SOME EARLY MIOCENE CARNIVORES

BY

ELMER S. RIGGS

CURATOR OF PALEONTOLOGY, RETIRED SEPTEMBER 15, 1942

GEOLOGICAL SERIES

FIELD MUSEUM OF NATURAL HISTORY

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NOTE TO LIBRARIANS

The accompanying publication, *Early Miocene Carnivores,* by Elmer S. Riggs, is the concluding number in Volume 9 of the Geological Series of Field Museum of Natural History. Volumes 7 and 8 of this series have also been closed, and the indexes, title pages, and lists of Contents of all three volumes will soon be issued.

In December, 1943, the name of Field Museum of Natural History was changed to Chicago Natural History Museum. In the future, technical geological publications of octavo size that are issued by this institution will bear the new name of the institution, and the general title *Fieldiana, Geology.* They will carry successive numerical designations that are continuous with those of volumes that have been issued in the Geological Series of Field Museum. Geological publications of quarto size will be entitled *Fieldiana, Geology Memoirs,* and their numerical designations will be similarly continuous with the former Memoirs Series. Technical publications of other Departments in the Museum will be treated in the same manner.

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SOME EARLY MIOCENE CARNIVORES

The early Miocene carnivores of the Great Plains region of North America include forms that are referred to four well-known families, the Canidae, Felidae, Mustelidae, and Procyonidae. Members of these families vary widely in numbers and in size and strength.

The carnivores of this stage apparently are derived in part from forms that are known to have existed during the preceding White River Oligocene, and in part from stocks that are entirely strange to any known earlier fauna of the Great Plains region. Apparently the latter are immigrants from some remote locality. The sources of such immigrant forms are more or less conjectural.

The Canidae of the Lower Miocene stage are relatively abundant and are, for the most part, derivable from stocks that were common to the Oligocene of the White River stage. The lesser canid phylum represented by *Pseudocynodictis* carries over from the Brule clays of the earlier epoch as a practically uninterrupted line.[1] Likewise, the larger canid phylum represented in the Brule clays by the genus *Daphoenus* leads almost directly to *Daphaenodon*, of the Great Plains and the Great Basin regions. Other recorded genera of the early Miocene are less nearly related.

The Felidae, represented in the White River stage by three well-known genera, are almost entirely absent from the records of the Lower Miocene in the Great Plains region.[2]

This reduction of a numerous and virile group of carnivores over so large an area perhaps may be attributed to general changes in environmental conditions and also to the appearance of a comparatively new and sturdy rival group, the large mustelines, rather than to any general elimination of the felids.[3] The change in the region about the Black Hills from conditions of flood-plain deposition to one of wind-borne sands with occasional lagoon and channel deposits, may well have been accompanied by changes of temperature and of food supply resulting in important animal migrations.

[1] Scott (1937) points out this sequence in the John Day beds of Oregon; a specimen (P14797) from the Gering of Nebraska is evidence of a similar sequence there.

[2] *Nimravus sectator* Matthew (1907), Lower Rosebud, South Dakota, is a definitely identified form; another is reported as a "felid."

[3] It is well known that at least two genera of Oligocene felids continued in the John Day stage and elsewhere in the Great Basin region.

At the beginning of Miocene time the Mustelidae present a more elusive problem than any of the other families. From the White River series have been described two genera of mustelines, *Mustelavus* and *Bunaelurus*,[1] both rather advanced in the structure of the sectorial teeth and in the reduction of the anterior premolars. They also have several basicranial characters that designate them as members of the musteline family. The Lower Miocene formation has produced a variety of small mustelines, most of them having definite family characteristics, but many of them a little weaker in dental development. The crowns of the molar and premolar teeth are not so high and the accessory cusps are more reduced and often worn away in older individuals. Some of the smaller forms are definitely progressing toward the genus *Martes*, which has been recognized from the Upper Miocene. There have been reported also a number of intermediate-size mustelines, comparable to the virile stock represented by the holotype of *Oligobunis crassivultus*[2] of the John Day formation. Nearly related to the holotype of this genus in structural characters, in relative strength of jaw and dentition, and of a size fitting them to prey upon larger animals, are the sturdy forms that have been referred to the genera *Aelurocyon* and *Megalictis*. These animals are too large and too highly specialized to have been derived from the known mustelines of the White River Oligocene; therefore I regard them as immigrants. Of the smaller forms included under the genus *Promartes*, some nearly complete skulls and a large part of an associated skeleton are described in this paper. Two referred species are discussed. The larger form, *Aelurocyon*, is described from an articulated skeleton.

Procyonids have been recognized from the Lower Miocene since 1899. Two genera have been described, *Phlaocyon*,[3] from Colorado and Nebraska, and *Aletocyon*,[4] from the Harrison beds of eastern Wyoming. The first was believed to be, in a general way, ancestral to *Procyon* and the last not far from the ancestry of *Ailurus*. In a recent preliminary paper (1942) I introduced the genus *Zodiolestes* as a member of the Procyonidae. The holotype of this form, consisting of an articulated skeleton, is described in detail here.

[1] *Bunaelurus* Cope (1883); *Mustelavus* Scott and Jepsen (1936).

[2] Various smaller species which recently have been referred to *oligobunis* are in this paper referred by me to the genus *Promartes*.

[3] Matthew (1899, p. 19).

[4] McGrew (1941), on the basis of dental characters, believed *Aletocyon* to be nearer to the procyonines than to the pandas.

The drawings used to illustrate this paper are made in projection, either by use of the pantograph or by direct projection. As such, they should be essentially accurate. The scale of reduction, in a few instances, can not be indicated by a simple fraction. In those instances the scale of reduction is indicated by a near fraction and marked as "approximate." For exact data, see measurements.

I wish to express my obligation to Professor G. W. Bain of Amherst College, to the late Walter Granger of the American Museum of Natural History, to Mr. Leroy Kay of the Carnegie Museum, and to Dr. Claude Hibbard of the University of Kansas for the privilege of studying important specimens in those institutions; to Mr. Bryan Patterson of this Museum for the benefit of conclusions derived from the study of the auditory region in carnivores; to Mrs. Margaret Hough for special studies in the structure of the ear; and to the Department of Zoology of this institution for the continued privilege of using specimens for study and comparison. Drawings used in illustration are by my classmate, the late Sydney Prentice of the Carnegie Museum, and by the late Carl F. Gronemann, Staff Illustrator, and Mr. John C. Hansen, Department Artist, both of Field Museum.

Family **Mustelidae**

Promartes Riggs

This genus was proposed (1942) to receive certain smaller species of mustelines, some of which had been referred to *Oligobunis* Cope.

Promartes olcotti Riggs

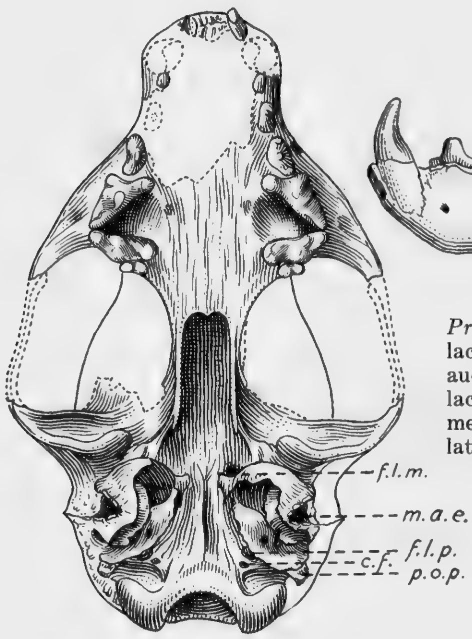
Promartes olcotti Riggs, Field Mus. Nat. Hist., Geol. Ser., 8, p. 59, 1942.

The holotype of this genus (F.M. No. P15178) consists of a broken skull with mandibles almost entire, and more than half the skeleton. The specimen was collected by Mr. T. F. Olcott, who was a member of a Museum expedition to Nebraska and Wyoming in 1906. An interesting feature of the occurrence was that it was found in association with the jaws of a species of *Palaeocastor* and embedded in the body of a horizontal branch of a *Daimonelix*[1] in situ.

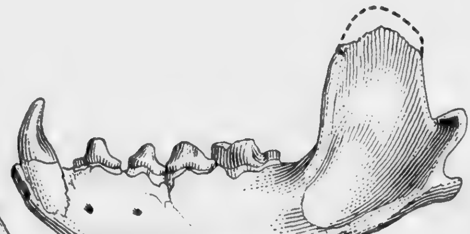
[1] The two specimens were recorded by the collector as "carnivore and rodent." When the collection was being prepared in the laboratory, the rodent was recognized and the section of the corkscrew with its contents was labeled "fragmentary rodent" and returned to storage. Many years afterward the carnivore was recognized and prepared.

SKELETON

The *skull* of *Promartes olcotti* (figs. 23, 24) may conveniently be compared with that of the recent species, *Martes actuosa*. It is somewhat shorter and broader than that of the recent forms, the palate is broader, and the basicranium somewhat shorter. The palate is



a



b

FIG. 23. *a*, detail view of holotype, *Promartes olcotti*. *f.l.m.*, foramen lacerum medium; *m.a.e.*, meatus auditorius externus; *f.l.p.*, foramen lacerum posticum; *c.f.*, carotid foramen; *p.o.p.*, paroccipital process. *b*, lateral view, mandible of the same.

more deeply excavated beside the upper carnassial teeth; the posterior nares open farther forward; the mastoid process is broader anteroposteriorly, and more prominent. The auditory bullae are well expanded; they are more laterally compressed and their anterior surfaces approach more closely to the posterior margins of the glenoid fossae. There is no inferior lip to the meatus; the sulcus tympanicus is somewhat larger than that of the recent species. A sharp crest extends above the opening of the meatus connecting the posterior margin of the zygomatic arch with the mastoid process. There is a small paroccipital process which is free from the bulla at its extremity. M^2 is present but greatly reduced.

The *mandible* is much more massive and deeper in the symphysis than that of *Martes actuosa* (fig. 23). The dentition in the holotype is worn at the apices of the premolars and carnassial. The first premolars both above and below should be considered as vestigial; one of the lower pair is absent from the holotype and one of the upper pair is absent from the paratype. $P^{\underline{1}}$ is tubercular in form and placed closely beside the canine; $P^{\underline{2}}$ and $P^{\underline{3}}$ are strong, functional teeth, increasing in size and closely set together. $P^{\underline{4}}$ is a typical musteline carnassial, strong and low-crowned; the protocone is

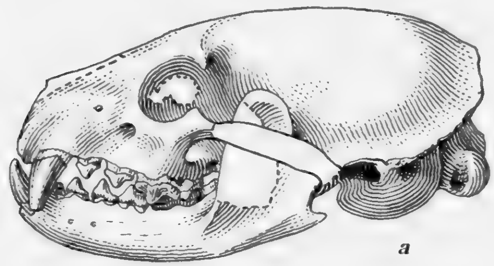
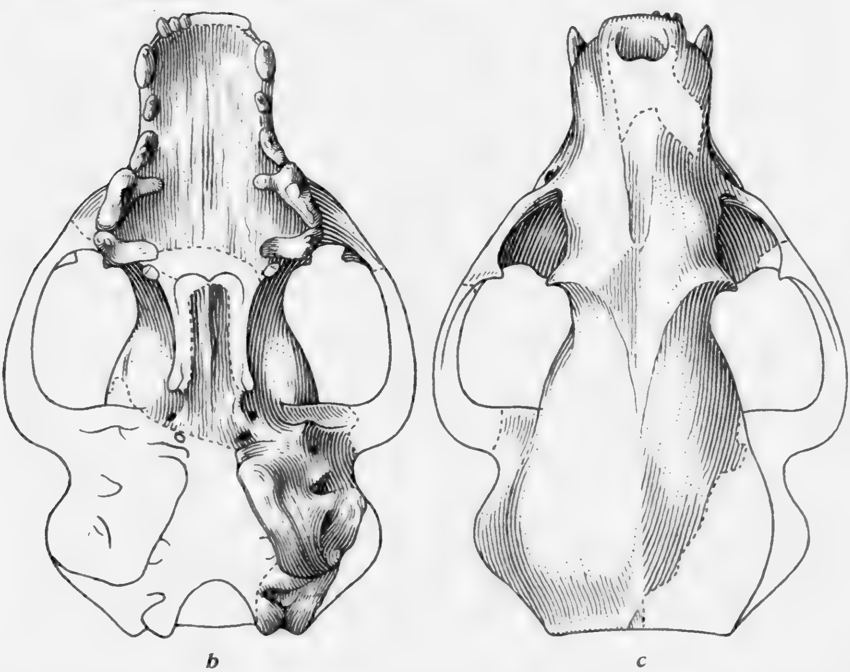


FIG. 24. Skull of paratype, *Promartes olcotti*. *a*, lateral view, $\times \frac{3}{4}$; *b*, palatal view, $\times 1$; *c*, dorsal view, $\times$ 1.



mesial and advanced in position. $M^{\underline{1}}$ has a long narrow crown set almost transverse to the cranial axis; the second molar is much reduced in size but preserves two distinct cusps.

