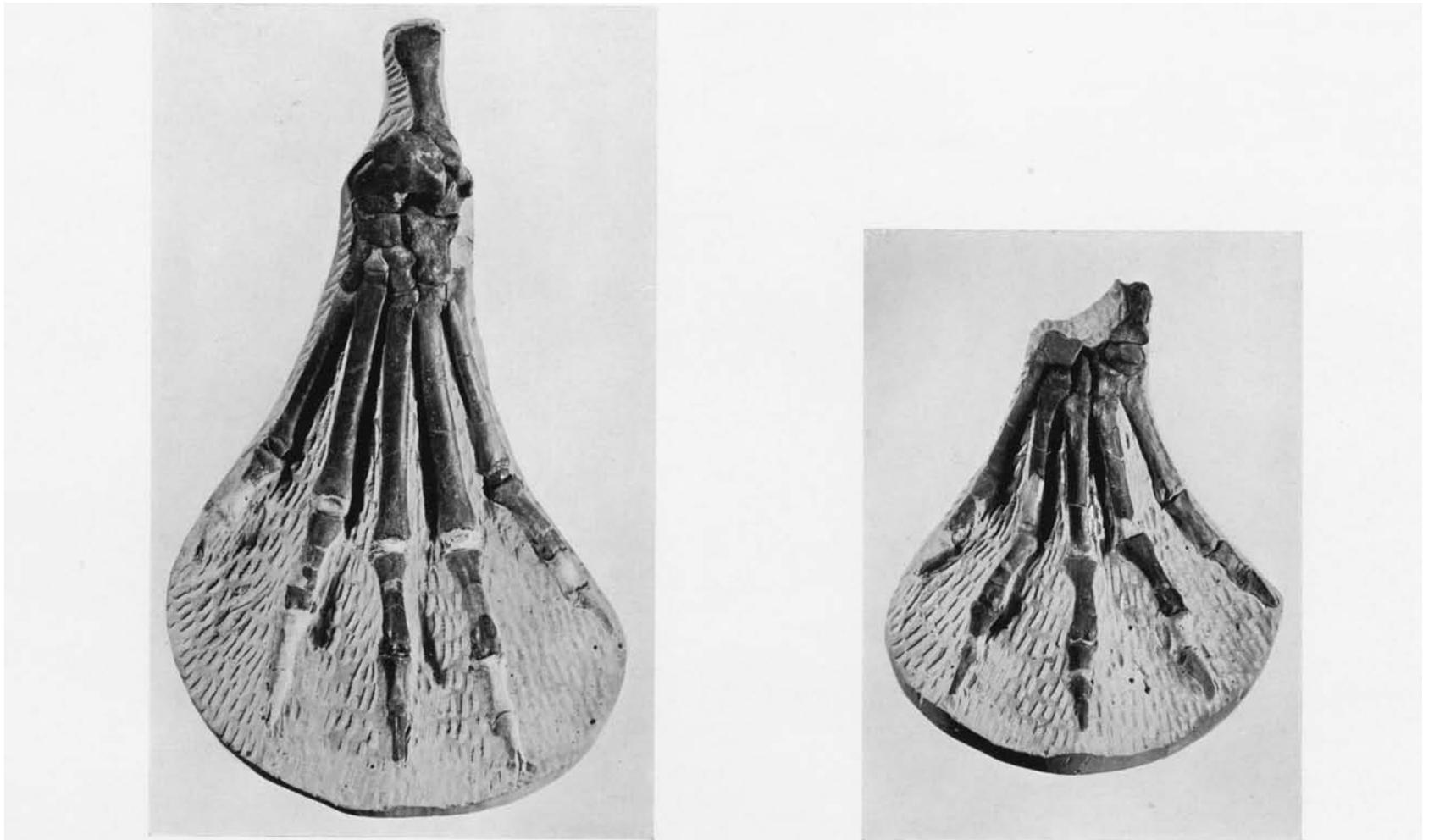
5, *Hapalodectes compressus*, x $\frac{1}{1}$



1, *Tritemnodon agilis*, x $\frac{1}{4}$



2, *Sinopa rapax*, x $\frac{1}{4}$



1. Pes and Manus of Sinopa, x $\frac{1}{1}$



a, Cercoleptes, x $\frac{1}{1}$ b, Vulpavus, x $\frac{1}{1}$ c, Uintacyon, x $\frac{1}{1}$ d, Limnocyon, x $\frac{1}{1}$ e, Sinopa, x $\frac{1}{1}$

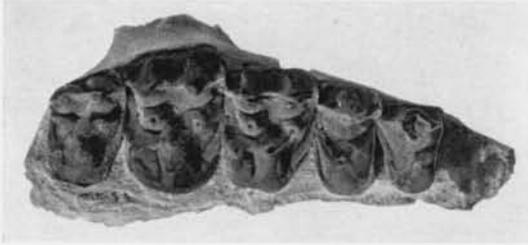
2. ASTRAGALI OF CARNIVORA.



