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# Contributions in Biology and Geology

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Number 43

March, 1981

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Formation, Southern Green River Basin,  
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**ISBN: 0-89326-070-3**

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**Milwaukee Public Museum Press**

**Published by the Order of the Board of Trustees**

**Milwaukee Public Museum**

**Accepted for publication March 2, 1981**

507 M648 CBG no.43 c.2

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Geology and paleontology of  
the Bridger Formation

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**Part 5. *Harpagolestes macrocephalus* and  
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Mesonychids**

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*Abstract:* A newly-collected specimen of a relatively young individual of *Harpagolestes macrocephalus* from the lower part of the Bridger Formation permits more complete description of the species than was possible previously. This specimen allows confirmation of much of Wortman's (1901) description, and also allows elaboration of information preserved in the little worn teeth and moderately well preserved basicranium. The peculiarities of the basicranium, including the massive laterally-extended mastoid process which is fused to the postglenoid process, are compared with those of three other mammalian groups — the sabre-toothed carnivores, the brontotheriid perissodactyls, and the primitive piglike artiodactyls. Substantial functional similarities are seen with the artiodactyls — achaenodontids and entelodontids. The stratigraphic record suggests that the mesonychids gave way to the structurally and, presumably, ecologically similar achaenodontids and entelodontids at the beginning of the Oligocene.

### INTRODUCTION

Recent collecting in the Bridger Formation by the Milwaukee Public Museum not only has developed extensive statistically-significant samples of small vertebrates, but also has yielded anatomically useful specimens of uncommon large taxa. This paper reports on a partial skull of the large mesonychid condylarth *Harpagolestes macrocephalus*. It is of special importance because it is a fairly young individual with almost unworn teeth and the basicranial area reasonably intact. This permits a more detailed description and comparison of the species than was previously possible, some functional speculations about large mesonychids, and comments on the diversity and disappearance of the middle and late Eocene large mesonychids.

Museum acronyms used below:

AMNH—American Museum of Natural History, New York

MPM—Milwaukee Public Museum, Milwaukee, Wisconsin

PU—Princeton University, Princeton, New Jersey

USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

YPM—Peabody Museum of Natural History, Yale University, New Haven, Connecticut

### Middle and Late Eocene Mesonychids

Wortman (1901) initially recognized *Harpagolestes* as the largest mesonychid from North America when he described *H. macrocephalus* from a partial skull, fragments of dentaries, and an associated humerus from the lower Bridger Formation near Millersville, Wyoming. The additional material described below increases the known sample of the species to four individuals, and it remains the only known Bridgerian species of *Harpagolestes*.

Four species of *Harpagolestes* are currently recognized in Uintan rocks (Szalay and Gould, 1966). *H. leotensis* (Peterson, 1931) is represented by a single worn ramus from the Uinta C near Ouray, Utah. Scott (1888) described *Mesonyx uintensis* from the Uinta B near White River, Utah. Osborn (1895) added several more specimens, including skulls, to that species and Matthew (1909) referred *M. uintensis* to Wortman's *Harpagolestes*. This is currently the best known species, with at least seven individual specimens reported. Matthew (1909) also added the species *H. immanis* based on an incomplete skull and jaws from a locality, probably of early Uintan age, on the north side of Haystack Mountain in the Washakie Basin, Wyoming. The holotype remains the only specimen referred to that species. Finally, Thorpe (1923) described *H. brevipes* from a Uinta Formation locality near White River, Utah. This, the largest species of the genus, is also known only from one published specimen.

To the south, Gustafson (personal communication, 1980) collected a single specimen referred to *Harpagolestes* sp. cf. *uintensis* from the Candalaria local fauna of southwestern Texas. This assemblage is probably late Uintan in age, making the Texas specimen the latest North American record of the genus.

Shikama (1943) named another species of *Harpagolestes*, *H. koreanicus*, from three isolated upper teeth found in an upper Eocene coal bed in Korea. Szalay and Gould regarded those teeth as insufficient for a diagnosis. They had better material and named another species, *H.*

*orientalis* Szalay and Gould, 1966, from two partial skulls from the late Eocene of Inner Mongolia, and noted a similarity of size of *H. koreanicus* and *H. orientalis*.

