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MACHAEROIDES EOTHEN MATTHEW, THE SABER-  
TOOTH CREODONT OF THE BRIDGER EOCENE

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THE 1940 Smithsonian Institution expedition to the Bridger Basin of Wyoming had unusual good fortune in securing skeletal remains of the rare creodont *Machaeroides eothen*. The materials, consisting of skull, lower jaws, and other skeletal portions of one individual, were found by Franklin Pearce in low exposures, probably of Bridger "C," immediately to the north of Twin Buttes, about 30 miles southwest of Green River, Wyo. Previous finds of this remarkable sabertooth form, so far as known, are limited to the lower jaw portions described by Matthew<sup>1</sup> in 1909.

The skull, U.S.N.M. No. 17059, was found with the lower jaws in a position of articulation, and although essentially complete there has been a small amount of transverse crushing and distortion so that the right side of the skull is higher than the left. The remainder of the skeleton includes portions of the vertebral column, both humeri and femora, the right radius and ulna, an incomplete left tibia, and fragments of the pectoral and pelvic girdles. The feet were not present except for a carpal and two metacarpal bones.

Matthew readily appreciated the indications in the lower jaw portions of *Machaeroides eothen* of a modification nearly paralleling that of the machairodont forms among the Fissipedia. In the materials he had at hand these modifications were not too evident, and R. H. Denison<sup>2</sup> was inclined to consider the *M. eothen* jaw as resembling *Felis* and not truly "sabertooth." The

<sup>1</sup>Matthew, W. D., *Mém. Amer. Mus. Nat. Hist.*, vol. 9, pt. 6, pp. 462-463, 1909.

<sup>2</sup>Denison, R. H., *Ann. New York Acad. Sci.*, vol. 37, p. 181, 1938.

National Museum specimen, however, leaves no doubt of the direction and extent of specialization, which quite parallels that seen in the machairodonts but not to the extent exhibited in the Uinta *Apataelurus kayi* described by Scott.<sup>3</sup> Structurally no characters are observed in the illustrations of the lower jaws of *A. kayi* that would preclude derivation of this form from *M. eothen*, with the characteristics attendant upon sabertooth development reaching a high degree of specialization within an interval of time suggesting a comparatively rapid evolutionary tempo.

Matthew regarded *Machaeroides eothen* as an oxyaenid type of creodont, closely related to forms included in the subfamily Limnocyoninae, to which he allocated it (p. 410),<sup>4</sup> having created, however, the subfamily name "Machairoidinae" on an earlier page (330). Denison<sup>5</sup> retained the supergeneric separation, which was entirely justified by the discovery of *Apataelurus*, recognizing a natural phyletic subfamily. However, Denison removed the Limnocyoninae and Machaeroidinae from the Oxyaenidae and placed them in the Hyaenodontidae. Justification for this was claimed on the basis of morphological differences between the Oxyaeninae and Limnocyoninae and similarities between the Limnocyoninae and Proviverrinae, particularly between *Prolimnocyon* and *Sinopa*. Separation from the Oxyaenidae seems supported, and, moreover, carnassial specialization, which has been the key to their supposed affinity, may well have developed independently in the two groups. I cannot, however, but regard the carnassial differentiation that so readily distinguishes the Limnocyoninae from members of the Hyaenodontidae as being of fundamental importance, and hold that the morphological similarities may be as easily attributed to similar adaptation or parallelism. It is in a similar manner that the Machaeroidinae so markedly resemble the machairodonts, although obviously not derived one from the other. Derivation of the Limnocyoninae from an early proviverrine stock is not disproved and may be reasonable as suggested by the similarity of lower jaws belonging to forms of *Prolimnocyon* and *Sinopa mordax*, but their divergence must originate in a primitive form with molars as yet undifferentiated as to carnassials, and where  $M^2$ , for example, has not taken on characteristics so markedly different in the two groups.

<sup>3</sup> Scott, W. B., Ann. Carnegie Mus., vol. 27, art. 6, pp. 113-120, 1938.

<sup>4</sup> Matthew, W. D., *ibid.*

<sup>5</sup> Denison, R. H., *ibid.*, p. 181.