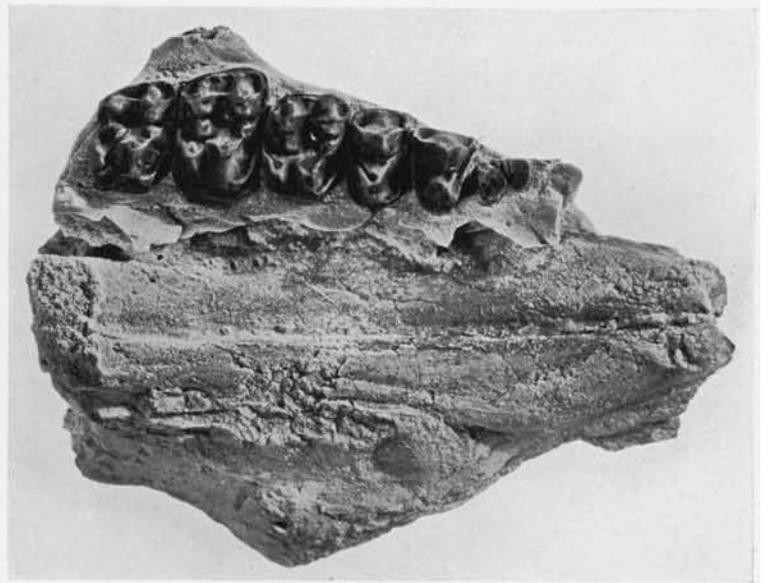
a, Hyopsodus, x $\frac{3}{1}$ b, Erinaceus, x $\frac{3}{1}$ c, Pantolestes, x $\frac{1}{1}$ d, Centetes, x $\frac{3}{1}$