$P_{\overline{1}}$ is reduced to a small tubercle, present in one mandible and absent in the other. The succeeding premolars are too much worn to show minute details; $P_{\overline{2}}$ has a well-developed secondary cusp. The talonid of $M_{\overline{1}}$ is concave, with a slightly elevated lateral margin; $M_{\overline{2}}$ retains two distinct roots.

In describing the bones of the skeleton it is convenient to use the fisher, *Martes penanti*, as a basis of comparison.

Vertebrae.—The axis, three cervicals, eight dorsals, five lumbars, one sacral, and parts of five caudal vertebrae belong to the holotype

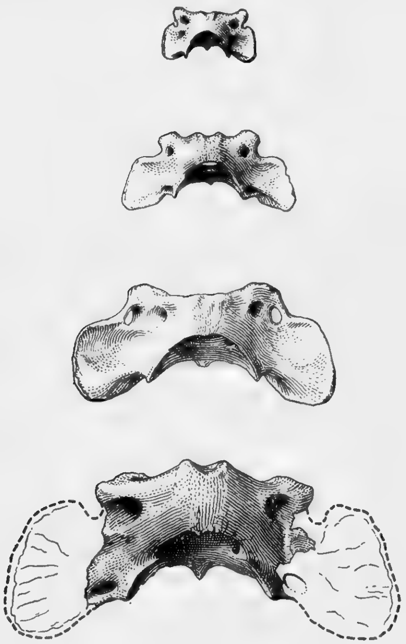


FIG. 25. Atlas, comparative series. From above downward: *Bassariscus, Zodiolestes, Gulo, Aelurocyon.* All × ½.

(fig. 25). The centrum of the atlas is not longer than in one lumbar; it is broad and flattened at the anterior end and has a moderate keel on the inferior surface. The odontoid process is relatively short and decurved near the extremity. The cervicals are short and broad; the neural canal is widely open. The centra of the dorsals are rounded on the inferior surface as in the lumbars. The first sacral centrum has an articular surface concave on the superior and convex on the inferior surface; the arch is low and the spine is a mere median crest. Other vertebrae of the sacrum are lacking. Four broken caudal vertebrae offer no evidence of variation from the early marten type.

The *scapula* in *P. olcotti* (fig. 26) is distinctive. In it, the fossa for the teres major and minor is so far developed as to be separated from the fossa of the subspinatus by a secondary spine. This structure is evidently an adaptive character and is found in varying degree in other related species. In the fisher there is only a slight thickening of the axillary margin near its upper extremity. The metacromion is apparently placed low on the spine, although the process itself is broken away. The anterior lip of the glenoid fossa is short; the coracoid process is broken at the extreme end.

The *humerus* (fig. 27) is perhaps the most distinctive element in the postcranial skeleton. In this species it is a moderately stout bone, strongly curved in the shaft antero-posteriorly and having a broad deltoid area which covers the anterior surface of the shaft and extends below the middle. The supinator ridge is more promi-

a b

FIG. 26. Scapulae: *a, Promartes olcotti*, × ½; *b, Martes penanti*, × ¾.

nent than that in the fisher, extending along more than a third of the shaft. The inner condyle is likewise more strongly developed than in the fisher and, unlike it, extends below the margin of the trochlea. There is no trace of a postcondylar fossa, a character slightly marked in the recent martens but prominent in *Aelurocyon* and *Megalictis* (see pp. 89, 95). The inner condyle has an even greater development in the American badger, *Taxidea americana*, where it appears to be an adaptation for burrowing.

The *ulna* is equal in length to the humerus, as restored (fig. 27). It has a relatively long olecranon, is narrow antero-posteriorly and much less flattened in its transverse diameter than that of the fisher. The shaft is laterally curved and bears a sharp crest on the mesial surface of the distal end.

The *radius* is likewise curved anteriorly in the shaft; it bears two distinct tubercles at the point of insertion for the tendon of the biceps. The articulation for the ulna extends two-thirds of the way around the head, showing that the manus was capable of supination.

The *fore foot* in this specimen consists of a scapho-lunar, four metacarpals, and a number of phalanges, including unguals. The entire foot from the scapho-lunar to the tip of the ungual in the third digit is somewhat longer than the radius of this animal. The scapho-lunar is short in the axial direction of the foot and is strongly

a *b* *c* *d*

FIG. 27. *Promartes olcotti*, holotype; bones of the fore leg. *a*, humerus, front view; *b*, humerus, side view; *c*, ulna; *d*, radius. All × 1.

convex proximally; the facet for the radius extends down to the margin of the trapezoid. The facets for the trapezium and the trapezoid are distinct. The first metacarpal is much stronger than that of the fisher, being almost as heavy in the shaft as the second and the third metacarpals of this animal. The first phalanges are moderately curved; the second are not modified for retractility. The unguals are hooded but rather narrow and straight.

Of the *pelvis*, only the posterior half of the ilium and the entire pubis with included acetabulum are preserved. These parts, in comparison with recent species, offer no distinctive characters.

The *femur*, a little longer than the humerus as restored, is slender and straight in the shaft (fig. 28). The head and great trochanter are inclined forward on the shaft, making a decided curve in the vicinity of the lesser trochanter. This character is not observed in *Martes americana* or in the fisher, although it is present to some degree in the holotype of *P. gemmarosae.* The facet for the patella extends but little above the superior surface of the condyles; the latter are rather widely separated.

The *tibia* (fig. 28) is about one-tenth shorter than the femur and is strongly curved in the shaft, laterally as well as antero-posteriorly. The lateral condyle is much larger than the mesial one; it is strongly

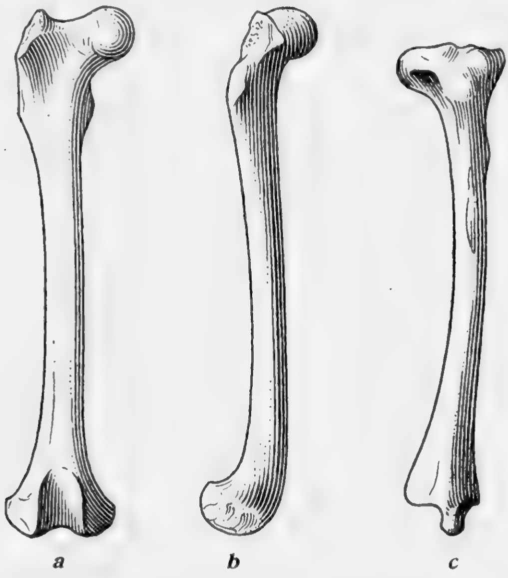


FIG. 28. *Promartes olcotti,* holotype; bones of the hind leg. *a,* femur, front view; *b,* femur, side view; *c,* tibia. All approx. × 1.

convex antero-posteriorly but slightly concave in the lateral direction. The mesial condyle is concave in both directions. This structure indicates a freedom of rotation in the knee joint.

Hind foot.—The astragalus is marked on the proximal surface by a wide, shallow groove, the lateral surface of which is angular and more elevated than the mesial; the latter is rounded and terminates anteriorly in a crest which extends along the neck toward the center of the head. The head is much compressed vertically and the capitular facet is indented at the superior margin. As in recent mustelines, the facet for the sustentaculum is advanced to a position on the inferior surface of the neck and is connected with the capitular facet by a short crest.

The *calcaneum* presents no distinctive characters other than that the facet for the cuboid is rounded, somewhat oblique to the axis of the bone and that the lateral margin of the facet is more prominent than the small infero-mesial tubercle. The remainder of the foot consists of a fifth metatarsal and some phalanges; the unguals of the fore foot show unmistakable evidence of being hooded.

The general characters of this animal indicate a size and strength considerably greater than that of *Martes americana*. The skull is 7 mm. longer and is much broader in the facial region. The leg bones

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MEASUREMENTS

(*In millimeters*)

No. P15178, holotype

SKULL	
Length of upper dental series, canine to last molar	34.3
Breadth across crowns of first molars	32
LOWER JAW	
Axial length	59.8
Length of lower dental series $P_{\overline{1}}$–$M_{\overline{2}}$	32.7
Lower second molar to condyle	19.2
Height of coronoid process above inferior margin	27
SCAPULA	
Greatest length	52
HUMERUS	
Breadth, distal end	20
ULNA	
Length over all	70
Length of olecranon from lip of sigmoid notch	12
RADIUS	
Greatest axial length	52.5
Ischium, length from margin of acetabulum	21
FEMUR	
Length, head to margin of inner condyle	73.3
TIBIA	
Greatest length	64.2
ASTRAGALUS	
Greatest length	13
CALCANEUM	
Greatest length	18
Length metacarpal III	19
Length metatarsal III	26

are perhaps one-fourth stronger, the scapula and the pelvis are correspondingly stronger. The development of the deltoid area and the supinator and pronator attachments of the humerus indicate an arboreal animal; the great area for insertion of the teres major especially points to arboreal habits. This character I have found in similar development only in certain species of marmosets, and to an even higher degree in the great sloths.

The genus *Promartes* appears to be ancestral to *Martes*, species of which are known from upper Miocene to Recent time. The transition might be accomplished by such changes in the dentition as elimination of the vestigial $M^{\underline{2}}$ and broadening of the mesial lobe of $M^{\underline{1}}$. This change would be possible from the fossil form *P. alcotti* to such recent species as *M. americana*, which has a correspondingly reduced premolar series; in *M. penanti* the first premolar is actually stronger than in the fossil species cited. Other characters offer no obstacle to such a transition.

Promartes lepidus Matthew

Oligobunis lepidus Matthew, Bull. Amer. Mus. Nat. Hist., **23**, p. 194, 1907.

Horizon.—Lower Rosebud, Lower Miocene, South Dakota.

This species was described in 1907, based upon the facial region of a skull with associated mandible and nearly entire dentition. The species was referred to *Oligobunis* Cope, this in turn based upon an incomplete skull and mandible.

The Field Museum collection includes a posterior half of skull, P12155, with one sectorial tooth and an associated pair of mandibles with dentition complete excepting the incisors. The locality is Raw Hide Butte, Wyoming, and the horizon apparently the upper levels of buff sand, designated by Peterson as Upper Harrison beds. This specimen agrees with the holotype of *P. lepidus* in so far as they have parts in common. The Field Museum specimen is therefore referred to this form, and the species is transferred to *Promartes*. From this specimen and from the holotype, which I have been permitted to examine, the following specific characters are derived:

Length of skull in specimen P12155 (estimated), 95 mm.; cranial index (estimated), 31.5; $M^{\underline{2}}$ tubercular and one-rooted; bullae well expanded and paroccipital process closely applied to it; lower dental series but little curved laterally and interlocking with the upper series. $P_{\overline{1}}$ present but vestigial and slightly displaced mesially from the dental series; $P_{\overline{2}}$ and $P_{\overline{3}}$ have basal cingula on the posterior margins, $P_{\overline{4}}$ has the posterior accessory cusp. In $M_{\overline{1}}$ the talonid is concave at the crown with lateral margin slightly elevated; the apex of the paracone is slightly lower than that of the metaconid; $M_{\overline{2}}$ is a functional, bilobate tooth.

The mandible is 65 mm. in length, and the dental series 41 mm. in length. The ramus is appreciably stronger than that of *P. olcotti*, the dentition correspondingly stronger. The coronoid process is broad but does not overhang the condyle as in *Oligobunis crassivultus*. Other differences are that the teeth are in nearly straight line and are not set oblique to the axis of the ramus.

Promartes vantasselensis Loomis

Oligobunis vantasselensis Loomis, Amer. Jour. Sci., (5), p. 321, 1932.

Horizon.—Harrison beds, Lower Miocene, Wyoming.

