# BULLETIN 15

TEXAS MEMORIAL MUSEUM

# PLIOCENE CARNIVORES OF

# THE COFFEE RANCH

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# Pliocene Carnivores of the Coffee Ranch

## (Type Hemphill) Local Fauna

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Plate I. Part of the skeleton of *Machairodus catocopis* (TMM 41261—8) in the field block. Note lumbar, sacral, and proximal caudal vertebrae below, radius and ulna at upper right, articulated cervical and thoracic vertebrae in center, and pelvis at upper left. Many of the bones had been removed when this photo was made, and others were still buried in the matrix.

# Pliocene Carnivores of the Coffee Ranch
# (Type Hemphill) Local Fauna

WALTER W. DALQUEST[*]

## Abstract

New material collected in the Coffee Ranch quarry, Hemphill County, Texas, represents eight species of Carnivora. Included in the fauna is an apparently new species of *Pseudaelurus*. Abundant material makes possible a detailed description of the bone-eating dog, *Osteoborus cyonoides*. The saber-toothed cat, *Machairodus catocopis*, is described from a largely complete skeleton. Specimens include teeth, previously unknown, of the rare wolverine, *Plesiogulo marshalli* and a very large bear, *Indarctos oregonensis*.

## Introduction

The Coffee Ranch quarry in Hemphill County, Texas has furnished important fossils of extinct mammals of middle Pliocene age. This local fauna, described in 1930, 1931 and 1932, was so distinctive that similar kinds of mammalian faunas from elsewhere in North America are referred to the Hemphillian fauna (Wood, et al., 1941), and the time during which the faunas lived is designated the Hemphillian land-mammal age (Evernden, et al., 1964). The Coffee Ranch local fauna is the type local fauna of the Hemphillian fauna. Potassium-argon dates for the Hemphillian stage range from 5.2 to 10 million years BP (Evernden, et al.: 164).

The Coffee Ranch quarry was designated "Locality 20" by Matthew and Stirton (1930a) in their first account of the fossil mammals discovered in Hemphill County. The list of 28 fossil-bearing localities in Hemphill County, of which the Coffee Ranch quarry was number 20, did not appear until two years later, however (Reed and Longnecker, 1932: 66). For an account of the discovery and early work at the quarry, see Matthew and Stirton (1930a: 171).

The first paper concerning the Coffee Ranch quarry fossils by Matthew and Stirton (1930a) dealt with the bone-eating dog (*Osteoborus cyonoides*). This was followed (1930b) by a study of the fossil horse remains. Burt (1931) published an

account of the saber-toothed cat (*Machairodus catocopis*). Following Matthew's death, Stirton completed an account of the rhinoceroses (Matthew, 1932). Descriptions of the remainder of the fauna were promised (Matthew, 1932: 411) but never appeared. Specimens from the Coffee Ranch have been mentioned briefly in a number of works dealing principally with other matters, and Webb (1965) has described a new species of camel from the deposits. No papers devoted to mammals from the Coffee Ranch have appeared since 1932, however, and no important collections had been made at the locality since 1929, until field parties from Midwestern University began collecting in 1956. In the summers of 1963 and 1964, large bulldozers were used to push aside the overburden of volcanic ash and clay, to expose fresh matrix. The large collection subsequently obtained includes remains of many carnivorous mammals, which furnish the basis of the present report. Earlier accounts of several taxa can now be expanded and one new species recognized.

## Acknowledgments

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# Geology, Occurrence and Taphonomy

The Coffee Ranch quarry is located in the southwestern part of Hemphill County (Fig. 1). For a detailed description see Reed and Longnecker (1932: 66; their locality 20). The locality is also shown on their geologic map of Hemphill County.

The Coffee Ranch fossils accumulated in a lake or bog of moderate but unknown area. The lacustrine sediments were later buried under 30 feet or more of sandy aeolian deposits and are now exposed in vertical section in the face of a steep hillside. To the south the sediments continue into the hill for an undetermined distance, while the portion that once extended northward has been destroyed by erosion of Red Deer Creek. The exposure is lenticular in profile and some 300 feet long.

A measured section of the quarry is given by Reed and Longnecker (1932: 59–60). Their section was apparently measured near the edge of the lenticular deposit. Closer to the center the sediments measure:

1. Overburden of buffy, sandy clay and soil    25.0 feet
2. Volcanic ash  ............  9.0
3. Compact bentonitic clay  ............  2.0
4. Greenish gray sand with some clay  ......  2.0
5. Reddish brown, sandy clay, variable in thickness in the deposit and with sharp but contorted contact with beds above and beneath  ............  1.0
6. Greenish sand and sandy clay with some pebble bands and thin calcareous sandstone layers  ............  5.5
7. Slick, hard, reddish brown clay with calcareous crusts and nodules  ............  0.2
8. Buff-colored aeolian sandy sediments of the Ogallala formation; bottom not exposed in this area.

Vertebrate fossils occur in all beds of the lake deposit. Some rich concentrations were found in the volcanic ash, but in most of the ash layer bones are few and scattered. In the thinner lamina of ash, near the bottom of this bed, ripple marks and footprints of birds and mammals are common.

The dense, bentonitic clay just beneath the vol-

canic ash contains an abundance of bones, but many of these are crushed and broken. A few good specimens were collected here, however, and most of the fossils of small mammals, such as mice and shrews, were obtained by washing the clay.
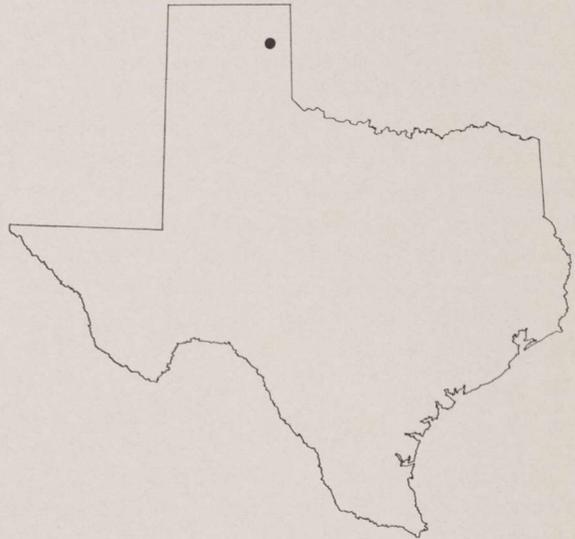
Most of the greenish, sandy clay beneath the bentonitic clay holds relatively few fossils, and these usually are poorly preserved. Some good specimens were found in the lower part of this bed, just above the contact with the hard, brown, sandy clay of Bed 5.

The brown, sandy clay bed yielded only scattered fragments and a few poorly preserved fossils. Over extensive areas it is completely barren. The bulk of the fossils, and most of the complete bones, were found in the greenish sand of Bed 6.

Little evidence of stratification is apparent in Bed 6, but there are occasional layers of pebbles, caliche gravel, or indurated, calcareous sandstone. The layers are often extensive but rarely exceed an inch in thickness.

Bones, bone fragments, and teeth may be found

throughout Bed 6 but are most common in the following zones: free in the sand about one foot beneath the contact with Bed 5; in and just above the pebble or gravel layers; just above the sandstone layers; and at the bottom of the greenish sand bed, resting on the slick, reddish, calcareous clay at the bottom of the deposit. Some depressions in the ancient lake bottom, a yard or more in diameter and two feet or more in depth, were filled with jumbled masses of ribs, limb bones, vertebrae, jaws, and other elements, derived from mammals of several different genera. The specimens in such pockets were often so interlocked that the individual bones could be separated only with great difficulty.

The history of the deposit may be interpreted as follows: sand and dust settled in the basin of the shallow, seasonal lake to form a sandy mud. Bones of animals that died in or near the lake, and that escaped destruction by scavengers, settled through the mud to rest near the bottom. Other bones, which may have accumulated on the surface when the lake was dry, settled through the mud when the lake again filled with water.

The lake must have been dry for extended periods, for the sandstone layers probably were formed when rainwater leached carbonates downward through a dry substratum. The pebble and gravel layers doubtless formed when heavy rains washed rock debris from nearby caprock hills and cliffs out onto a firm, sandy flat, not onto soft mud. Sandstone and pebble layers were later buried under accumulating sandy mud, but each hard layer served as a trap to catch bones sinking down through the soft sediments above them.

The hard, brown, sandy clay deposit (Bed 5) may have formed under somewhat different climatic conditions. The amount of clay and carbonate in this bed suggests slower deposition, and the reddish brown color suggests that the sediments were usually exposed to the air. Slow deposition and swift drainage or evaporation would also account for the scarcity of fossil bones in this bed.

After the brown, sandy clay accumulated there was a return to original conditions, and greenish sand again formed. Vertebrate bones sank through the sand to a level just above the hard, brown bed.

The new period of deposition of greenish sand was brief. The site then became a meadow or shallow bog where mice, shrews, and rabbits lived, and whose remains were preserved in the bentonitic clay. Dust, fine sand, and fine volcanic ash form the bentonitic clay.

Increased volcanic activity to the west then showered the hills about the lake basin with a dust of volcanic ash. Each heavy rain washed the ash into the shallow water of the lake. As the ash became waterlogged it sank to form a mud which, when the lake periodically became dry, retained ripple marks and footprints of wading animals. Additional ash settled and rains washed it into the basin to refill the lake and cover the hardened layer of ash with a new layer of mud, preserving bones and footprints. Layer after layer of such volcanic dust was washed into the lake until nine feet had accumulated. The hard ash bed completely filled the closed depression of the lake bed, sealing the fossils and sediments beneath like a cork in a bottle. The capped deposit was then buried in the continuing accumulation of aeolian sediments of the Ogallala formation, until exposed by erosion of Red Deer Creek.

*Osteoborus* was doubtless the major scavenger at the fossil site. On one slab of volcanic ash, ten feet long and six feet wide, a small ungulate rib was exposed when the slab was split open. Surrounding the rib were numerous footprints of bone-eating dogs. A few feet away the trackway of a saber-toothed cat, the footprints evenly spaced and unhurried, went past the clustered dog foot prints. One can only conjecture that the cat frightened the dogs away from their meal.

The name "bone-eating" dog may be validated by other than anatomical features. Found in the bentonitic clay were numerous small clusters of bone chips. These sometimes were evenly but densely distributed through fist-sized areas of clay that were not otherwise marked off from the surrounding matrix. The bone chips were rarely more than 10 mm. in greatest dimension, and presumably represent the disintegrated feces of *Osteoborus*.

The dogs were possibly cannibalistic, as the hunting dogs of Africa are reputed to be. The species is the most common carnivore in the deposit, represented by more than 50 skulls and jaw fragments. Yet very little postcranial material was recovered and much of that is damaged. For example, the humerus of *Osteoborus* is represented by eight distal portions but not a single proximal end. Doubtless the scapulae and meaty proximal ends of the humeri were devoured, but the distal ends, where there is little flesh, were less attractive. Lower leg and foot bones are more common, but vertebrae with protruding neural spines and transverse processes appear to have been heavily gnawed and largely destroyed.

The *Osteoborus* series included only two specimens with milk teeth. Fifty-four adult dentitions were arbitrarily separated into four age categories: young (little or no wear on teeth), medium-aged (moderate tooth wear), old (considerable wear on all teeth), and very old (teeth worn almost flat). Upper dentitions were separated as follows: 7 young, 10 medium, 2 old, and 3 very old. Lower dentitions included: 9 young, 13 medium, 8 old, and 2 very old. Maximum mortality seems to have occurred among the fully mature animals.

Vultures, too, probably aided in scattering bones at the quarry. On a number of bones, protruding processes and sharp edges appear to have been damaged by nibbling or pecking, but there are no distinct tooth marks. This is especially apparent in the skeleton of the saber-toothed cat, described later. The broken edges of the cranium of this specimen have a pecked, nibbled appearance, while many of the transverse processes and neural spines of the vertebrae are damaged or missing on one side only. No actual remains of vultures were discovered, however. The only bird tracks found in the volcanic ash appear to be of a heron-like form, and the only large bird bone found was identified as a hawk by Dr. Pierce Brodkorb of the University of Florida.

Many bones were broken or crushed by the feet of large mammals wading in the mud of the shallow lake. Rhinoceroses were probably responsible for much of this damage. One rhinoceros skull showed clearly that a heavy foot had crushed the frontal area. The skull lay in the matrix in three pieces: cranium and two separated maxillaries, with a mass of bone splinters between them. The three parts, reassembled, showed a gaping hole where the foot had descended. The skull of the saber-toothed cat also was clearly damaged in this fashion. The articulated skeleton (Plate I) lay in greenish sand matrix a few inches above a layer of sandstone. Atlas and axis were separated from the other cervical vertebrae by three inches and the basicranium of the skull lay three inches ahead of them. The main weight of the crushing foot had come to rest on the anterior left part of the skull. The right maxillary with canine and carnassial had been pressed down until it lay on the sandstone layer. A right premaxillary, doubtless of the same skull, was found a short distance away. Both glenoid processes were broken free and lay in the matrix beneath their natural positions, but the remainder of the zygomatic arches were splintered. The remainder of the skull (left maxillary) was not found. The toothless skull of a wolverine, *Plesiogulo*, also appears to have been crushed by a wading mammal, but the damage is less distinctive.

In the accounts that follow, all measurements of specimens are in millimeters. Specimen numbers are: MU, Midwestern University, Wichita Falls, Texas, and TMM, Texas Memorial Museum, Austin. Figured specimens are in the collection of the latter.

# Taxonomic Synopsis

Order Carnivora   Bowdich
  Suborder Fissipeda   Blumenbach
    Family Canidae   Gray
      Subfamily Caninae   Gill
        *Vulpes* cf. *V. shermanensis*   Hibbard
      Subfamily Borophaginae   Simpson
        *Osteoborus cyonoides*   (Martin)
    Family Ursidae   Gray
        *Indarctos oregonensis*   Macdonald
    Family Mustelidae   Swainson

      Subfamily Mustelinae   Gill
        *Plesiogulo marshalli*   (Martin)
      Subfamily Melinae   Burmeister
        *Pliotaxidea* cf. *P. nevadensis* (Butterworth)
    Family Felidae   Gray
      Subfamily Nimravinae   Trouessart
        *Pseudaelurus hibbardi*   Dalquest
      Subfamily Machairodontinae   Gill
        *Machairodus catocopis*   Cope

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# Accounts of Species

## *Vulpes* cf. *V. shermanensis* (Hibbard)

Two edentulous lower jaws and a number of isolated teeth belong to a fox approximately the size of an adult red fox, *Vulpes vulpes*. Jaw MU6866 lacks the ascending ramus but has the alveoli of the canine and cheek teeth. When this jaw is placed beside the jaw of a red fox from north-central Texas, from which the teeth have been removed, the alveoli of the canine, premolars and carnassial match closely, but the alveoli for $M_2$ and $M_3$ are more widely spaced, and the jaw is longer in the corresponding region. The distance from the anterior edge of the canine alveolus to the posterior edge of the alveolus for $M_3$ is 79.0 mm., or slightly greater than in the jaws of several red foxes from Texas.

Four isolated $M_1$'s (MU4362, 4363, 6406, 6497) are similar to the lower carnassials of red foxes from Texas in size and morphologic details, but in each tooth the metaconid is distinctly larger and more prominent. Except for this difference, and the larger $M_2$ and $M_3$, the lower jaw of the Hemphill fox is quite like that of modern red foxes. Canid lower jaws are usually conservative, however, and if complete upper jaws or skulls were available, greater differences between them would probably be found.

## *Osteoborus cyonoides* (Martin)

The bone-eating dog is the commonest carnivore in the Coffee Ranch Quarry. Four skulls (Table 1), 18 maxillaries or maxillary fragments with teeth, 32 lower jaws or mandibular fragments containing teeth, numerous isolated teeth, and isolated bones representing most of the skeleton were recovered.

In spite of the abundance of cranial fragments, postcranial material is uncommon and fragmentary. No useful remains of pelvis or sacrum were obtained, and only the proximal portions of two scapulas. A femur is nearly complete but only fragments of humeri were found. Lower leg and foot elements are more common. A number of vertebrae were taken but only some of the cervicals and posterior thoracics can be identified with confidence.

DESCRIPTION.—An excellent skull, jaws, and some postcranial bones of this dog were briefly described and figured by Matthew and Stirton (1930a), but only a few measurements were given. The following data, based on newly-collected specimens, augment the work of Matthew and Stirton.

*Skull*.—MU7408 is the broken skull of a young dog. The permanent teeth are in place and are scarcely worn. The skull lacks the tip of the rostrum, the teeth anterior to the second premolars, and the right $M^2$, as well as part of the anterior dorsal skull roof. The skull had been broken into three pieces: basicranium and two maxillaries. No point of bone-contact between the three pieces remained. The missing parts have been restored with plaster, but measurements of breadth are not usable.

MU3229 is the skull of a young-adult dog, with the teeth scarcely worn except that the tips of the fourth premolars show some wear. The right $I^1$, right and left $P^1$'s, right zygomatic arch, and right posterior portion of skull are missing. The skull is embedded in a hard calcareous matrix and has not been completely prepared.

MU5049 is also the skull of a young-adult dog, a bit older than MU3229. Missing are all teeth anterior to the $P^2$'s, the right $M^2$, the left $M^1$ and $M^2$ and left zygomatic arch. There is also some minor crushing and breakage.

MU5862 is from an older animal, and a moderate amount of wear is present on even the canines and incisors. Missing is the right $P^1$, right and left $P^3$ and left $M^2$, as well as all of the skull posterior to the palate. Additional material includes 18 maxillary fragments, some with the premaxillaries attached.

The four skulls are from animals considerably younger than the nearly-perfect specimen figured by Matthew and Stirton (1930a, Plates 21, 24, 25, 26), but they are essentially similar in shape. The braincase is narrow but the remainder of the skull is broad and powerful. The zygomatic arches are stout and broad posteriorly. Rostrum and palate are broad. The breadth is accentuated by the short-

ness of the muzzle, which results from the shortening of the premolar region of the skull and reduction of the premolars. The frontal region is greatly bulged, in the manner typical of hyaenoid dogs. The zygomatic arches are narrow anteriorly but, posterior to the orbits, flare widely to permit passage of the enormous masseter muscles. The orbits are small and diagonally constricted by the bulged forehead above and flared arches behind. In life the eyes must have been strongly slanted. The sagittal crest is very heavy, and the occipital crest is strong and projects posteriorly above. It is transversely truncated posteriorly rather than ending in a point, as in *Canis*. The head, in life, might have resembled somewhat that of a modern bulldog, but the expanded frontals and powerful muscles of the temporal region and of the jaws must have appeared quite different.