In addition to *Harpagolestes*, eight other genera of mesonychids are known from the middle and late Eocene of North America and middle Eocene to early Oligocene rocks of eastern Asia and one from the middle Eocene of Europe. A second large eastern Asian mesonychid is *Andrewsarchus*, described by Osborn in 1924 from a single skull found in late Eocene rocks of Inner Mongolia. Osborn's *A. mongoliensis* is by far the largest member of the family, with a skull 834 mm long, about twice the size of the skulls of *H. uintensis* and *H. macrocephalus*.

Suyin *et al.* (1977) described a second species, *A. crassum*, based on two isolated lower premolars from late Eocene rocks of Guangxi, southern China. Determination of possible synonymy with *A. mongoliensis* is difficult, as despite apparent similarity in size, the *A. crassum* type materials are not directly comparable with any part of the *A. mongoliensis* holotype. A third Inner Mongolian late Eocene form, *Mongolonyx dolichognathus*, a *Harpagolestes*-sized animal, was described by Szalay and Gould (1966).

Two other mesonychid genera, *Honanodon*, with both large (*H. macrodontus*) and small (*H. hebitis*) species, and *Hapalodectes lushienensis*, a *Mesonyx*-sized animal, are known from the late Eocene of Honan in northern China (Chow, 1965).

The only known early Oligocene mesonychid is also from Inner Mongolia. *Mongolestes hadrodens* (Szalay and Gould, 1966) approximates *Mesonyx* in size and is relatively derived, as it lacks M<sub>3</sub>.

Mesonychids have been reported from early or middle Eocene rocks of Pakistan by Pilgrim (1940) and by Dehm and Oettingen-Spielberg (1958). Subsequent work on these taxa, *Gandakasia* and *Ichthyolestes*, suggests that they are substantially derived with respect to typical mesonychids and are better placed in the Cetacea (Gingerich, *et al.*, 1979; West, 1980). The isolated presumed mesonychid tooth illustrated by West (1980) actually is an artiodactyl premolar (Gingerich, personal communication, 1980).

The European Lutetian contains *Dissacus*, the last survivor of the family on that continent (Szalay and Gould, 1966).

The other North American species are *Mesonyx obtusidens* Cope 1884 and *Synoplotherium vorax* (Marsh, 1867), both Bridgerian in age, and Duchesnean *Hessolestes ultimus* Peterson 1932. Several skulls and skeletons of *Mesonyx obtusidens* and *Synoplotherium vorax* have been described (Scott, 1888; Cope, 1884; Wortman, 1901). Each of these monospecific genera is now represented in the five largest Bridger

Formation collections (AMNH, MPM, PU, USNM and YPM), with *Mesonyx* considerably more abundant than *Synoplotherium*. Together with *Harpagolestes* they show a pronounced size range, with *Synoplotherium* about 20% to 25% larger than *Mesonyx*, and *Harpagolestes* about 20% to 25% larger than *Synoplotherium*. Two genera, *Harpagolestes* and *Hessolestes*, both with large-sized species only, are known to persist into the late Eocene in North America.

A similar pattern seem to be present in the late Eocene of China and Inner Mongolia, as there is a considerable size range from *Hapalodectes* through *Andrewsarchus*. Only a single relatively small species of *Mongolestes* persisted into the early Oligocene.

#### *Harpagolestes macrocephalus* Wortman 1901

**Materials available.**—The holotype of *H. macrocephalus* is a rostrum and palate with associated dentary fragments and right humerus (YPM 11901) collected from Bridger B strata near Millersville, Wyoming, in 1873 but not catalogued until 1909. The skull and jaws have been substantially reconstructed in plaster; figures 1 and 2 show the extent of this reconstruction. Two specimens of isolated teeth are also referable to *H. macrocephalus*: USNM 299485, an M<sup>2</sup> collected in 1965 near Millersville, and YPM 13009, fragments of lower teeth collected in 1873, also from the Bridger B near Millersville. The recovery in 1978 of MPM 4959, a partial skull with the upper cheek tooth dentition and basicranial area and an associated atlas (figures 3-5) thus adds significantly to the sample of *H. macrocephalus*. This specimen was collected at MPM locality 2784 along upper Leavitt Creek in the middle of Bridger B.

