ASIATIC MESONYCHIDAE
(MAMMALIA, CONDYLARTHRA)

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STEPHEN JAY GOULD

A restoration of *Mesonyx* by Charles R. Knight. The painting is an excellent approximation of the presumably carnivorous middle Eocene mesonychid

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INTRODUCTION

MESONYCHIDS HAVE OFTEN been considered one of the more aberrant groups of the little-understood early Tertiary mammals. Our ideas of the ecological relations of modern mammals are not always adequate for us to interpret the functions and interactions of the primitive types that made up the faunas of the world during the first half of the Tertiary. The present investigation, which originally started as a brief taxonomic treatment of several new Asiatic mesonychids, does not claim to be definitive or to explain fully the role of these animals in the faunas in which they occur. It is an attempt to view mesonychid diversity in terms of various adaptive levels in relation to broad adaptive zones.

The Central Asiatic Expeditions of the American Museum of Natural History collected many fine specimens during the 1920's and 1930's; these are gradually being described and studied in relation to allied forms found in various faunas around the world (e.g., Dawson, 1964; Radinsky, 1965; the present paper; and others). In this work we treat Asiatic mesonychids found in the collection of the American Museum of Natural History and all the pertinent literature on the family. Many mesonychid genera and species greatly need revision, but such an undertaking would be possible only if a study of all the known specimens of the family were undertaken. An attempt has been made, however, to survey or comment on all the genera and to give a comprehensive picture of the major outlines of mesonychid radiation in Asia, North America, and Europe. As this study progressed, it became apparent that there was a previously unknown diversity among Asiatic forms of the family. A consequent revision of the prevailing concepts of mesonychid dispersal and distribution patterns became imperative.

Radinsky (1964) should be consulted for further information on Eocene and Oligocene localities of the Central Asiatic Expeditions in Inner Mongolia.

With the exception of the sections on the stratigraphy of the Mongolian mesonychid-bearing formations (pp. 132–133), the genera *Gandakasia* and *Ichthyolestes* (pp. 150–152) and the correlation of size and shape in mesonychid lower cheek teeth (pp. 161–164), which are by Gould, Szalay is responsible for the contents of this paper.

STRATIGRAPHY OF MONGOLIAN MESONYCHID-BEARING FORMATIONS

As INTERPRETED BY Berkey and Morris (1927), the Tertiary history of the Gobi is one of sporadic gentle deformation of a stable basement, producing basins of large geographic extent and low relief. The gentle and intermittent nature of uplift resulted in long intervening periods of erosion, producing paraconformities that are very difficult to detect on lithologic criteria. "The beds of successive formations of later age often lie so nearly parallel that the actual physical break, caused by one of these erosion epochs, can rarely be seen" (Berkey and Morris, 1927, p. 212). Moreover, the local nature of deposition results in complex facies relationships which greatly enhance difficulties of correlation. "There is an enormously complex interlocking and interweaving of formations, no single one extending continuously, or free from par-

tial destructive erosion for very great distances" (Berkey and Morris, 1927, p. 212).

Type areas and a proposed correlation (indicated by dashed line) of mesonychid-bearing formations are presented in table 1. The accompanying map (text fig. 1) shows the geographic distribution of type formations in the Shara Murun region. (Telegraph Line Camp is approximately 75 miles northeast of Tukhum.)