*Superior dentition.*—There is a greater amount of individual variation in the series of upper jaws of *O. cyonoides* than in a comparable series of skulls of the modern coyote, *Canis latrans*. Variation in the relative size and crowding of the teeth is especially apparent. In skull MU3229 the teeth are small and widely spaced. The individual teeth are separated by short spaces, and the long axes of the premolars are parallel to the axis of the tooth row. The alveolar length, from $P^2$ to $M^2$, is relatively and actually long (63.8 mm.). In skull MU5862 the teeth are relatively large and the toothrow short ($P^2$–$M^2$ 58.5 mm.). The teeth are in contact, and the anterior premolars crowded until they are rotated out of the axis of the tooth row. Even more extreme crowding is seen in some maxillary fragments.

There is considerable variation in the size and shape of the small, anterior premolars. Unworn teeth may be elongate or broadly oval. There may be a single central cusp or three distinct cusps. There is an equal amount of variation in size of the carnassial and upper molars. In some, the upper $P^4$'s are more than 20 percent larger than others. The difference is so great that, were only the largest and smallest teeth available, one might place them in separate species.

There is little variation in the shape of the carnassial and first molar, however. The parastyle is well developed and present on every specimen at hand. Vanderhoof and Greggory (1940, footnote p. 160) state that the parastyle on $P^4$ is "a demonstrably variable character, especially in *Osteoborus*, where it ranges from total absence to large size," but earlier in the same paper (p. 144) these authors

list the parastyle as a character of the genus *Osteoborus*. Canid dentitions are variable and that of *O. cyonoides* unusually so. It would not be surprising if occasional individuals lacked the parastyle. In the more than 20 specimens available, however, the parastyle is present and strong in all.

The first incisors of *O. cyonoides* are small, the second only slightly larger, and the third strong and stout, resembling the canine in shape but only about half its size. Poorly developed basal cusps are present on $I^2$ and at least sometimes on the posterior base of $I^3$. The huge cusps of the upper incisors of *Aelurodon* are not even approximated by *O. cyonoides*. Few measurements of the upper incisors are possible for $I^1$ and $I^2$ are rarely retained in the fossils, and $I^3$ is only slightly more common. The canines are stout and short but otherwise doglike. Their roots are heavy, and the tooth is often retained in the fossil jaws.

The three anterior premolars are small and graduated in size, with the first the smallest. This tooth is usually lost from the fossil jaws. $P^2$ is two-rooted. It is almost always oriented anteroposteriorly in the jaw and is firmly fixed and usually present in the fossils. $P^3$ is larger than $P^2$, but, if the tooth row is crowded, this tooth is rotated or forced out of alignment between $P^2$ and $P^4$. It is less firmly fixed in the jaw than $P^2$, and is more often missing in fossil jaws. Many premolars were lost in life and their alveoli almost completely obscured by bone growth.

$P^4$ is a large, strong tooth. There is, at most, only a trace of the protocone, but the tooth is noticeably broader anteriorly where the protocone seems to have been taken into the body of the tooth. The root remains lingually. The bulk of the tooth consists of the small but distinct parastyle, large paracone, and metacone.

$M^1$ is a large, stout tooth. It is well fixed in the jaw and seldom lost in fossils. $M^2$ is much smaller and is quite variable in size. It is often lost in fossil specimens. Because $P^1$ and $M^2$ are so often lost, they are not included in measurements of length between teeth (Table 2). In the measurements of length of the individual teeth, the longest axis is given as length of the premolars, regardless of the orientation in the jaw. Breadth is the greatest width at right angles to the long axis. The length of $M^1$ was taken with the jaw of the caliper placed against the flat, posterior face of the tooth and width was taken with the jaw against the flat, labial side of the tooth. All of the measurements given in Table 2 were taken from jaws containing $P^4$, $M^1$, and other

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teeth. Measurements indicated with "a" are from alveoli where the tooth is lost. No isolated teeth are included in the table.

*Mandible.*—The lower jaw of *O. cyonoides* is short, deep, and thick. The ascending ramus is strongly developed. The lower border of the mandible, posterior to $M_2$, curves upward and backward, so that the angular process is well above the inferior border of the horizontal ramus. The articular condyle is heavy and strong. The coronoid process is very high and strong. The height of the ascending ramus is as long as or longer than the tooth-bearing part of the horizontal ramus. The masseteric fossa is large and deep, crossed with diagonal ridges and rugosities for attachment of powerful muscles. These rugosities seem to be best developed in animals with worn teeth, and doubtless increased with age.

*Inferior dentition.*—Variation in the lower dentition, in spacing and relative size of teeth, is equal to that in the upper teeth (Table 3). In the large teeth, $P_4$ and $M_1$, there is little variation in structure but much in size. The largest carnassials are fully 20 percent larger than the smallest. No such great variation was noted in the lower molars of the coyote.

*Osteoborus* typically lacks the first lower premolar, but this tooth is present in one lower jaw and its single-rooted alveolus is present in another. The $P_1$ that is present is nearly as large as the $P_2$ in the same jaw.

Characters that separate the lower dentition of *Osteoborus* from that of its descendant, *Borophagus*, include the stepped posterior face of $P_4$ and the presence of a metaconid on $M_1$. That these are always lacking in *Borophagus* remains to be determined, but they are present in all of the 34 $M_1$'s and 28 $P_4$'s of *Osteoborus* from the Coffee Ranch.

The lower incisors of *O. cyonoides* are not preserved in any of the 32 lower jaws available. Their alveoli are present in some cases, and some isolated specimens that probably are lower incisors of *Osteoborus* were found. The lower incisors appear to have been small and simple. The canine is short, thick, and strong, with a heavy root. $P_1$ has been lost from most specimens. $P_2$ and $P_3$ are small, oval teeth. In unworn specimens, three small, low cusps can usually be distinguished but these vanish with moderate wear. The teeth vary considerably in size from jaw to jaw, but $P_3$ is invariably larger than $P_2$. $P_2$ is often lost in fossil jaws.

$P_4$ is a large, strong, thick tooth, triangular in lateral view and, in unworn teeth, strongly inclined posteriorly. The posterior face is invariably stepped. This tooth is rarely lost from fossil jaws.

$M_1$ is a very large, strong, crushing tooth. The trigonid is subject to heavy wear, and in old animals is worn down to the level of the talonid. The tooth is strongly attached in the jaw and seldom lost.

$M_2$ is a moderately large and prominent tooth. It seems to receive relatively little wear, and it is often lost from fossil jaws. $M_3$ is a tiny, almost vestigial tooth that is usually lost in fossil jaws. Even the alveolus is sometimes absent, indicating that the tooth was lost during the life of the animal.

Measurements of length of the lower tooth rows do not include $M_3$. Measurements of length of individual teeth were taken parallel to the long axis of the tooth, regardless of its position in the tooth row, and breadth was measured at right angles to the length.

*Postcranial skeleton.*—Most vertebrae are so fragmentary that recognition of their place in the spinal column is uncertain or impossible. The following are identified with reasonable certainty: Atlas (MU 7560), Axis (MU5693), third cervical (MU3872), fifth cervical (MU4504), seventh cervical (MU 5692), eleventh thoracic (MU5503), twelfth thoracic (MU5686), and thirteenth thoracic (MU 5507). These vertebrae are slightly stouter and heavier than vertebrae of the modern coyote (*Canis latrans*) but are otherwise quite similar.

Some measurements of the atlas are: length of top of neural arch, 14.5; length of bottom of neural arch, 11.3; least breadth just posterior to transverse processes, 39.5; greatest breadth across transverse processes, 93.7; maximum breadth, internal, of articular surfaces for occipital condyles, 40.6; breadth across articular surface for axis, 35.1.

Some measurements of the axis are: length of centrum to end of odontoid process, 48.0; breadth across articular surfaces for atlas, 31.9; breadth across posterior zygapophyses, 35.2; breadth of posterior epiphysis of centrum, 19.0. The anterior part of the neural spine has been broken away and lost. Measurements of other vertebrae are given in Table 4.

The proximal portions of two scapulae apparently belong to *Osteoborus*, but only one of these (MU 6021) belongs to an adult. Measurements: anteroposterior diameter of glenoid fossa, 33.0; transverse diameter of glenoid fossa, 21.8; least constriction of neck above glenoid fossa, 26.4.

The limb material is sufficient to show that the humerus and femur were considerably longer and much stouter than the bones of a coyote of comparable size. Radius, ulna, and tibia (no complete fibulae were found) are almost the same length as the comparable bones in the coyote, but are much stouter. Relatively, the humerus and femur of the coyote are shorter than those of *Osteoborus*. The humerus of *Osteoborus* differs radically in structure from that of *Canis*. The distal end is greatly expanded. The olecranon fossa is very wide, and a large entepicondylar foramen is present. This foramen is absent in *Canis*. The proximal end of the humerus of *Osteoborus cyonoides* is unknown.

The other long bones are typically canid, except for their unusual thickness. The metapodials are relatively short and thick but otherwise similar to the metapodials of the coyote.

### Canid, species undetermined
### (Fig. 2)

Among the specimens obtained at the Coffee Ranch is the partial skull of a large canid. The skull is broken across the preorbital region, just anterior to the termination of the nasals. Both zygomatic arches are missing, though the left glenoid process is present. Part of the parietal of the right side is broken away. The remainder of the skull is well preserved.

The interorbital region is broad and the postorbital processes are wide and strong. The postorbital region is strongly constricted. The lamb-doidal crest is long, reaching maximum height at the anterior margin of the parietals and then decreasing in height posteriorly, becoming obsolete just ahead of the occipital crest. The occipital crest is strong and broad, transversely truncated posteriorly. Preserved cranial foramina are similar to those of *Canis* and *Osteoborus*.

The preserved part of the skull is extremely slender and elongate. It bears a distinct resemblance to the skull of *Tomarctus euthos* (McGrew) from the lower Pliocene Burge fauna of Nebraska. The skull is clearly of a young animal, and cranial sutures are distinct.

Donald E. Savage has examined this specimen and believes it to be a large late juvenile *Osteoborus*. The specimen is as large as the comparable part of an adult *Osteoborus* (length from end of nasals to end of occipital crest 124.2 vs. 135.0 in *Osteoborus*). The posterior and ventral parts of the specimen resembled the skull of *Osteoborus* except that the lambdoidal crest is much lower. In canids the lambdoidal crest increases in size and prominence with age, especially in male animals.

The greatest difference between the fragmentary skull and the skull of *Osteoborus* is the nature of the frontal region. In *Osteoborus* the interorbital region is much wider and the frontals are greatly bulged. In the fragmentary skull the interorbital region is narrower (38.9 mm. vs. 50.9 in *Osteoborus*) and the frontal curvature is as smooth and gentle as in a modern red fox (*Vulpes vulpes*). If a straight line from the posterior ends of the nasals to a point on the lambdoidal crest 100 mm. posterior to the
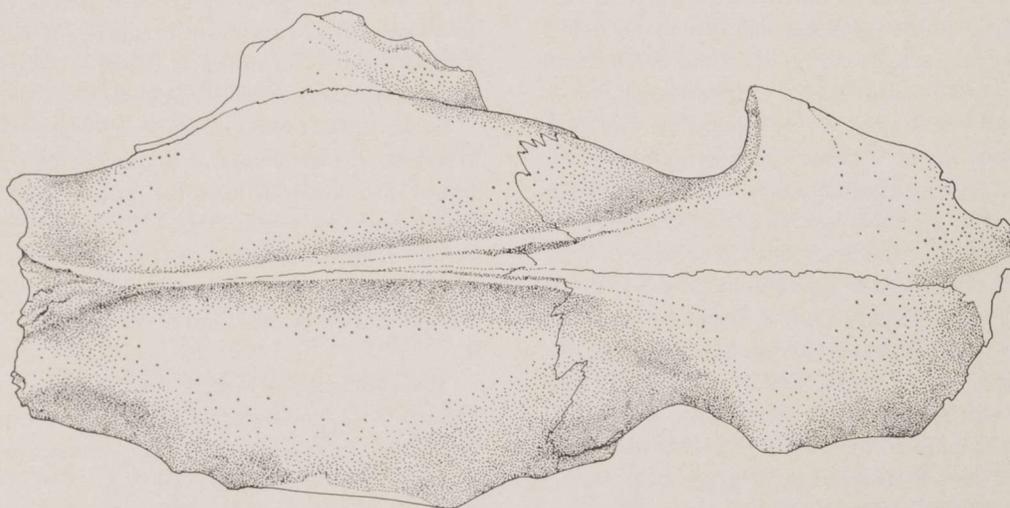


Fig. 2. Cranium of an undetermined canid (TMM 41261—4), in dorsal view. X 1.0 natural size.

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nasals be taken as a base line, the frontals of *Osteoborus* (young-adult specimen) arch 19 mm. above the base line while the frontals of the fragmentary skull rise only 7 mm. above the base line.

If the fragmentary skull belonged to *Osteoborus*, it suggests that the distortion of the frontal region of the skull, typical of this genus and *Borophagus*, of the upper Pliocene, developed rather abruptly between the late juvenile and early adult stages. I know of no comparable changes in the skull during ontogeny of modern canids. If the fragmentary skull is not a juvenile *Osteoborus*, it may represent a late surviving species of *Tomarctus*, otherwise unknown. It is not *Canis*.

## *Indarctos oregonensis* Macdonald
### (Figs. 3–4)

Remains of a very large bear are among the rare elements of the Coffee Ranch local fauna. Matthew and Stirton (1930a) listed *Hyaenarctos* from the Coffee Ranch but the material has never been figured or described. The present collection includes a fragmentary lower jaw with $P_4$ to $M_3$, an isolated unworn lower $M_1$, and two fragmentary lower molars.

DESCRIPTION.—A small part of the ascending ramus is present in the jaw (TMM41261–1), and only a small amount of the upper margin of the mandible holds the molars in place. $P_4$ was in place in the matrix but free of the bone. The teeth are beautifully preserved and almost unworn. They are huge, even when compared with those of an Alaskan brown bear.
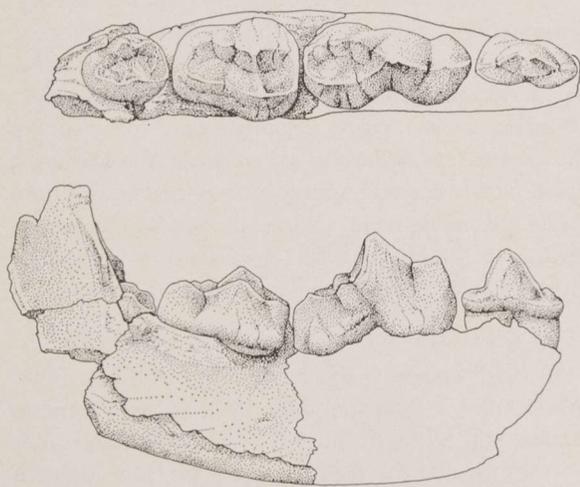


Fig. 3. Lower jaw of *Indarctos oregonensis* with P4–M3 (TMM 41261–1). X .50 natural size.

The central cusp of $P_4$ is high. The anterior cusp is low but trenchant. The posterior cusp is poorly developed. There is a low cingulum about the posterior third of the tooth, posterior to the central cusp. The enamel has many faint vertical striations, most pronounced on the labial side of the tooth.

$M_1$ is elongate. The trigonid is narrower transversely than the talonid. There is a low cingulum on the lingual side of the paraconid. The carnassial notch is distinct but narrow, with the posterior edge of the blade of the paraconid and the anterior edge of the blade of the protoconid in contact for a vertical height of approximately 5 mm. The metaconid is a small, rounded cone on the lingual side of the tooth, posterior to the protoconid. The entoconid is smaller and posterior to the metaconid. The post-entoconid cusp is still smaller and posterior to the entoconid. The three cusps, metaconid, entoconid and post-entoconid, form an evenly stepped series on the lingual side of the tooth. The hypoconid is a low, elongated cusp, as long as but lower than the entoconid and post-entoconid together, on the opposite side of the tooth. There is a low intra-protoconid-hypoconid cusp opposite the metaconid. There is a low, faint cingulum on the labial side of the talonid. The enamel is finely wrinkled and vertically striated, especially on the labial side.

The $M_2$ is somewhat triangular, with the trigonid much broader than the talonid. In American Pleistocene and Recent bears (*Ursus, Tremarctos, Arctodus*, etc.) this tooth is rectangular or hourglass shaped. The metaconid is very large, larger and higher than the protoconid. The paraconid is obscure or absent. Inward-reaching crests from metaconid and protoconid meet in a low "V" to form a loph across the tooth and separate the occlusal surface into two distinct basins. The anterior basin is closed anteriorly by a ridge-like cingulum. The transverse loph on the $M_2$ of the Hemphill bear is quite similar to that of *Arctodus* (Kurtén, 1963). The entoconid is small and the post-entoconid is equal in size. The hypoconid is larger and higher. A narrow ridge or cingulum connects the hypoconid with the post-entoconid around the posterior border of the tooth to close the basin of the talonid. The enamel of the tooth is finely wrinkled and vertically striated.

The crown of $M_3$ is a rounded triangle in occlusal view. In the specimen, the tooth is set so that its occlusal surface is parallel with the occlusal surface of $M_2$, but the tooth is so far back in the jaw that all but its anterior edge was buried in the

rising curve of the ascending ramus of the mandible. Considerable bone had to be ground away to expose the crown. The root appears to be developed. Either the tooth was not completely erupted or it was "impacted" in the manner of some human lower third molars.

The protoconid is a low swelling on the labial side of the tooth. The remainder of the crown consists of a wrinkled basin surrounded by a narrow cingulum or ridge that is continuous with the external (labial) edge of the protoconid.