**Description.**—The rostral part of YPM 11901 was described in detail by Wortman (1901). He pointed out the elongate muzzle, posteriorly spread nasals, large extra-orbital lacrimal exposure, posteriorly situated orbits, moderate-sized premaxillae, large infraorbital foramina, suggestion of a postorbital process and high sagittal crest, narrow palate, posterior position of the internal nares, narrow narial groove, and prominent pterygoid wings. He also described the strongly arched zygoma with a ventrally directed process at the anterior end, and the large glenoid fossa with prominent postglenoid processes. Since the posterior part of YPM 11901 is broken, Wortman's discussion of the basicranial and occipital area is inadequate. The dentaries are incomplete, but Wortman did observe that they are deep, have a low coronoid process, a broad shallow masseteric fossa, and an inflected angular process. The extreme wear on the dentition of YPM 11901 precluded effective description of the teeth, both lower and upper. Wortman reported a *Mesonyx*-like dental formula with only two upper molars and a molariform P<sup>4</sup> and a long diastema between P<sup>1</sup> and P<sup>3</sup>.

Apart from the left cheek teeth and the right glenoid region, there is little overlap between the parts of the skull preserved in YPM 11901 and MPM 4595. Since the specimens supplement each other so well, the following description of MPM 4595 greatly expands knowledge of *Harpagolestes macrocephalus*.

**Basicranium.**—Although the bone is significantly crushed and broken away, the general anatomy of the basicranium of MPM 4595 is clear (figures 3 and 6). The basicranium is short, the braincase is small (although this size is predicted by the scaling method of Emerson and Radinsky [1980]), and the postglenoid region is markedly constricted.

The dorso-ventrally flattened occipital condyles are preceded by small condylar foramina which, in turn, are immediately posterior to the posterior lacerate foramina. These openings are in a depression flanked medially by the basioccipital bone, anteriorly by the modestly inflated bulla, posteriorly by the large occipital condyles, and laterally by a broad groove beneath the internal end of the mastoid process. The bulla, present only on the right side and lacking much of the delicate bone, clearly has a crenulated surface.

The area between the lateral corners of both occipital condyles and the posterior margin of the enlarged mastoid process is broken away along the occipital-periotic suture on both sides of the skull. There is a modestly-developed, posteriorly-directed paroccipital process just medial to the sutural break.

The mastoid process of the periotic is massively developed, laterally extended, and has an extensive external exposure. It is located well dorsal to the level of the basicranial axis. The ventral edge of the mastoid process is fused to the posterior part of the glenoid process of the squamosal so the external auditory meatus is completely enclosed. The free lateral end and the postero-ventral surface of the mastoid both are heavily pitted and rugose, indicative of a prominent muscle insertion. It is likely that *H. macrocephalus* had a large and powerful sternocleidomastoid muscle.

The glenoid fossa is flanked by a prominent postglenoid process, the full ventral extent of which is missing on both sides. The preglenoid process is substantially smaller than the postglenoid. The glenoid fossae are cylindrical and suggestive of only minor lateral condylar movement.

Immediately anterior to the bullar-basioccipital contact is a prominent anterior lacerate foramen, and the foramen ovale opens above (dorsal to) a flange of the squamosal extending to the basisphenoid. Broken bases for pterygoid wings extend posteriorly to the region of the foramen ovale, although they are so damaged that the degree of closure of the narial canal cannot be determined.

The zygomatic arch bends forward at the lateral end of the glenoid fossa. The jugal is straight, fusing with the maxillary close behind the last upper molar. At the point of fusion there is a modest ventral bulge of rugose bone, possibly marking the anterior border of the superficial masseter origin. This feature was also noted by Wortman on YPM 11901. On the other hand, there is no indication on MPM 4595 of a jugal part of the postorbital process suggested by Wortman.

**Skull reconstruction.**—The part of the *H. macrocephalus* skull preserved in MPM 4595 suggests some errors in the reconstruction of YPM 11901, previously illustrated photographically by Szalay and Gould (1966, pl. 16) and here drawn in figures 1 and 2. The reconstruction appears to have been loosely based on the much more complete skull referred to *H. uintensis* by Osborn (1895). Nonetheless, the Yale reconstruction omitted the area of the mastoid and paroccipital processes. There is no bone preserved in that area on YPM 11901, although the two linear regions of fusion of the mastoid and glenoid processes are present. The basicranium of YPM 11901 is made completely of plaster, and includes imaginary antero-posteriorly elongate bullae with prominent posterior paroccipital processes (compare with figure 3). Thus MPM 4595 provides the first actual data on the relative development and position of the bulla and the petiotic and occipital bones.