The name Irdin Manha was applied by Granger and Berkey (1922, p. 5) to clays, sands, and gravels exposed in the Irdin Manha escarpment where it is crossed by the Kalgan to Ulan-Bator telegraph line 20 miles south-southeast of Iren Dabasu (now called Erhlien). The name Irdin Manha was later restricted to the upper 30 feet, while the lower red clays and fine silts were termed Arshanto.
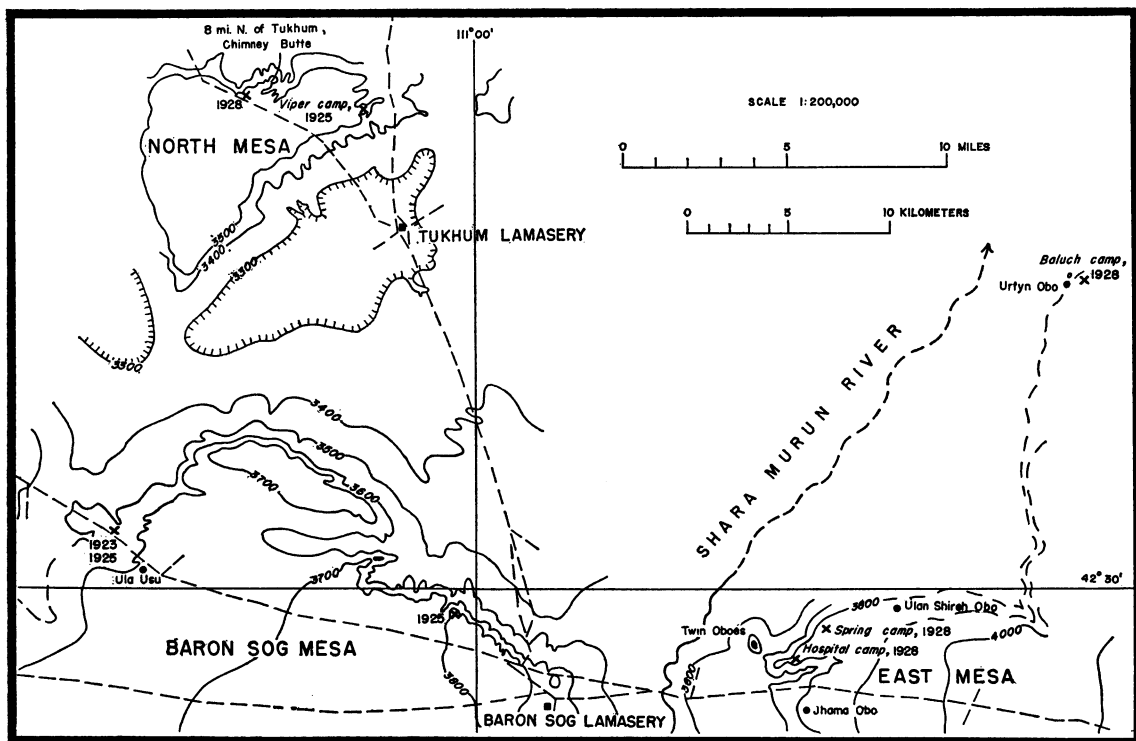

FIG. 1. Topographic map of the Shara Murun region, showing the collecting localities and camps of the Central Asiatic Expeditions. From Radinsky (1964).

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TABLE 1

CORRELATION CHART OF THE MONGOLIAN MESONYCHID-BEARING FORMATIONS

Age		Type Area	
	Telegraph Line Camp	North Mesa	Baron Sog Mesa
Oligocene			Baron Sog Formation Ulan Gochu Formation
Late Eocene	Irdin Manha Formation— Arshanto Formation	—Ulan Shireh Formation—	Shara Murun Formation —Tukhum Formation

Radinsky reported (1964, p. 3) that tapiroids from the Arshanto are probably early late Eocene in age. Mesonychid diversity in type Irdin Manha beds is surprisingly high. The 83-cm. skull of giant *Andrewsarchus* and a tiny lower molar of *Hapalodectes serus* were recovered here; in addition, the presence of three other genera filling intermediate rungs of the size continuum may be inferred from individual teeth described in this paper (A.M.N.H. Nos. 20131, 20132, 20133, 26267, 26288, 26303). *Mongolonyx*, new genus, another large form, is catalogued as coming from "Irdin Manha, 7 miles W. of Camp Margetts." Camp Margetts is 18 miles west of the type Irdin Manha region, and the correlation between the two areas is uncertain (see Radinsky, 1964).

Osborn (1929) designated 50 feet of red clay exposed in the northern and eastern parts of Baron Sog Mesa as the Ulan Gochu Formation. These strata form part of a superposed series of four formations named, from oldest to youngest, Tukhum (red beds), Shara Murun (200 feet of varicolored clays, predominantly gray), Ulan Gochu, and Baron Sog (15–20 feet of white clay and sands). The Eocene-Oligocene boundary is said to occur between the Shara Murun (latest Eocene) and Ulan Gochu (lower Oligocene). *Mongolestes*, new genus, and unallocated teeth described in this paper are cata-

logued as "Ulan Gochu" from Jhama Obo and Twin Oboes, East Mesa (see map of Shara Murun region). Correlation of these beds with the type Ulan Gochu is questionable.

The name Ulan Shireh Formation was given by Berkey, Granger, and Morris (1929) to 150 feet of predominantly red, multicolored clays exposed at North Mesa, Shara Murun Region. *?Harpagolestes orientalis*, new species, and unallocated teeth came from these type Ulan Shireh beds.