3. ASTRAGALI OF INSECTIVORA.

f, Mesonyx, x $\frac{3}{1}$



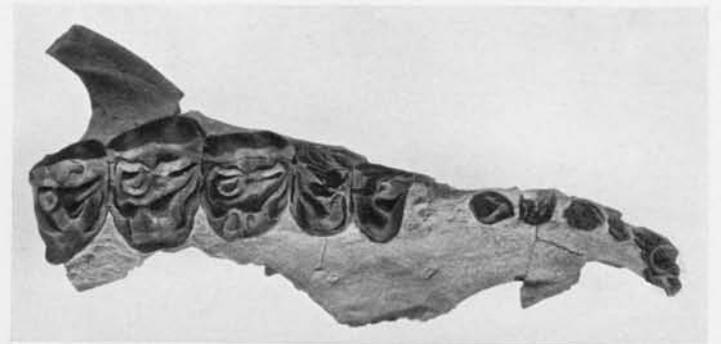
1, *Hyopsodus marshi*, x $\frac{3}{1}$



2, *Hyopsodus paulus*, x $\frac{3}{1}$



3, *Hyopsodus paulus*, x $\frac{3}{1}$



4, *Hyopsodus lepidus*, x $\frac{3}{1}$



4, *Hyopsodus lepidus*, x $\frac{3}{1}$



5, *Hyopsodus paulus*, x $\frac{3}{1}$



6, *Hyopsodus lepidus*, x $\frac{3}{1}$



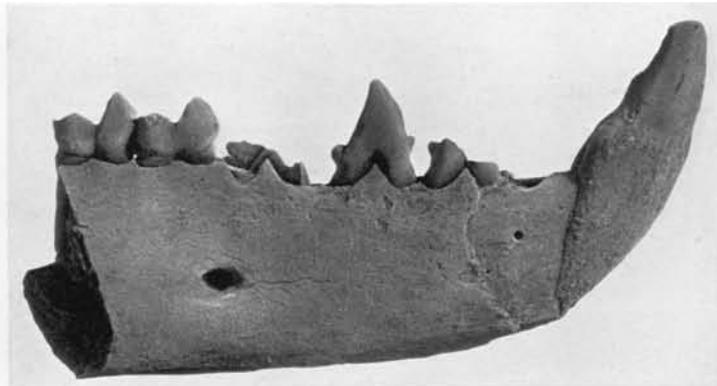
7, *Hyopsodus paulus*, x $\frac{3}{1}$



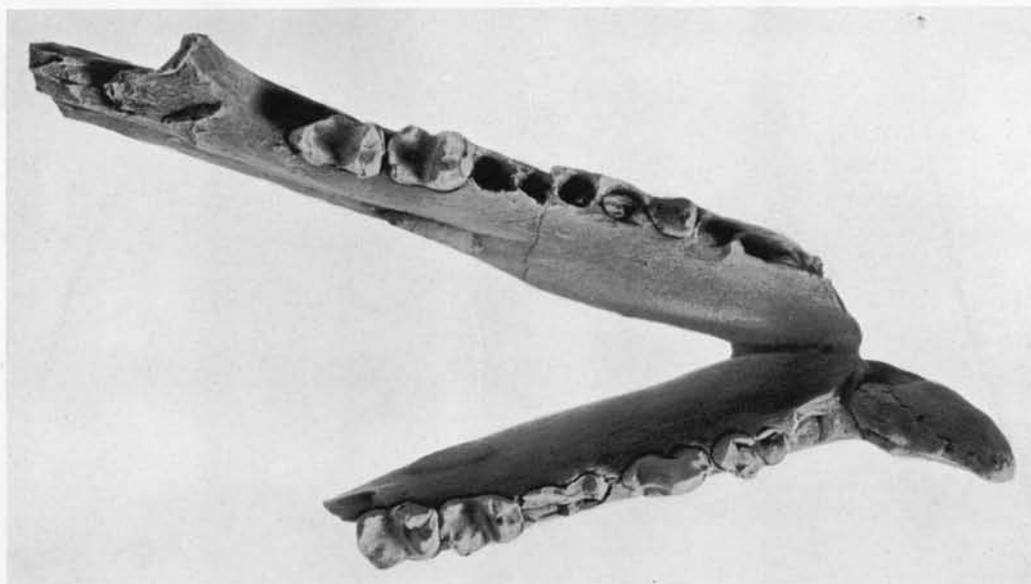
8, *Hyopsodus minusculus*, x $\frac{3}{1}$