The isolated $M_1$ (TMM41261–2) is also from the right side. It is smaller than the $M_1$ of TMM 41261–1, and the talonid basin is deeper. The roots had not developed. The lingual border of the tooth, between the paraconid and protoconid, is more notched than in TMM41261–1, so that the trigonid and talonid are not so distinctly set off from one another. In other respects the tooth is like TMM41261–1. Metaconid, entoconid and postentoconid are similarly stepped.

Comparison of the present material with *Indarctos oregonensis* Merriam, Stock and Moody (1916), and *Hyaenarctos gregoryi* Frick (1921) is not possible, for those species were based on upper teeth. *Indarctos nevadensis*, however, is based on a lower jaw with unworn canine and $P_1$–$M_1$. It is directly comparable with the Coffee Ranch teeth, but only $P_4$ and $M_1$ are present in both specimens. The teeth in the jaw from Nevada are slightly smaller but are so similar in shape and details of tooth structure, including the stepped metaconid-entoconid-postentoconid on $M_1$, that identity seems probable. Individual variations of greater extent are seen in the $P_4$ and $M_1$ of modern *Ursus*. Whether *I. nevadensis* is actually a species distinct from *I. oregonensis* remains to be determined when lower jaws of the latter are discovered. For comparison of *I. nevadensis* with old-world species see Macdonald (1959).

*Agriotherium schneideri* Sellards, described from the Pliocene Bone Valley formation of Florida, is a bear of approximately the same size as the specimen from the Coffee Ranch. The holotype is a right lower jaw with $P_4$–$M_2$ and the alveolus for $M_3$. The teeth are worn and it is difficult to determine whether the cusps of the talonid of $M_1$ were "stepped" like those of the Texas bear.

The $M_2$ of the holotype jaw of *A. schneideri* differs strikingly from the Coffee Ranch specimen in that talonid and trigonid are approximately equal in breadth and the tooth is almost rectangular. In
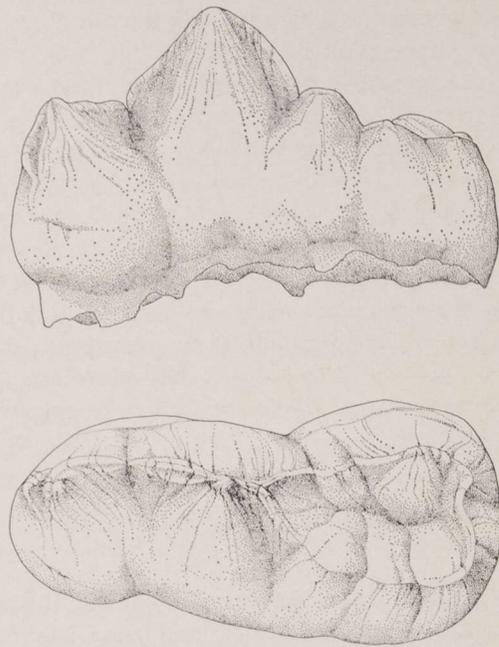


Fig. 4. Lower carnassial of *Indarctos oregonensis* (TMM 41261–2) in lingual and occlusal views. X 1.5 natural size.

the bear from Texas the $M_2$ is more triangular. Maximum breadth is near the base of the enamel, and not affected by wear until extreme old age.

Savage (1941) figures and give measurements of the teeth of a lower jaw of a bear from the Pliocene Optima local fauna of Oklahoma. The measurements of the $M_2$ are similar to those of the Coffee Ranch specimen. Anteroposterior and transverse diameters of the $M_2$'s of the specimens from Texas, Oklahoma and Florida are respectively: 34.2 x 25.5; 32.5 x 25.1; 26 x 20.

Donald E. Savage has suggested (personal communication) that all of the American Pliocene bears may belong to one genus, namely *Agriotherium*. Certainly the group is in need of revision. Pending such revision it seems best to refer the Texas bear to *Indarctos oregonensis*, the species it most closely resembles among described forms. Savage's specimen from Oklahoma would appear to belong to the same species. *Agriotherium schneideri* appears to be at least specifically distinct.

*Pliotaxidea* cf. *P. nevadensis* (Butterworth)

A small badger is represented by two lower jaws. MU1334 is a right mandible lacking the ascending ramus and all teeth but $M_1$. The alveoli and roots of the other cheek teeth are present. The molar is well worn and closely resembles the tooth from Oklahoma figured by Hesse (1936:60) and later re-

ferred to *Pliotaxidea nevadensis* by Hall (1944:15). The tooth is 10.3 mm. long and 5.5 mm. wide.

MU8066 is a left mandibular ramus, complete except for the alveoli of the incisors. Only $P_2$ and $P_3$ are present. The roots of most of the other teeth are visible in their alveoli. The distance from the anterior edge of the canine alveolus to the posterior edge of the articular condyle is 48.6 mm. The distance from the anterior edge of the canine alveolus to the posterior edge of the alveolus of $M_2$ is 32.1 mm. The maximum depth of the jaw beneath $M_1$ is 5.7 mm.

Hall (1944) has shown that the Pliocene old-world *Parataxidea* Zdansky is distinct from the Pliocene American *Pliotaxidea*, and that the former is close to the ancestry of the modern old-world *Meles* while the latter may be the direct ancestor of the modern American *Taxidea*. Long (1965) presents evidence that *Taxidea* and *Meles* should be placed in separate sub-families.

## *Plesiogulo marshalli* (Martin)
## (Fig. 5)

This wolverine-like mustelid is represented by the posterior half of a lower first molar (MU5132) and



Fig. 5. *Plesiogulo marshalli* (TMM 41261–12), upper MI in occlusal view. X 1.5 natural size.

the unworn crown of an upper first molar (TMM-41261–12). The fragmentary lower tooth is almost identical in size and details of structure to the tooth

in the photograph of the holotype lower jaw (Martin, 1928). The upper tooth lacks roots, but the crown is perfect. Its greatest dimensions are $19.5 \times 16.3$ mm. The least breadth across the median constriction is 9.3 mm. The enamel, even on the strong cingulum and low cusps, is delicately wrinkled and denticulate.

A skull without teeth, MU8068, is also referable to this species. It is crushed, and has lost both zygomatic arches and other important details. It shows, however, that the skull of *P. marshalli* was similar in shape and in general construction to the skull of the modern wolverine: broad through the rostrum and across the interorbital region with a large infra-orbital foramen, and narrow, cylindrical braincase.

## *Pseudaelurus hibbardi*, new species
## (Fig. 6)

*Holotype.*—Left lower jaw (TMM41261–3), lacking canine, front of canine alveolus and anterior tip of jaw with incisors, and all of ramus posterior to $M_1$. Most of symphysis, $P_3$, $P_4$ and $M_1$ present.

*Locality.*—Coffee Ranch quarry, Coffee Ranch local fauna, from gray sand bed six feet beneath volcanic ash layer, middle Pliocene, Hemphill County, Texas.

*Fauna.*—Hemphillian.

*Diagnosis.*—Size of large puma. Carnassial notch open in upper $P^4$ and lower $M_1$; $P_1$ absent; vestigial $P_2$ possibly present; $P_3$ and $P_4$ small and thin but $M_1$ relatively very large. Ramus straight, deep and stout, especially anteriorly. Symphysis strong, with angle between ventral and anterior surfaces of ramus acute. Metaconid on lower $M_1$ of moderate size.

*Referred material.*—Right lower jaw fragment (TMM41261–5) with part of canine alveolus, alveolus of $P_3$, a well-preserved $P_4$, and part of the
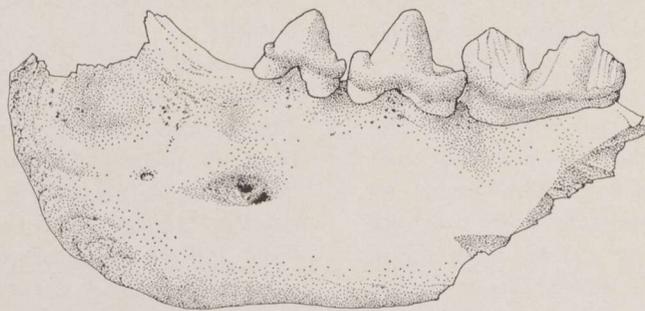


Fig. 6. Lower jaw of holotype of *Pseudaelurus hibbardi* with P3–MI (TMM 41261–3), in labial view. X 1.0 natural size.

alveolus of $M_1$; isolated upper carnassial (MU 6389); scapula (TMM41261–15); humerus (TMM41261–16); radius (TMM41261–17); astragalus (TMM41261–19); two calcanea (TMM 41261–21, 22); navicular (MU6389).

DESCRIPTION.—The ramus of the lower jaw is thick and deep, especially anteriorly. The alveolus of the canine is very large, of round-oval shape, and the jaw is almost bulbous about the canine alveolus. The angle between the ventral border of the jaw and the front of the jaw is acute. The diastema is short, and contains a tiny pit that may be an alveolus for a vestigial $P_2$. The lower $P_3$ has a posterior basal cusp but only a slight swelling in place of an anterior basal cusp. There is no posterior cingular cusp. Lower $P_3$ and $P_4$ are relatively small and thin, and closely placed in the tooth row. Lower $P_4$ has anterior and posterior basal cusps. Lower $M_1$ large and heavy with broadly open carnassial notch and moderately well-developed metacone. Referred upper $P^4$ with broadly open carnassial notch. Referred postcranial elements exactly comparable to bones of large puma.

COMPARISONS.—Hibbard (1934) has described *Adelphailurus kansensis* from the Edson Beds, Sherman County, Kansas, and *Pratifelis martini* from the Lost Quarry, Wallace County, Kansas; both species are from deposits of Hemphillian age.

*Adelphailurus kansensis*, as noted by Hibbard (1934: 246) is not closely related to *Pseudaelurus*. It is, instead, very close to *Panthera*. A cast of the holotype was compared with the skull of an African leopard, and the resemblances are numerous. Differences include a shorter diastema, more laterally compressed canine, very slightly more open carnassial notch, and some minor details of the teeth. *Adelphailurus* may well be the direct ancestor of the leopard, and the genus is not strongly differentiated from *Panthera*.

Differences between *Adelphailurus kansensis* and *Pseudaelurus hibbardi* are numerous. In the upper $P^4$, the carnassial notch of *P. hibbardi* is broadly open rather than almost closed. The diastema of the upper jaw of *Adelphailurus* is very short, and when the lower jaw of a leopard is placed in occlusion with it, the canine of the leopard will not enter the diastema of the maxillary. With canine removed, the leopard jaw articulates fairly well with the *Adelphailurus* maxillary, and the teeth almost occlude. The lower jaw of *Adelphailurus* was almost certainly similar to the leopard lower jaw but lighter in build, and the lower canine must have

been much smaller. In *Pseudaelurus hibbardi* the canine was enormous and the lower jaw very heavy. When placed with the maxillary of *Adelphailurus*, the teeth do not occlude and the lower canine is almost exactly below the upper canine.

The holotype of *Pratifelis martini* is a left lower jaw, and is thus comparable with the type of *Pseudaelurus hibbardi*. In *Pratifelis* the lower jaw is slender, light and curved. In *P. hibbardi* the jaw is straight, heavy and deep. The lower canine of *Pratifelis* was small, in *P. hibbardi* it was very large. The lower $P_3$ and $P_4$ of *Pratifelis* are quite similar to those of *P. hibbardi* except that the $P_3$ of *Pratifelis* has a posterior cusp and a posterior cingular cusp. In *P. hibbardi* there is only a posterior basal cusp. Both $P_3$ and $P_4$ of *Pratifelis* are thinner than the premolars of *P. hibbardi*. The $M_1$ of *P. hibbardi*, on the other hand, is both longer and wider than the molar of *Pratifelis*. A striking difference is the broadly open carnassial notch of *P. hibbardi*. *Pratifelis* was a highly aberrant cat. It does not belong in the genus *Pseudaelurus*, and shows little similarity to *P. hibbardi*. Both were cats approximately the size of the puma.

*Pseudaelurus thinobates* Macdonald, known from Clarendonian and early Hemphillian faunas of California, Texas and Oklahoma (Kitts, 1958), resembles *P. hibbardi* in several respects, including the heavy symphysis, large, deep ramus, swollen anteriorly for the enormous canine, and the steep angle of the anterior face of the jaw. The carnassial notch, in *P. thinobates*, is broadly open as it is in *P. hibbardi*. *P. thinobates*, however, is much larger than *P. hibbardi*, being approximately the size of an African lion rather than the size of a large puma.

Kitts (1958) has placed *P. thinobates* in a new genus, *Nimravides*. The characters of *P. hibbardi* and *P. pedionomus* Macdonald bridge the gap between *P. thinobates* and typical *Pseudaelurus*, such as *P. intrepidus* (Leidy). *Nimravides* is best considered a subgenus until the late Tertiary felids are revised.

*Pseudaelurus pedionomus* Macdonald was described from the lower Pliocene of Nebraska. Among described fossil cats, this form is most similar to *P. hibbardi*. In both the ramus is deep and heavy, and the canine large. The two are of similar size. In *P. hibbardi* the jaw is more swollen anteriorly, and the canine alveolus is larger. $P_1$ and $P_2$ are present in *P. pedionomus*, but only a tiny $P_2$ may occur in *P. hibbardi*. The diastema (C-P3) is much less in *P. hibbardi* than in *P. pedionomus*.

The premolars of *P. pedionomus* are longer and wider than those of *P. hibbardi*, and the molar is slightly longer and wider. The metaconid is better developed in *P. hibbardi* than in *P. pedionomus*. In *P. pedionomus* there is a distinct gap between P₃ and P₄, but no such gap occurs in *P. hibbardi*. There are two mental foramina in *P. pedionomus*, one beneath the center of the diastema and one beneath the anterior root of P₃. In *P. hibbardi* there is a single mental foramen beneath the anterior root of P₃.

Some of the differences listed may be subject to individual and sexual variation. The enormous canine alveolus and swollen anterior end of the ramus in *P. hibbardi* are present in two different specimens, however, and are probably valid species characters. They readily serve to separate *P. hibbardi* from *P. pedionomus*. *P. pedionomus*, *P. thinobates* and *P. hibbardi* seem to represent a line of large, heavy-jawed cats (subgenus *Nimravides*) with *P. hibbardi* the last known member of the group.

The postcranial elements referred to *P. hibbardi* are splendidly preserved and almost complete. The elements are so similar to the same bones of a large puma, even to details of shape of muscle scars and curvature of scapular blade, that one may suppose that the body shape was very much like that of the puma. Macdonald (1948a) thought that *P. pedionomus* was lynxlike, with some pumalike characters. I would judge *P. hibbardi* to have been quite puma-like in its habits.

#### *Machairodus (Heterofelis) catocopis*   Cope
#### (Plate 1; Figs. 7–11)

Remains of a large saber-toothed cat from the Coffee Ranch quarry all seem to pertain to a single species. Materials include a largely complete skeleton, several upper and lower jaws, and numerous isolated teeth and bones. Burt (1931) has briefly described and figured a number of bones of *Machairodus catocopis* from the Coffee Ranch. The new material is much superior to that available to Burt, and it is possible to correct some errors in his work and greatly extend the knowledge of this interesting cat.

DESCRIPTION.—The most important specimen is the skeleton TMM41261-8. It is of an old saber-tooth, possibly a female, for some of the bones
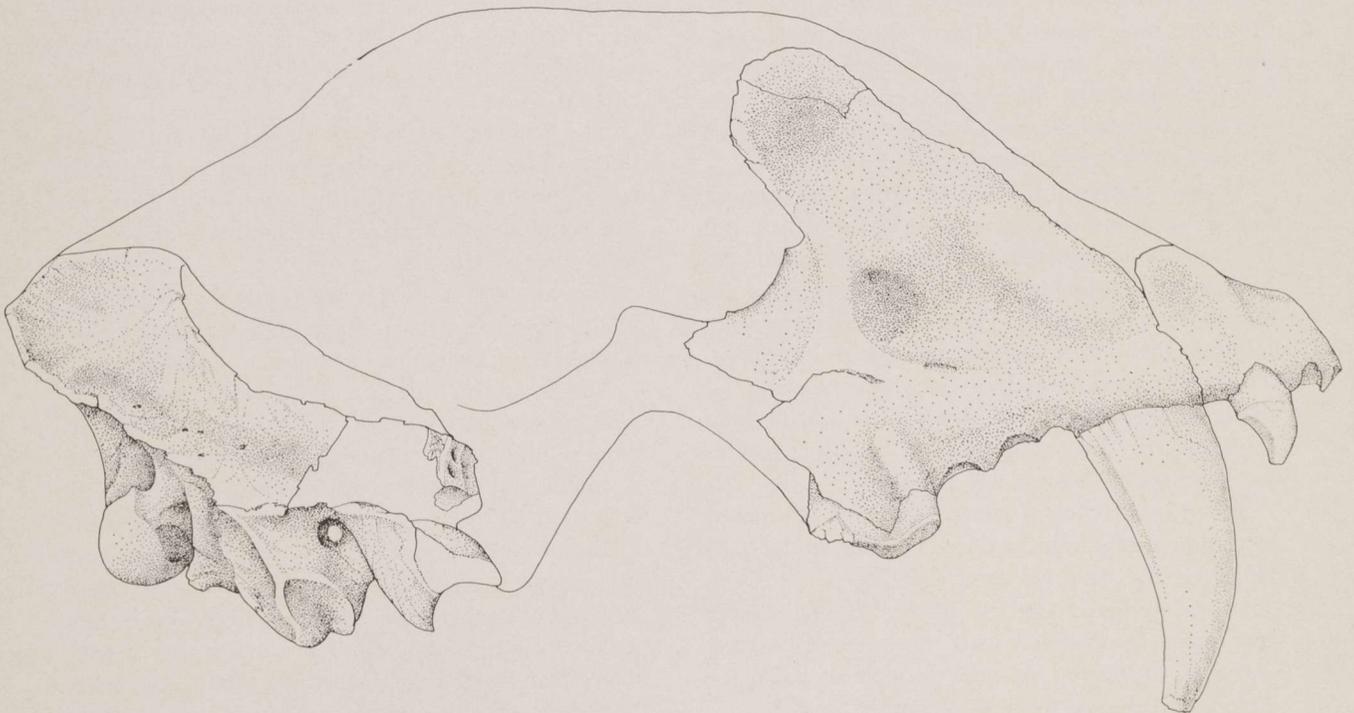


Fig. 7. Restoration of skull of *Machairodus catocopis* based on the basicranium and right maxilla of TMM 41261–8, and on associated premaxilla probably belonging to the same individual. Approx X .50 natural size. The length of the gap in the center of the skull was determined by articulating the lower jaw of TMM 41261–8 in the glenoid fossa and placing upper and lower dentitions in occlusion.

are only of moderate size when compared with other specimens from the quarry. The bones were found articulated or closely associated, and much of the skeleton was removed in a single large block of matrix (Plate 1). The following descriptions, unless otherwise stated, are based on this specimen.