Inasmuch as it seems advisable to exclude the Limnocyoninae from the Oxyaenidae, and since I am unable to reconcile it with the Hyaenodontidae on the basis of carnassial differentiation, I propose, at the risk of censure, that the Limnocyoninae and Machaeroidinae be given family recognition as the Limnocyonidae.

*Description of skull* (pl. 45).—The skull of *Machaeroides eothen* is significantly smaller than that of *Limnocyon verus* but much larger than *Thinocyon velox*, corresponding closely in size to *Sinopa rapax* among its less closely related contemporaries. The skull is moderately slender but with a noticeably deep rostrum, high sagittal crest, and a narrow occiput.

The rostrum, in addition to depth, exhibits a well-inflated maxillary portion covering the long root section of the canine, extending parallel and immediately posterior to the suture joining the premaxilla. The nasals extend posteriorly in a nearly V-shaped wedge between the frontals, terminating fully as far back as the postorbital processes. In *Thinocyon* and *Limnocyon* the nasals as exposed terminate distinctly forward of this position. The postorbital processes of the frontals are moderately well developed and, although possibly not complete, do not appear so prolonged as in *Thinocyon*. The lachrymal bone in *M. eothen* is large and extends well forward of the orbit and exhibits a most unusual feature in that the lachrymal foramen enters the skull anterior to the orbital rim and anteroventral to the lachrymal crest or tubercle. A smaller foramen also enters the lachrymal bone outside and immediately dorsal to the lachrymal tubercle. This arrangement was not observed in other creodonts, but it occurs in marsupials and sloths. Matthew,<sup>6</sup> however, noted that the lachrymal foramen in *Limnocyon* was very near the orbital rim.

The cranial portion of the skull is characterized by an exceedingly small brain case, relatively much smaller than in *Thinocyon*, and a very high sagittal crest, which joins a high but narrow occipital crest. The latter is overhanging but, quite unlike *Limnocyon*, is noticeably constricted transversely immediately above the occipital condyles. A prominent vascular foramen is noted at the suture between the parietal and squamosal at a position about over the trough for the audital tube, and one also in the posterior portion of the temporal fossa, presumably at about the juncture of the parieto-squamosal and parieto-occipital sutures.

In ventral aspect the palatal portion of the skull shows no unusual features. No evidence exists of the grooves and ridges

<sup>6</sup> Matthew, W. D., *ibid.*, p. 438.

characterizing the later fissiped sabertooth cats. However, palatal excavations between the deuterocone or protocone portions of successive 3-rooted teeth, for reception of the much-elevated protoconids of the lower cheek teeth, are as well developed as in several of the other creodonts. The posterior margin of the palate is extended posteriorly a very short distance below the narial passage, somewhat as in *Limnocyon*. The palatal margin outside the narial passage, however, shows a conspicuous notch for the palatine vein, with well-developed tuberosities on both the palatal and maxillary sides of the groove.

The zygomatic arch arises from perhaps a slightly higher position on the relatively deep rostrum of *Machaeroides eothen* than it does in *Limnocyon verus*, although in *M. eothen* the left arch is broken down to a position below normal on that side of the skull. The depth of the arch is moderate, but because of crushing the extent to which it is expanded laterally cannot be determined. Posteriorly the arch terminates at a position relatively low with respect to the basicranial surface. The zygomatic process of the squamosal projects conspicuously downward from the basicranium, placing the glenoid surface for articulation of the lower jaw at a much lower level than observed in other creodonts, a condition noted in machairodonts and in the sabertooth marsupial *Thylacosmilus atror*. This lowering of the fulcrum gives leverage to the temporal muscle acting on a coronoid process of reduced height. The reduction of the coronoid presumably permitted the lower jaw to open wide enough for the mandible to clear the sabertooths, apparently much wider than necessary in other carnivores, except *Apataelurus* and the machairodonts.

The basicranial portion of the skull is the least distorted by crushing and is relatively elongate and clearly much narrower than in *Limnocyon verus*. The paroccipital process shows very little development and does not project posteriorly as in *Limnocyon verus*. However, in addition to the downward-projecting pedestallike base for the glenoid surface, the mastoid process, as in the machairodonts, is very well developed, projecting downward and forward, and noticeably expanded in an anterointernal-posteroexternal direction. The mastoid process is moderately developed in most creodonts including *Limnocyon*, but nowhere in the suborder is it relatively so important, particularly in a forward medial extension, as in *M. eothen*, and in *Apataelurus* by inference. Its prominence and rugosity demonstrate the strength and importance of the sterno-cleido-mastoid muscle, the actions of which include depressing the head, as in striking with the

sabers. The mastoid process is essentially a part of the mastoid portion of the periotic; however, the extent to which the squamosal enters into its composition cannot be determined, limited possibly to a portion of the anterior surface of the process.