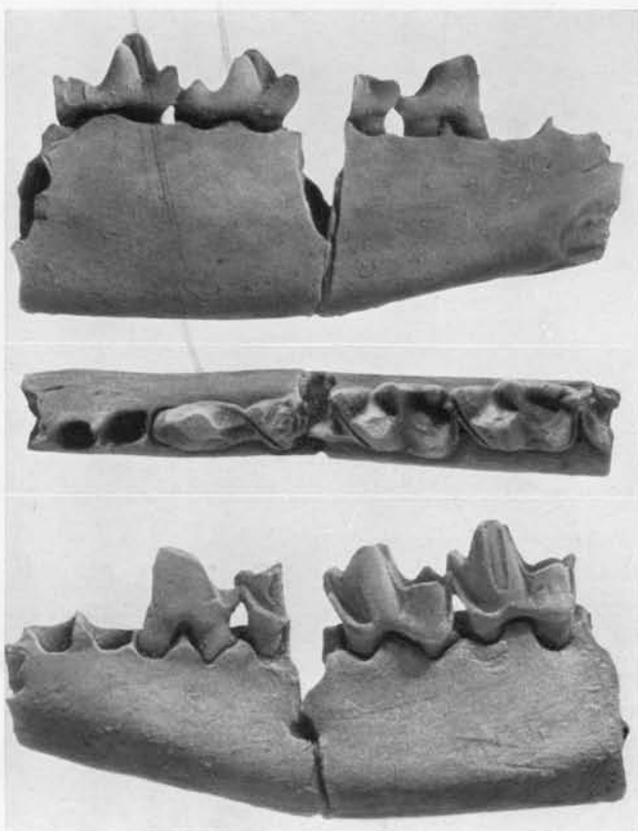
1, *Phenacops incerta*, x $\frac{3}{1}$



2, *Pantolestes elegans*, x $\frac{3}{1}$



2a, *Pantolestes elegans*, x $\frac{3}{1}$



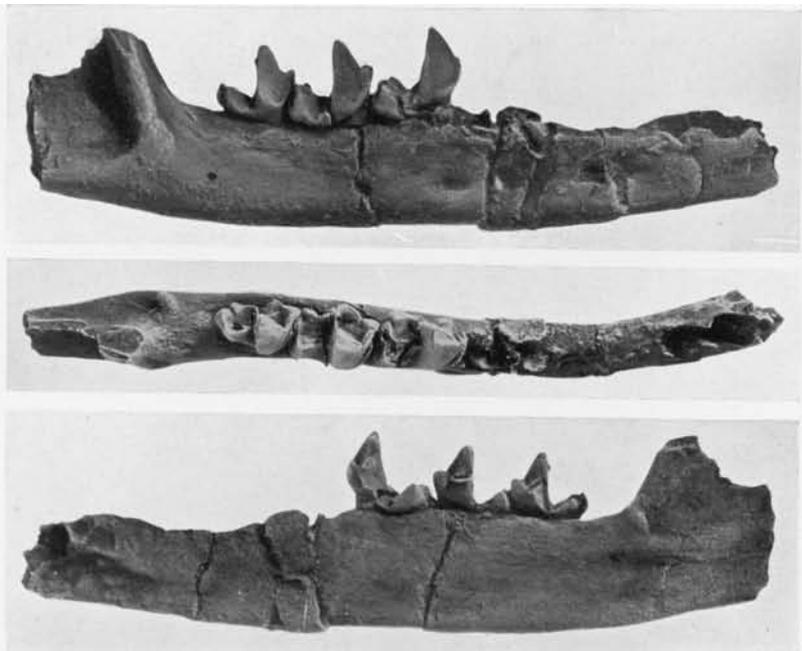
4, *Peratherium* sp., x $\frac{6}{1}$



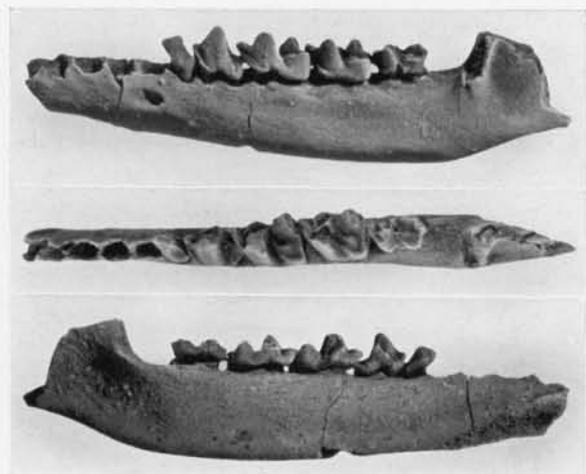
3, *Hyopsodus minusculus*, x $\frac{3}{1}$



5, *Proscalops miocænus*, x $\frac{6}{1}$



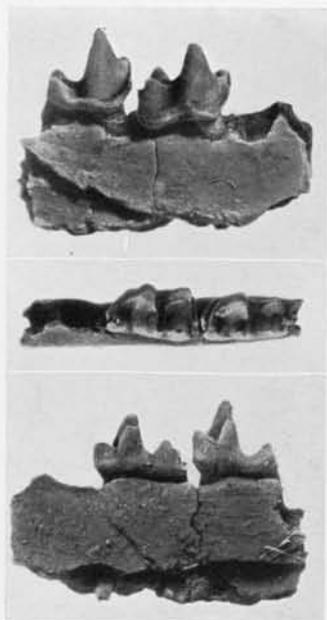
1, *Myolestes dasypelix*, x $\frac{6}{1}$



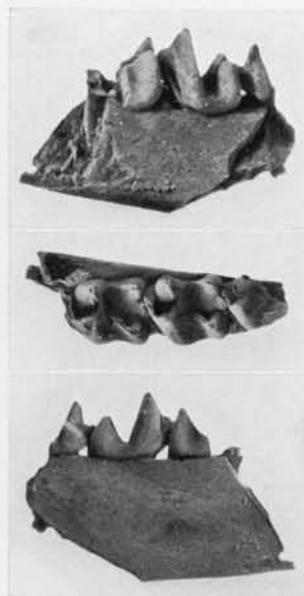
2, *Entomolestes grangeri*, x $\frac{6}{1}$