In the following accounts, comparisons are primarily with the bones of *Smilodon californicus* Bovard, the saber-tooth from the Rancho La Brea, of California. *Smilodon* is not particularly close to *Machairodus catocopis* in morphological details, but it is the best-known of the saber-toothed cats. Nearly all of the bones of the skeleton have been figured in the classic work of Merriam and Stock (1932), and the tables in that publication show the expected range of variation in measurements of the skeleton elements. Bones from the Rancho La Brea are preserved in many museum collections, and most of the bones of the skeleton of *Smilodon californicus* were available for direct comparison.

The skeleton of *Homotherium serum* (Cope), from the late Pleistocene deposits in Friesenhahn Cave, Texas, has been described in the important work by Meade (1961). (For use of *Homotherium* Fabrini rather than *Dinobastis* Cope, see Churcher, 1968.) *Machairodus catocopis* resembles *Homotherium serum* more closely than it does *Smilodon*. However, few bones of *Homotherium* were available for direct comparison with *Machairodus*, and most of the stated differences between *Machairodus catocopis* and *Homotherium serum* are based on the figures and measurements given by Meade.

*Skull.*—The skull had been stepped on, presumably by a large mammal such as a rhinoceros, and the anterior left portion destroyed. The top of the braincase, including all but the posterior inch of the sagittal crest, is missing. The glenoid processes were found in the matrix beneath their natural positions. The right maxillary with canine and carnassial, and premaxillary with P³ and alveoli of I¹ and I², were found nearby. The occipital and basicranial regions are almost complete and well preserved.

There is no point of contact between the maxillary and basicranium. In the restoration of the skull (Fig. 7), the distance represented by the missing bone was approximated by placing the right lower jaw ramus in occlusion with the upper carnassial, and then fitting the articular condyle of the mandible in the glenoid fossa of the basicranium.

The skull is long and slender, like the skull of *Homotherium*. The occipital crest projects far backward, as it does in *Homotherium*, and is constricted anteriorly, behind the braincase, more than in *Smilodon*. Only the posterior part of the sagittal crest remains, but it is prominent as in other large cats. The edges of the occipital crest have been damaged but it is apparent that the crest, in posteroventral view, is broad and rounded, not triangular. The infraorbital foramen is large and oval, as in *Homotherium*. The premaxillary is strong and juts forward, more as in *Homotherium* than as in *Smilodon*.

The braincase appears to have been more expanded, and rounded at the sides, than in *Smilodon*. The parts of the sides that remain are almost vertical, even slightly inclined outward above. In *Smilodon* the sides converge above, so that the braincase appears almost triangular in section.

The basicranium is well preserved and important. The ventral surfaces of the glenoids are separated from the top of the mastoid processes by a space of 10 mm. In a *Smilodon* of comparable size the separation is less, about 6 mm.

The audital bulla of the left side is complete, and that of the right side partly so. The bullae are relatively larger than in any available specimen of *Smilodon*, but their size is known to vary widely in *Smilodon*.

The opening to the eustachian canal is wide (12 mm.) but narrows swiftly to a narrow slit, partially divided internally by a sharp ridge on the posterior surface.

The external auditory meatus is almost round and is situated, as in *Smilodon* but not as in the true cats (*Panthera*, *Felis*), in the deep cavity between the zygomatic arch above and the mastoid process below.

The jugular foramen is in a triangular depression at the posterointernal corner of the audital bulla. This area is usually more rounded in *Smilodon*.

The foramen ovale is a deep, round opening, 6 mm. wide, separated from the eustachian canal by a bar of bone 3.6 mm. wide. The foramen rotundum is similar to the foramen ovale in shape and size and is located 10.7 mm. anterior to it. There is a groove in the alisphenoid between the two foramina, and the groove is partially spanned by a bar of bone. The bar of bone is present on both sides, and is thus a short alisphenoid canal. The canal is not as well developed as in dogs. Mawby (1965) has mentioned the existence of this canal in *M. catocopis*. It appears to be absent in other sabertooths, and in *Felis* and *Panthera* as well. It may be simply a persistent primitive character in *M. catocopis*.

*Superior dentition.*—The specimen best showing the upper dentition is TMM41261–10, the upper jaw of a young-adult sabertooth with the alveolus of I¹ broken away, both I² and I³ present canine alveolus and P³ and P⁴ present (Fig. 8). An associated canine probably belongs to the same jaw. The following description is based primarily on this specimen, but is augmented by TMM41261–8 and other specimens when helpful.

I¹ is not preserved, but the alveoli in two premaxillaries suggest that it was a bit smaller and more compressed than I². I² is a strong tooth with a heavy internal cingulum and large basal cusps at anterior and posterior margins. It is a much stronger and more triangular tooth than the I² of *Smilodon*. The I² of *Homotherium* appears to be similarly large and triangular but has a basal cusp only on the posterior edge. This may be a minor and variable feature.

I³ is a large, strong triangular tooth, as it is in *Homotherium*. It has a strong basal cusp on the anterior margin, but posteriorly there is only a heavy cingulum and a low swelling in place of a basal cusp. In *Homotherium* there is a strong posterior cusp. The anterior edge does not seem to be serrate, as it is in *Homotherium*. The posterior edge is serrate for less than half of its length. Resemblance to *Homotherium* is strong; differences are minor and probably subject to individual variation.

The upper canine is compressed, relatively as much as in *Smilodon*. It is serrate anteriorly and posteriorly for the entire length of the enamel. It is relatively and actually a much smaller tooth than it is in *Smilodon*, but is a bit longer than the canine of *Homotherium*.

Burt (1931:264) described the alveolus for a single-rooted P² in *Machairodus* and characterized the genus (p. 271) as having P² "vestigial or absent." None of the maxillaries on hand have an alveolus for P² and all are well preserved in the area such a tooth would occupy. The presence of the upper P² must have been a rare or abnormal occurence in *Machairodus*.

P³ is a much larger tooth than it is in either *Homotherium* or *Smilodon*. There are three major cusps and a well developed posterior basal cusp, plus a strong anterior cingulum with several small cusps along its anterior edge.
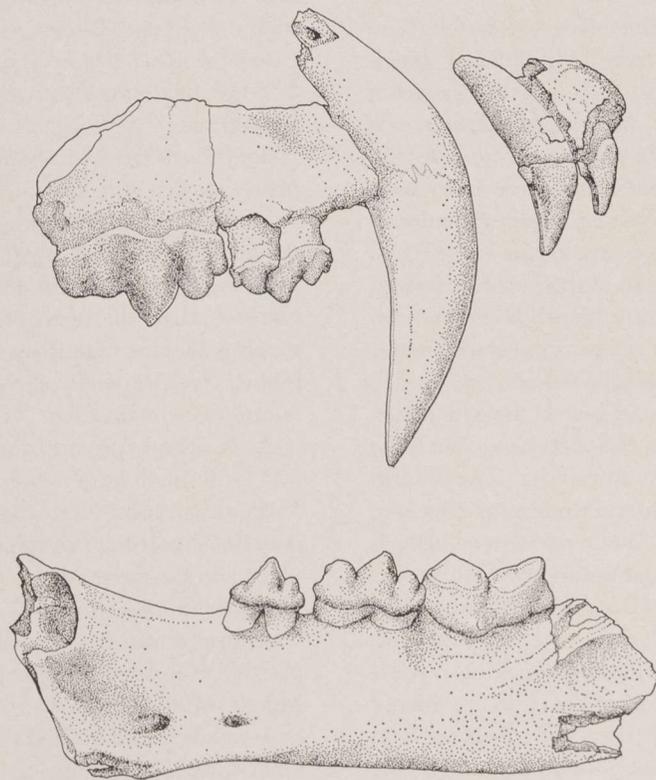


Fig. 8. Right upper (TMM 41261–10) and left lower (TMM 41261–9) jaws of young adult *Machairodus catocopis*, in lateral view. X .50 natural size.

P$^4$ is very similar to the same tooth in *Smilodon*. The paracone averages shorter and the metacone longer, but both of these characters are variable in *Smilodon*. The P$^4$ appears to be larger in *Machairodus* than in *Homotherium*.

Burt (1931:264) has termed the uper P$^4$ of *Machairodus* "relatively longer, narrower and more brachydont than the corresponding tooth in *Smilodon*." Measurements indicate that the carnassial of *Machairodus* falls into the upper range of measurements of *Smilodon* in length, and near the mean in width. The tooth does not seem to me to be more brachydont than that of *Smilodon*.

The internal (protocone) root of P$^4$ is said by Burt to be better developed than it is in *Smilodon*. This is not always true, and in one tooth the internal root is firmly fused to the anterior root for the entire length. In *Homotherium* the upper P$^4$ lacks the internal root.

The upper cheek teeth of *Machairodus* are primitive in having a larger, more complicated P$^3$ than either *Smilodon* or *Homotherium*, having the internal root present on P$^4$, and in being more upright, less backward-inclined. The upper dentition is not so primitive, however, as it appeared from the few specimens available to Burt.

*Mandible.*—The mandible (Fig. 8) is long and straight, as long as the longest mandibles of *Smilodon* and *Homotherium*. It is relatively deep, but thinner than in *Smilodon*. Mawby (1965:585) has characterized the mandible of *Machairodus* as relatively slender, but the specimens show it to have about the proportions of *Smilodon* and *Homotherium*. The average length is about the same as in those genera, while the depth of the jaw averages, at most places, in the upper range of *Homotherium* measurements and in the upper range or greater than the same measurements of *Smilodon*.

The lateral flanges extend below the symphysis, as in both *Smilodon* and *Homotherium*, but they are not well developed anteriorly. They form rounded ridges on the anterior edges of the jaw, rather than keels of bone. The articular condyle is low, as in *Homotherium*, but not so low as in *Smilodon*. The angular process of *M. catocopis* is less inflected than that of *Smilodon*. The most striking difference separating the mandible of *M. catocopis* from that of the two Pleistocene cats is the relatively high, sloping, triangular, coronoid process. The coronoid process of *Smilodon* is much lower, and that of *Homotherium* lower and flatter yet.

There are two mental foramina in *M. catocopis*: a large anterior foramen located beneath or slightly anterior to the center of the diastema, and directed internoposterioly, and a posterior foramen, oval in shape and located just beneath the anterior root of P$^3$. The foramina vary in size from specimen to specimen but are uniform in their positions. Both are near the lower margin of the jaw with the posterior foramen usually, perhaps always, lowest. Similar foramina are seen in Meade's figure of *Homotherium* (1961: Plate 1), and are described in *Ischyrosmilus* by Mawby (1965). *Smilodon*, however, has a single large mental foramen located near the center of the diastema, and sometimes an additional small foramen located farther forward.

*Inferior dentition.*—The lower incisors of *Machairodus catocopis* are not present in any of my specimens, nor in any of Burt's specimens. The lower canines are present, though worn, in two rami. In both the canines are round in cross-section, both through the root and across the enamel of the crown. The alveolus is also round. These lower canines are not at all as described by Burt. The supposed lower canine figured by Burt (1931: Plate 45) is flat and triangular, with a root longer than the depth of the lower jaw of *Machairodus* at the alveolus of the canine. The elongated alveoli shown in Burt's Plate 46 may result from breakage. The canine of *Machairodus* is essentially as in *Smilodon*, but the teeth are too worn to disclose details of basal cusps.

The cheek teeth of *Machairodus catocopis* are set nearly vertically in the jaw, thus differing markedly from both *Smilodon* and *Homotherium*, in which the teeth are strongly inclined posteriorly. The teeth are thinner, less curved and folded on their lateral surfaces, than the teeth of *Smilodon*; they are not brachyodont as stated by Burt, but are relatively higher than the teeth of *Smilodon*, and perhaps of *Homotherium* as well.

P$_3$ is always present, larger than in *Homotherium*, and much larger than in the rare specimens of *Smilodon* that have this tooth. There are three main cusps and a strong posterior cingulum. The tooth is placed on the outer edge of the jaw in *Machairodus*, labial to the longitudinal axis of P$_4$ and M$_1$. It is separated from P$_4$ by a short distema. A similar position is figured for the jaw of *Homotherium* by Meade (1961: Plate 1), but in *Homotherium* the P$_3$ is smaller and tipped backward rather than almost upright in the jaw.

P$_4$ is large, about as in *Smilodon*, but is simpler, with three major cusps, a strong posterior cingulum,

and small posterior cingular cusp. The $P_4$ of *Machairodus* is similar to that of *Homotherium* but not so strongly tipped backward in the jaw.

$M_1$ resembles the same tooth in *Smilodon* but is relatively longer, more slender, and less inclined posteriorly. The protoconid blade is longer than the paraconid blade, as in *Smilodon*. There is no metaconid and, as Burt concluded, *M. catocopis* probably does not have a metaconid on the $M_1$.

The lower dentition of *Machairodus catocopis* is of a simple and generalized marchairodont type. There are no aberrant features. There is a greater resemblance to teeth of *Homotherium* than to *Smilodon*.

*Vertebrae.*—The vertebral formula of *Machairodus catocopis* appears to have been: cervicals, 7; thoracics, 13; lumbars, 7; sacrals, 3; caudals, 2 plus ?.

Burt (1931) has figured the damaged axis and atlas of *Machairodus* but the other vertebrae were hitherto unknown. The skeleton (TMM41261–8) lacks only the fourth, ninth and tenth thoracic vertebrae and all caudals posterior to C2. Most of the vertebrae, especially the thoracics, have suffered some damage to projecting parts, such as neural spines and transverse processes. The damage is often confined to the side of the bone that lay upward in the matrix.

The cervical vertebrae are approximately the size of those of *Homotherium*, but are much smaller than the cervicals of *Smilodon*. The latter are powerful, with high neural spines and broad, wide transverse processes. The vertebrae of *Homotherium* are more like those of *Machairodus* but, though no larger, appear more robust. The sixth to seventh cervicals of *Homotherium* are unknown, but the third to fifth have broader, stronger transverse processes and apparently had longer, stronger neural spines. The neck and neck musculature of *Machairodus* was probably not as powerful as in *Homotherium* and *Smilodon*.

The atlas (Figs. 9, 10) of *Machairodus* differs markedly from that of both *Smilodon* and *Homotherium* in having a much broader, more catlike, transverse process. As in the true cats, the anterior margin of the process extends outward and then sweeps backward in a smooth curve. In the Pleistocene saber-tooths the anterior margin of the transverse process is inclined steeply backward, forming a narrow blade. The process of *Machairodus* extends posteriorly to about the level of the middle of the axis, as it does in other saber-tooths. The dorsal surface of the neural arch is as in *Smilodon*, with a strong notch anteriorly. The ventral surface is narrow but has a strong median spine posteriorly. The neural canal is marked internally by large shelf-like spurs of bone at the upper level of the odontoid process. The spurs are relatively much more prominent than in the puma, and more prominent than figured in *Smilodon*. They have not been described in *Homotherium*.

The axis (Figs. 9, 10) is well preserved. In lateral view the top of the neural spine is flatter and straighter than in *Smilodon*, and the posterior end is longer and more slender. The odontoid process is relatively larger and the transverse processes turn more downward, less backward, than in *Smilodon*. In posterior view the neural spine is slender, not broad as in *Smilodon*. It comes almost to a sharp edge dorsally, rather than being broad and flat above. The neural spine of *Machairodus* is catlike, and resembles that of the puma more than it does *Smilodon*. In *Machairodus*, however, the posterior part of the spine is deeply excavated ventrally, above the posterior zygapophyses. There are no such depressions in the spine of the puma. The neural spine of the axis of *Homotherium* is not known.

The third cervical vertebra (Fig. 10) seems to resemble closely that of *Homotherium* except that the transverse process is narrower, and as seen from above does not appear to be bifurcated distally. The transverse process is relatively longer and broader, more laterally inclined, than in *Smilodon*. The presence of hyperapophyses cannot be determined for the part of the arch that would support them is missing. The centrum is keeled ventrally.

On the fourth cervical, there is a median longitudinal keel of bone on the dorsal surface of the neural arch, and a slightly thickened, raised area near its center represents the vestige of the neural spine. There are distinct neural spines on this vertebra in *Smilodon* and *Homotherium*. The transverse process has an anterior extension that reaches past the anterior epiphysis of the centrum. There is no such extension in *Smilodon*. The lateral wall of the neural arch has a deep depression, such as is present in *Panthera atrox*, but not *Smilodon*. Such depressions are present on the third through sixth cervical vertebrae. The centrum is keeled ventrally.