This species is based upon a skull and mandibles almost entire. Through the courtesy of Amherst College the holotype of the species

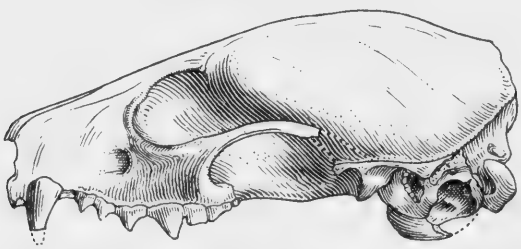


FIG. 29. *Promartes vantasselensis.* Skull of holotype refigured; × 1.

was lent for study (fig. 29). In the interest of accuracy it has been refigured.[1] The skull is very similar in proportions to skulls of recent American martens, notably *M. americana* and *M. caurina*. Comparison will be made with the latter species. It has a similar outline as seen from the dorsal aspect, a similar though slightly more elevated occiput, and a similar lateral view, including the characteristic upward curve of the zygomatic arch in the martens. The length and the general configuration of the basicranial region are similar; the length of the dental series and of the temporal arcade are almost identical. The bullae are well inflated but vary in outline

[1] Attention should be called to inaccuracies in the illustrations which accompanied the type description. The upper sectorial and $P^{\underline{2}}$ and $P^{\underline{3}}$ have crowns of moderate length. The scale of the figure of skull in side view should be given as a little more than 5/4, and the scale of the figure of upper dentition should be given as 2/1. See measurements, op. cit., p. 322.

from the recent form; the position of the posterior nares cannot be determined in the fossil; the structure of the internal ear has been studied only in part. The floor of the meatus, which is extended into a lip in the recent species, cannot be determined from the fossil. The structure of the internal ear shows differences, but nothing that may be considered important.

The molar-premolar dentition is little worn; the premolars and sectorial are more pointed, but not essentially different from the dentitions of the smaller species of the genus, especially *P. olcotti*. The ramus of the mandible is stronger in the fossil than in the recent species of martens. The masseteric fossa is similar in outline but deeper in the fossil; the coronoid process is equally elevated but broader in the crest, the posterior margin is slightly recurved.

In the present knowledge of the fossil species, it cannot be said that *P. vantasselensis* is directly ancestral to any species of living martens but the general structure of the skull and the relative developments in a number of variants as cited above, lead to the conclusion that this species is in a general way ancestral to the smaller American martens. Also, the general structure of the skull and the dental formula indicate some relationship to *Bunaelurus* of the Oligocene, but the structure of the upper sectorial and of the first molar, as well as various characters of the basicranium, bar it from close relationship to that genus. It is much more closely related to *Promartes olcotti*.

Promartes gemmarosae Loomis

Oligobunis gemmarosae Loomis, Amer. Jour. Sci., (5), p. 317, 1932.

Horizon.—Lower Rosebud, Lower Miocene, South Dakota.

This species was described from a nearly entire but imperfectly preserved skeleton. The same difficulties that were encountered by others in undertaking to classify early mustelines and procyonids on the basis of dental characters apparently were realized by Loomis. The specimen is not well preserved and at the time it was described had not been removed from the slab of matrix where parts of it were concealed. Such studies as I could make, aided by further preparation, have led me to transfer the species to the genus *Promartes*. The length and slenderness of the skull are characters common to this species and to *Oligobunis darbyi* Thorpe. The unusual length of the legs in this species is a marked character, but cannot be considered as of more than specific value. The structure of scapula and of pelvis is typical of the early martens. Treating this species as a viverrine on the basis of comparison with the dentition of *Herpestes* does not appear justifiable.

Some errors appear in the figures published with the type description. A new figure of the scapula (fig. 30) shows the suprascapular area as triangular, and that a prominent process for attachment of

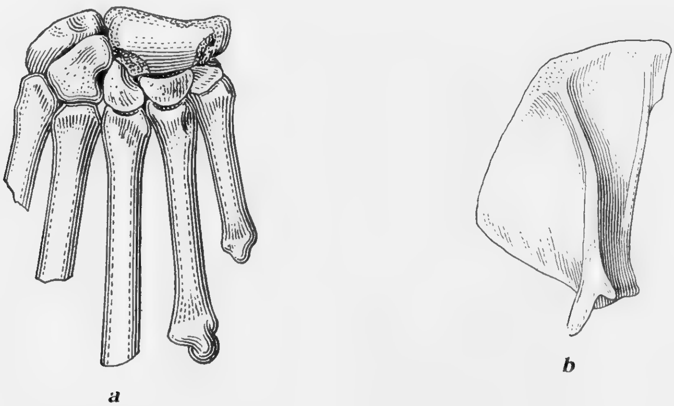


FIG. 30. *Promartes gemmarosae,* holotype. *a,* fore foot, × 2; *b,* scapula refigured, approx. × ¾.

the teres major is present and extends along the distal portion of the axillary border. The fore foot is refigured in order to represent more accurately the arrangement of the carpals (fig. 30).[1] Measurements were given in the type description.

Oligobunis darbyi Thorpe

Horizon and locality.—Monroe Creek beds, Lower Miocene, Pine Ridge, Nebraska.

This species was described from a skull and jaws in Peabody Museum, Yale University. A cast of the specimen together with published figures shows the following characters: Skull long and narrow, facial region short, cranial region elongated; $P_{\overline{1}}$, $P^{\underline{1}}$ and $M_{\overline{2}}$ reduced to vestiges; $M_{\overline{2}}$ a functional tooth reduced in size and well worn in this specimen; bullae expanded, oblique in position, stylomastoid process closely applied. The tympanic region shows no distinctive characters, the teeth appear to be somewhat stronger

[1] I regret that a more detailed study of this skeleton cannot be given in this connection. This could be done only by removing it from the matrix.

than those of *Promartes;* the coronoid process is recurved and overhangs the condyle. Some of these characters appear to ally the species with the mustelines of larger size, such as *Oligobunis crassivultus.* Definite determination of the relationships must await a study of the tympanic region or some knowledge of the skeleton.

Aelurocyon Peterson

Genotype *Aelurocyon brevifacies* Peterson.

The holotype is an incomplete skull and mandible with associated parts of the skeleton. The dentition is nearly complete but the nasals and basicranium are missing. No classification of this genus was made at the time of description, although it was compared with the mustelines, *Gulo* and *Mellivora.* In a later paper (1910) the genus was referred by its author to the Mustelidae. So far as this writer knows, no further information on this genus has been published and no other species has been referred to it.

Aelurocyon brevifacies Peterson

Aelurocyon brevifacies Peterson, Ann. Carnegie Mus., **4**, p. 68, 1906.

Three specimens collected by the Field Museum Expedition of 1906 have been referred to this species. The locality at which they were found is the north fork of Raw Hide Creek (J. M. Creek) about two miles above its junction with the west fork of that stream; the horizon apparently is Harrison beds. Credit for collecting these specimens is due to the late John B. Abbott, member of the Field Museum of Natural History Expedition of 1906 and long a member of the paleontological staff of the Museum.

The first and most important specimen is an articulated skeleton (P12154) lacking the anterior half of the skull and lower jaw, most of the feet, and parts of other bones. The second is a pair of lower jaws (P12283) having the condyles, the angles, and the symphysis weathered but the rami, coronoid processes, and dentition preserved in their natural relations. The third specimen (P12152) consists of a weathered mandible with two teeth in position, together with three other sectorial and two canine teeth, the shafts of various leg bones, an os penis, and a number of metapodials and phalanges. The specimens were recorded as *Aelurocyon* species and the skeleton was long exhibited in a slab mount with parts in position as found. As no complete skull was known, identification had been regarded as uncertain. Recent comparison of the jaws with the holotype of

Peterson's species, made possible by removing the skeleton from the original slab of matrix, has convinced this writer that the series of specimens is of the same form and should be referred to *A. brevifacies.* The following characterization of this genus is based upon the holotype of *A. brevifacies,* lent to this museum for study, and upon the specimens cited above:

Mustelines of relatively large size; upper and lower jaws massive; sagittal crest prominent; dentition $I\frac{?}{?}$, $C\frac{1}{1}$, $P\frac{3-4}{3-4}$, $M\frac{2}{2}$; $P\frac{1}{1}$ and $M\frac{2}{}$ vestigial; lower carnassial with reduced internal cusp;[1] coronoid process recurved and overhanging the condyle; otic bullae moderately inflated; paroccipital process free from bulla and prominent; superior arch of atlas elevated and overhanging the condylar facets of same; scapula with axillary process; humerus with strong deltoid crest and inner condyle extending below the trochlea; inner condyle of humerus excavated posteriorly by postcondylar fossa; metacarpus and metatarsus short and stout, unguals not preserved. Vertebral formula: 7, 14, 6, 4, ?; ilium convex on lateral surface, inferior border massive; os penis uniformly curved and exceeding femur in length.

SKELETON

The *skull* of this specimen (P12154; fig. 31) consists of the posterior half, including the cranium, basicranial region with bullae broken, the base of the right arch and the right mandible as far as the fourth premolar tooth. The parts common to the two specimens have a similar structure, and the measurements, as far as they can be compared, agree quite closely with those of the holotype of this species. The cranium is long and rather low; the sagittal crest is narrow and sharp, extending forward to a point opposite the middle of the temporal arcade. The mastoid process is prominent and laterally directed; the auditory bullae, preserved in part only, appear to have been rather broad and low as in *Gulo.* There is no alisphenoid canal. The paroccipital process is prominent, extending backward to a point opposite the lateral extremity of the condyle. The auditory meatus was apparently extended into a rather elongate tube, though the extremity of that structure is broken. The postglenoid process firmly encloses the condyle of the mandible at its mesial extremity. The basioccipital region is broad and flat, showing no evidence of a median keel.

[1] This character is described by Peterson (1910) as reduced. The teeth of specimens in Field Museum are too much worn to show this structure.

The *mandible* in specimen P12154 includes only the posterior half of the right side with $M_{\overline{2}}$ in position (fig. 31). The condyle is elongated transversely and but little elevated above the angle. The latter is produced into a slender point which extends beyond the condyle;

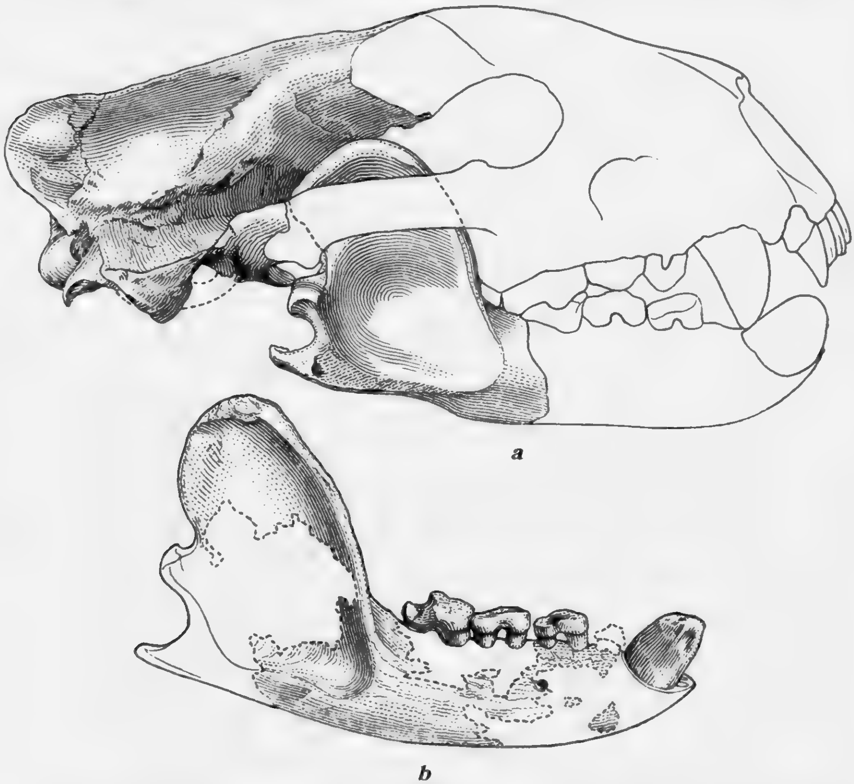


FIG. 31. *Aelurocyon brevifacies.* *a*, restored skull and mandible, No. P12154; *b*, right mandible of pair, No. P12283. Both × ½.

the coronoid process is broad and its posterior margin overhangs the condyle. The masseteric fossa is deeply excavated and bounded anteriorly by a sharp ridge which extends upward as far as the crest. Mandibles No. P12283, length approximately 145 mm., are very similar in structure and retain most of the teeth (fig. 31). $P_{\overline{1}}$ is not preserved in any specimen though it may have been present; $P_{\overline{2}}$ is likewise missing from all of the Museum specimens though present in the holotype. The canine is strong but much worn at the crown. $P_{\overline{3}}$ and $P_{\overline{4}}$ are worn at the crown; a vestigial paraconid is present on $P_{\overline{4}}$. $M_{\overline{1}}$ is likewise much worn and present in left ramus only.