The skull proportions are also a bit different in MPM 4595 than in the Yale reconstruction. Comparisons of figures 1 and 3 show that the posterior part of the skull is more compact than indicated by YPM 11901, that the basicranial area is shorter, and that the jugal bones angle inward from the lateral end of the glenoid fossa to the rear of the maxillary rather than being virtually parallel.

Neither specimen retains the occipital or sagittal crests. However, the mechanical considerations of the massiveness of the skull and jaws and the elongate maxillary and premaxillary areas necessitate a well-developed temporal and nuchal musculature. *H. uintensis* (AMNH 1882) shows the nuchal area of the skull to be expanded, but MPM 4595 suggests that this expansion is concentrated along the sagittal crest in *H. macrocephalus*.

**Dentition.**—The worn dentition of the holotype permits only the outlines of the teeth to be described. MPM 4595, a much younger individual with the teeth in a very early wear stage, shows details of cusp development (fig. 4).

Szalay and Gould (1966), in agreement with Wortman (1901), presumed the dental formula of *Harpagolestes* to be  $I_{\frac{3}{2}}^1, C_1^1, P(\frac{3+4}{4})^1, M_{\frac{3}{2}}^2$ . MPM 4595 retains  $P^3$  through  $M^2$ , without apparent diastema, and it plus other *Harpagolestes* specimens confirms the posterior part of the above dental formula. Measurements of all teeth referable to *H. macrocephalus* are given in Table 1.

The upper third premolar is an elongate tooth, with the central paracone the highest cusp. A lower posterior cusp is somewhat broader than the paracone, and a small internal bulge affects the outline of the tooth but lacks a cusp. This two-rooted tooth lacks a cingulum and is premolariform. It appears to be more complex than is the equivalent tooth of YPM 11901.

The antero-external half of P<sup>4</sup> is missing. The tooth is three-rooted and clearly molariform (in the mesonychid style). The paracone is at or slightly posterior of the midline, and there is a low, posterior-facing metacone. The protocone is well developed, much larger than the metacone, and situated slightly forward of the paracone. There is no hypocone or cingulum. The protocone of P<sup>4</sup> of MPM 4595 is located much farther forward than it is on YPM 11901, although this cusp on the Yale specimen is very heavily worn. The metacone of MPM 4595 is better developed.

The first upper molar is the largest upper cheek tooth. It has a prominent paracone with a much lower connate metacone. The parastyle, well developed, is aligned with the two major external cusps and is much lower than even the metacone. There is a posterior bulge in the metastyle position, but no cusp is developed. The protocone is large and is separated from the paracone by a deep, sharp valley. The protocone is wider and broader than the paracone, but is not as high. There is neither hypocone nor cingulum. It is not possible to compare this tooth with M<sup>1</sup> of YPM 11901 because of the excessive wear on the Yale specimen.

The upper second molar of MPM 4595 is virtually identical to USNM 299485 with its prominent external paracone and completely connate, though very low, metacone. There is a low parastyle on the antero-external corner of the tooth. A deep valley separates the paracone from the well developed but low protocone. There is no hypocone and no cingulum. The M<sup>2</sup> on MPM 4595 is heavily worn on its anterior end, but virtually unworn posteriorly.

The wear on all the teeth of *H. macrocephalus* is horizontal from the apices of the cusps. This is suggestive of a grinding-crushing habit. The P<sup>3</sup> of hyaenas shows a similar pattern.

Of the heavily worn lower cheek teeth of YPM 11901, only M<sub>3</sub> retains any topography, probably because of the absence of an occluding upper third molar. All these teeth are two-rooted and trenchant. M<sub>3</sub> has a single high anterior cusp and a sloping shelflike posterior cusp.

Three fragmentary lower teeth (YPM 13009) are probably referable to *H. macrocephalus*, but contribute little information. They are smaller than are the teeth of YPM 11901, but show the typical mesonychid trenchant form with a large slanted anterior cusp followed by a deep

groove and a low, rather bulbous, posterior cusp. It is not possible to assign these three fragmentary teeth to particular positions in the tooth row.

**Atlas.**—Associated with the skull (MPM 4595) is a nearly complete atlas (fig. 5), missing only parts of the dorsal arch and the right transverse process. As in *Mesonyx* (Scott, 1888) and *Synoplotherium* (Wortman, 1901), it is relatively short with small, non-protruding transverse processes. Both the atlanteal foramen and vertebroarterial canal are well developed. The maximum width of the atlas is estimated to be 148 mm., the height 70 mm., and the maximum length about 52 mm.