The neural spine of the fifth cervical is broken off, but the remaining portion indicates that it resembled that of *Smilodon* but was smaller. The centrum is relatively broad with a strong median
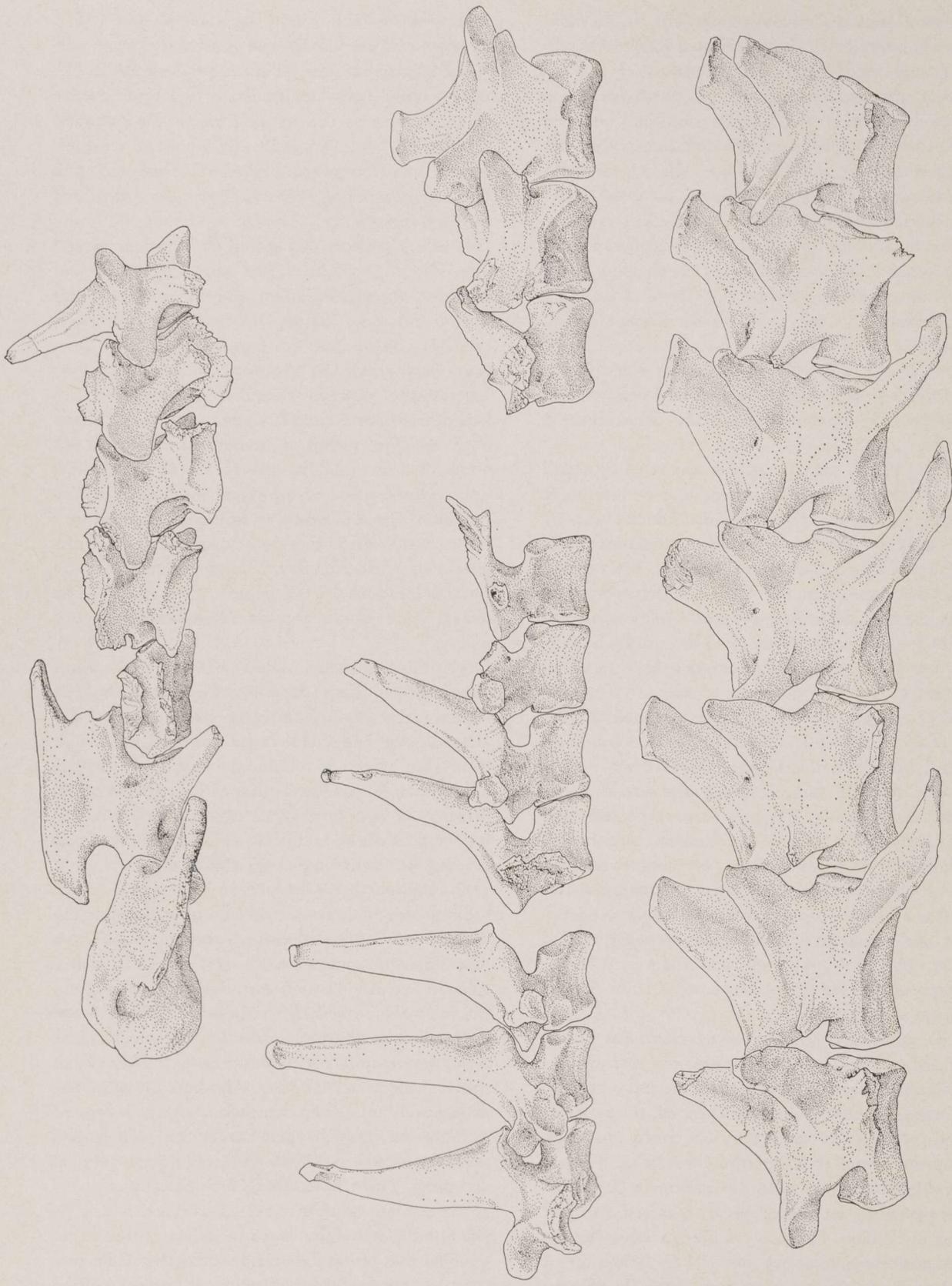
Fig. 9. Vertebral column of *Machairodus catocopis* from skeleton TMM 41216–8. Thoracics 4, 9, and 10 are missing. Approx. 7 .50 natural size. Note lumbar sequence is, drawn from the right side in order to show transverse processes which are missing on the left side probably as a result of the activities of scavengers. Other vertebrae are shown from the left.

ventral keel. The vertebrarterial canal is rounded, not slitlike as in *Smilodon*. It resembles the canal of *Homotherium*. The inferior lamella of the transverse processes do not extend downward in a triangle, as in *Smilodon*, or a roundish plate as in *P. atrox*, or in a squarish plate as in *Felis concolor*. Instead the lamella forms a roundish oval plate. The anterior zygapophyses, as seen in lateral view, are rounder and more vertically placed than in *Smilodon*.

The spine of the sixth cervical, to judge from the part of the base remaining, was similar to that of *Smilodon*, but smaller. The anterior zygapophyses are more horizontal than those of *Smilodon*, appearing almost flat in front view. The inferior lamella is narrower than that of *Smilodon*, with the ventral surface sinuous in lateral view. Otherwise the vertebra is much like that of *Smilodon*. The sixth cervical of *Homotherium* is unknown. The seventh cervical vertebra is well preserved and the neural spine is present. It is much smaller and more slender than the spine of *Smilodon*, with a smaller distal swelling. The neural canal is rounder, less triangular, than the neural canal of *Smilodon*. The anterior zygapophyses are more horizontal and the transverse processes extend more ventrally, less laterally, than in *Smilodon*. The vertebra is more deeply indented between anterior and posterior zygapophyses. The neural canal is shorter, so that more of the centrum is visible in dorsal view. Otherwise the vertebra is like that of *Smilodon*. The seventh cervical of *Homotherium* is unknown.

The first three thoracic vertebrae (Fig. 10) were articulated with the last cervical. The fourth thoracic was not found. Vertebrae T5 to T8 were scattered but closely associated with the skeleton. T9 and T10 were missing. T11 had been dragged forward and lay partly beneath the last cervical. T12 and T13 were articulated and lay a few inches away from the articulated lumbar series.

The thoracic series of *Machairodus catocopis* differs from the thoracic vertebrae of *Smilodon* and *Homotherium* in numerous ways. The most striking differences are in the much smaller, weaker neural spines and more slender, weak transverse processes placed lower on the neural arches. The back musculature of *M. catocopis* was not nearly so strong, especially in the shoulder region, as that of *Smilodon* or *Homotherium*.

The neural spine of T1 is thin transversely but broad anteroposteriorly at the base. It narrows swiftly above to arch back in saberlike form to a narrow, scarcely swollen tip. In *Smilodon* and *Homotherium* the neural spine is thick and deep, uniformly deep through its length, and broadly swollen at the tip. The centrum, in *M. catocopis*, is shallower than in *Smilodon*. The anterior zygapophyses are more vertical and the transverse processes extend almost horizontal rather than downward as in *Smilodon*. There is a shallow keel on the under side of the centrum, and a depression on each side of the keel, as in *Homotherium*. The ends of the transverse processes extend far forward, so that a line connecting their anterior tips lies 10 mm. in front of the centrum.

T2 bears the largest, heaviest neural spine in the series. The spine is still narrow and slender as compared with the neural spine of T2 of *Smilodon* and *Homotherium*. There is a slight keel on the ventral side of the centrum, missing in *Homotherium* and *Smilodon*. A line connecting the anterior tips of the transverse processes lies 2 mm. ahead of the centrum, but in *Smilodon* and seemingly also in *Homotherium*, such a line would fall far behind the anterior epiphysis of the centrum.

The neural spine of T3 is slender, narrowing smoothly and uniformly above to form a long, slender triangle with a slight terminal swelling. It is smaller, thinner, more tapering, and has a smaller terminal button, than the corresponding spine of *Smilodon*, and is also more upright, with less backward inclination. There is a slight ventral keel on the centrum. The T3 of *Homotherium* is unknown.

The neural spine of T5 is thicker at the base than in the more anterior vertebrae. It tapers uniformly upward to form a long, slender triangle with scarcely any terminal button. The spine is much smaller and narrower, anteroposteriorly, than in *Smilodon* or *Homotherium*. The lateral depression on the spine of *Homotherium*, described by Meade, is lacking in *M. catocopis*. The centrum bears a scarcely perceptible keel.

In T1 to T5 the neural spines are generally upright. From T6 posteriorly they are strongly inclined backward. In *Smilodon* and *Homotherium* all of the thoracic neural spines are strongly inclined backward. The erect anterior spines are typical of the felines, and the thoracic vertebrae of *M. catocopis* resemble those of *Felis concolor*, the puma, in this respect.

The neural spine of T6 is thicker than in the more anterior vertebrae, and rounder in cross section. It tapers rapidly, but not so rapidly as the spine of T5. It is smaller and lighter than the spines of T6

of *Smilodon* and *Homotherium*. The centrum is not keeled ventrally.

The part of the spine of T7 remaining suggests that it was larger and more posteriorly inclined than the neural spine of T6. It was probably smaller than in *Smilodon* and *Homotherium*. The transverse processes are relatively longer and lighter than those of *Smilodon*. The centrum is not keeled, nor are any of the centra posterior to T5 keeled.

The broken base of the spine of T8 indicates that it was strongly inclined backward. The vertebra throughout appears smaller and lighter in build than that of *Smilodon*. The posterior zygapophyses are almost horizontal.

T11 has no neural spine but there is a low, sharp-edged ridge or keel on the dorsal side of the neural arch. The posterior zygapophyses are elongated, and almost vertical. In the known *Homotherium* and typical *Smilodon*, T11 bears a large, strong, posteriorly inclined neural spine. However, Merriam and Stock figure (1932: 86) a "spineless type" of 11th thoracic vertebra that is a rare form in *Smilodon*. This closely resembles the present specimen of *M. catocopis*. The centrum of *M. catocopis* is relatively deeper than that of *Smilodon*, but the dorsal side (the ventral surface of the neural canal) is channeled and not flat or nearly flat as in *Smilodon*. As a result of the channeling, the centrum

is heart-shaped in posterior view, and only slightly less so in front view.

The neural spine is undeveloped in T12, represented only by a low, knife-edged ridge 22 mm. long and 4 mm. high. There is a strong spine in T12 of *Homotherium* and *Smilodon*. The anapophyses are well-developed but there are no metapophyses remaining on the damaged anterior edge of the anterior zygapophyses.

The neural spine of T13 is short, broad, and erect. Small metapophyses are present. The anapophyses are as in *Smilodon*. The centrum is channeled dorsally, but is too broad to appear heart-shaped. There is no ventral ridge on the centrum, as in *Homotherium*.

Relative to the thoracic vertebrae, the lumbars are stout and strong (Figs. 9, 10). They are smaller than the lumbars of *Smilodon* but comparable in strength, and were even more firmly united in articulation. The zygapophyses are almost vertical and parallel, with the lower edges of the anterior zygapophyses curved inward, thus permitting almost no side-to-side movement. The neural arch is notched posteriorly, and the posterior face of the neural spine bears a deep groove, into which the anterior edge of the succeeding spine fits when the column is flexed. There was thus considerable vertical freedom of movement of the hip region. The
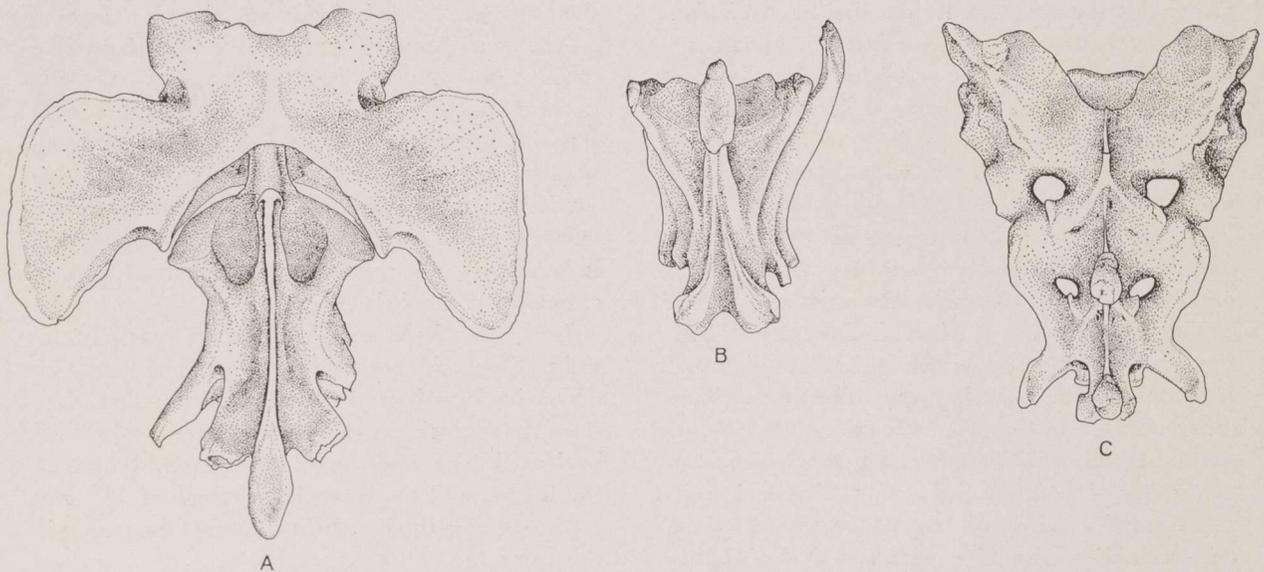


Fig 10. Vertebrae of *Machairodus catocopis* skeleton (TMM 41261–8), viewed from above. A, atlas and axis; B, third lumbar; C, sacrum. Approx. X .50 natural size. Note the anterior position of the neural spine and the deep groove in the posterior face of the spine for the reception of the neural spine of lumbar 4 when the vertebral column is deeply flexed.

functional implications of these conditions are discussed below. Anapophyses and metapophyses appear to have been less developed than in *Smilodon*.

The most striking difference between the lumbar vertebrae of *M. catocopis* and those of *Smilodon* is the forward position of the neural spine in *Machairodus*. There the neural spines slope anteriorly, with the anterior edge upright and the posterior edge angled forward. In *Smilodon* the reverse is true, and the neural spines slope backward.

In lateral view, the neural spine of L1 is strongly inclined forward, and the metapophysis is less prominent than in *Smilodon*. The anterior zygapophyses are almost vertical. The transverse processes are strongly inclined downward; they are almost horizontal in *Smilodon*. The posterior zygapophyses are narrower and closer together than in *Smilodon*. The anapophyses, as a result, are closer together and almost parallel. Seen from above, the neural spine lies over the anterior edge of the vertebra, with the button on the top of the spine extending forward past the edge of the interzygapophyseal notch. There is a deep notch between the posterior zygapophyses, and the neural spine is deeply grooved for approximately half of the length of its posterior side, for the reception of the neural spine of L2 when the vertebral column is flexed.

In L2, the neural spine is notched and grooved posteriorly, for the reception of the spine of L3, but the groove is not so deep as in the spine of L1. The anterior zygapophyses are almost vertical. The posterior zygapophyses are more widely separated than those of *Smilodon*. There is no ridge on the ventral surface of L1 or on the anterior half of the centrum of L2, but a ridge begins on the posterior half of L2. In *Smilodon* and *Homotherium* the anterior lumbars are ridged ventrally.

In L3 the neural spine is strong but so situated anteriorly that, when seen from directly above, more than half of the interzygapophyseal notch is obscured by the terminal button of the spine. The posterior zygapophyses are farther apart than those of L2, and much more so than those of L1. The notch and groove in the posterior face of the neural arch and spine are like those of L2. The centrum is heavily ridged ventrally.

The anterior zygapophyses of L4 are not so erect as those of L1–3, and are like those of *Smilodon*. The notch and groove in the posterior face of the neural arch and spine are broader and shallower than in the more anterior vertebrae. The posterior zygapophyses are more widely separated than those

of *Smilodon*. The transverse process is like that of *Smilodon*.

The neural spine of L5 is like that of L3, but the terminal button is smaller. The anterior zygapophyses are as in *Smilodon*. The posterior zygapophyses are similar to those of *Smilodon*, but the notch between them is deeper when seen in dorsal view. The groove for the front of the neural spine of T6 is only about one-third of the length of the spine of vertebra L5. The centrum is very strongly keeled.

L6 is much like that of *Smilodon* but the transverse process is longer, wider, and more downward-turned. The anterior zygapophyses are cupped, like those of *Smilodon*, but the walls external to the zygapophyses are much thinner than in *Smilodon*. The posterior zygapophyses are smaller than those of *Smilodon* but have a similar notch between them. The neural spine bears a groove posteriorly for the spine of L7, as it does in *Smilodon*. Only the anterior half of the ventral surface of the centrum bears a ridge.

The metapophyses of L7 do not extend so far forward as in *Smilodon*, and the centrum extends forward beyond them, as seen in dorsal view. In *Smilodon* the anterior margins of the metapophyses extend forward past the end of the centrum, and there are excavations in the wall of the neural arch between the bases of the transverse processes and the metapophyses, lateral to the centrum. There are no such excavations in *Machairodus*. The posterior zygapophyses are more widely separated than those of *Smilodon*. There is no ridge on the ventral surface of the centrum.

The sacrum, in dorsal view (Fig. 10), is less squarish, more tapering posteriorly, than the sacrum of *Smilodon*. It seems also to taper more than the sacrum of *Homotherium*. The dorsal openings of the sacral foramina are round-oval in shape, and are relatively larger and more prominent than in *Smilodon*. The transverse process of S3 is longer, narrower, than in *Smilodon*. In anterior view the anterior zygapophyses are flatter and more horizontal than those of *Smilodon*. The neural canal is shallower. The lateral rugosities, where the ilium was attached, are large and show that there was a powerful attachment between pelvis and sacrum.

The sacrum of *M. catocopis* seems to resemble that of *Homotherium* more than *Smilodon*. However, structural differences between the three genera are slight, and possibly within the range of individual variation in any one of them.

Only the proximal two caudal vertebrae were

recovered, in articulation with the sacrum. The first caudal has a slender transverse process and a small but distinct neural spine. In *Smilodon* the transverse process is short and wide, and there is no neural spine. In C2 there is no neural spine but the neural arch is complete. The transverse process is shorter and wider than in C1. In *Smilodon* and *Homotherium* the neural arch is incomplete in C2, and may be incomplete in the C1 of *Homotherium*. Both Pleistocene genera are known to have had short tails. The complete neural arch of the second caudal vertebra of *Machairodus* suggests a longer and more catlike tail.

*Ribs.*—A few ribs of skeleton TMM41261–8 were complete but most were damaged and many were missing. The ribs are generally catlike. They are relatively small and thin as compared with those of *Smilodon*.

*Pectoral girdle and fore limb.*—Both scapulae were present but most of the blades were crushed and shattered and could not be saved. The ventral parts were complete, along with parts of the scapular spines and some of the anterior and posterior margins of both specimens.

The suprascapular notch seems to be unusually deep, relatively deeper than in *Homotherium*, *Smilodon*, or *Felis concolor*. The neck of the scapula, in consequence, is much constricted. Beyond the scapular notch, the anterior border of the blade curves abruptly outward, as though to form a broad blade, as in *Felis*, but not enough remains to be sure of this. The posterior border is straight, as in *Homotherium* and the puma.