3, *Myolestes* sp., x $\frac{6}{1}$



4, *Entomacodon minutus*, x $\frac{6}{1}$



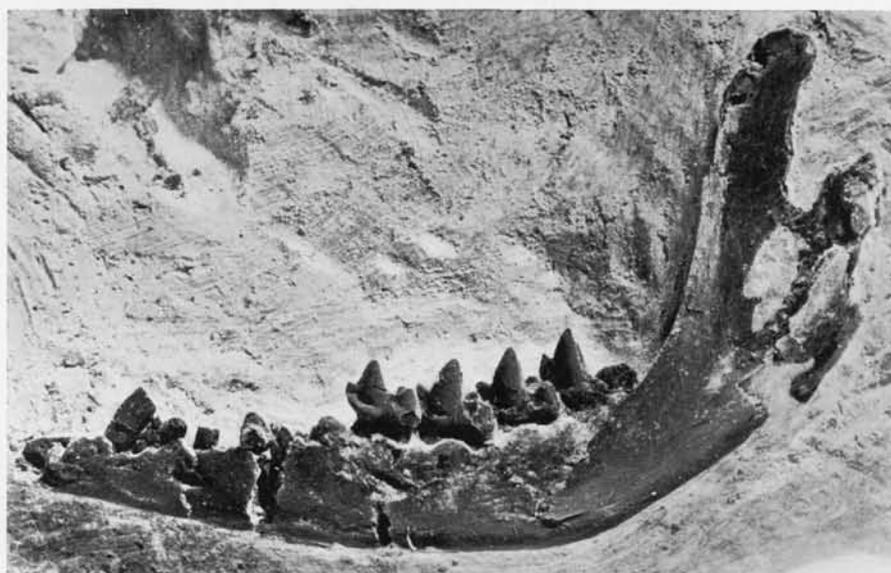
5, *Nyctitherium curticens*, x $\frac{6}{1}$



6, *Nyctitherium nitidum*, x $\frac{6}{1}$



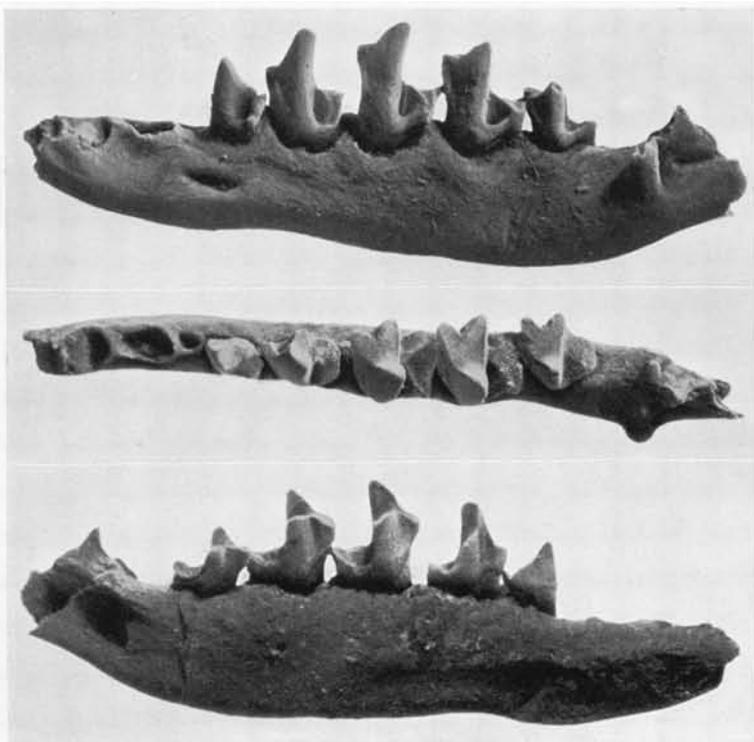
8, *Nyctitherium velox*, x $\frac{6}{1}$