### *Harpagolestes* Feeding Habits

Hypotheses on the feeding habits of *Harpagolestes macrocephalus* and all other large mesonychids must take into account the following anatomical attributes: 1) the massive skull with relatively shortened braincase; 2) the fusion of the laterally extended mastoid process with the posterior side of the glenoid process; 3) the ventral position of the glenoid fossa; 4) the rugosity on the zygoma; and 5) the bunodont, simple, often horizontally heavily worn cheek teeth accompanied by enlarged round canines.

Rather substantial similarities may be seen in the basicranial region of the stabbing cats (such as *Hoplophoneus* [Scott and Jepsen, 1936] and *Smilodon* [Merriam and Stock, 1932]), and the marsupial sabretooth *Thylacosmilus* (Riggs, 1934; Turnbull, 1976, 1978 and personal communication, 1980). Specimens of these taxa all have enlarged mastoid processes which approach the posterior surface of the postglenoid and, in the case of some specimens of *Smilodon*, actually fuse with it. In these taxa the mastoid process is highly rugose and undoubtedly served as the origin for a large sternocleidomastoid muscle (Matthew, 1910; Merriam and Stock, 1932; Turnbull, 1976) used in the stabbing action. However, the anterior part of the skull in these taxa is markedly shortened, the canines are enlarged into bladelike stabbing devices, and the cheek teeth are highly specialized for shearing. There is no indication of elaboration of masticatory muscles, although the vertical orientation of the temporalis allows a strong carnassial bite (Emerson and Radinsky, 1980). This is quite different from *Harpagolestes* and is most unlikely that the large mesonychids stabbed with their enlarged but rounded canines.

Brontotheriid perissodactyls also have enlarged mastoid processes which are closely appressed, but not fused to the postglenoid process. They also show prominent ventrally-elongate paroccipital processes at the medial end of the mastoid, and the mastoid itself is ventrally extended, rather than laterally as in the mesonychids. A further difference from mesonychids is the position of the broadly open glenoid fossa of brontotheres which is dorsal to the level of the basicranial axis. The

enlarged mastoid suggests, as in the mesonychids, an enlarged sternocleidomastoid muscle, but the shape and position of the glenoid fossa indicates a jaw mechanism typical of herbivores and quite unlike that of the mesonychids.

A much higher degree of similarity is seen with several large bunodont artiodactyls, including the late Eocene achaenodontids (or advanced helohyids *vide* Gazin, 1955) such as *Achaenodon* (Peterson, 1919) and, to a somewhat lesser extent, the Oligocene-Miocene entelodontids *Archaeotherium* (Scott, 1940; Russell, 1980) and *Dinohyus* (Peterson, 1909). These animals have greatly enlarged and laterally extended mastoid processes which are fused to the back of the glenoid process, enclosing the external auditory meatus in exactly the same fashion as in *Harpagolestes macrocephalus*. The laterally-directed mastoid is well dorsal to the basicranial axis level, again as in *Harpagolestes*. Both achaenodonts and entelodonts have rounded, bunodont teeth, which differ from those of mesonychids in the presence of molar hypocones. Canines are also enlarged but retain the primitive oval cross-section. Entelodonts have elongated the facial part of the skull far more than have the achaenodonts which, in this character, are more similar to *Harpagolestes*. Entelodonts have a widely flaring zygoma with prominent bony flanges, variously interpreted as either attachment areas for large masseter muscles (Russell, 1980) or simple ornamental bosses. The expanded rugose area at the anterior end of the jugal part of the zygoma in *H. macrocephalus* may represent a more subdued version of this enlarged muscle attachment or ornamental area.

If this analogy with achaenodonts and, perhaps, entelodonts is appropriate (it has been noted previously by Osborn, 1895 and 1925; Szalay and Gould, 1966; and Szalay, 1969), the large mesonychids are best regarded as study omnivores. They compare poorly with hyaenas, as pointed out by Matthew (1915) and have proportions and dentitions markedly different from most other Carnivora. Modern ursids are mesonychid-like in the organization of their jaws and dentitions, although ursid basicrania do not have an enlarged mastoid region. Szalay and Gould (1966) and Szalay (1969) made a strong case for bone-crushing and carrion-feeding, based on muscle development, dental wear patterns, and the presence of functional large incisors and canines. In addition, the ventral position of the glenoid fossae and relatively small coronoid process on the dentary indicate a potentially wide gape. The prominent cranial crests and expanded jugals with rugosities are further suggestions of a well-developed jaw musculature. All of these characters are adequate substantiation of an omnivorous habit.