Vertebrae.—The vertebral column, as found, was articulated and continuous from cranium to sacrum with most of the ribs in position. The vertebrae had suffered somewhat from being dissolved by percolating waters and in places from weathering at the surface. Missing parts have been reconstructed by comparison with other mustelines and in part with the canid, *Daphoenus vetus,* of similar size. The vertebral column as a whole is somewhat longer than that of *Daphoenus;* the lumbar region is relatively less strong (fig. 37).

The *atlas* (figs. 25, 32) is similar in size to that of the gray wolf, *Lupus nubilis.* Its structure is nearest to that of *Zodiolestes.* The superior arch is more massive in proportion to size than that of *Gulo.* There is a rugose prominence at the crest and an emargination of the anterior border similar to that observed in the atlas of *Zodiolestes* and in *Felis concolor.* The arch projects well above the margins of anterior articular facets as in the latter form; at the median line it projects forward beyond them. The neural opening is almost circular; the inferior arch is narrow as in *Gulo.* The anterior external foramina open laterally into wide fossae. The margin of the lateral process is notched for the passage of the vessels but not bridged over to form a foramen. The inferior surface of the root of the lateral process is excavated by another large fossa which gives entrance for the arterial canal. The canal passes obliquely upward and backward and emerges on the superior surface beside the margin of the posterior facet. The structure of the superior arch and the position of the foramina are similar to those in the holotype of *Zodiolestes.*

In the *axis* of this specimen, only the arch with postzygapophyses, the greater part of the spine and the odontoid process are preserved. The spine is high and relatively short, overhanging the postzygapophyses and terminating anteriorly in a thickened tuberosity. The odontoid process is rather short and truncated (fig. 32).

The *cervical vertebrae* are known from molds in the matrix and from the fourth, which was preserved. The centra were broader than long and moderately concavo-convex at the articulations. The inferior surface of the fourth centrum is marked by a median and two lateral keels. The lateral process in the sixth is well rounded in the shaft but little recurved distally. The spine on the seventh, as shown by a fragment in the matrix, was rather high and tapering.

The first and second *dorsal vertebrae* have these transitional characters: The anterior zygapophyses in the first are widely spaced as in the cervicals; they face obliquely inward though presenting almost plane articular surfaces. The posterior pair are a little more closely apposed and are plano-convex in form, embraced by the plano-concave facets of the succeeding vertebra, in a manner similar to the articulations of the lumbar vertebrae. In the second dorsal vertebra the transition from cervical to dorsal type of articulation is completed, the posterior zygapophyses having the usual closely apposed and essentially plane facets. A similar transition is observed in a specimen of *Gulo*, but in *Taxidea* the facets between these vertebrae are essentially plane. In *Zodiolestes*, in which the structure of atlas is similar to that of the specimen under description, the transition from cervical to dorsal type of articulation is accomplished in the first dorsal vertebra. The transverse process of the first dorsal is strong and subtriangular in section; the facet for the rib articulation

FIG. 32. Atlas of *Aelurocyon brevifacies*, No. P12154. *a*, anterior view; *b*, posterior view. Both × ½.

is concave and directed obliquely outward and downward. The capitular facet covers the antero-lateral half of the centrum.

The length of spines in the anterior series of the dorsal vertebrae cannot be determined from these specimens. The anticline is at the twelfth vertebra. The spines from the thirteenth dorsal to the fifth lumbar are broad and inclined slightly forward. The zygapophyses throughout the lumbar series are widely spaced and strongly interlocking. Such lumbar centra as are preserved, notably 4 and 6, are smooth on the inferior surface and much broader than long. No reliable evidence as to other processes can be derived from this specimen.

The *sacrum* is so poorly preserved as to give rise to some uncertainty. It has been restored as having four vertebrae in its composition. Parts of four vertebral centra are imbedded in the original matrix. The first and second centra, as shown (fig. 37), have parts missing, but it does not appear possible that they could be combined to form one centrum; the third and fourth centra are evident. Other parts preserved are one anterior and both posterior zygapophyses, two spines, and parts of the lateral masses of the first sacral vertebra. Of the caudal series, parts of only two arches remain.

There are fourteen pairs of *ribs*. Between the right and left sides, sixteen rib heads are preserved, from which the structure of ten can be determined. The first rib is relatively strong, with the head set at an angle of 82 degrees to the upper margin of the shaft. The tubercular facet extends well over on the posterior surface.

The *scapula* is relatively long and narrow as compared with other carnivores of equal strength (fig. 33, *a*). The spine extends obliquely

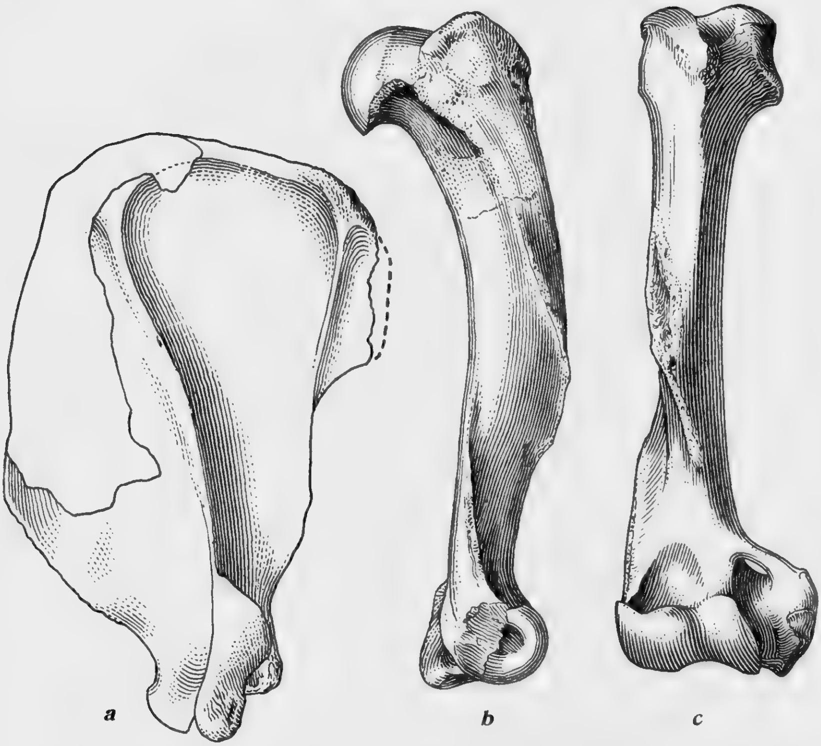


FIG. 33. *Aelurocyon brevifacies*, No. P12154. *a*, scapula; *b*, humerus, lateral view; *c*, humerus, anterior view. All × ½.

across the suboval blade; a prominent process for attachment of the teres major muscle arises from the upper third of the axillary border, forming a broad process. A rather strong but simple acromion process projects over the proximal articulation. The glenoid facet is broad and suboval in outline, the margins forming a rounded angle antero-laterally. The coracoid process is reduced to a tubercle surmounted by a short, medially inflected hook, as in *Gulo*. The posterior margin of the blade turns outward in the middle third of its length and continues in the upper third to form a secondary spine, separating the axillary process from the subscapular fossa. This spine is almost as prominent relatively as that in *Promartes olcotti*.

The *pelvis* is unfortunately incomplete (fig. 34). The ilium is distinguished by having the lateral surface of the blade uniformly convex. The inferior margin of the blade is thickened and massive, meeting the lateral surface in a decided angle; the tubercle for attachment of the rectus femoris is unusually prominent. The ischiatic

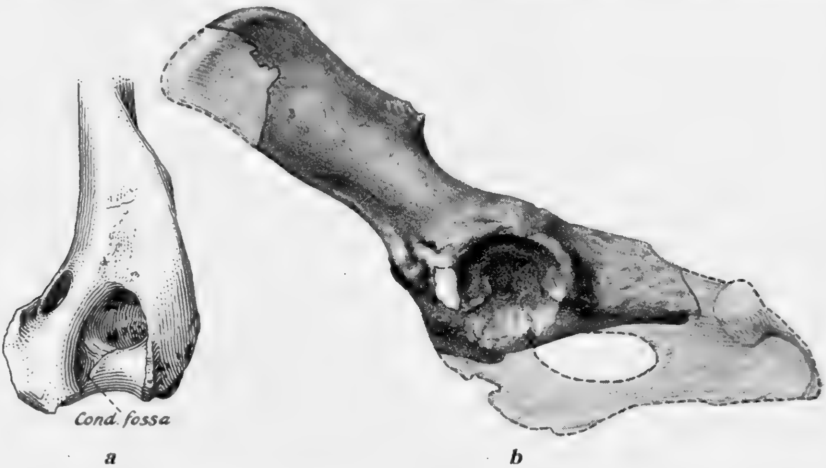


FIG. 34. *Aelurocyon brevifacies*, No. P12154. *a*, humerus, posterior view, distal third in detail; *b*, pelvis in lateral view. Both × ½.

tubercle has been restored in this specimen from related forms but was apparently deflected laterally, giving to the ischium a strongly concave outline as seen from above. The pubic arch is broken away close to the acetabulum.

The *humerus* of this form is highly characteristic and deserves a detailed description (fig. 33, *b*, *c*). The right humerus is almost entire and but little distorted; the left is somewhat weathered at the proximal end but has been restored from the opposite one. This bone is rather short and stout, strongly curved in the antero-posterior direction and well expanded at the distal extremity. The great tuberosity does not extend above the head; the lesser tuberosity has the form of a crest, oblique to the direction of the shaft and similar to that of *Gulo*. The deltoid area is broad at the proximal end, extending well over on the lateral surface. The crest is strongly marked and extends over the entire middle third of the shaft. It consists of two diverging, curved, and rugose lines which join in their lower extension to form a single crest. These attachments for the deltoid muscles are relatively stronger than those observed in the felid *Hoplophoneus* of the Oligocene, or in *Taxidea.* The attachment for the triceps muscle is marked by two rugose fossae on the lateral and the mesial surfaces of the shaft posterior to the greater and lesser tubercles, respectively. The antero-superior boundary of the lateral fossa is marked by an oblique crest; that on the mesial surface excavates the posterior surface of the lesser tuberosity.

The supinator ridge extends above the lower extremity of the deltoid crest as in *Gulo,* but is relatively less prominent than in *Taxidea.* The inner condyle is prominent and rugose, extending below the trochlea as in *Promartes.* The entepicondylar foramen is oval in outline as is common among mustelines, having its center opposite the superior margin of the trochlea. The epitrochlear fossa is deep but not perforate; a second recess, which for lack of other name may be designated as the postcondylar fossa, excavates the inner condyle opposite the superior margin of the articular surface, as may be seen to some extent in *Taxidea* and in smaller martens of recent age (fig. 34). In addition to its much greater size, the humerus of *Aelurocyon* differs from that of *Promartes* in the greater extension and the lateral expansion of the deltoid crest and in the presence of the postcondylar fossa. It differs chiefly in size from a larger specimen which will be described below as belonging to a species of *Megalictis. Aelurocyon* is clearly a burrowing animal as may be seen by comparison of the humerus and the scapula with the well-known recent burrowing form, *Taxidea taxus.*

The *ulna* of this species has a somewhat greater length than those of *Daphoenus vetus* or *Hoplophoneus primaevus,* and is about one-fourth stronger (fig. 35). The olecranon is but little longer than the breadth of the great sigmoid notch; it is strongly inflected as in *Gulo* and the inferior margin is turned inward in the form of a prominent tubercle. The styloid process bears a strong, rounded terminal facet; that for articulation with the radius is small and elevated. The tubercle for interosseous ligament is elongated and terminates well above the facet. The radius is rounded in the shaft and well expanded at the articular ends. The head is somewhat flattened antero-posteriorly; the contact with the ulna is outlined on the lateral surface by a low ridge, indicating a limited capacity for rotation. The insertion for the supinator tendon is likewise but faintly marked. The distal facet is broad antero-posteriorly and laterally placed, leaving a large meso-terminal surface for ligamentary attachment.

Fore foot.—Only the scapho-lunar and metacarpal II are preserved. The metacarpal is a short, stout bone as measurements will indicate (26.0 mm.), and deeply concave at the proximal articulation.