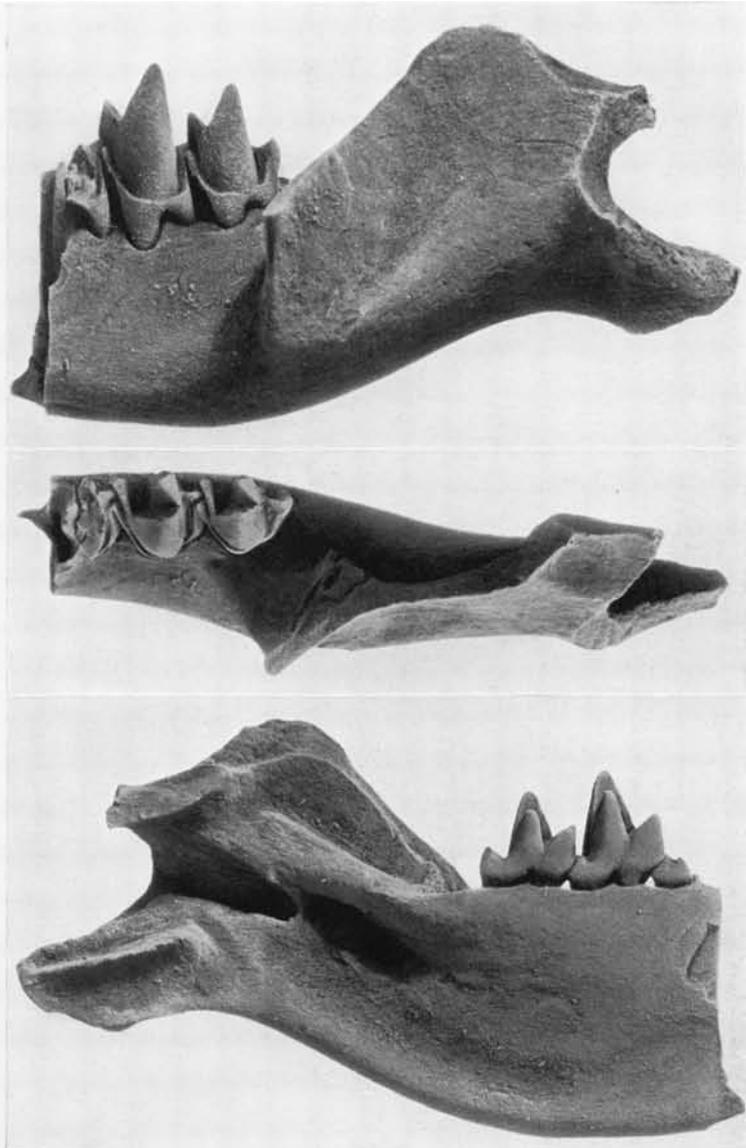
9, *Peratherium* sp., x $\frac{6}{1}$



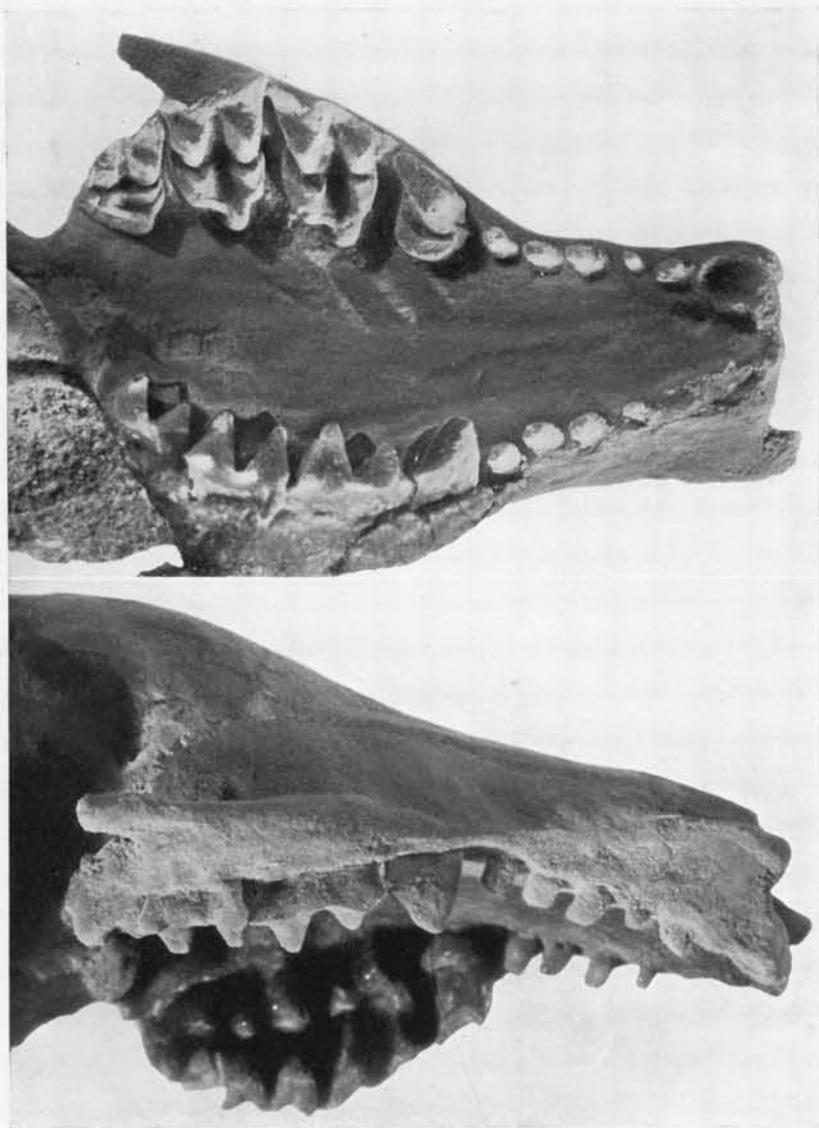
7, *Nyctitherium nitidum*, x $\frac{6}{1}$