#### DIVERSIFICATION AND DISAPPEARANCE

The large mesonychids, *Mesonyx*, *Synoplotherium*, *Hessolestes* and

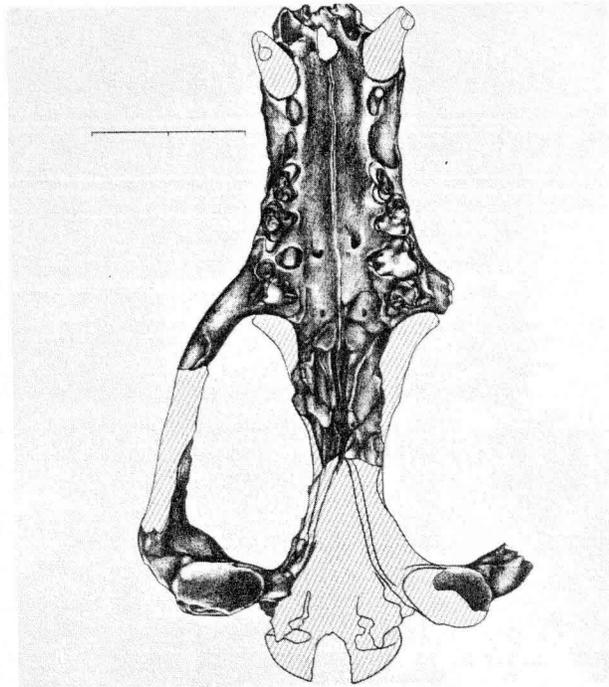
*Harpagolestes* in North America and *Hapalodectes*, *Honanodon*, *Mongolonyx*, *Harpagolestes* and *Andrewsarchus* in eastern Asia, underwent a modest middle and late Eocene radiation. Although a total of six species of *Harpagolestes* have been described, only two North American species (*H. macrocephalus* and *H. uintensis*) are known from more than a single published specimen. Asian species are also poorly represented. Because of the extreme wear on the teeth of most specimens, the similarity in size of several of the described species, and our general ignorance of possible sexual dimorphism and intraspecific variation, it is not possible to assess the validity of each of these species. When adequate samples are available, it may well be that all will fit comfortably in a single species. In the absence of adequate samples, all the currently-valid taxa must be retained.

The geologic range of *Mesonyx*, *Synplotherium*, *Hessolestes* and *Harpagolestes* in North America and *Hapalodectes*, *Honanodon*, *Mongolonyx*, *Harpagolestes* and *Andrewsarchus* in eastern Asia is relatively short, extending from early middle Eocene through late Eocene, a period of about ten million years. Only *Mongolestes* is known to have persisted into the Asian early Oligocene. Up to five or six species were present in both middle and late Eocene time, although it seems that no more than three or four coexisted geographically or temporally, and then they were usually clearly differentiated by size. This modest differentiation of the larger mesonychids coincided geographically with the Uintan development of the similar-sized Achaenodontidae in North America. The virtual extinction of the larger mesonychids on both continents preceded the diversification of the entelodonts in the Oligocene throughout the Holarctic. As shown above, the large mesonychids and the achenodont and entelodont artiodactyls show substantial anatomical, and probably functional and behavioral similarities. Therefore, it is here proposed that the larger mesonychids were ecologically replaced at the end of the Eocene by the large bunodont entelodont artiodactyls after a period of coexistence of the mesonychids and achenodontids.

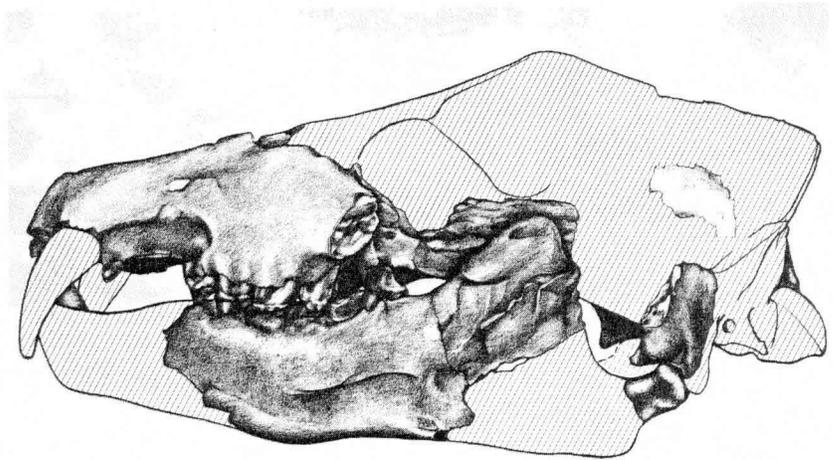
TABLE 1

Measurements, in millimeters, of teeth of *Harpagolestes macrocephalus*.