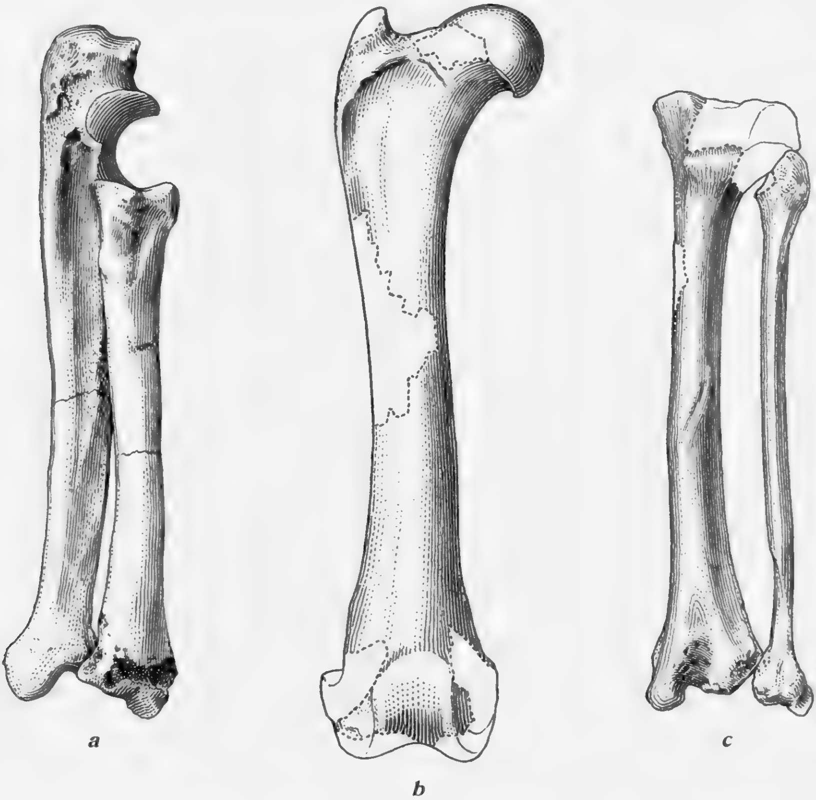


FIG. 35. *Aelurocyon brevifacies*, No. P12154. *a*, lateral view of ulna and radius; *b*, anterior view of femur; *c*, anterior view of tibia and fibula. All approx. × ½.

Femur.—In this specimen both femora are preserved but neither has the great trochanter or the lateral wall of the digital fossa entire (fig. 35). The femur is somewhat longer than that of a male specimen of *Daphoenus vetus* and is stronger in the shaft and broader in the extremities. The head is appreciably larger in diameter; the pit for the ligamentum teres appears on the postero-mesial surface of the head somewhat as in *Taxidea*, rather than on the mesial surface as in the Oligocene canids and felids. The lesser trochanter is conical in form and is directed posteriorly; a rugose line extends from it obliquely down the shaft. The same position of the lesser trochanter is observed also in the femur of the contemporary *Zodiolestes;* in the smaller *Promartes olcotti* the trochanter is directed postero-mesially as it is in *Daphoenus* and in the recent *Cryptoprocta.* Linea aspera are not well defined on the femur of *Aelurocyon* nor are they found as well marked on other Miocene mustelines as they are in the Oligocene *Daphoenus.* This may be due to imperfect preservation. The condyles are equal in size and the intercondylar notch is relatively narrow; the facet for the patella is short and broad as in the short-legged machairodonts.

The *tibia* is appreciably shorter than that in a specimen of *Daphoenus,* but broader at the articular ends and heavier in the

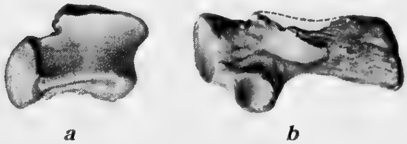


FIG. 36. *Aelurocyon brevifacies,* No. P12154. *a,* astragalus, superior view; *b,* calcaneum. Both × ½.

shaft (fig. 35). The cnemial crest is prominent; the surface immediately below is rounded. At the middle of the shaft and on the anterolateral surface there is a slight rugosity, observed also on the tibia of *Promartes olcotti* but not in carnivores of other families. The internal malleolus is short and truncated; the distal facet does not cover the entire end of the bone as in the Oligocene canids, but leaves a wide margin for ligamentary attachment.

The *fibula* is of equal strength to that of *Daphoenus.* An interesting feature of this specimen is that the right tibia and fibula had been fractured during the life of the individual. The tibia in the lower fourth had thrust past at the fracture and had partly healed but a permanent exostosis remained. The fibula had fractured in the shaft above the middle but had successfully healed and the external malleolus was left projecting beyond the astragalus. As a result, the astragalus and the calcaneum had become diseased and in part atrophied.

The left *astragalus* has lost the head by weathering (fig. 36). This bone differs but little in proportions from that of *Daphoenus.* The trochlear facet does not extend quite around the proximal end, indicating that the animal was subdigitigrade; the head is deeper in the vertical dimension and its facet is joined with the facet for the sustentaculum by a narrow bridge, as observed in *Zodiolestes.*

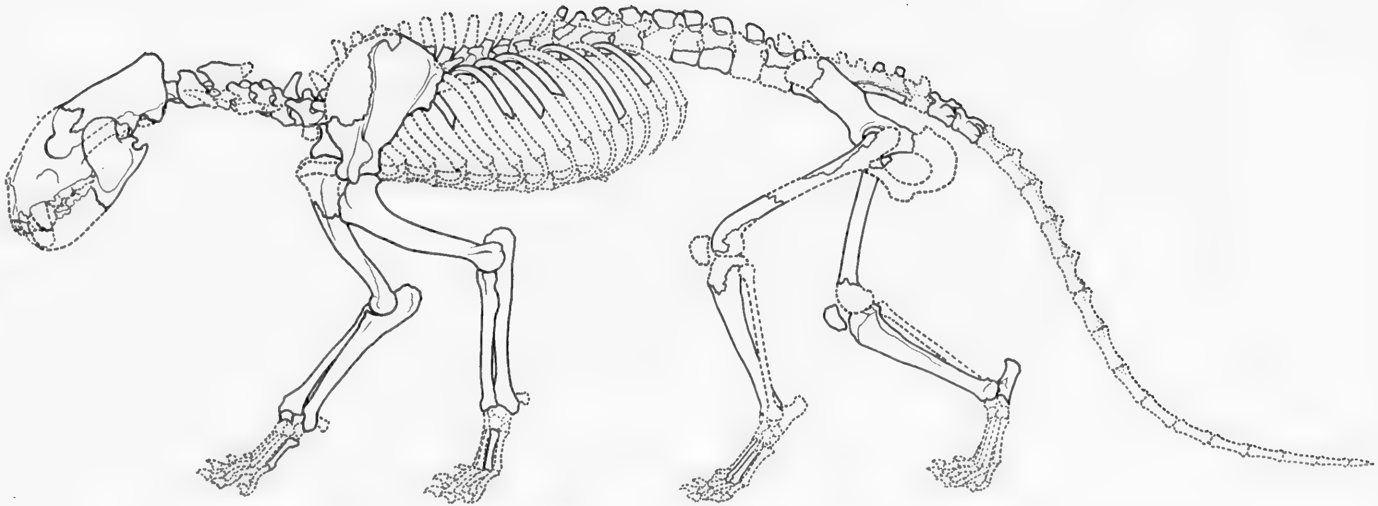


FIG. 37. *Aelurocyon brevifacies.* Skeleton restored from specimens P12154 and P12283, as figured in detail above; × 1/6.

Of the *calcaneum*, only the diseased bone is available for description (fig. 36). It is short and stout, presenting a massive and rugose extremity for attachment to the tendon of achilles and a rounded and concave facet for the cuboid.

Metatarsals I, II, and III are preserved. The first is much reduced in size; length 29 mm. The proximal end is enlarged and bifurcate posteriorly, presenting a small facet for Mt. II. The latter is a stout bone but so broken at the anterior end that it offers no characters for description. Mt. III is somewhat longer (length 48 mm.) than II, stout in the shaft and oblique in the anterior articulation.

MEASUREMENTS

(*In millimeters*)

HUMERUS	
Axial length	178
ULNA	
Length	180
RADIUS	
Length	142
FEMUR	
Greatest length as restored	201
Breadth across condyles	41
TIBIA	
Greatest length	169
FIBULA	
Length	156
CALCANEUM	
Length	54

Megalictis Matthew

Megalictis ferox Matthew

Megalictis ferox Matthew, Bull. Amer. Mus. Nat. Hist., **5**, pp. 175–204, 1907.

This is the largest known form of the Mustelidae. The genus is based upon two specimens designated by Matthew as holotype and paratype. The first includes a fragmentary skull with upper sectorial and upper and lower molars. The paratype includes the humerus, the tibia, and most of the fore and hind feet.

A fragmentary specimen in the Field Museum collections (P12135) includes the proximal and distal ends of the humerus and the femur with anterior half of the ulna and a number of vertebral centra. These make it possible to add some characters to the knowledge of this great musteline.

The *humerus*, as restored and figured, is somewhat longer than that of the paratype (fig. 38). The head and the great tuberosity are equal in height; the bicipital groove is broad and shallow as in *Aelurocyon*. The attachments for the triceps muscle consist of deep pits, bounded superiorly by two sharp crests which continue backward from the inferior margins of the capitular surface. The distal end of the humerus is most characteristic, as in other mustelines. The mesial condyle extends below the trochlea in a rugose prominence. The olecranal fossa is moderately deep, and extending from it mesially is the postcondylar fossa. The latter opens downward along the margin of the articular surface and is not so deep proportionately as in a specimen of *Aelurocyon* described above. The anterior fossa is broad and shallow; the supinator ridge is more rounded and less prominent than that in the smaller form.

The *ulna* is known from the anterior half only (fig. 38). There are no important differences between this bone and that of *Aelurocyon* except size.

The *femur*, so far as may be determined, has general characteristics similar to those of *Aelurocyon* (fig. 38). The head is well rounded, with a pit for the ligamentum teres placed near the center of the articular area, but opening downward. The great trochanter rises to a level with the head; its lateral surface is broad and rugose to a point below the level of the lesser trochanter. The digital fossa excavates the posterior surface of the great trochanter, opening upward in a narrow cleft. The lesser trochanter is relatively small. The condyles are almost equal in size and are separated by a narrow intercondylar notch. The surface for the patella is broad and does not extend above the superior margin of the condyles.

This specimen was found in a small residual deposit of the Upper Harrison beds, as described by Peterson, lying directly upon an eroded surface of the *Daimonelix* beds. Allowing for a considerable interval of time between the two formations, these two large mustelines, *Megalictis* and *Aelurocyon*, might have been successors in the same line. The rapid development of these larger forms, apparently from animals of such type as *Oligobunis crassivultus* of the John Day beds or *Paroligobunis* of the Lower Miocene of Nebraska, indicates an unusually rapid expansion in this line. The great strength and the apparent voracious nature of the beasts may account for their supplanting the sabertooth cats in the Great Basin area during Lower and Middle Miocene time. Their disappearance was apparently as sudden as their development was rapid.

Upper Miocene deposits have yielded no evidence of these sturdy and destructive invaders.

MEASUREMENTS

(*In millimeters*)

No. P12135

HUMERUS	
Breadth across head and great tuberosity	63.5
Greatest breadth of distal end	67.0
FEMUR	
Breadth across condyles	56.5
ULNA	
Length of olecranon beyond margin of sigmoid notch, projection	44.0

Family **Procyonidae**

Three genera of Lower Miocene carnivores have been referred to this family. These genera may be divided into two groups: (1) Forms having broad, multicuspidate molars, imperfectly differentiated sectorials, and an alisphenoid canal include *Aletocyon* and *Phlaocyon*. (2) Those with narrow-crowned molars, well-differentiated sectorials, and no alisphenoid canal include *Zodiolestes* and are most nearly related to the living *Bassariscus*.