The foramina of the basicranium show certain significant differences in relative position from those in *Limnocyon verus* or in *Thinocyon velox*. For the most part these maintain a primitive, creodont arrangement with differences noted in *Machaeroides eothen* that are in part due to structural modification attendant upon sabertooth development. The alisphenoid canal, if present, is decidedly long as in *Limnocyon*, but with the posterior opening confluent with or not distinguished from the foramen ovale, so that it was not certainly identified in the material at hand. In *Limnocyon verus* the posterior opening of the alisphenoid canal is shown by Matthew<sup>7</sup> as well forward of the foramen ovale. The foramen ovale in *M. eothen* is located medial to the postglenoid process, at the root of the pterygoid wing of the alisphenoid. The postglenoid foramen enters the skull at the base of the posterior surface of the postglenoid process but exhibits a groove for about half the length of this surface before closure is complete. The foramen lacerum medius is in a customary position antero-internal to the exposed portion of the petrosal. From a position medial to the promontorium of the petrosal a narrow cleft extends posteriorly along the outwardly convex lateral margin of the basioccipital to the foramen lacerum posterius, about halfway to the occipital condyles. The internal carotid evidently entered the brain case at some point along the anterior part of the cleft and adjacent to the petrosal. The condylar or hypoglossal foramen is well forward of the condyles and separated by a thin partition from the foramen lacerum posterius, quite unlike *Limnocyon* or *Thinocyon* but resembling certain specimens of the Oligocene *Daphoenus* in this respect. The stylomastoid foramen shows as a groove on the medial margin of the mastoid process. Dorsally this is completely enclosed, presumably by bone belonging to the mastoid portion of the periotic, at the root of the mastoid process, posterolateral and very close to the promontorium of the petrous portion.

*Machaeroides eothen* is without a tympanic bulla, and the tympanic ring was not preserved. The site of the audital tube is a deep and compressed U-shaped trough between the postglenoid and mastoid processes, extending laterally and somewhat posteriorly from below the anteroexternal portion of the

<sup>7</sup> Matthew, W. D., *ibid.*, fig. 55

petrosal. In *Limnocyon* and *Thinocyon* the trough is more widely open and relatively shorter. The petrosal is partially exposed on both sides of the skull of *M. eothen*. It exhibits an acutely projecting promontorium located immediately inward from the medial margin of the mastoid process. The petrosal is more broadly rounded ventrally in *Thinocyon*. The fenestra rotunda in *M. eothen* is large and faces posteriorly and slightly outward and downward below the flattened ventral surface of the posterior portion of the petrosal. The anterior surface of the petrosal is broad and flattened, facing anterolaterally and ventrally and joining the medial surface in a bluntly rounded angle that extends anteromedially and dorsally from the promontorium. The fenestra ovale faces slightly forward of lateral and is situated very deep in the mesotympanic fossa, almost directly above but well separated from the promontorium. It is much higher in position than the fenestra rotunda and is very much above the lip of the trough for the audital tube. Further description of the petrosal and its relation to the cranial cavity is not undertaken, inasmuch as such additional information cannot be obtained without damage to the skull.

*Upper dentition.*—The dental formula for the upper teeth of *Machaeroides eothen* is 3-1-4-2, as noted by Matthew in *Limnocyon* and as observed in *Thinocyon*. Moreover, the first upper molar is the carnassial as in these forms and as in the Oxyaenidae. The teeth resemble those in the Limnocyoninae with certain exceptional characteristics which for the most part are modifications seemingly accompanying sabertooth development.

The incisors are slender, recurved, conical teeth adapted for piercing and with transversely flattened roots. Unlike *Limnocyon* they increase in size from first to third,  $I^3$  being much more robust and with a root portion about twice as long as in  $I^2$ .  $I^3$  in *Limnocyon* is much smaller than  $I^2$  and may not be present in some individuals, as indicated by Matthew.<sup>8</sup> In *Thinocyon* the three are subequal and slightly spatulate.