The left humerus is nearly complete but the right lacks the proximal quarter. The humerus (Fig. 11) is vastly different from that of *Smilodon*. Although it is approximately the same length it is much more slender, with a mid shaft diameter approximately half that of a large *Smilodon*. At the distal end, the *Smilodon* humerus is about two inches wider. The humerus of *Machairodus* is also straighter in both anteroposterior and transverse view. There are numerous other differences but all are associated with the relative slenderness of the *Machairodus* bone. Some of these differences have been noted by Burt.

The humerus of *Homotherium*, figured by Meade, is as long as that of *Machairodus* but stouter, and is more slender than that of *Smilodon*. In bulk and general appearance it is intermediate between *M. catocopis* and *Smilodon*.

The ulna (Fig. 11) is known from both sides of the skeleton (TMM41261–8) and an isolated specimen. The bone is approximately the length of the ulna of *Smilodon* but much more slender. The ulna of *Homotherium* is slightly longer and slightly stouter than the ulna of *Machairodus*. In *Smilodon* the anterior dorsal surface of the olecranon bears a high, distinct crest, but in both *Machairodus* and *Homotherium* the crest is relatively and actually much lower. *M. catocopis* differs from both *Homotherium* and *Smilodon* in lacking the deep, elongated depression on the shaft ventral to the facet for the articulation of the proximal end of the radius.

The radius (Fig. 11) is known from three specimens, two of which were isolated finds. The radius is very slender compared with that of *Smilodon*. It closely resembles the radius of *Homotherium*, but seems to be a bit more slender and curved. The neck of the proximal end appears more constricted, and the distal end of the shaft wider in relation to the rest of the shaft, than in *Homotherium*. There is considerable variation in all these proportions, however, as may be seen from the measurements.

*Manus.*—The following elements are available: 5 scapholunars, 1 pisiform, 1 metacarpal I, 1 MC II, 3 MC III's, 1 MC IV, and numerous phalanges.

The scapholunars display some individual variation but are, in general, like the bone in *Smilodon* and *Homotherium*. However, they differ markedly and uniformly from the scapholunar of *Smilodon* in that the "beak" is much narrower and more prominent.

The pisiform is much smaller than the pisiform of *Smilodon*, and appears stouter through the head, and less twisted. The cuniform articulation is relatively long, as compared with that of *Smilodon*, and the "heel" is therefore relatively longer but more slender. The pisiform resembles that of *Felis concolor* and *Panthera atrox* more than it does *Smilodon*.

The first metacarpal is short and stout, like the MC I of *Smilodon*, and as in *Smilodon*, has an oblique ridge across the dorsal surface. This ridge is less developed than in *Smilodon*. There are numerous other minor differences, but the general resemblance to *Smilodon* is close. On the other hand, the MC I of *Panthera atrox*, *Felis concolor*, and other true cats available, is quite different. The MC I of sabertooths seems quite distinctive.

Metacarpals II, III, and IV are long and slender compared with the manus of *Smilodon*. They are also very straight, especially on the ventral surface, compared with large true cats. The distal keel is not

Fig. 11. Limb bones of *Machairodus catocopis*, from left to right; humerus, ulna, radius, tibia, femur. The tibia (TMM 41261—14) and femur (TMM 41261—13) are isolated discoveries. The other elements are from the skeleton (TMM 41261—8). X .50 natural size.

"hooked" under, as in *Smilodon*. The proximal articular surface of MC II is triangular in shape, of MC III squarish with a deep, broad notch, and of MC IV broad above and notched laterally. The notch lateral to the unciform facet is shallow, as in *Smilodon*, not deep as in *Panthera atrox*.

No effort has been made to assign the numerous phalanges to their proper place. However, the single ungual phalanx found with the skeleton appears to have been from the fore foot. It is large and strongly hooded. It resembles the hooded terminal phalanx of *Smilodon* in details of shape as well as size. Since the limb and foot bones of *M. catocopis* are uniformly smaller and more slender than those of *Smi-*

*lodon,* the claws must have been relatively huge.

*Pelvis and hind limb.*—The innominate resembles that of *Smilodon* but is thinner and lighter in build. The distinct constriction anterior to the acetabulum in *Smilodon* is absent in *M. catocopis.* The ischium also appears to be more twisted.

The distal ends of both femora of TMM41261–8 were missing, as were all other bones of the hind legs, save for a few foot elements. The following description is based principally on TMM41261–13, a nearly complete femur, augmented by additional material.

The femur of *M. catocopis* is long, straight and slender (Fig. 11). It thus differs markedly from the femora of *Smilodon,* and is more like the femora of the true cats, such as *Panthera* and *Felis.* In *Smilodon* the lesser trochanter is more distinct from the head than it is in true cats, and in *Homotherium* and *Machairodus* also, where the lesser trochanter is placed closer to the head of the femur. The femur of *Homotherium* appears, in figures, to be stouter and more curved than that of *Machairodus.*

The tibia of *M. catocopis,* known from two isolated specimens, is as long as in *Smilodon* and *Homotherium,* but straighter and more slender (Fig. 11). It resembles the tibia of *Homotherium* more than it does that of *Smilodon.* The anterior notch in the distal end is much deeper than it is in either *Smilodon* or *Homotherium.* Tibiae tend to be featureless bones, but the difference in the anterior notch is striking. Burt (1931, Plate 47) has figured a *M. catocopis* tibia with a similarly deep notch. The significance of this character is not clear.

*Pes.*—The following complete or nearly complete specimens are available: 7 astragali; 3 calcanea; 1 cuboid; 1 navicular; 7 metatarsal II's; 1 MT III; 2 MT IV's; 1 MT V; and numerous unstudied phalanges.

Even the largest astragalus is smaller than the astragalus of a medium-sized *Smilodon.* The wall posterior to the deep groove between the calcaneal articulations, thick in *Smilodon,* is thin in *M. catocopis.* The bone appears more catlike than the astragalus of *Smilodon,* and probably of *Homotherium* also.

The calcaneum, compared with that of *Smilodon,* is shorter and not so broad. The distal end of the heel is more notched. The facet for the articulation of the navicular is smaller and less prominent. The major astragalar facet is smaller and more vertical. The calcaneum of *M. catocopis* is similar, in general, to that of *Homotherium* but the heel is distinctly

longer and more notched distally. The heel is also less swollen at the distal end.

The cuboid is generally similar to that of *Smilodon,* but there are numerous minor differences in addition to much smaller size. The facet for articulation with the navicular is relatively smaller and the facet for the ectocuniform is larger, with a median constriction not present in *Smilodon.* The facet for metatarsal IV is prominent, as in *Smilodon,* but the facet for metatarsal V is scarcely indicated. The groove for *M. peroneus longus* is relatively deeper and set closer to the distal border than it is in *Smilodon.*

The navicular is much like that of *Smilodon* but smaller. The surface for the astragalar articulation is narrower and rounder than in *Smilodon.* The facet for articulation with the mesocuniform is low, not so prominent, as it is in *Smilodon.* The bone is also thinner dorsoventrally.

The metatarsals are markedly longer and more slender than those of *Smilodon.* They are also much straighter, and this is especially marked in MT III, the longest and straightest of the metatarsals. The ventral keel of the distal articulation of the metapodials of *Smilodon* is often "hooked" downward and backward. None of the metatarsals of *M. catocopis* are hooked.

A number of minor differences are noted in the shape of the proximal articular surfaces of the metatarsals. Notable is the complete absence, on all seven specimens of MT II, of an articular surface for a rudimentary MT I. Instead there is a prominent crest on the lateral surface of the bone which would virtually preclude articulation with another metatarsal. There is an articular facet in *Smilodon,* and a vestigial metatarsal I. Seemingly *M. catocopis* lacked MT I.

REMARKS.—The skull, jaws and dentition of *M. catocopis* indicate a rather primitive, unspecialized machairodont. The skull is long and low, and cranial foramina are typically machairodont except that the alisphenoid canal is present. The mandible is deep, but the coronoid process is not as reduced as in the Pleistocene sabertooths, and the mandibular flange is not so well developed. The existence of the upper $P_2$ and triangular, flattened lower canine, noted by Burt as aberrant features, are not confirmed by the present material. The cheek teeth are high but compressed. The upper carnassial still retains the lingual (protocone) root, but reduction is evident and fusion of the root with

the outer roots sometimes occurs. In the lower dentition, P₃ is a large, broad tooth, whereas it is reduced or absent in the later sabertooths. The cheek teeth of both upper and lower jaws are set nearly upright, rather than strongly inclined backward. Resemblance of skull, jaws and teeth of *Machairodus catocopis* to *Homotherium* is much closer than it is to *Smilodon*. The dentition of *Machairodus* is so generalized that the dentition of *Homotherium* could be derived from it.

The body proportions are unusual. The head seems to have been disproportionately large, and the neck stout. The trunk was slender, and lacked the powerful muscles typical of the fore part of the body of *Smilodon*, and to a more limited degree, *Homotherium*. The front legs were excessively slender and if shorter than those of *Homotherium*, were relatively long compared with their thickness. The feet were large, and the claws as large as those of *Smilodon*.

The lumbar region was specialized for freedom of movement in the vertical plane, but almost rigid laterally. The pelvis and sacrum are strongly built. The hind limbs are long, as long as in *Homotherium*, and the hind feet seem disproportionately long and slender.

The slim body, long, slender limbs, and elongated, slender feet, along with the curious adaptation of the lumbar region, may have been a specialization for a swift, bounding gait. Certainly the ability of the hip region to flex vertically was highly developed. The lumbar vertebrae of the cheeta (*Acinonyx jubatus*) show almost the reverse of the kind of specialization noted in *M. catocopis*. In the cheeta the neural spines are small and well separated, and the zygapophyses are almost horizontal. The cheeta captures its prey in a swift, dashing run. Agile twisting of the hip region is necessary to follow and inter-cept the dodging prey. The lumbar vertebrae of the puma (*Felis concolor*) have zygapophyses intermediate between the relatively vertical type of *Machairodus* and the relatively horizontal type of *Acinonyx*. Perhaps the Pliocene cat overtook large but clumsy prey in a series of long, bounding leaps, fixed its huge claws in the skin of its victim, and drove the long canines into the flesh to inflict gashes through which the prey quickly bled to death.

Evans (1961: 19) presents strong evidence that the principal prey of *Homotherium* at Friesenhahn Cave was the young of mammoths and mastodons. Adult elephants might have been killed as well, but their remains would have been left where killed, rather than dragged back into the cave. To judge from the few fossils recovered, mastodons were extremely rare in the Coffee Ranch area when the deposits were forming. Rhinoceroses, especially *Aphelops*, were common, and their remains are abundant. Fossils of young animals are no more common, relative to the remains of adult animals, than is usually the case of fossil deposits. *Aphelops* may have been the principal prey of *Machairodus*, and both young and adult animals were probably eaten.

Some individual *M. catocopis* lived to a considerable age, and some teeth were found that had been worn nearly to the gums. An extreme case is represented by maxillary MU5634. This jaw has the teeth so worn as to be scarcely recognizable. Only the canine and the carnassial remain, and the other teeth seem to have been lost in life. The canine is worn until it is almost semicircular, nearly as wide as long. The carnassial is so worn that only a bit of enamel remains at the base, scarcely a square millimeter in area. This individual, in its old age, must have competed with the bone-eating dogs for the carrion left by more active predators.

# Speculation as to Faunal Relationships of the Carnivores

Hemphill County was probably a grassland when the Coffee Ranch fauna lived. Grazing mammals are represented by abundant fossils, but browsing forms are rare. At least some bushes must have existed nearby, probably in canyons, for remains of mastodon, pigs, deer and ground sloths are occasionally found. The relative scarcity of browsers, however, precludes terming the area a savannah.

The climate was probably warm and dry, not unlike the present climate of the area. The angular caliche gravel, preserved in the greenish sand layer, shows the presence of caliche caprock in Hemphillian times. Caliche forms and is preserved under semiarid conditions.

The lake, where the bones collected, was seasonal and probably of the playa type. Permanent-water vertebrates, such as fishes, alligators, and aquatic turtles, are absent from the fauna. Of the numerous fossils found, only one was an articulated skeleton. Thousands of isolated complete and fragmentary bones were so scattered that they could only have been strewn over a dry surface. Tooth marks are present on many bones, and others show the evidence of crushing in the jaws of the bone-eating dog. This damage would scarcely have occurred if the bones were under water.

The Coffee Ranch local fauna includes species of fairly modern mammalian types, whose faunal relationships can be guessed on the basis of existing descendent or related types, and extinct lineages with no living relative. In the case of many small forms, the place they occupied in the middle Pliocene fauna seems clear. For example, *Copemys* is so similar, morphologically, to modern deer mice (*Peromyscus*) that one may feel confident that they were nocturnal seed-eaters that occupied burrows dug in sandy soil or nests placed in crevices in rocks. Similarly, *Hypolagus* was a rabbit and probably had much the same habits, and took the same place in the fauna, that the cottontail, *Sylvilagus*, occupies today. One cannot make similar assumptions for the hoofed mammals. *Aphelops* and *Teleoceras* are so distinct, morphologically, from living rhinoceroses,

that one cannot judge the ecological relationships of the extinct forms from knowledge of the African and Asiatic species. This is equally true of the several species of camels and horses of the Coffee Ranch fauna.

The carnivora of the Coffee Ranch include both modern and extinct lineages. *Vulpes shermanensis* was certainly much like a modern red fox in appearance and probably habits. It doubtless preyed on birds, rabbits, small rodents, and insects. It may have competed with the bone-eating dogs for carrion, in the manner that jackals compete with hyenas in the Old World today. The fox was probably much too swift, agile, and intelligent to be captured by the thick-legged *Osteoborus*.

The dentition and type of tooth wear attests to the hyenoid food habits of *Osteoborus*. Whether the dogs were strictly scavengers is doubtful, for some remains of small mammals were found in what, presumably, were scats. They may have been active predators as well as scavengers. They could scarcely have been swift runners, for their legs were curiously proportioned: long humerus and femur, short lower limbs, and stubby feet. Cursorial types usually show an elongation of the lower, not the upper, limbs. Perhaps they lived in packs, as some canids do today. Perhaps their activities were restricted to the immediate vicinity of water holes. This might account for the abundance of hyenoid dog remains in late Tertiary deposits.

*Indarctos* is a rare species, and perhaps was only an occasional visitor to the lake. This huge bear could have had little to fear from any other mammal of the fauna. Too little is known of its structure to guess at its habits or its place in the fauna.

*Pliotaxidae* is so similar to the modern badger, except for smaller size, that it probably had similar habits. Doubtless it was a powerful burrower that fed on insects and small vertebrates, especially rodents that it dug from underground nests.

*Plesiogulo* is the Pliocene equivalent of the modern wolverine, and may have had similar habits. Presumably it was a generalized but active carni-

vore, preying on a variety of birds and small mammals, and even overcoming quite large prey when occasion permitted. It may have been swift and vicious enough to hold off carnivores such as *Osteoborus*, as the modern wolverine defies wolves in the treeless subarctic. It may, like the wolverine, also have employed skunk-like musk.

*Pseudaelurus* was a pumalike cat and probably had pumalike habits. If so it probably inhabited the cliffs and canyons, coming to the water only rarely. Prey of suitable size included the abundant horses and smaller camels, as well as peccaries and deer.

Possible habits of *Machairodus* have been discussed. Probably this cat crept to a point near its prey, mainly rhinoceroses, and captured it in a bounding charge. Doubtless vegetation near the lake's edge was taller and more suitable for cover than better grazed grassland. Yet, it is doubtful that the sabertooth was restricted to the vicinity of the lake or fossils would have been more numerous.

The general aspect of the carnivore fauna of the Coffee Ranch fauna was, except for the bone-eating dog and saber-toothed cat, quite modern. Foxes, coyotes and badgers occur in the region today, and bears and pumas lived nearby in historic times. The wolverine now occurs only far to the north. The hoofed-mammal fauna, in contrast, bears little resemblance to modern North American forms. The two rhinoceroses, four horses, four camels, dimunitive antilocaprid, deer, and mastodon, have no close relatives in our fauna. Only the peccary is similar to existing species.

TABLES

TABLE 1

Measurements of *Osteoborus* skulls

| | MU5044 | MU3229 | MU5686 | MU7408 |
|---|---|---|---|---|
| Occipital condyles to alveoli of incisors | 192.0 | ...... | ....... | ....... |
| Zygomatic breadth | 143.0a* | 141.0a | ....... | ....... |
| Breadth across fourth premolars | 83.3 | 89.3 | 79.0 | ....... |
| Breadth across second premolars | 51.0 | 51.3 | 45.9 | ....... |
| Breadth across canines | ...... | 51.2 | ...... | 49.8 |
| Breadth across incisor row | ...... | 31.2 | ...... | 32.0 |
| Least interorbital breadth | 50.9 | ....... | ....... | ....... |
| Least postorbital constriction | 30.2 | ....... | ....... | ....... |
| Breadth across infraorbital foramina, anteriorly | 47.6 | ....... | 41.5 | ....... |
| Breadth across occipital condyles | 37.7 | ....... | ....... | 35.8 |
| Length, incisors to back of $M^2$ | ...... | 103.8 | 96.0 | ....... |
| Length, canines to back of $M^3$ | ...... | 85.4 | 80.0 | ....... |

\* Approximate.