Zodiolestes Riggs

This genus of carnivores was named and described in a preliminary paper (Riggs, 1942) published by this Museum a short time ago. The specimen upon which it was based has been in the Museum collections for a number of years and has offered a problem in classification. Its dental formula and its tooth structure seemed to place it in the Mustelidae. The full premolar dentition, with functional first pair, and the longer facial region were noted as inconsistent with known mustelids but were taken to indicate a somewhat less specialized development than species described from the Lower Miocene or those now included in the genus *Promartes*. As more complete specimens made it possible to determine the basicranial structure in the smaller mustelines of the period, it became evident that the relatively broad and short basicranium of the doubtful specimen could not be aligned with any of those species. Similar distinctions barred it from any grouping with known canids of the Oligocene or the Lower Miocene. Careful comparisons were made with the recent genus *Cryptoprocta*, and again the basicranial

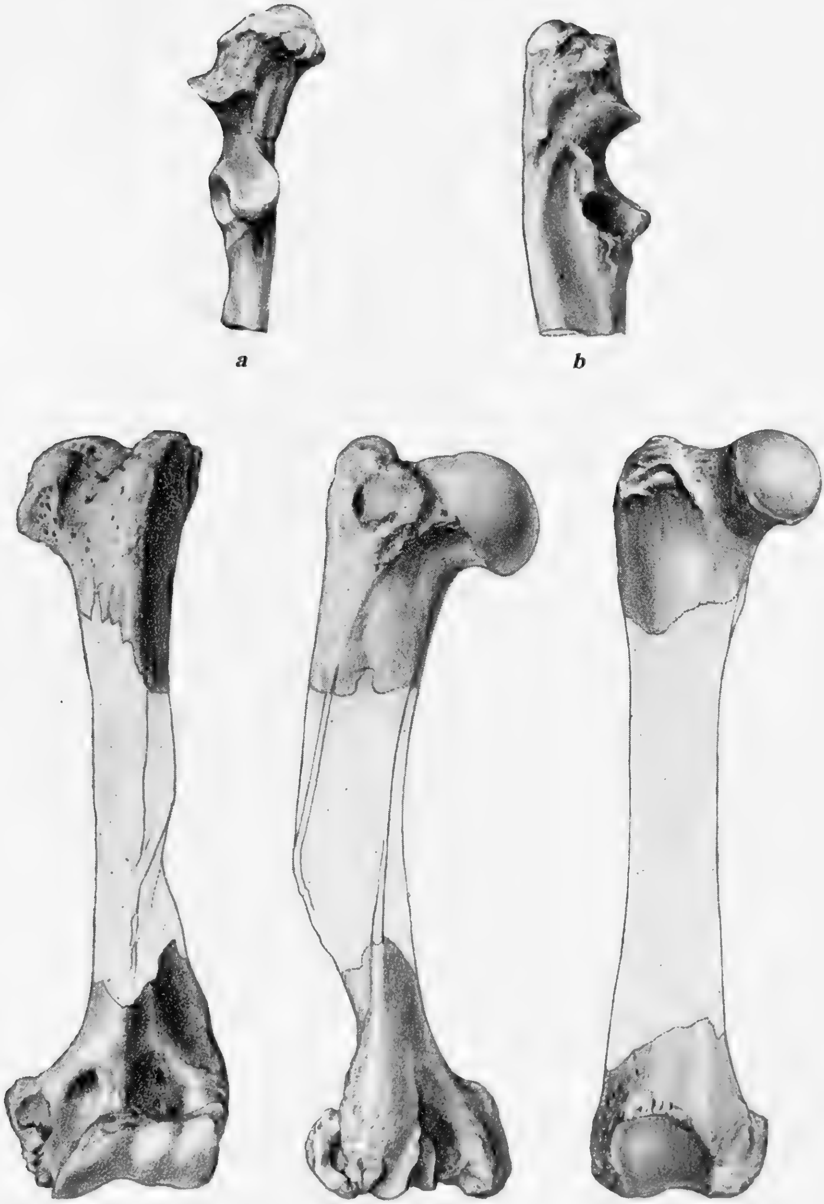


FIG. 38. *Megalictis ferox*, No. P12135. *a*, *b*, proximal end of ulna; *c*, anterior view, *d*, lateral view of restored humerus; *e*, anterior view of restored femur. All × 2/5.

region was found an obstacle. However, many characters of the two postcranial skeletons proved to be very similar.

In this difficulty, one of my associates in the Museum[1] suggested that a study of the inner ear be made. This was done, comparing the ear-structures in a series of carnivores both recent and fossil, and the conclusion was reached that the ear was essentially that of a procyonid. While known fossil specimens of this family are rare and only a skull of *Amphianasua* was available from South American fossil faunas, the Museum was fortunate in having good comparative material of the recent genera and many points of similarity were found with *Bassariscus,* in skeleton as well as in the cranium and particularly in the ear. Surprising as this conclusion is—finding an almost typical mustelid dentition in association with a procyonid basicranium and ear—the study has been so thoroughly done that the result may be accepted as offering little room for doubt. An added consideration is that the cephalo-cranial index is identical with that of such primitive canids as *Pseudocynodictis* and close to that of the procyonids. This affords good reason for removing the holotype of *Zodiolestes* from its former determination as a mustelid. Also, the structure of the deltoid crest and the development of the inner condyle in the humerus of this form are more nearly like those of *Cryptoprocta* and *Bassariscus* than any of the known Miocene mustelids.

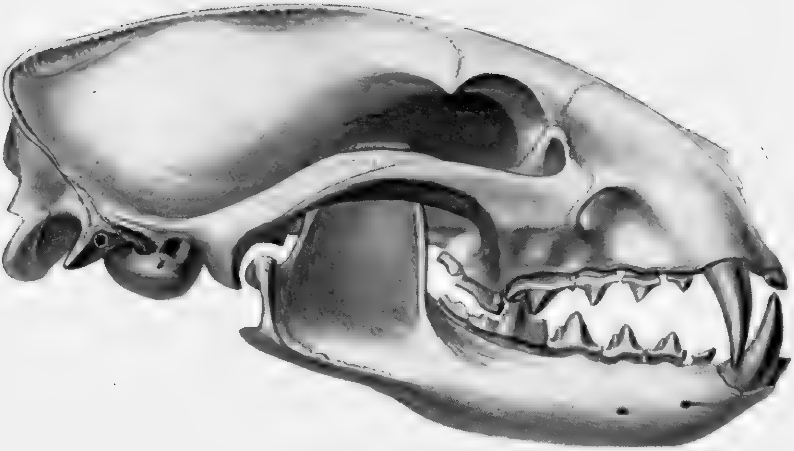
For convenience, the generic characterization of *Zodiolestes,* published in an earlier paper as referred to above, is repeated here.

Small carnivores, size and proportions similar to those of *Cryptoprocta.* Dentition mustelid-like; formula $\frac{3}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{2}{2}$, all teeth functional; parametacone and metaconid of carnassials moderately developed . . . sagittal and lambdoidal crests prominent; alisphenoid canal absent; basicranium broad and short. Tympanic region procyonid-like, agreeing with living genera in structure and especially in the presence of a fossa in superficies meatus of squamosal and in flooring of medial part of fossa muscularis major by periotic; differing in that tympanic does not form a bony external auditory meatus; paroccipital process closest to that of *Bassariscus* but stouter and more posteriorly directed.

To the above it may be added that the scapula has an axillary process in the superior fourth of axillary margin; the humerus has a simple but elongate deltoid crest, inner condyle not excavated by a second posterior condylar fossa and not extending below the trochlea.

The following description of the auditory structures in this genus is given by Margaret Hough (1944):

[1] Mr. Bryan Patterson, Assistant Curator of Paleontology.



a

b

FIG. 39. Skull and mandible of *Zodiolestes daimonelixensis*, No. P12032. *a*, lateral view, approx. × 9/10; *b*, palatal view, × 9/10.

Carotid canal formed by the tympanic along the medial wall of the bulla; a foramen stylomastoideum primitivum is present and the facial canal must have been ligamentous in its external third; tympanohyal lodged in a groove on the surface of the bulla.

Relationships.—There is no doubt whatever that *Zodiolestes* should be classified with the Procyonidae on the basis of the ear region.

Zodiolestes daimonelixensis Riggs

Zodiolestes daimonelixensis Riggs, Field. Mus. Nat. Hist., Geol. Ser., 8, p. 59, 1942.

This species was named for the peculiar spiral form *Daimonelix*, in which the holotype of this species was found embedded. The skeleton was found coiled about in a lifelike position at the middle of the spiral. Clearly this spiral form was, at the time the animal entered, an opening in the sand in which the animal found harborage (figs. 44, 45).

SKELETON

In structure the holotype of this species has no close parallel among known mammals. The dentition is of a primitive canid-mustelid type. The size and the general outline of the skull are nearest to *Cryptoprocta* of Madagascar. The basicranium has the shortness characteristic of canids and procyonids, the auditory region is closest to the latter groups; the postcranial skeleton is of the size and general proportion of *Cryptoprocta.* Comparisons are therefore made with a number of genera, especially *Bassariscus* and *Cryptoprocta.*

The outlines of the facial and the supracranial regions of the *skull* are similar to those of *Cryptoprocta;* the temporal arcade is longer, the cranium correspondingly shorter (figs. 39, 40). The arches are equally strong; there is no postorbital process on the jugal; the bridge over the infraorbital canal is broader than in the recent form. The premaxillaries are narrow and extend almost as far as the anterior extremity of the frontals (fig. 40). The nasals taper posteriorly and terminate above the anterior rim of the orbit. The teeth are low-crowned, straight in alignment and inter-mesh with the opposing series. The basicranial region is broad; the auditory bullae are well rounded, widely spaced from the median line and center with the auditory meatus as in *Aletocyon* and in *Bassariscus.* The posterior nares open just back of the last molars.

The *mandibles* are moderately strong in the ramus, the inferior outline is gently curved. The coronoid processes are broad and slightly recurved but their posterior margins do not overhang the condyles as in *Oligobunis crassivultus* and *Aelurocyon*. The masseteric fossae are deep and are bounded anteriorly by sharp ridges which extend as far as the superior crest of the coronoid process. The entire structure of the skull and mandible is finely modeled, in decided contrast with the heavy structure of the recent *Procyon*. Nevertheless, the short and broad basicranium, the lipless meatus, the rounded

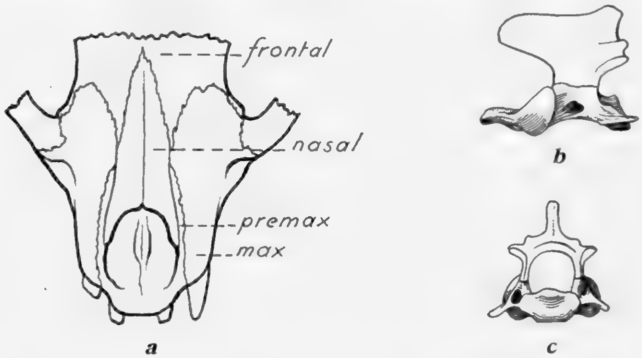


FIG. 40. *Zodiolestes daimonelixensis*, No. P12032. *a*, detail of nasal region; *b*, axis, lateral view; *c*, axis, posterior view. All × ¾.

bullae centering with the meatus, the detached paroccipital process and the structure of the auditory region, all point to basic procyonid relationship.

Vertebral column (fig. 43).—The presacral series of vertebrae, with the exception of some of the processes, is preserved entire. As the skeleton was articulated when found, and was later prepared and photographed in that position, there can be no doubt as to the series being intact (fig. 45). The vertebral formula is C–7, D–13, L–7, S–3, C–?. The column as a whole is somewhat lighter in the cervical and the anterior dorsal series than in *Cryptoprocta* but in the lumbar series it becomes heavier and the processes become stronger.

The series of cervical vertebrae, measured over the centra, is 8 mm. shorter than that of *Cryptoprocta*. The atlas is not so broad in the arches and is lighter throughout (fig. 25). The anterior atlantar foramen opens laterally on the surface as in *Bassariscus*, but not in a fossa. The lateral margin of the transverse process is rounded where the vertebral artery passes over it, but not indented.

The posterior opening of the arterial canal, like the anterior opening, may be seen from the dorsal view. In the latter characteristic the atlas of *Zodiolestes* is nearer to that of *Aelurocyon* than to any of the recent procyonids or the American mustelids. Of the axis, only the centrum, the odontoid process, and the transverse processes are preserved (fig. 40). The centrum has a keel on the inferior surface which is bifurcate posteriorly. The odontoid process is tapering in outline and decurved at the extremity.

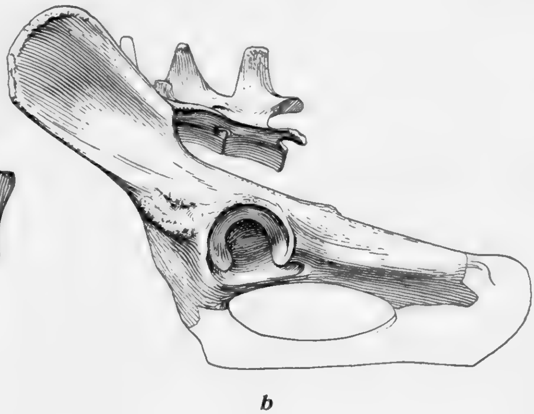
The succeeding five cervicals are similar in size and in general characters to those of *Cryptoprocta*. In the fourth and fifth a pair of small, pointed processes spring from the posterior margin of the neural arch mesad to the postzygapophyses; similar processes were probably present on the second and third, but those portions of the arches are not preserved. The neural spines throughout these five vertebrae are long and tapering (fig. 43).