The enlarged canine is preserved only on the left side and is broken away a short distance below the alveolus. It is removed from  $I^2$  by a short diastema. The tooth as exposed has no cingulum, is nearly oval in cross section, and has a long gently curved root section, as inferred from the inflated portion of the maxilla. In Matthew's<sup>9</sup> illustration of *Limnocyon verus* the upper canine appears to have an exposed cingulum and the short crown is

<sup>8</sup> Matthew, W. D., *ibid.*, p. 434.

<sup>9</sup> Matthew, W. D., *ibid.*, fig. 53.

noticeably recurved below this point. The length of the canine in *M. eothern* cannot be determined from the present material; however, if this tooth extended as far as the flange of the lower jaw it would have had a length of about 3 cm. beyond the alveolus. The canine shows no evidence of serrations along the anterior or posterior margins.

The premolars of *M. eothern* are 1-, 2-, 3-, and 3-rooted, respectively.  $P^1$ , preserved only on the right side when found but subsequently lost, is a small, simple, conical tooth without an accessory cuspule and separated by a diastema from both the canine and  $P^2$ . In both *Limnocyon* and *Thinocyon*  $P^1$  is 2-rooted and exhibits a small posterior cuspule.  $P^2$  of *M. eothern*, in addition to being 2-rooted, retains a vestige of a posterior cuspule. The tooth is relatively much smaller and transversely more compressed than in *Limnocyon*.  $P^3$ , on the other hand, is much better developed than in *Thinocyon* and apparently than in *Limnocyon*. This tooth, preserved only on the left side, has a minute parastyle and a rather well developed posterior cusp or crest, approximating  $P^4$  in this respect. The lingual root is slender but extends markedly inward from about midway of the tooth length and supports a very small deuterocoene.  $P^4$  is relatively robust with a prominent parastyle before and a trenchant cusp posterior to the large backward sloping primary cusp. The deuterocoene portion is broad and well defined, extending lingually from the midportion of the tooth. The deuterocoene portion does not project forward as it does in *Thinocyon* or (to a less degree) in *Limnocyon*. The deuterocoene is situated on the lingual margin of the talon and is connected with the primary cusp by a low crest across the forward part of the talon. A small, shallow basin is enclosed between this forward crest and the low lingular crest around the posterior margin of the talon.

The difference in development of the various premolars is rather striking in comparison with related forms.  $P^1$  and  $P^2$  are relatively small and less progressive, probably reduced from an earlier but more advanced state, paralleling the machairodonts in this respect, as an accompanying factor in sabertooth specialization.  $P^3$ , however, has retained a more advanced stage of development and undoubtedly continued to be a significant and functional tooth in the later and more advanced *Apataelurus*, as indicated by the well-developed and trenchant  $P_4$  with which it occludes in the lower jaw of the Uinta form.

$M^1$ , the upper sectional tooth in *Machaeroides eothern*, has taken on a very trenchant appearance as compared either with the

preceding  $P^4$  of *Machaeroides* or with  $M^1$  in *Limnocyon* and *Thinocyon*. The talon portion is much reduced and far forward in position, the deuterocone being but a very small cusp at the anterolingual angle of the tooth. The posterior crest is elongate and the greater part of the lingual face of the tooth forms a flat shearing blade which, though oblique, is directed more nearly longitudinal than in either *Limnocyon* or *Thinocyon*. The paracone and metacone of  $M^1$  are closely connate, more so than in *Limnocyon*, approximately as in *Tritemnodon*. The parastyle is but weakly developed, being represented only by an enlargement of the cingulum anteroexternal to the paracone.

$M^2$  has a nearly transverse shear and is characterized in distinction from that in *Limnocyon* and *Thinocyon* in having lost all trace of the metacone. Also, the talon is reduced to a very subdued projection from the paracone, the shear being effected essentially by the paracone and parastyle, whereas in *Limnocyon* and *Thinocyon* the talon participates very largely in the shearing structure, cutting against the metaconid and occluding with the talonid of  $M_2$ . The reduction of the talon of  $M^2$  in *M. eothen* accompanies the loss of the metaconid and extreme reduction of the talonid of the lower carnassial.