1, *Micropternodus borealis*, x $\frac{6}{1}$



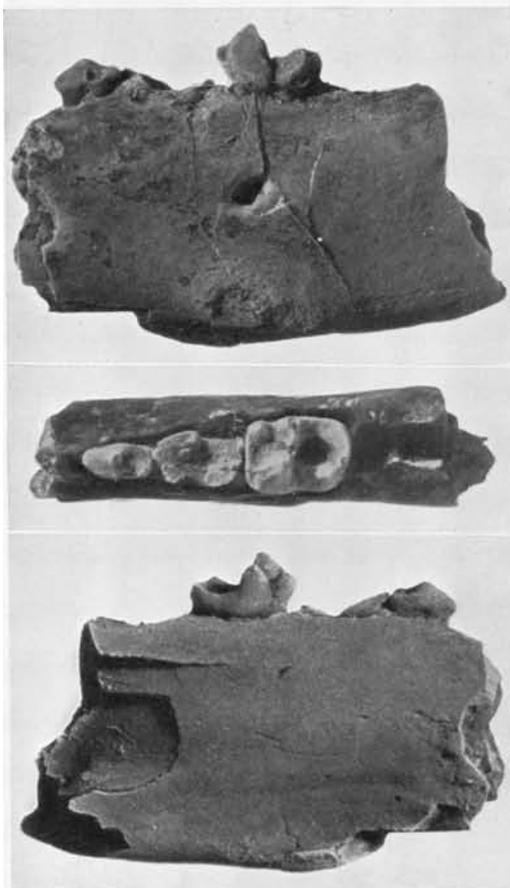
2, *Apternodus mediaevus*, x $\frac{6}{1}$



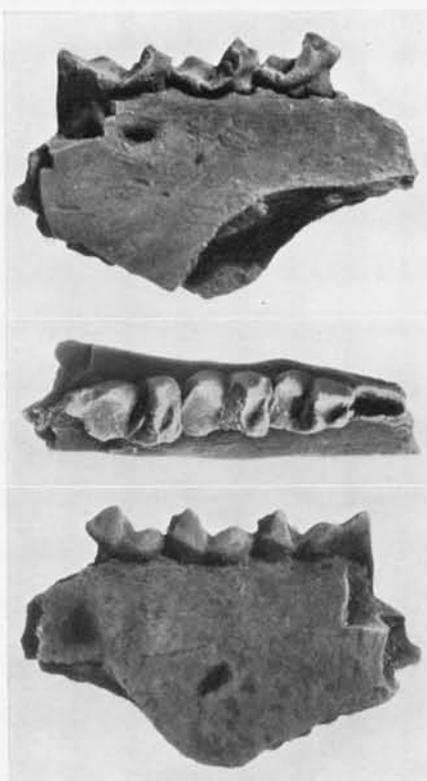
3, *Proscalops secundus*, x $\frac{6}{1}$



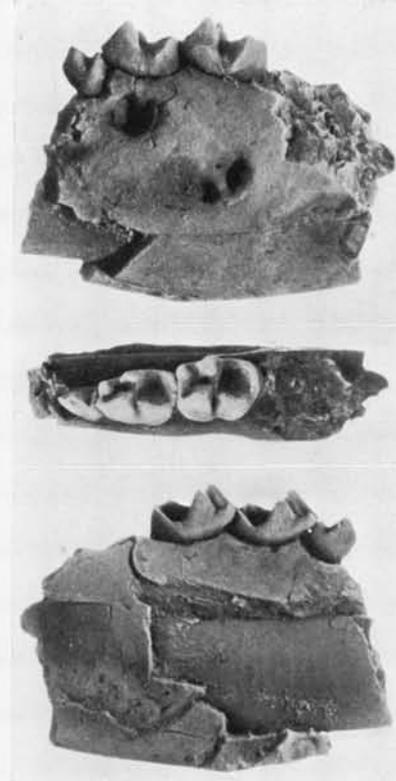
4, *Proscalops secundus*, x $\frac{3}{1}$