The dorsal vertebrae are thirteen in number and of the type common to small and active arctoid carnivores. The series is 8 mm. shorter than the same in *Cryptoprocta*. The neural spines are equally long and more massive in proportions than in that form. Throughout the series they are broader antero-posteriorly. The tenth marks the change in type of postzygapophyses; the eleventh has a short spine. The succeeding dorsal vertebrae have increasingly broad and anteriorly inclined spines, grading imperceptibly into those of the lumbar series. The first two transverse processes of the dorsal vertebrae are laterally directed and stronger than those of the succeeding units. With the fifth, a small, hook-like process appears at the antero-lateral extremity and continues in the succeeding units as far as the tenth. A corresponding posterior process is present on the fifth, sixth, seventh, and tenth. Only two of the mid-dorsal centra may be described as keeled.

The lumbar vertebrae, as a series, are 10 mm. longer than the same series in the specimen of *Cryptoprocta*. The spines of the anterior three are broader and more expanded at their extremities; the last four are similar to those of the recent form. The transverse processes are less curved, somewhat longer, more laterally directed and in the last three are expanded at their extremities. The last vertebra is much broader across the postzygapophyses.

The *sacrum* is made up of three co-ossified vertebrae. It is equal in length to that of *Cryptoprocta*, and is narrower and more tapering posteriorly; the centrum of the last vertebra is not so large. These characters indicate that the tail was not so long or so powerful as in the recent animal. The neural spines increase in height from anterior to posterior. The second and third are separate as in *Bassariscus.*

The *scapula* is similar in size to that of *Cryptoprocta* (fig. 41); the base of the spine is longer, the anterior border is convex below and slightly concave above, as in *Bassariscus;* superiorly it is rounded, the axillary border somewhat shorter. The superior axillary margin is produced into a process for attachment of the teres major as in the latter form. The blade of the spine inclines posteriorly so as to



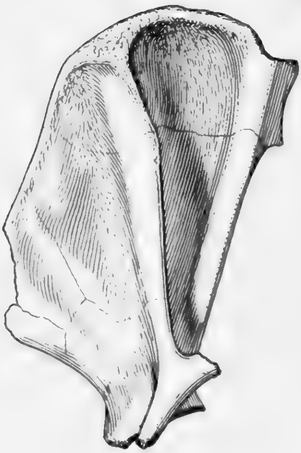


FIG. 41. *Zodiolestes daimonelixensis,* No. P12032. *a,* scapula; *b,* pelvis and sacrum. Both × ¾.

enclose the infra-scapular fossa. The coracoid process is proximal; the acromion and metacromion are closely joined as in *Bassariscus,* the two processes forming a bar, oblique to the direction of the spine as is common to some mustelines.

The *pelvis* as preserved in this specimen includes the ilium, the ischium, and the descending branch of the pubis, all of the right side, together with the greater part of the left ilium (fig. 41). Contact with the sacrum is perfect. From these important parts the pelvis has been restored by comparison with that of *Nasua,* the living procyonid nearest its size. The pelvis is characterized by the unusual length of the ischium from acetabulum to tubercle and by the oblique direction of the ilium, upward and laterally, as compared with the supra-acetabular margin. The crest of the ilium is uniformly rounded, showing nothing of the antero-inferior angle common to this element in both *Bassariscus* and *Nasua*. The attachment for the rectus femoris is a prominent tubercle.

The *humerus* is 5 mm. shorter than that of *Cryptoprocta;* it is rounded in the shaft and curved antero-posteriorly as in *Bassariscus* (fig. 42). The deltoid crest is strongly marked and extends well below the middle of the shaft. The muscular and ligamentary attachments are more strongly developed throughout than in *Cryptoprocta,* less so than in *Gulo*. The supinator ridge rises as a sharp crest extending along the lower third of the shaft and affording another procyonid character. The inner condyle does not extend below the articular facet as in the American mustelines; the entepicondylar foramen is small, rounded, and placed low on the shaft as in *Bassariscus* and *Nasua*.

The *ulna* is equal in length to the humerus of the same individual, being 2 mm. longer than that of the specimen of *Cryptoprocta*. The olecranon is laterally compressed as in *Bassariscus,* less curved in its dorsal outline. The dorso-lateral angle is moderately inflected but not produced into a strong tubercle as in *Promartes* and *Aelurocyon*. The styloid process is laterally compressed but prominent.

The *radius* has lost some 15 mm. of the proximal end by erosion, as determined by comparison with the ulna. The meso-distal angle is notched, apparently for the passage of the extensor tendon.

The *fore foot* of *Zodiolestes* is longer than that of *Cryptoprocta* but similar in strength (fig. 42). The metacarpals are from one-fifth to one-sixth longer. The scapho-lunar has its proximal articulation extended farther over upon the anterior surface, indicating a semi-digitigrade position of the foot; the distal surface is less pointed and is not notched into the magnum. Likewise, the trapezoid is not notched into the distal surface of the scapho-lunar. The magnum, on its anterior face, approaches the form of a right triangle, the longer dimension divided in its contacts between the trapezoid and the scapho-lunar. The unciform is less narrowly pointed at its proximal end and separates the elements of the proximal row more widely. The two proximal facets of the unciform are concave; that for the ulna is larger, accounting for the larger facet on the styliform process of that bone.

The *femur* of the left side is preserved almost entire; of the right side only the proximal half remains (fig. 42). It is 6 mm. shorter than the femur of *Cryptoprocta* and is stronger and more curved in

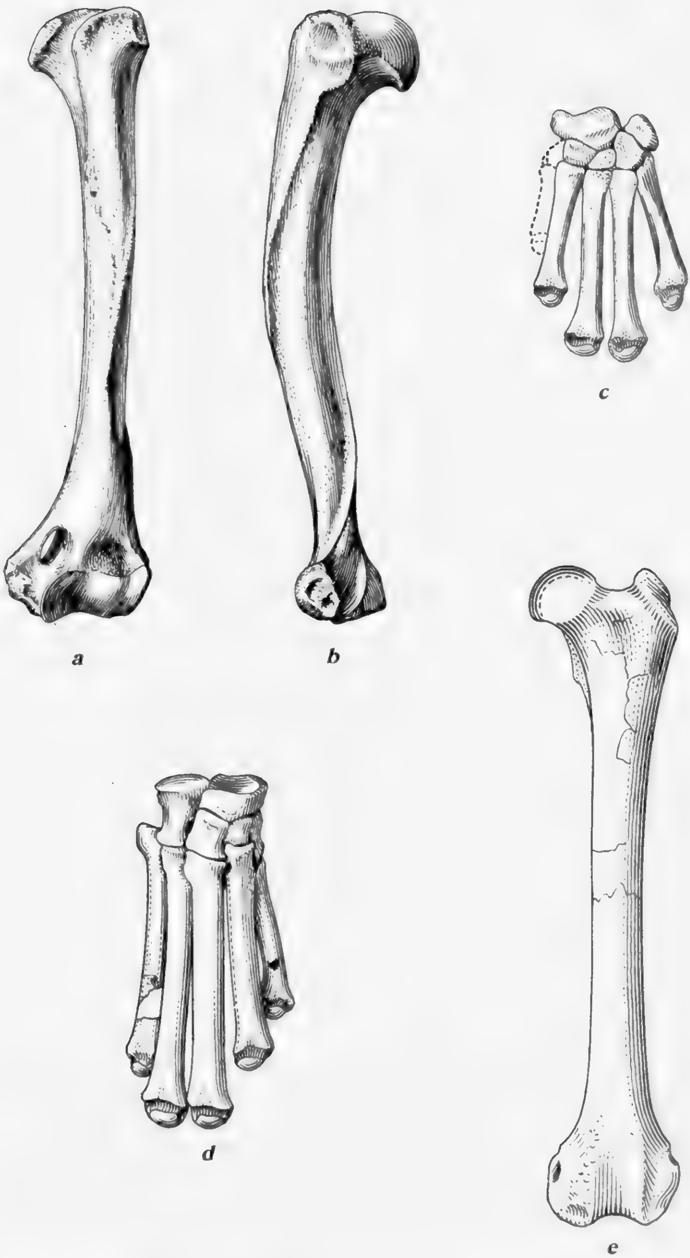


FIG. 42. *Zodiolestes daimonelixensis*, No. P12032. *a*, humerus, anterior view; *b*, humerus, lateral view; *c*, fore foot; *d*, hind foot; *e*, femur. All approx. $\times \frac{3}{4}$.

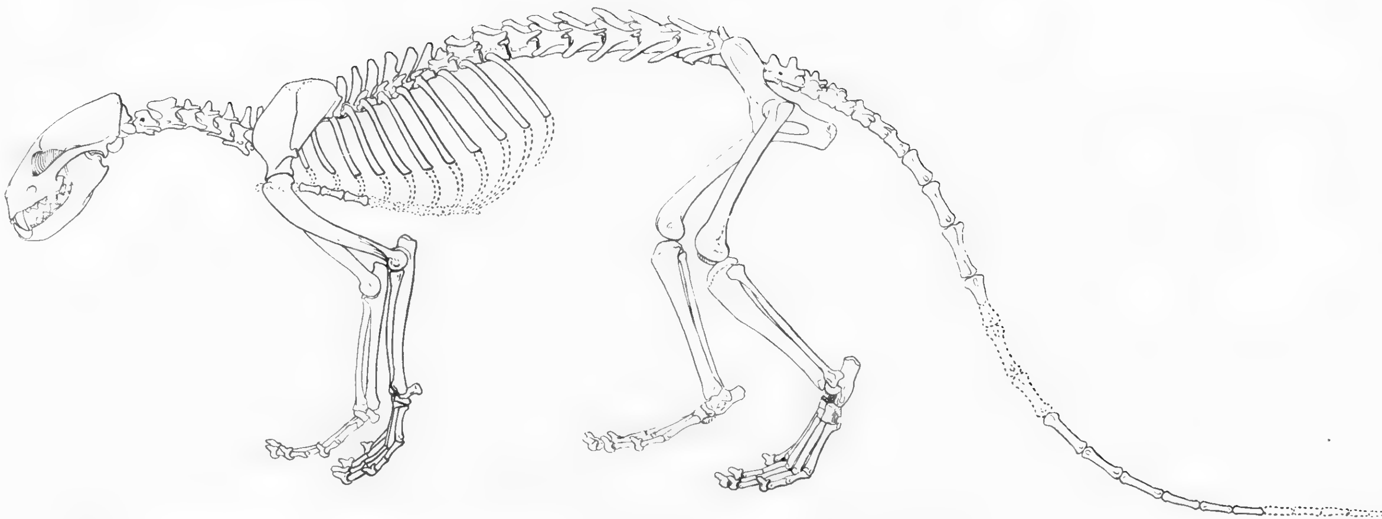


FIG. 43. Restored skeleton of *Zodiolestes daimonelixensis* drawn from Field Museum specimen, No. P12032. Approx. × 1/5.

the shaft. The head is directed obliquely forward on the shaft and does not rise above the great trochanter.