*Mandible* (pl. 46, a, b).—The lower jaw of *Machaeroides eothen* has been briefly described and figured by both Matthew and Denison, and the relationship to other creodonts discussed at length. However, the specimens available to them for study were incomplete, lacking particularly the extremity of the flange, coronoid process, and the crowns of the canine and carnassial teeth. Restorations of these parts in drawings were conservative in indicating less modification from the limnocyonine pattern than the more complete material demonstrates.

The lower jaw is relatively very deep and transversely slender compared to jaws belonging to forms of the Limnocyoninae. Its flange projects downward to a greater extent than anticipated but not to the extent shown in *Apataelurus kayi*, and much less than in *Hoplophoneus*. In *M. eothen* it projects but a little below the dorsoventrally elongate symphysis and curves gently outward so that the width across the extremities of the flanges is greater than at any point above. The deep symphyseal surface has a nearly straight, steeply inclined anterior margin, which makes an abrupt angle with lower margin. The coronoid process of the lower jaw appears truncated and much reduced from the large and fully developed coronoid observed in *Limnocyon* and *Thinocyon*. The reduction, nevertheless, has not gone so far as that in *Apataelurus*.



Moreover, the condyle is lower with respect to the tooth row. The angle, less widely separated from the condyle, does not curve downward from the nearly straight lower margin of the jaw but preserves the alignment practically to its extremity, more so than in *Apataelurus*. The masseteric fossa is well defined with a sharp masseteric crest anterodorsally; however, the fossa, as in *Apataelurus* and also *Patriofelis*, extends farther forward beneath the carnassial than in *Limnocyon* and *Thinocyon*. The mental foramina are beneath  $P_1$  and the posterior root of  $P_2$  and placed relatively low on the side of the jaw.

*Lower dentition.*—The lower teeth are all present, although the right canine and  $P_2$  as well as the left carnassial and median incisors are slightly damaged. The lower incisors of *Machaeroides eothen* were most certainly reduced to two. The lateral of these is the larger of the two, and both, as in the case of the upper incisors, are piercing type structures with transversely flattened roots. In lateral view the canine appears moderately robust at the alveolar border but is transversely flattened and tapers rapidly to a point only a little above the closely adjacent incisors. Moreover, it shows a pronounced scar or bevel vertically along its posterolateral surface, worn through occlusion with the superior canines.

The cheek teeth appear decidedly slender, and the two anterior premolars, both of which, however, retain two roots, are of rather small size.  $P_3$  is about intermediate in size and development between  $P_2$  and  $P_4$ . It has a crested talonid, almost as in  $P_4$ ; a structure but very feebly expressed in  $P_2$ .  $P_3$  is without a paracoid, whereas in  $P_4$  this cusp is low but distinct. Both  $P_3$  and  $P_4$  are more progressive than in *Limnocyon* and *Thinocyon*; however, in *Apataelurus*  $P_3$  has become relatively much reduced in size.  $P_4$  in both *Machaeroides* and *Apataelurus* has become a relatively large and functionally significant tooth, actually exceeding  $M_1$  in size in both forms.

The two molars possess somewhat more distinctive structural characters than the premolars in characterizing *Machaeroides*. In  $M_1$  the metaconid is but moderately developed and pressed close to the protoconid. The talonid is much reduced in size and trenchant in character. In *Limnocyon* and *Thinocyon* the relatively wider and more robust  $M_1$  has a better-developed metaconid and a large, deeply basined talonid. In *Apataelurus* the trenchant heel persists and evidence remains of a metaconid that has not been entirely obliterated by the shearing function imposed on the tooth.

The carnassial,  $M_2$ , in *M. eothen* exhibits more noticeable modifications than  $M_1$  toward a sabertooth specialization. The metaconid is lost, except for a slight rugosity on the posterointernal margin of the backward sweeping protocone. The talonid is reduced to little more than a vestige, although its expression is somewhat better in the specimen figured by Matthew.<sup>10</sup> The tooth is almost catlike in appearance, quite unlike that in *Limnocyon* or *Thinocyon* where the carnassial is very much like  $M_1$  except for its greater size and higher trigonid. In *Apataelurus* the lower carnassial has almost or quite reached the stage exhibited by *Smilodon* in its modification for shearing, but still preserving a vestige of its trenchant talonid.