Lophiatelid tapiroids catalogued as coming from the "lower red beds" at Ula Usu (Baron Sog Mesa) and presumably from the Tukhum Formation are of species identical to those found in the type Ulan Shireh beds. They are very similar to forms of the Irdin Manha strata and older than those of the Shara Murun (Radinsky, 1964). In addition, we describe in this paper specimens very probably of the same mesonychid species as cf. *Mesonyx* among unallocated teeth from the Ulan Shireh and Irdin Manha beds, thus further supporting the proposed correlation.

The situation is admittedly somewhat discouraging. Of the three new forms described, only one comes from a type area. The two new genera derive from beds of which the proposed correlation to type strata cannot now be established with any satisfaction. No two specimens illustrated in this paper were found in direct superpositional relationship.

IN THIS SECTION two new genera and a new species of Asiatic mesonychid are described, and all Asiatic taxa of the family are critically evaluated.

In order to give an adequate picture of the degree of adaptive radiation of the Mesonychidae and to place the poorly known mesonychid phylogeny into a proper taxonomic framework for future studies, two new subfamilies have been erected: the Hapalodectinae and the Andrewsarchinae. Both these subfamilies are represented in Asia, and the Andrewsarchinae appear to be endemic to the Asian continent.

It is pointed out here that, with the exception of *Hapalodectes*, not one genus can be said for certain to have been present both in North America and in Asia. Species of cf. *Pachyaena*, cf. *Mesonyx*, and cf. *Harpagolestes*, however, appear in the Mongolian record. *?Harpagolestes orientalis*, on the other hand, may prove to be generically distinct from *Harpagolestes*. The temporal and geographic distribution of the family is separately treated below.

Many insufficiently known mesonychid forms from both continents have been consistently dumped into the genus *Harpagolestes* (e.g., see Shikama, 1943), creating a rather confusing state for this taxon. We have tried to remedy the situation in part by critically reviewing all published literature on *Harpagolestes*, with the addition of comments or needed redescriptions of all available specimens. Although a full revision of *Harpagolestes* is beyond the scope of this work, we feel that the information summarized here may be of some value.

All the unallocated Asiatic mesonychids in the collections of the American Museum of Natural History have been described, illustrated, and discussed; although many probably represent new species and genera, they are an inadequate basis for new taxa.

ORDER **CONDYLARTHRA** COPE, 1881

SUPERFAMILY **MESONYCHOIDEA** OSBORN, 1910

FAMILY **MESONYCHIDAE** COPE, 1875

SUBFAMILY **MESONYCHINAE** WORTMAN, 1901

INCLUDED GENERA: *Dissacus, Pachyaena,* *Mesonyx, Harpagolestes, Hessolestes, Mongolonyx, Mongolestes.*

KNOWN DISTRIBUTION: From middle Paleocene to late Eocene in North America, from late Paleocene to early Eocene in Europe, and from early Eocene to ?early Oligocene in Asia.

REVISED DIAGNOSIS: Mesonychids with high, conical, and blunt cusps on upper cheek teeth; paracone and metacone usually connate; no trace of hypocone; P[4] fully molariform; cingula and additional cuspules anterior to paracone and posterior to metacone either present or absent. Lower cheek teeth all premolariform; talonids single crested; metaconids present, vestigial, or absent; protoconid tallest and most prominent cusp on lower cheek teeth. Feet from plantigrade to highly cursorial condition; ungual phalanges hooflike, fissured.

MONGOLONYX, NEW GENUS

TYPE: *Mongolonyx dolichognathus,*[1] new species.

KNOWN DISTRIBUTION: Late Eocene of Inner Mongolia, in "Irdin Manha" beds.

DIAGNOSIS: *Mongolonyx* is clearly distinct from *Dissacus* and *Mesonyx* in having much bulkier and relatively larger teeth. The new genus is easily differentiated from *Dissacus* and *Pachyaena* by the absence of cingula from the upper teeth of both genera, by the loss of M[3], and by the lack of any traces of a metaconid on the trigonids of the lower molars.

In *Harpagolestes*, in contrast to *Mongolonyx*, the crowns of the anterior lower cheek teeth lean to the rear, and the enamel-dentine line of these teeth is arcuate; neither of these tendencies is observed in *Mongolonyx*. On the diagnostic P[4] of *Mongolonyx* the large paraconid stands parallel to the protoconid, while in *Harpagolestes* the paraconid invariably forms an angle with the protoconid. The anteroposteriorly flattened paraconid of the M[3] also renders the new genus distinct from *Harpagolestes*.