The *tibiae* are both broken, but between the two all of the anatomical characters can be determined. They are apparently a little shorter than the femur of the same animal. This bone as a whole is

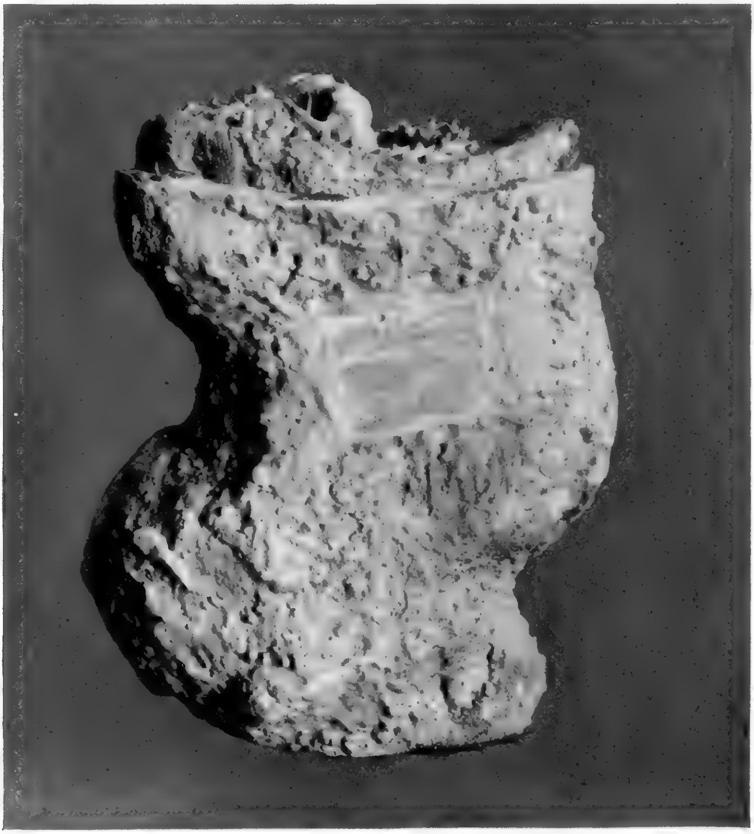


FIG. 44. Photograph showing the holotype specimen of *Zodiolestes daimonelixensis* in relief on the lower half of a spiral of a daimonelix in plaster wrappings. The upper half of the spiral had been removed. Approx. × ¼.

considerably stronger than that of *Cryptoprocta*. The distal end bears a distinct facet for articulation with the fibula. The *fibula* is straight in the shaft, angular, and moderately expanded at the extremities. A spine-like process extends mesially from the proximal end just below the facet. The distal end bears a distinct facet for the tibia above that for the astragalus.

The *hind foot,* consistent with the strength of the pelvis and the hind leg, is larger and stronger than that of *Cryptoprocta* (fig. 42). The first digit is appreciably reduced, the fifth is almost as strong as the second. The third and fourth metatarsals are equal in length. The astragalus is rather deeply concave proximally; the facet for the navicular is elongate in the transverse direction, and its center is opposite the terminus of the external angle. The calcaneum has a

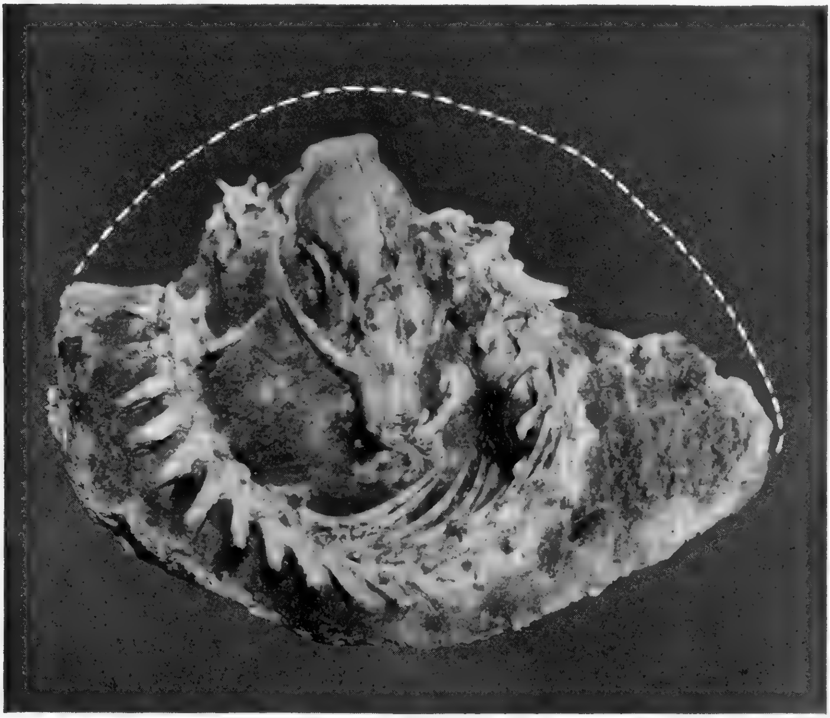


FIG. 45. Sectional view of *Daimonelix* spiral, showing the skeleton of *Z. daimonelixensis* as it was found coiled and embedded in the sandy mass of the spiral.

prominent tubercle on the lateral surface opposite the sustentaculum; the anterior end bears a rounded and moderately concave facet; the mesocuneiform meets the navicular in a well-defined articulation. The unguals are hooded but not retractile.

In conclusion, it may be pointed out that *Zodiolestes* was an animal of similar size, proportions, and muscular development to *Cryptoprocta* (fig. 43). It retained the full complement of premolar teeth and molars of similar structure to those of the smaller, lower

Miocene *Promartes*. The short and broad basicranium with rounded bullae, detached and backwardly directed paroccipital processes and the procyonid-like structure of the auditory region, at once distinguish it from *Cryptoprocta* or from any of the American Mustelidae. While it must be regarded as a form detached and apart from known procyonids, the basicranial characters and the structure of the inner ear definitely group it with the Procyonidae.

MEASUREMENTS

(In millimeters)

SKULL	
Length, condyle to incisors	114
Breadth across arches	73
Breadth across mastoid processes	49
Length of dental series	52
Breadth across crowns of first molars	37
Molar II to posterior margin of glenoid fossa	31
Projection—posterior margin of glenoid fossa to margin of condyles	32
Length of sagittal crest	53
Greatest breadth of cranium	44
Anterior margin of orbit to anterior margin of canine alveolus	31
LOWER JAW	
Greatest length, condyle to incisor alveolus	83
Height of coronoid process above inferior margin	36
Occipital condyle to margin of molar II	36
Length of lower dental series	51
VERTEBRA	
Atlas	
Breadth across transverse processes	46
Breadth of superior arch	8
Breadth of inferior arch	4
Axis	
Length of centrum including odontoid process	26
Breadth of anterior articulation	18
Breadth of centrum, posterior end	11
Fifth cervical vertebra	
Axial length of centrum	12
Breadth across prezygapophyses	19
Dorsal Vertebra I	
Axial length of centrum	11
Breadth across transverse processes	21
Height of spine above base of centrum	33
Lumbar Vertebra I	
Length of centrum	19
Breadth across prezygapophyses	8
Height of spine above base of centrum	23

VERTEBRA—*Continued*	
Lumbar Vertebra VII	
Axial length of centrum	19
Breadth across transverse processes	52
Breadth across prezygapophyses	19
Height of spine above base of centrum	28
SCAPULA	
Axial length	72
Length of axillary border	64
Greatest breadth	39
Breadth of articular end	16
HUMERUS	
Axial length	107
Breadth across head and great tuberosity	23
Greatest breadth at distal end	26
ULNA	
Length	109*
Olecranon length from margin of sigmoid notch	12
RADIUS	
Axial length	83
Breadth at proximal end	12
Greatest breadth of distal end	15
FORE FOOT	
Length from scapho-lunar to distal end of third metacarpal	43
Metacarpal I, axial length	18
Metacarpal II, axial length	27
Metacarpal III, axial length	33
Metacarpal IV, axial length	32
Metacarpal V, axial length	25
PELVIS	
Greatest length, crest of ilium to tubercle of ischium	101*
Ilium, length from margin of acetabulum	49
Ilium, breadth of anterior end	23
Ischium, length from margin of acetabulum	45*
Breadth of acetabulum	15
FEMUR	
Greatest length over head and inner condyle	122
Breadth over head and great trochanter	29
Greatest diameter of head	13
Diameter of middle of shaft	11
Greatest breadth across condyles	24
TIBIA	
Greatest length	118*
Greatest breadth at proximal end	25
Breadth cnemial crest to posterior margin	26
Greatest breadth at distal end	17
FIBULA	
Length	110

*Estimated.

HIND FOOT	
Greatest length, extremity of calcaneum to end of fourth metatarsal	94
Calcaneum, greatest length	33
Astragalus, greatest length	22
Metatarsal I, length	29
Metatarsal II, length	40
Metatarsal III, length	47
Metatarsal IV, length	49
Metatarsal V, length	—

CONCLUSIONS

From the character of known mustelines of Lower Miocene age, it appears that there were two stocks of these animals present in the Great Plains region. First, an indigenous stock descended from known Oligocene forms, of small size and apparently of active habits. These forms include the early, marten-like group, designated by the genus *Promartes*. It may be that other small forms will not fall within this genus. Second, a larger and stronger stock of mustelines, earliest known as *Oligobunis crassivultus* of the John Day formation but represented also by other strong-jawed forms such as *Paroligobunis* of the Great Plains region. Along with these animals and probably descended from the same stock, were the larger mustelines, *Aelurocyon* and *Megalictis*, sturdy and voracious killers and strong rivals in their field of depredation. These animals appear to have driven out most of the felids and to have remained as a prominent group well into Middle Miocene time. Before the end of the Miocene they had disappeared and the felids, filtering back into the Great Plains region, were again becoming more numerous.

The canids as a family appear to have held their own against the rivalry of the larger mustelids. The smaller line as represented by *Pseudocynodictis* apparently disappeared early in the Lower Miocene. The stronger canid line, in sequence to the Oligocene *Daphoenus* and the Lower Miocene *Daphaenodon*, held their own. Later the great bear-dogs appeared as dominating carnivores. With the large mustelines out of the race, and the procyonids never strong enough to play an important part, the balance of power became established between the great canids and surviving felids. Difference in habits between cat and dog families appears to have been early established, the one lying in wait or stalking while the other pursued its prey, either overtaking it by greater swiftness of foot or by driving it to exhaustion. Their rivalry, because of different hunting habits, has never been pushed to the point of exterminating either family.

ZODIOLESTES COMPARED WITH OTHER PROCYONIDS

	Zodiolestes holotype	*Aletocyon* holotype	*Phlaocyon* holotype*	*Bassariscus*, referred specimen
Skull dimensions in mm.	119 × 76	114 × 67	91 × 60	81 × 48
Palate length†	51.5 mm. = 43.3%	53. mm. = 46.4%	43 mm. = 47.2%	35.0 mm. = 44. %
Basicranium length‡	33 mm. = 27.3%	31.5 mm. = 27.6%	25 mm. = 27.5%	24.5 mm. = 30.8%
Paroccipital process	Free and backwardly directed		Process free	Below meatus, process small but free‡
Mastoid process	Moderately developed	Less developed than in *Zodiolestes*	Little developed	Moderately prominent
Alisphenoid canal	Not present	Present	Present	Not present
Precondylar foramen	Separate from foramen lac. post.	Separate from F.L.P.		Separate from F.L.P.
Foramen lac. medium	Concealed by bulla as in *Felis*	Concealed by bulla	Not concealed	Not concealed
Maxillo-palatine suture	Crosses median line opposite ant. margin of P^4	Not determined	Crosses opposite center of P^4	Crosses opposite ant. margin of P^4
Palate	Narrow as in *Martes pennanti*	Moderately wide	Intermediate	Intermediate
Ant. palatine foramina	Small and rounded	Small	Medium size elongate obliquely	Moderately large

* From description by Wortman and Matthew, 1899.

† Measured on median line, incisors to line drawn across posterior margins of last molars.

‡ Measured on median line, condyles to line drawn across posterior margins of glenoid cavities.

ZODIOLESTES COMPARED WITH OTHER PROCYONIDS—*Continued*

	Zodiolestes holotype	*Aletocyon* holotype	*Phlaocyon* holotype*	*Bassariscus*, referred specimen
Premaxillaries	Slender, approach ant. process of frontals	Do not approach frontals	Elongate, meeting frontals	Widely separate from frontals
Jugal bone	Approaches glenoid cavity	Approaches glenoid cavity	Ends just outside glenoid cavity	
Upper sectorial tooth	A strong protocone present		Protocone and internal conule present	A protocone and cingulum present
Upper M^2	Much reduced	Strong	Conule present; P^4, M^1, M^2, strong low-crowned teeth	Reduced but functional
Atlas	No second anterior foramen. Posterior opening of canal visible from dorsal view		Posterior opening of canal presents slightly upward	No second ant. foramen; posterior opening of canal not visible from above
Scapula	Axillary process on superior fourth of border			Axillary process on superior fourth of border
Humerus, deltoid crest	Extends below middle of shaft		"Humerus more slender than in Procyon"	Deltoid crest extends to middle of shaft
Entepicondylar foramen	Oval in outline placed low on shaft			Foramen small
Postcondylar fossa	A trace only			No trace

* From description by Wortman and Matthew, 1899.

Of the Procyonidae much less is known. We have a glimpse of two multicuspidate forms in the Lower Miocene and now we have in *Zodiolestes* a procyonid which has retained the sectorial function of the carnassial teeth. This appears to have been a form of terrestrial animal quite as alert as the cat or the fox. Up to this time it is known from one specimen only; its source and its ultimate fate are as yet unknown.

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