1, *Apatemys bellus*, x $\frac{6}{1}$



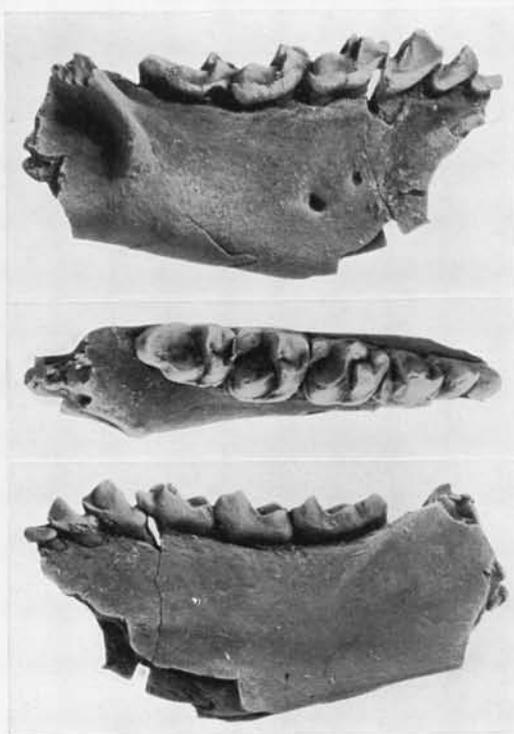
2, *Apatemys bellus*, x $\frac{6}{1}$



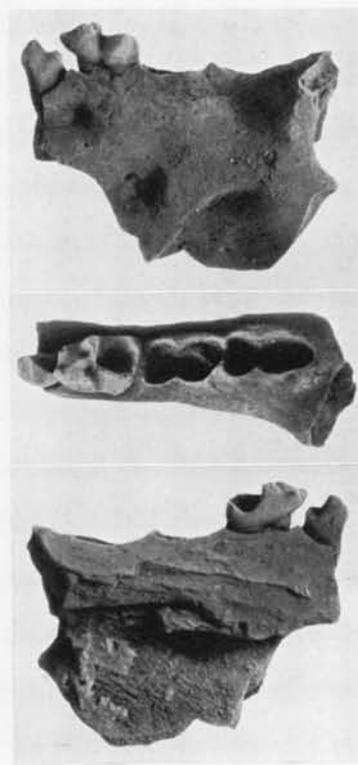
3, *Apatemys bellulus*, x $\frac{6}{1}$



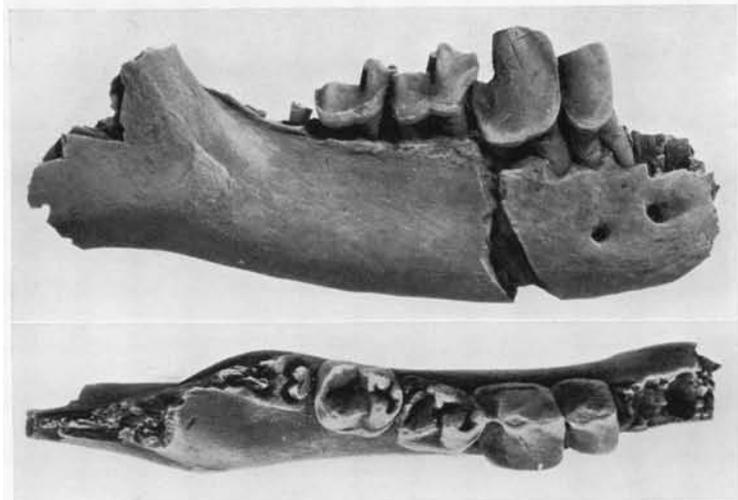
6, *Uintasorex parvulus*, x $\frac{6}{1}$



5, *Trogolemur myodes*, x $\frac{6}{1}$



4, *Apatemys bellulus*, x $\frac{6}{1}$



7, *Anaptomorphid* gen. indesc., x $\frac{6}{1}$



7a, *Anaptomorphid*, gen. indesc., x $\frac{6}{1}$

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