TABLE 1.—Measurements (in millimeters) of skull, mandible, and dentition of *Machaeroides eothen*, U. S. N. M. No. 17059

Greatest length of skull from anterior margin of premaxillae to posterior margin of occipital condyles.....	a	135
Distance from anterior margin of premaxillae to posterior nasal aperture.....	a	65
Greatest depth of maxillae above $P^3$ .....	a	32
Width of palate between canine alveoli.....	a	16
Greatest width of basicranial region across mastoid processes.....	a	48
Length of upper dentition from $I^1$ to $M^2$ inclusive.....	a	62
Length of upper dentition from anterior margin of canine alveolus to $M^2$ inclusive....	a	55
Width across $I^1$ to $I^3$ inclusive.....		75
Length of cheek tooth series, $P^1$ to $M^2$ inclusive.....		42
Length of diastema anterior to $P^1$ ; posterior to $P^1$ .....	3.5:	2.5
Length of premolar series, $P^1$ to $P^4$ inclusive.....		30
Length of molar series, $M^1$ to $M^2$ .....		11.3
Canine—anteroposterior diameter at alveolus: transverse diameter.....	8.5:	5
$P^1$ —anteroposterior diameter: greatest transverse diameter.....	3.2:	2.1
$P^2$ —anteroposterior diameter: greatest transverse diameter.....	5.4:	2
$P^3$ —anteroposterior diameter: greatest transverse diameter.....	8 :	5
$P^4$ —anteroposterior diameter: greatest transverse diameter.....	10 :	8.2
$M^1$ —anteroposterior diameter: greatest transverse diameter.....	9.4:	7.5
$M^2$ —anteroposterior diameter: greatest transverse diameter.....	3.5:	8.1
Length of lower jaw from anterior extremity to condyle.....		92
Depth of symphysis of lower jaw measured along anterior face.....		26
Depth of flange of lower jaw below diastema between canine and $P_1$ .....		22
Depth of lower jaw below $P_2$ .....		16.5
Depth of lower jaw below $M_2$ .....		16.5
Height of coronoid process above inferior margin of ramus.....		28
Length of lower dentition from anterior margin of canine to $M_2$ inclusive.....		57.5
Length of cheek tooth series, $P_1$ to $M_2$ inclusive.....		43.5
Length of diastema anterior to $P_1$ ; posterior to $P_1$ .....	8 :	2
Length of premolar series, $P_1$ to $P_4$ inclusive.....		28.8
Length of molar series, $M_1$ and $M_2$ .....		15.9
Canine—anteroposterior diameter at cingulum: transverse diameter.....	6.7:	3.5
$P_1$ —anteroposterior diameter: greatest transverse diameter.....	3.6:	1.6
$P_2$ —anteroposterior diameter: greatest transverse diameter.....	4.7:	2
$P_3$ —anteroposterior diameter: greatest transverse diameter.....	7.6:	3
$P_4$ —anteroposterior diameter: greatest transverse diameter.....	9.1:	4
$M_1$ —anteroposterior diameter: greatest transverse diameter.....	8.6:	4
$M_2$ —anteroposterior diameter: greatest transverse diameter.....	8.7:	4.4

*Vertebrae*.—Among cervical vertebrae preserved of *Machae-*

<sup>10</sup> Matthew, W. D., *ibid.*, fig. 71.

*roides eothen* are the atlas, axis (badly crushed), and three others including the seventh. The transverse processes are not complete on the atlas, but sufficient remains to show that the groove or notch at the anterior extremity for the anterior course of the vertebral artery and the inferior branch of the spinal nerve is not covered but widely open as in *Thinocyon*. The posterior opening of the vertebral foramen, however, is distinctly on the posterior border of the transverse process, not dorsal to it as described by Matthew for *Thinocyon*.

The two intermediate cervicals between the axis and the seventh show a well-developed inferior lamella with the forward ridge well separated from the forward extension of the transverse process by the opening of the vertebral canal. These also show a well-developed forward projecting hyperapophysis beginning superior to the postzygapophysis and extending forward half to three-quarters of the way to articular surface of the anterior zygapophysis. It is lower than the spine and more compressed transversely.