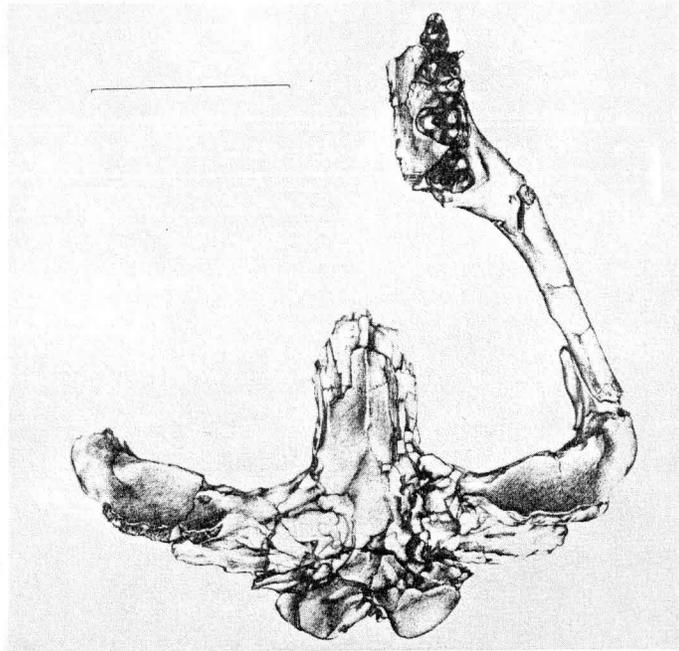
	YPM 11901		MPM 4595		USNM 299745
	Left	Right	Left	Right	Left
P <sup>3</sup> L	22.0	21.7	21.5		
W	12.2	12.7	14.5		
P <sup>4</sup> L	22.0	24.5	23.4		
W.	20.2	19.5	—		
M <sup>1</sup> L	24.8		27.9	28.0	
W	25.8		27.3	27.3	
M <sup>2</sup> L	20.5	19.7	23.2	21.7	21.5
W	22.6	23.5	23.2	22.7	23.2
P <sub>4</sub> L	27.0				
M <sub>1</sub> L	30.4				
W	14.3				
M <sub>2</sub> L	30.1				
W	15.4				
M <sub>3</sub> L	24.3				
W	14.0				



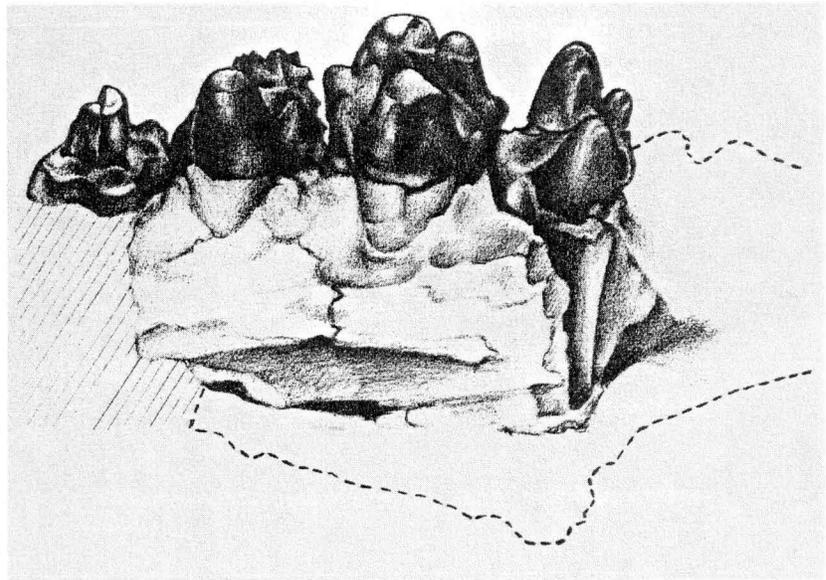
**Figure 1.** Palatal view of YPM 11901. Cross-hatched areas have been reconstructed in plaster. Scale represents 10 cm.