Mongolonyx differs from *Mongolestes* in retaining an M[3] and in having a relatively straighter, shallower, and longer jaw.

The lower canines of *Mongolonyx* are set

[1] *Mongolonyx*, Mongolian "claw"; *dolichognathus*, long jaw.

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very close to each other (the position is not due to a crushing of the type of the type species), and this fact differentiates the new genus from all other mesonychid genera, with the possible exception of *Pachyaena*. The paracone of M^2 is twice as large as the protocone of the same tooth. P_2 is diagnostically very small, lacking a heel.

Tooth formula: $I_?^?$, C_1^1, P_4^4, M_3^2.

Mongolonyx dolichognathus, new species

Plates 10 and 11, plate 12, figure 1;
text figure 2; table 2

TYPE: A.M.N.H. No. 26661, lower jaw with several well-preserved teeth and coronoid processes broken off; collected during the 1930 Central Asiatic Expedition; field number 895.

HYPODIGM: The type and A.M.N.H. No. 26662 (field no. 907), a complete left maxilla with P^2–M^2 in place.

HORIZON AND LOCALITY: "Irdin Manha" beds, 7 miles west of Camp Margetts of the 1930 Central Asiatic Expedition, Inner Mongolia.

DIAGNOSIS: This is the only known species of the genus. The skull, as inferred from the mandibles and the maxilla, must have been in the size range of the recent Alaskan brown bear.

DESCRIPTION: The type specimen is a fairly well-preserved lower jaw with both the back of the right mandible and the ascending ramus of the left mandible broken. The specimen shows an unusually (for an advanced mesonychid) deep and extensive masseteric fossa, probably indicating the presence of large and strong m. zygomaticomandibularis. The bony wall separating the latter muscle and the m. temporalis profundus is very thin, only a little more than 4 mm. thick at some places on the level of the tooth row. The masseteric fossa extends under the entire length of the last molar. The angle of the jaw is strongly inflected, as in most mesonychids, forming a broad shelf approximately 8 cm. in length. The dental foramen forms an unusually large, very long, and wide cavity. The condyle (preserved only on the left ramus) is broad and strong. The tooth row diagnostically bulges out the superior half of the otherwise not very bulky horizontal ramus. The closely set canines (as shown by their alveoli)

and a constricted symphyseal region characterize the anterior part of the lower jaw.

Lower Dentition: The incisors, canines, and the first premolars are missing. The large lower canines were set close together; the distance between their inferior extremities was not more than 10 mm. The first premolar was single-rooted and peglike. The second premolar, preserved only on the left side, was a relatively small, two-rooted tooth, with one large cusp and a trenchant ridge posterior to this cusp. The crown of the left P_3 was broken; it is evident, however, that the heel was well set off and had a large hypoconid. The protoconids do not lean backward on P_3 and P_4, as they do in *Harpagolestes*, for example. The lower fourth premolar is probably the most diagnostic tooth of this species. The anterior fourth of the crown bears a large paraconid. This area of the tooth is set off from the protoconid by a groove which originates close to the inferior border of the enamel line. The paraconid stands almost parallel to the protoconid, while in other genera, such as *Harpagolestes* and *Pachyaena*, the paraconid leans forward, forming an angle with the protoconid. The hypoconid of P_4 shows almost no signs of wear, probably because the anterior portion of M_1 (unfortunately broken on both sides in the type specimen) receives the principal wear caused by P^{3-4}. The first lower molar is broken on both sides to such extent that the morphology of this tooth is completely obscured. On M_2 the paraconid has its usual relation to the protoconid, the former cusp leaning forward, forming an angle with the protoconid. The second lower molar is otherwise not diagnostic of the species. The talonid is broken off from both M_3's, but the paraconid is very characteristic on the tooth. This cusp is flattened anteroposteriorly against the somewhat reduced protoconid, giving the impression that, figuratively speaking, the paraconid was gradually but not entirely pushed into the anterior surface of the protoconid. The paraconid (what there is of it) and the protoconid are parallel to each other, both oriented normally to the horizontal ramus. The protoconid, which is only very slightly worn on its apex, bears no sign of a metaconid. Judged from the size of the protoconid, the last molar was a considerably smaller tooth than P_3, P_4, M_1, or M_2.