The first eight dorsal vertebrae were found in articulation with the last cervical, and the centra of seven additional vertebrae, not in articulation, were preserved, at least four of which belong to the lumbar series. The anterior dorsals show elongate transverse processes for articulation with the ribs, and moderately high but rapidly tapering spines. The spine of the first dorsal appears to be the longest, and possibly the only one to have an anteroposteriorly expanded tip. The centra identified as lumbar are very elongate, dorsoventrally flattened, and with the articular faces markedly sloping, downward and backward with respect to the longitudinal axis.

*Limb bones* (pl. 46, c-f).—The humerus of *Machaeroides eothen* is distinctly larger and more robust than in *Limnocyon verus*. The deltoid and ectocondylar ridges are wide and flaring, and both extend for a greater proportion of the length of the shaft than in *L. verus*. The development of the deltoid crest together with the high and widely expanded acromion of the scapula furnishes good leverage and indicates the importance of the deltoid muscle, which functions in raising the arm outward. The prominence and length of the ectocondylar ridge denote good leverage for the supinator longus in flexing and supinating the forearm. The greater and lesser tuberosities are well developed with large rugose surfaces for the muscles used in rotating the humerus. The distal end of the humerus exhibits a large, oval entepicondylar foramen and well-developed condyles, particularly the inner, which has a very rugose

anterodistal surface for attachment of flexor muscles for the manus and forearm.

The radius and ulna are longer than in *Limnocyon verus* and noticeably curved. Both elements are noticeably flattened transversely and anteroposteriorly expanded in their distal portions, although a part of this is recognized as due to crushing. The olecranon of the ulna is relatively robust and bent somewhat inward but is not so long as in *L. verus*. The shaft of the ulna is not convex anteriorly, as described for *L. verus*, but, if anything, is concave anteriorly. The radius shows a compound curve, concave forward in the proximal portion and convex forward in the medial and distal portions. The proximal portion of the radius also has a well-developed bicipital tuberosity, turned slightly inward from the shaft of the ulna, for insertion of the biceps. Moreover, the distal portion of the radius is very much expanded anteromedially above the prominent styloid process. This expansion supports the place of insertion for the distal end of the supinator longus muscle which had its origin on the well-developed supinator ridge of the humerus.

Remains of the manus include the scapholunar and the third and fifth metacarpals. The scaphoid, lunar, and centrale are fused, although a groove showing the line of separation between the scaphoid and lunar can be seen across a portion of the radial facet. The distal facets for articulation with the magnum, unciform, and trapezoid are deeply concave and separated from one another by sharp angles. The metacarpals appear short and stout, a characteristic noted in machairodonts in comparison with true felids.

TABLE 2.—Measurements (in millimeters) of the limb bones of *Machaeroides eothen*, U. S. N. M. No. 17059

Length of humerus.....	104
Anteroposterior diameter of proximal end of humerus.....	26.5
Transverse diameter of proximal end of humerus across tuberosities.....	23
Transverse diameter of distal end of humerus.....	31.5
Greatest length of radius.....	78.8
Greatest diameter of proximal end of radius.....	13.5
Greatest diameter of distal end of radius.....	18.3
Length of ulna .....	102
Anteroposterior diameter of olecranon below tuberosities.....	13.5
Greatest diameter of distal end of ulna .....	13
Greatest length of scapholunar.....	18
Length of metacarpal III.....	27
Length of metacarpal V.....	21
Length of femur parallel to axis of shaft.....	118
Diameter of proximal end of femur across head and greater trochanter, perpendicular to axis of shaft.....	a 85
Transverse diameter of shaft of femur at midsection.....	17.5
Transverse diameter of distal end of femur across condyles, excluding tuberosities.....	16
Transverse diameter of distal end of femur across tuberosities.....	18