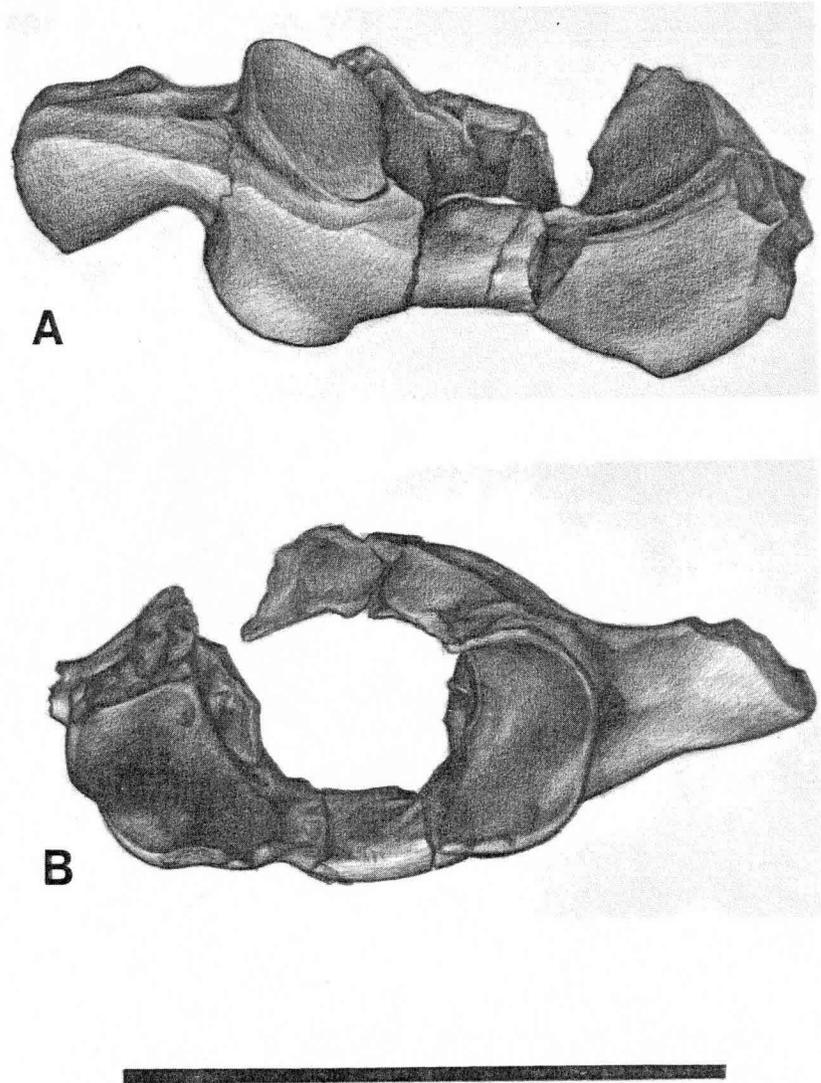
**Figure 2.** Lateral view of YPM 11901. Cross-hatched areas have been reconstructed in plaster. Scale represents 10 cm.



**Figure 3.** Palatal view of MPM 4595. Scale represents 10 cm.



**Figure 4.** Lingual view of upper left cheek teeth of MPM 4595, anterior to left. Scale represents 10 cm.



**Figure 5.** Atlas of MPM 4595. **A.** Dorsal view, anterior end directed upward. **B.** Posterior view. Scale represents 10 cm.

### ACKNOWLEDGMENTS

The MPM *Harpagolestes* specimen was prepared by Mr. Rolf Johnson of the Milwaukee Public Museum. Drs. Robert M. Hunt, University of Nebraska Museum, William D. Turnbull, Field Museum of Natural History, Chicago, and Leonard Radinsky, University of Chicago, assisted with the anatomical interpretations, and Drs. Hunt and Radinsky critiqued an early version of the paper. Drs. Turnbull and Richard H. Tedford, American Museum of Natural History, New York, graciously allowed access to collections in their respective charges. The drawings were made by Ms. Susan Speerbrecher, Milwaukee Public Museum.

This research was supported by grants from the National Science Foundation.

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