TABLE 2

Measurements of *Osteoborus* upper dentitions. Figures in parentheses are measurements of 18 randomly-chosen, young-adult coyotes (*Canis latrans*) of unknown sex, trapped in Wichita County, Texas.

| | N | Mean and standard error | Standard deviation | Coefficient of variation |
|---|---|---|---|---|
| Length $P^2$–$M^2$ | 8 | 57.51 ± 2.15 | 5.26 | 9.14 |
| | (18) | (59.84 ± 0.48) | (1.98) | (3.30) |
| Length $P^2$–$M^1$ | 8 | 53.81 ± 1.39 | 3.40 | 6.32 |
| | (18) | (54.21 ± 0.49) | (2.00) | (3.69) |
| Length $P^4$–$M^2$ | 9 | 45.07 ± 0.98 | 2.76 | 6.13 |
| | (18) | (36.84 ± 0.32) | (1.31) | (3.54) |
| Length $P^4$–$M^1$ | 12 | 38.39 ± 0.54 | 1.78 | 4.63 |
| | (18) | (30.56 ± 0.32) | (1.30) | (4.25) |
| Length $P^2$ | 11 | 8.99 ± 0.21 | 0.67 | 7.46 |
| | (18) | (10.96 ± 0.16) | (0.68) | (6.17) |
| Breadth $P^2$ | 11 | 5.20 ± 0.11 | 0.34 | 6.35 |
| | (18) | ( 3.93 ± 0.06) | (0.26) | (6.68) |
| Length $P^3$ | 10 | 11.45 ± 0.25 | 0.76 | 6.63 |
| | (18) | (12.42 ± 0.19) | (0.78) | (6.27) |
| Breadth $P^3$ | 10 | 5.92 ± 0.15 | 0.44 | 7.39 |
| | (18) | ( 4.29 ± 0.08) | (0.32) | (7.39) |
| Length $P^4$ | 16 | 24.94 ± 0.36 | 1.40 | 5.61 |
| | (18) | (19.23 ± 0.21) | (0.88) | (4.60) |
| Breadth $P^4$ | 16 | 12.54 ± 0.20 | 0.79 | 6.30 |
| | (18) | ( 9.29 ± 0.16) | (0.68) | (7.29) |
| Length $M^1$ | 15 | 15.91 ± 0.34 | 1.27 | 7.96 |
| | (18) | (13.41 ± 0.16) | (0.67) | (4.97) |
| Breadth $M^1$ | 15 | 19.39 ± 0.30 | 1.12 | 5.76 |
| | (18) | (15.18 ± 0.15) | (0.62) | (4.10) |

## TABLE 3

Measurements of *Osteoborus* lower dentitions. Figures in parentheses are measurements of 18 randomly-chosen, young-adult coyotes (*Canis latrans*) of unknown sex, trapped in Wichita County, Texas

| | N | Mean and standard error | Standard deviation | Coefficient of variation |
|---|---|---|---|---|
| Length $C–M_2$ | 6 | $85.50 \pm 1.85$ | 4.14 | 4.84 |
| | (18) | $(86.66 \pm 0.55)$ | (2.27) | (2.62) |
| Length $P_2–M_2$ | 8 | $69.75 \pm 0.90$ | 2.38 | 3.42 |
| | (18) | $(65.65 \pm 0.39)$ | (1.61) | (2.46) |
| Length $P_4–M_2$ | 15 | $53.91 \pm 0.48$ | 1.79 | 3.32 |
| | (18) | $(41.74 \pm 0.32)$ | (1.31) | (3.14) |
| Length $P_4–M_1$ | 17 | $42.50 \pm 0.34$ | 1.33 | 3.13 |
| | (18) | $(32.13 \pm 0.28)$ | (1.16) | (3.62) |
| Length $M_1–M_2$ | 13 | $38.75 \pm 0.54$ | 1.86 | 4.81 |
| | (18) | $(30.62 \pm 0.23)$ | (0.93) | (3.04) |
| Length $P_2$ | 8 | $6.81 \pm 0.20$ | 0.54 | 7.92 |
| | (18) | $( 9.71 \pm 0.13)$ | (0.55) | (5.62) |
| Breadth $P_2$ | 8 | $4.84 \pm 0.14$ | 0.38 | 7.87 |
| | (18) | $( 4.15 \pm 0.06)$ | (0.24) | (5.86) |
| Length $P_3$ | 12 | $8.63 \pm 0.19$ | 0.64 | 7.39 |
| | (18) | $(10.82 \pm 0.15)$ | (0.62) | (5.76) |
| Breadth $P_3$ | 12 | $5.74 \pm 0.11$ | 0.38 | 6.63 |
| | (18) | $( 4.52 \pm 0.06)$ | (0.26) | (5.79) |
| Length $P_4$ | 18 | $16.66 \pm 0.21$ | 0.88 | 5.30 |
| | (18) | $(12.19 \pm 0.11)$ | (0.46) | (3.81) |
| Breadth $P_4$ | 17 | $10.69 \pm 0.13$ | 0.53 | 4.93 |
| | (18) | $( 5.25 \pm 0.07)$ | (0.29) | (5.51) |
| Length $M_1$ | 18 | $27.58 \pm 0.29$ | 1.22 | 4.41 |
| | (18) | $(21.05 \pm 0.22)$ | (0.89) | (4.24) |
| Breadth $M_1$ | 18 | $11.77 \pm 0.13$ | 0.52 | 4.44 |
| | (18) | $( 8.15 \pm 0.08)$ | (0.33) | (4.07) |
| Length $M_2$ | 12 | $12.63 \pm 0.21$ | 0.70 | 5.52 |
| | (18) | $(10.06 \pm 0.15)$ | (0.61) | (6.08) |
| Breadth $M_2$ | 11 | $8.65 \pm 0.16$ | 0.51 | 5.89 |
| | (18) | $( 6.72 \pm 0.11)$ | (0.44) | (6.50) |

## TABLE 4

Measurements of *Osteoborus* vertebrae

| | Cervicals | | | Thoracics | | |
|---|---|---|---|---|---|---|
| | 3 | 5 | 7 | 11 | 12 | 13 |
| Length of centrum | 29.4 | 18.8 | 18.6 | 22.3 | 24.4 | 27.5 |
| Breadth anterior zygapophyses | 32.0 | 37.2 | 37.7 | 17.5 | ...... | 18.7 |
| Breadth posterior zygapophyses | 27.8 | 38.3 | 33.2 | ...... | 16.0 | 15.9 |
| Height of centrum anteriorly | 12.2 | 8.8 | 12.3 | 13.5 | 14.7 | 15.0 |
| Breadth of centrum posteriorly | 20.0 | 20.1 | 27.0 | 22.0 | 23.5 | 23.5 |

## TABLE 5

### Measurements of *Osteoborus* limb bones

|  | Number | Mean | Minimum | Maximum |
|---|---|---|---|---|
| *Humerus* |  |  |  |  |
| Anteroposterior diameter, midshaft | 5 | 20.9 | 19.3 | 23.3 |
| Transverse diameter, midshaft | 5 | 15.9 | 14.7 | 16.6 |
| Transverse breadth of distal end | 9 | 49.6 | 45.1 | 52.0 |
| Least anteroposterior diameter, distal end | 9 | 14.3 | 13.3 | 15.5 |
| *Radius* |  |  |  |  |
| Greatest length | 1 | 160.0 | ...... | ...... |
| Transverse breadth of proximal end | 5 | 21.5 | 20.9 | 22.6 |
| Anteroposterior diameter of proximal end | 5 | 15.2 | 14.8 | 16.0 |
| Transverse diameter, midshaft | 4 | 14.4 | 13.1 | 17.5 |
| Anteroposterior diameter, midshaft | 4 | 10.7 | 9.3 | 12.8 |
| Transverse breadth of distal end | 2 | 27.7 | 26.6 | 28.8 |
| Anteroposterior diameter of distal end | 2 | 18.8 | 18.5 | 19.0 |
| *Ulna* |  |  |  |  |
| Greatest length | 1 | 190 |  |  |
| Anteroposterior length of top of olecranon | 1 | 34.9 |  |  |
| Greatest breadth of top of olecranon | 1 | 19.8 |  |  |
| Anteroposterior length at sigmoid cavity | 1 | 22.6 |  |  |
| Transverse diameter at tendon scar | 1 | 11.5 |  |  |
| Anteroposterior diameter of distal end | 1 | 16.8 |  |  |
| Transverse diameter of distal end | 1 | 11.0 |  |  |
| *Femur* |  |  |  |  |
| Length from top of head to distal end | 1 | 198.0 |  |  |
| Least vertical constriction distal to head | 1 | 18.0 |  |  |
| Anteroposterior constriction at head | 1 | 11.9 |  |  |
| Anteroposterior diameter at midshaft | 1 | 15.0 |  |  |
| Transverse diameter at midshaft | 1 | 17.9 |  |  |
| Anteroposterior diameter of distal end | 1 | 36.8 |  |  |
| Transverse diameter of distal end | 1 | 36.0 |  |  |
| *Tibia* |  |  |  |  |
| Greatest length | 2 | 174.0 | 172.0 | 176.0 |
| Anteroposterior diameter of proximal end | 2 | 30.9 | 30.5 | 31.3 |
| Transverse diameter of proximal end | 1 | 41.1 |  |  |
| Anteroposterior diameter at midshaft | 3 | 17.1 | 15.0 | 18.6 |
| Transverse diameter at midshaft | 3 | 14.2 | 13.1 | 15.1 |
| Anteroposterior diameter of distal end | 4 | 18.5 | 17.5 | 19.2 |
| Transverse diameter of distal end | 4 | 27.0 | 25.3 | 28.1 |
| *Astragalus* |  |  |  |  |
| Anteroposterior length | 6 | 29.8 | 28.2 | 31.7 |
| Transverse breadth of tibial surface | 6 | 18.8 | 17.1 | 20.3 |
| Least dorsoventral height | 5 | 14.3 | 13.7 | 15.0 |
| Least transverse constriction at neck | 6 | 11.9 | 11.3 | 12.8 |
| *Calcaneum* |  |  |  |  |
| Anteroposterior length | 1 | 55.8 |  |  |
| Greatest breadth of astragalar surfaces | 1 | 24.6 |  |  |
| Transverse diameter of distal end | 1 | 15.0 |  |  |
| Dorsoventral height of distal end | 1 | 20.0 |  |  |
| *Metacarpal II* |  |  |  |  |
| Greatest length | 2 | 47.2 | 46.8 | 47.5 |
| Greatest height of proximal end | 2 | 12.0 | 11.4 | 12.5 |
| Greatest height of distal end | 2 | 9.7 | 9.5 | 9.9 |

TABLE 5—(Continued)

|  | Number | Mean | Minimum | Maximum |
|---|---|---|---|---|
| *Metacarpal III* |  |  |  |  |
| Greatest length | 2 | 61.8 | 59.3 | 64.2 |
| Greatest height of proximal end | 2 | 13.3 | 13.1 | 13.5 |
| Greatest height of distal end | 2 | 11.4 | 11.1 | 11.7 |
| *Metacarpal IV* |  |  |  |  |
| Greatest length | 1 | 62.1 |  |  |
| Greatest height of proximal end | 1 | 12.1 |  |  |
| Greatest height of distal end | 1 | 8.5 |  |  |
| *Metatarsal II* |  |  |  |  |
| Greatest length | 1 | 52.7 |  |  |
| Greatest height of proximal end | 1 | 12.7 |  |  |
| Greatest height of distal end | 1 | 8.8 |  |  |
| *Metatarsal III* |  |  |  |  |
| Greatest length | 1 | 56.0 |  |  |

TABLE 6

Measurements of undetermined canid skull
(TMM41261–4)

| | |
|---|---|
| Length from end of nasals to end of occipital crest | 124.2 |
| Breadth across interorbital region | 39.0 |
| Breadth across postorbital processes | 46.9 |
| Postorbital constriction | 27.2 |
| Breadth across parietals | 55.0 |
| Breadth across occipital crest | 32.1 |

TABLE 7

Measurements of teeth of *Indarctos nevadensis*

|  | TMM41261–1 | MU3350 | Type (Macdonald, 1959) |
|---|---|---|---|
| P$_4$ anteroposterior length | 25.6 | ...... | 23.5 |
| transverse breadth | 14.2 | ...... | 14.7 |
| M$_1$, anteroposterior length | 45.0 | 43.1 | 40.5 |
| transverse breadth of trigonid | 19.2 | 19.1 | 17.8 |
| transverse breadth of talonid | 23.7 | 22.6 | 20.6 |
| M$_2$, anteroposterior length | 34.2 |  |  |
| transverse breadth | 25.5 |  |  |
| M$_3$, anteroposterior length | 19.7 approximate |  |  |
| transverse breadth | 20.1 |  |  |

TABLE 8

Measurements of *Pseudaelurus hibbardi*

| Lower Jaws | TMM41261–3 | TMM41261–5 |
|---|---|---|
| Anteroposterior diameter of canine alveolus | 17.0 | ...... |
| Diastema, C-P3 | 14.8 | 14.7 |
| P3, greatest anteroposterior diameter | 11.1 | ...... |
| P3, greatest transverse diameter | 5.5 | ...... |
| P4, greatest anteroposterior diameter | 15.5 | 15.2 |
| P4, greatest transverse diameter | 7.4 | 7.4 |
| M1, greatest anteroposterior diameter | 21.5 | ...... |
| M1, greatest transverse diameter | 8.9 | ...... |
| Paraconid, maximum anteroposterior diameter | 8.2 | ...... |
| Protoconid, maximum anteroposterior diameter | 8.5 | ...... |
| Length, P3-M1 inclusive | 47.4 | ...... |
| Width of mandible below center of P3 | 15.2 | ...... |
| Width of mandible below center of M1 | 12.8 | ...... |

| Upper Carnassial, P4 | MU6389 |
|---|---|
| Anteroposterior diameter | 24.6 |
| Greatest transverse diameter | 12.1 |

| Scapula | TMM41261–15 |
|---|---|
| Length, coracoid process to blade at end of spine | 185.0 approximate |
| Length of spine | 155.0 approximate |
| Height of glenoid fossa | 37.7 |
| Breadth of glenoid fossa | 26.7 |
| Least vertical diameter of neck | 33.7 |

| Humerus | TMM41261–16 |
|---|---|
| Greatest length | 232 approximate |
| Greatest proximal breadth | 51.0 |
| Greatest anteroposterior diameter of head | 41.2 |
| Greatest breadth of distal end | 54.8 |
| Greatest anteroposterior diameter of articulating surface of distal end | 16.9 |
| Anteroposterior diameter of trochlea | 31.6 |
| Anteroposterior diameter of capitulum | 29.1 |

| Radius | TMM41261–17 |
|---|---|
| Greatest length | 202.0 |
| Greatest proximal breadth | 26.3 |
| Greatest anteroposterior diameter, proximal | 18.5 |
| Midshaft breadth | 18.8 |
| Anteroposterior diameter at midshaft | 11.6 |
| Greatest distal breadth | 34.9 |
| Anteroposterior diameter at distal end | 21.0 |

| Astragalus | TMM41261–19 |
|---|---|
| Greatest length | 39.0 |
| Least dorsopalmar height | 15.2 |
| Least transverse breadth of neck | 19.1 |

| Calcanea | TMM41261–21 | TMM41261–22 |
|---|---|---|
| Greatest length | 74.6 | 75.7 |
| Width at sustentaculum | 29.8 | 29.6 |

| Navicular | MU6389 |
|---|---|
| Greatest length | 28.4 |
| Greatest breadth | 22.0 |
| Least height measured across at notch | 11.3 |

TABLE 9

Measurements of *Machairodus* mandibles

| | TMM 41261-8R | TMM 41261-8L | TMM 41261-9 | MU 3527 |
|---|---|---|---|---|
| Length from anterior end of symphysis to posterior end of condyle. | 225.0 | ....... | ....... | ....... |
| Length from anterior end of outer flange to posterior end of condyle. | 202.0 | ....... | ....... | ....... |
| Length of symphysis measured along anterior border. | ........ | 55.5 | 63.1 | ....... |
| Least depth of ramus below diastema. | 37.6 | 38.4 | 38.2 | 36.7 |
| Depth of ramus below posterior end of M/1. | 45.5 | 46.2 | 44.0 | ....... |
| Thickness of ramus below M/1. | 18.5 | 18.5 | 15.6 | 17.2 |
| Height from inferior border of angle to summit of condyle. | 41.2 | ....... | ....... | ....... |
| Height from inferior border of angle to summit of coronoid process. | 90.0 | ....... | ....... | ....... |
| Transverse width of condyle. | 43.8 | ....... | ....... | ....... |
| Greatest depth of condyle. | 16.2 | ....... | ....... | ....... |

TABLE 10

Measurements of *Machairodus* superior dentitions

| | TMM 41261-8 | TMM 41261-10 | MU 5670 | MU 1867 | MU 5373 |
|---|---|---|---|---|---|
| Length from anterior end of canine alveolus to posterior end of P4/. | 109a | ....... | ....... | ....... | ....... |
| Length from anterior end of P3/ to posterior end of P4/. | 66.0 | 73.4 | ....... | ....... | ....... |
| Length of diastema from posterior end of alveolus for C to anterior end of alveolus for P3/. | 10.4 | 9.8 | ....... | ....... | ....... |
| I2/, greatest transverse diameter. | ....... | 11.9 | ....... | ....... | ....... |
| I3/, greatest transverse diameter. | 12.3 | 11.5 | ....... | ....... | ....... |
| C/, anteroposterior diameter at alveolus. | 32.4 | ....... | 28.9 | ....... | ....... |
| C/, transverse diameter at alveolus. | 13.4 | ....... | 12.7 | ....... | ....... |
| Length of C from alveolar border to tip of tooth. | 88.0a | ....... | 78.0a | ....... | ....... |
| P3/, anteroposterior diameter. | ....... | 26.1 | ....... | ....... | ....... |
| P3/, greatest transverse diameter. | ....... | 10.8 | ....... | ....... | ....... |
| P4/, anteroposterior diameter. | ....... | 47.0 | ....... | 46.5 | 45.1 |
| P4/, greatest transverse diameter across protocone. | 17.6 | 16.4 | ....... | 16.4 | 18.8 |
| P4/, greatest anteroposterior diameter of base of paracone. | ....... | 15.2 | ....... | 15.4 | 14.6 |
| P4/, length of metacone blade. | ....... | 19.5 | ....... | 20.5 | 20.0 |