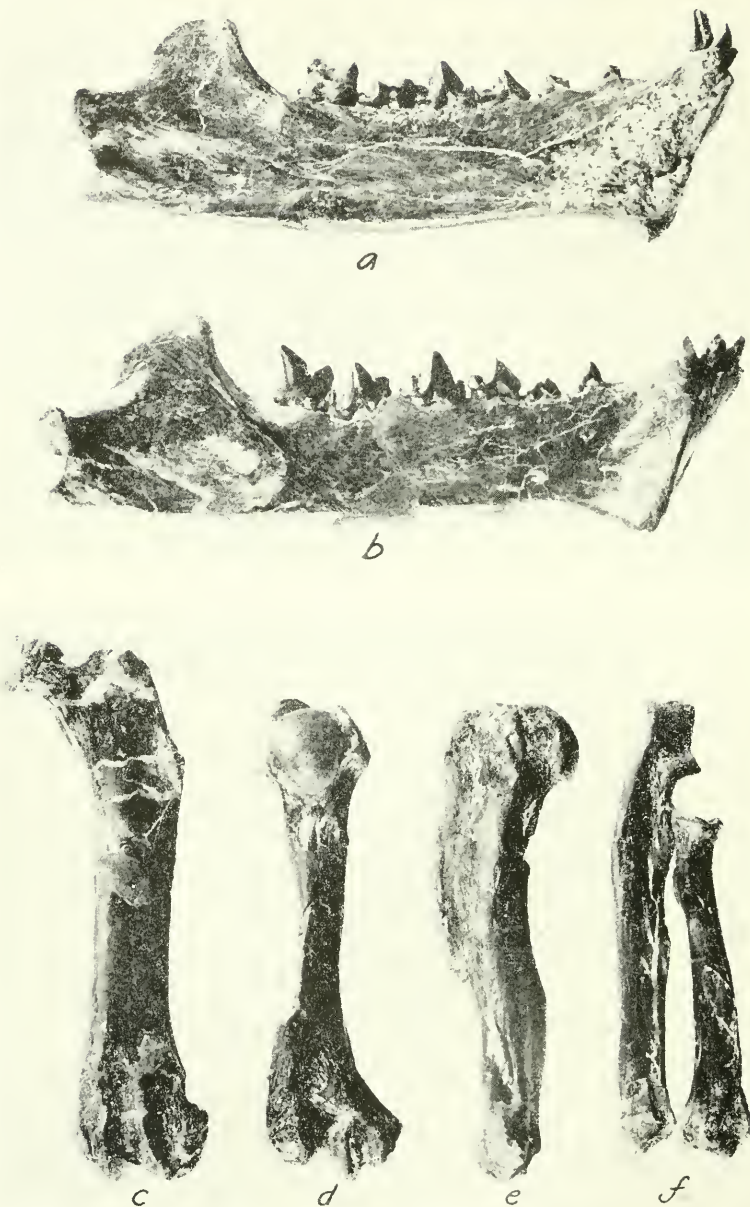
Both femora are preserved although the right is partly damaged. This element is longer and sturdier than in *Limnocyon verus* but otherwise has about the same curvature. The greater trochanter, though exhibiting an enlarged, rugose surface, does not project upward so far as in *L. verus*. The lesser trochanter is a posterointernal knoblike process situated at about the same height on the shaft as in *L. verus*, but the third trochanter is distinctly higher or more proximally located on the shaft, only slightly lower than the lesser trochanter. The distal extremity is relatively flattened on the dorsal surface and the patellar trochlea not so long as in *L. verus* but with the depression carried upward on the shaft well beyond the termination of the articulating surface.

The preserved portion of the tibia is relatively robust, and curved, as described for *L. verus*, but the cnemial crest is prominent and extends distally a greater distance. The proximal extremity is missing but the posterior surface shows a rather deep groove between the ridges supporting the condyles, emphasized in part by crushing. The distal extremity may not be entire. It terminates in a simple, nearly flat surface with a steep dorso-lateral slope for articulation with the astragalus. The internal malleolus may not extend much below the facet for the astragalus, but is incomplete.





*Machaeroides cothen* Matthew. Skull (U.S.N.M. No. 17059): *a*, Dorsal view; *b*, lateral view; *c*, ventral view; *d*, occlusal view of upper cheek teeth. Bridger Eocene, Wyoming. *a-c* three-fourths natural size; *d*,  $1\frac{1}{2}$  natural size. Drawing (*d*) by Mrs. Aime M. Awl.



*Machaeroides cothen* Matthew. *a, b*, Mandible (U.S.N.M. No. 17059): *a*, lingual view of left ramus; *b*, lateral view of right ramus. *c-f*, Limb bones (U.S.N.M. No. 17059): *c*, anterior view of left femur; *d*, posterior view of left humerus; *e*, medial view of right humerus; *f*, lateral view of right radius and ulna. Bridger Eocene, Wyoming. *a, b* natural size; *c-f* three-fifths natural size.