TABLE 11

Measurements of *Marchairodus* inferior dentitions

| | TMM 41261-8 | TMM 41261-9 | MU 3527 | MU 4360 | MU 6399 | MU 6397 | MU 5597 | MU 4544 | MU 4545 |
|---|---|---|---|---|---|---|---|---|---|
| Length from anterior end of C to posterior end of M/1. | 128.0 | 133.0 | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| Length from anterior end of P/3 to posterior end of M/1. | 81.2a | 83.1 | 81.0a | ...... | ...... | ...... | ...... | ...... | ...... |
| Length from anterior end of P/3 to posterior end of M/1. | 59.8a | 62.5 | 61.0 | ...... | ...... | ...... | ...... | ...... | ...... |
| Length of diastema measured between alveoli for C and P/3. | 34.5 | 36.1 | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| Length of diastema measured between alveoli for P/3 and P/4. | 3.7 | 3.8 | 3.4 | ...... | ...... | ...... | ...... | ...... | ...... |
| Length measured from posterior border of alveolus for C to anterior border of alveolus for P/4. | 53.9 | 57.3 | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| /C, greatest transverse diameter. | 11.4 | ...... | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| /C, greatest anteroposterior diameter at base of enamel. | 12.5 | ...... | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| P/3, anteroposterior diameter. | ...... | 19.4 | ...... | 21.7 | ...... | ...... | ...... | ...... | ...... |
| P/3, greatest transverse diameter. | ...... | 8.3 | ...... | 9.5 | ...... | ...... | ...... | ...... | ...... |
| P/4, anteroposterior diameter. | ...... | 28.6 | ...... | ...... | 28.7 | 28.9 | 27.9 | ...... | ...... |
| P/4, greatest transverse diameter. | ...... | 10.9 | ...... | ...... | 12.0 | 12.0 | 12.0 | ...... | ...... |
| P/4, basal length of principal cusp. | ...... | 11.1 | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| M/1, anteroposterior diameter. | 32.1 | 35.8 | 32.6 | ...... | ...... | ...... | ...... | 32.3 | 32.0 |
| M/1, greatest transverse diameter. | 13.8 | 12.4 | 13.7 | ...... | ...... | ...... | ...... | 12.4 | 13.6 |

TABLE 12

Measurements of *Machairodus* cervical vertebrae, TMM41261–8

### ATLAS

| | |
|---|---|
| Greatest width across transverse processes | 147.0 |
| Greatest width of anterior end across articulation for condyles | 68.6 |
| Greatest width across outer borders of articulation for axis | 62.0 |
| Length from anterior end of articulation for condyles to posterior end of articulation for axis | 64.7 |
| Length of neural arch along median line | 27.9 |
| Greatest length of transverse process taken oblique to axis of vertebra | 74.4 |
| Greatest height from ventral surface of inferior arch to dorsal surface of neural arch | 41.0 |

### AXIS

| | |
|---|---|
| Length of centrum to tip of odontoid process | 82.3 |
| Depth of centrum measured normal to floor of neural canal and across posterior epiphyses | 20.0 |
| Greatest transverse width across posterior epiphysis of centrum | 41.0 |
| Width across articulating surface for atlas | 59.7 |

| | 3RD. | 4TH. | 5TH. | 6TH. | 7TH. |
|---|---|---|---|---|---|
| Length between ends of zygapophyses | ...... | 56.7 | 48.8 | 45.6 | 44.5 |
| Length of centrum normal to posterior face | 37.7 | 36.4 | 32.5 | 29.3 | 28.8 |
| Width across anterior zygapophyses | ...... | ...... | 58.0 | 60.0 | 58.2 |
| Width across posterior zygapophyses | ...... | ...... | 56.5 | 57.3 | 54.3 |
| Width of neural canal at anterior end | 20.2 | 22.1 | 23.1 | 24.6 | 26.1 |
| Greatest transverse width of posterior epiphysis of centrum | 30.3 | 34.6 | 32.1 | 29.3 | 30.0 |

| | | | | |
|---|---|---|---|---|
| Greatest width across ends of transverse processes | 96.0 | 94.0 | 89.8 | ...... | ...... |
| Greatest length of transverse process from outer end to end of anterointernal projection of inferior lamella | 44.0 | 42.5 | 34.4 | ...... | ...... |
| Height from ventral border of posterior epiphysis of centrum to top of neural spine | ...... | ...... | ...... | ...... | 84.0 |
| Depth of centrum measured normal to floor of neural canal and across posterior epiphysis | 21.7 | 21.3 | 17.5 | 20.0 | 20.4 |

TABLE 13

Measurements of *Machairodus* thoracic vertebrae

| Thoracic vertebra number | Greatest length from anterior to posterior zygapophysis. | Length of centrum normal to posterior face. | Greatest width across facets of anterior zygapophyses. | Greatest width across facets of posterior zygapophyses. | Height of neural canal at anterior end. | Greatest width of centrum across capitular facets. | Depth of centrum posteriorly, measured normal to floor of neural canal. | Greatest width across ends of transverse processes. | Greatest anteroposterior diameter of outer end of transverse process. | Distance from bottom border of centrum posteriorly to top of neural spine. |
|---|---|---|---|---|---|---|---|---|---|---|
| 1. | 46.0 | 28.9 | 55.3 | 40.0a | 16.0 | 37.7 | 20.9 | 89.5a | 24.7 | 101.9 |
| 2. | 43.9 | 30.0 | 42.8 | 34.3 | 12.4 | 41.1 | 21.9 | 74.0a | 19.3 | 111.8 |
| 3. | 44.5 | 28.0 | 34.5 | 30.9 | 12.0 | 41.5 | 21.2 | 73.7 | 16.3 | 105.0 |
| 5. | 43.7 | 27.6 | 31.6 | 27.6 | 13.0 | 39.0 | 22.0 | ...... | ...... | .......... |
| 6. | 43.5 | 27.7 | 27.6 | 27.4 | 12.8 | 37.5 | 22.5 | 72.3 | 14.7 | ........ |
| 7. | ...... | 27.9 | 25.5 | ...... | 11.5 | 37.7 | 23.3 | ...... | ...... | .......... |
| 8. | 43.6 | 27.6 | 27.7 | 25.6 | 12.8 | 37.0 | 23.2 | 70.2a | 15.1 | ........ |
| 11. | 44.7 | 32.8 | 26.4 | 19.7a | 12.2 | 29.2 | 23.5 | ...... | ...... | 55.0a |
| 12. | 56.0 | 36.8 | 30.1 | 25.6 | 13.3 | 39.2 | 24.3 | 47.0 | ...... | 49.5 |
| 13. | 62.7 | 40.1 | 24.6 | 19.1 | 14.3 | 35.8 | 23.5 | 43.0a | ...... | 74.0 |

TABLE 14

Measurements of *Machairodus* lumbar vertebrae

| Lumbar vertebra number— | Length of centrum measured normal to face of posterior epiphysis and along median line. | Greatest length from anterior face of metapophysis to end of posterior zygapophysis. | Greatest width across metapophysis. | Greatest width across posterior zygapophysis. | Width of posterior epiphysis of centrum. | Depth of centrum measured normal to floor of neural canal and across posterior epiphysis. | Height from middle ventral border of anterior epiphysis of centrum to top of neural spine. |
|---|---|---|---|---|---|---|---|
| 1. | 44.1 | 64.0 | 45.8 | 23.6 | 35.7 | 23.9 | 72.0 |
| 2. | 46.4 | 65.4 | 44.3 | 29.2 | 35.5 | 25.3 | 74.2 |
| 3. | 49.3 | 66.6 | 45.6 | 29.3 | 35.8 | 27.3 | 77.9 |
| 4. | 53.1 | 69.4 | 45.9 | 29.0 | 37.3 | 28.0 | ....... |
| 5. | 54.6 | 70.6 | 44.2 | 31.1 | 38.2 | 28.3 | 88.9 |
| 6. | 56.5 | 69.1 | 44.4 | 30.1 | 39.5 | 26.6 | 83.9 |
| 7. | 50.1 | 62.5 | 48.4 | 55.9 | 38.3 | 26.3 | 76.9 |

TABLE 15

Measurements of *Machairodus* sacrum, TMM41261–8

| | |
|---|---|
| Greatest length measured parallel to median line. | 112.0 |
| Greatest width at anterior end and at outer surfaces for ilia. | 85.2 |
| Greatest width of third sacral vertebra across transverse processes. | 57.0 |
| Greatest width between dorsal surfaces of anterior zygapophyses. | 56.4a |
| Greatest depth of centrum of first sacral vertebra measured normal to floor of neural canal and across anterior epiphysis. | 22.8 |
| Greatest distance from dorsal margin of anterior zygapophysis to ventral border of surface joining with ilium. | 59.0 |

TABLE 16

Measurements of *Machairodus* caudal vertebrae, TMM41261–8

| | 1. | 2. |
|---|---|---|
| Greatest length of centrum measured parallel to central axis. | 26.5 | 26.8 |
| Width across anterior zygapophyses. | 19.1 | 23.9 |
| Width across posterior zygapophyses. | 14.4 | 24.0 |
| Height from middle of ventral border of centrum to top of neural spine or neural arch. | 31.0 | 34.1 |

## TABLE 17

Measurements of *Machairodus* scapula, TMM41261–8

|  | right | left |
|---|---|---|
| Greatest width of articulating end measured across glenoid cavity. | 62.1 | 61.1 |
| Greatest transverse diameter across glenoid cavity. | 35.0 | 35.1 |
| Least width of neck across articulating end. | 52.3 | 52.4 |

## TABLE 18

Measurements of *Machairodus* humerus

|  | TMM 41261-8R | TMM 41261-8L | MU 6865 | MU 6869 |
|---|---|---|---|---|
| Greatest length measured parallel to longitudinal axis. | ....... | 314.0 | ....... | ....... |
| Greatest transverse diameter of proximal extremity. | ....... | ....... | 63.3 | ....... |
| Greatest anteroposterior diameter of proximal extremity. | ....... | ....... | 86.4 | ....... |
| Transverse diameter at middle of shaft. | 23.4 | 21.5 | ....... | ....... |
| Anteroposterior diameter at middle of shaft. | 38.7 | 37.1 | ....... | ....... |
| Greatest width of distal extremity. | 71.0 | 73.8 | 74.3 | 74.6 |
| Least anteroposterior diameter of articulating surface for ulna. | 24.8 | 24.8 | 24.0 | 23.8 |

## TABLE 19

Measurements of *Machairodus* ulna

|  | TMM 41261-8R | TMM 41261-8L | MU 6870 |
|---|---|---|---|
| Greatest length measured parallel to longitudinal axis of ulna. | 316.0 | ....... | 353a |
| Greatest width of posterior surface of olecranon process. | ....... | 27.0 | ....... |
| Greatest transverse width of greater sigmoid cavity. | 35.0 | 37.4 | ....... |
| Anteroposterior diameter of shaft at proximal end of tendon scar. | 38.1 | 35.6 | 44.5 |
| Transverse diameter of shaft at proximal end of tendon scar. | ....... | 26.9 | ....... |
| Greatest anteroposterior diameter of distal extremity. | 29.7 | ....... | 30.0a |
| Greatest width of distal extremity. | 18.0 | ....... | 20.7 |

## TABLE 20

Measurements of *Machairodus* radius

|  | TMM 41261-8 | MU 5533 | MU 5271 |
|---|---|---|---|
| Length measured along internal border. | 267.0 | 247.5 | 285.0 |
| Long diameter of proximal end. | 33.0 | 29.8 | 36.0 |
| Greatest diameter taken at right angles to long diameter of proximal end. | 25.7 | 24.0 | 26.4 |
| Greatest diameter of shaft at middle. | 25.1 | 23.6 | 23.2 |
| Least diameter of shaft at middle. | 15.2 | 14.8 | 16.3 |
| Greatest width at distal end taken normal to internal face. | 50.4 | 43.6 | 61.7 |
| Greatest thickness of distal end. | 33.5 | 28.7 | 30.9 |

TABLE 21

Measurements of *Machairodus* scapholunar

|  | MU 5417 | MU 7911 | MU 7975 | MU 7941 |
|---|---|---|---|---|
| Greatest transverse diameter measured normal to external border of proximal surface. | 56.0 | 51.1 | 47.4 | 48.1 |
| Greatest dorsopalmar length. | 35.6 | 38.1 | 31.3 | 31.6 |
| Greatest proximal distal diameter. | 28.8 | 25.6 | 24.7 | 24.4 |

TABLE 22

Measurements of *Machairodus* pisiform, MU7867

| | |
|---|---|
| Greatest length from and measured normal to contact edge of ulnar and unciform facets to the head. | 35.5 |
| Long diameter of articulating end. | 23.0 |
| Long diameter of head. | 19.0 |
| Greatest proximal diameter of head normal to long diameter. | 13.2 |

TABLE 23

Measurements of *Machairodus* metacarpal I, MU5929

| | |
|---|---|
| Greatest length normal to proximal end. | 34.0 |
| Greatest width of proximal end. | 22.7 |
| Transverse width of distal articulating surface. | 17.5 |

TABLE 24

Measurements of *Machairodus* metacarpals

| | Greatest length | Greatest transverse diameter of proximal end | Greatest dorsoventral diameter of proximal end | Transverse diameter at middle of shaft | Dorsoventral diameter at middle of shaft | Greatest transverse diameter at distal end of shaft |
|---|---|---|---|---|---|---|
| Metacarpal II | | | | | | |
| TMM41261-8 | 97.1 | 20.6 | 23.7 | 10.1 | 14.1 | 16.6 |
| MU4872 | 101.0 | 24.3 | ...... | 13.5 | 13.5 | 21.2 |
| MU5891 | 106.0 | 21.5 | 24.6 | 11.5 | 14.2 | 20.5 |
| Metacarpal III | | | | | | |
| TMM41261-8 | 112.1 | 19.4 | 23.0 | 13.9 | 11.7 | 21.0 |
| MU5376 | 112.9 | 21.2 | 22.6 | 15.4 | 12.8 | 22.8 |
| MU5892 | 117.6 | 19.8 | 21.6 | 14.9 | 13.2 | 23.1 |
| Metacarpal IV | | | | | | |
| MU6875 | 107.3 | 19.3 | 20.4 | 14.1 | 12.5 | 19.2 |
| Metacarpal V | | | | | | |
| TMM41261-8 | 88.8 | 16.4 | 19.3 | 10.4 | 12.0 | 17.3 |

TABLE 25

Measurements of *Machairodus* femur

|  | TMM 41261-8R | TMM 41261-8L | TMM 41261-13 |
|---|---|---|---|
| Greatest length from top of greater trochanter to distal condyles, measured parallel to long axis. | ....... | ....... | 342.0 |
| Transverse diameter of proximal end, outer face of greater trochanter to inner side of head, taken normal to median longitudinal plane. | 74.1 | 73.3 | 79.4 |
| Greatest anteroposterior diameter of head. | 35.3 | 35.1 | 35.6 |
| Transverse diameter of shaft at middle. | 29.0 | 28.4 | 30.9 |
| Anteroposterior diameter of shaft at middle. | 25.1 | 28.0 | 26.6 |
| Greatest width of distal extremity. | ....... | ....... | 65.9 |
| Greatest anteroposterior diameter of distal extremity at right angles to longitudinal axis of femur. | ....... | ....... | 63.2 |
| Greatest width of intercondylar notch. | ....... | ....... | 14.5 |
| Greatest width of articular surface of inner condyle. | ....... | ....... | 26.0 |

TABLE 26

Measurements of *Machairodus* tibia.

|  | TMM41261-14 | MU3671 |
|---|---|---|
| Greatest length measured parallel to long axis. | 284.0 | 293.0 |
| Greatest transverse diameter of proximal end. | 64.5 | 68.4 |
| Transverse diameter of shaft at middle. | 26.2 | 30.8 |
| Greatest transverse diameter of distal end. | 50.7 | 52.5a |
| Greatest anteroposterior diameter of distal end. | 31.5 | 31.0a |

TABLE 27

Measurements of *Machairodus* astragalus.

|  | TMM 41261-8 | MU 5743 | MU 5744 | MU 5764 |
|---|---|---|---|---|
| Greatest length. | 47.1 | 51.3 | 49.2 | 47.3 |
| Greatest width. | 48.5 | 51.3 | 50.5 | 48.7 |
| Least distance across neck. | 19.1 | 21.0 | 19.7 | 20.9 |
| Greatest diameter of head. | 28.8 | ....... | 30.7 | 32.5 |

TABLE 28

Measurements of *Machairodus* calcaneum.

|  | MU 7562 | MU 7644 | MU 7536 |
|---|---|---|---|
| Greatest length. | 90.7 | 83.5 | 94.4 |
| Greatest width measured across astragalar facets As[1] and As[2]. | 36.7 | ....... | 40.5 |
| Greatest width across cuboid surface measured from astragalar facet As[3] to outer side. | 29.3 | 29.1 | 31.1 |

TABLE 29

Measurements of *Machairodus* cuboid, MU7949

| | |
|---|---|
| Greatest proximodistal diameter. | 28.7 |
| Greatest transverse diameter. | 22.7 |
| Greatest dorsoplantar length. | 29.1 |

TABLE 30

Measurements of *Machairodus* navicular, MU5963

| | |
|---|---|
| Dorsoplantar length. | 35.6 |
| Transverse diameter. | 26.1 |

TABLE 31

Measurements of *Machairodus* metatarsals

| Metatarsals number | Greatest length. | Greatest transverse diameter of proximal end. | Greatest dorsoventral diameter of proximal end. | Transverse diameter at middle of shaft. | Dorsoventral diameter at middle of shaft. | Greatest transverse diameter at distal end of shaft. |
|---|---|---|---|---|---|---|
| | | | Metatarsal II | | | |
| TMM41261-8R | 119.0 | 15.6 | 30.1 | 12.0 | 16.0 | 20.7 |
| TMM41261-8L | 118.7 | 16.4 | 27.4 | 11.0 | 13.9 | 20.3 |
| MU3353 | 107.0 | 16.3 | 27.8 | 11.7 | 13.5 | 20.1 |
| MU3884 | 105.1 | 16.0 | 30.0 | 12.0 | 15.4 | 20.0 |
| MU6874 | 102.4 | 14.4 | 27.1 | 11.9 | 13.5 | 18.8 |
| MU6879 | 104.5a | 14.4 | 27.6 | 11.3 | 13.5 | 18.9 |
| MU1868 | 104.7 | 14.5 | 25.1 | 11.0 | 13.3 | 17.8 |
| | | | Metatarsal III | | | |
| MU6873a | 123.5 | 21.7 | 29.2 | 15.6 | 14.1 | 22.0 |
| | | | Metatarsal IV | | | |
| MU6873b | 115.2 | 21.9 | 26.2 | 12.8 | 15.3 | 19.4 |
| MU6876 | 115.8 | 26.4 | 22.8 | 12.5 | 13.7 | 19.2 |
| | | | Metatarsal V | | | |
| MU1933 | 103.2a | 18.5 | 16.3 | 8.6 | 11.6 | 16.3 |

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