Upper Dentition: The maxilla containing the cheek teeth is slightly larger and deeper than the same bone of *Harpagolestes uintensis*. The very large alveolus for the root of the upper canine is slightly flattened mediolaterally, the crypt for this tooth extending far upward and backward into the muzzle (the medial wall of the maxilla, separating the canine from the nasal cavity, becomes very thin). The first upper premolar, judged from the alveolus, must have been a large, single-rooted, and procumbent tooth, situated close behind the canine. There are diastemata between P^1 and P^2, and between P^2 and P^3. P^2 is by far the smallest of the cheek teeth. It has two very closely set roots and, in spite of the flaked-off enamel, it is evident that the crown must have been equally as simple and single-cusped as that of its lower counterpart. The infraorbital foramen in the maxilla is more anterior in *Mongolonyx* that in either *Harpagolestes uintensis* or *?H. orientalis*. In *Mongolonyx* the foramen opens above the anterior root of P^3, while in *Harpagolestes* this structure opens above the anterior root of P^4. P^3 is much larger than the preceding P^2 and, despite the crushed crown, it can be recognized as the somewhat bulky but typical two-cusped mesonychid P^3 with the slight posterolingual shelf also seen in *Mesonyx* and *Harpagolestes*. The fourth molariform premolar is badly broken. The large paracone dominates the tooth, and the metacone is insignificant in size compared to the paracone. The protocone is slightly anterolabial on the tooth, close to the larger paracone. The first molar is badly broken; it is the widest of the cheek teeth. The last molar, M^2, is the best preserved and most diagnostic tooth in the maxilla. The paracone is at least twice the size of the protocone, while the small metacone is connate with the posterior wall of the paracone. M^2 is only about two-thirds as wide as the preceding M^1.

DISCUSSION: Taxonomically *Mongolonyx dolichognathus* is undoubtedly different from any of the previously known mesonychid genera. The evaluation of the distinctive morphological features of the new taxon from a functional point of view is, however, a difficult problem. Although the teeth have increased in relative size, an advanced feature, there is no reduction in the number of the
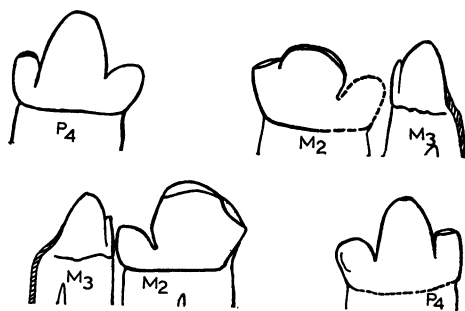
FIG. 2. *Mongolonyx dolichognathus*, left lower cheek teeth. The talonid of M_3 is broken off. *Above:* Buccal view. *Below:* Lingual view.

lower cheek teeth. The very long mandibles and the relatively narrow symphyseal region of the mandibles, with the canines set close to each other, only add to the puzzle of functional significance presented by the dentition.

The cheek teeth of *Mongolonyx*, mainly P^1 and P^3–M^2, are almost twice the size of the homologous teeth of *Harpagolestes uintensis* which is of similar size. The difference is very striking, but it is hazardous to speculate on whether the relatively larger teeth of *Mongolonyx dolichognathus* represent a different adaptation, or whether the increased surface area of wear simply means an accentuation of the crushing ability of the tooth row.

MONGOLESTES, NEW GENUS

TYPE: *Mongolestes hadrodens*,[1] new species.

KNOWN DISTRIBUTION: Early Oligocene of Inner Mongolia in the Shara Murun region; "Ulan Gochu" Formation.

DIAGNOSIS: *Mongolestes* is clearly differentiated from all other known genera of mesonychids in having an unusually steep mandibular symphysis. The loss of M_3 and the relatively very large teeth distinguish *Mongolestes* from *Dissacus*, *Mesonyx*, *Pachyaena* (*P. gigantea* and *P. ponderosa* also have very large teeth), *Hapalodectes*, and *Harpagolestes*. (*Mongolonyx* also has relatively large teeth compared to those of the above genera.)

Mongolestes also differs from *Dissacus* and *Pachyaena* in the absence of cingula on the upper teeth and in the lack of any trace of a metaconid on the trigonids of the lower cheek teeth.

[1] *Mongolestes*, Mongolian robber; and *hadrodens*, bulky tooth.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF *Mongolonyx dolichognathus*, NEW GENUS AND NEW SPECIES (A.M.N.H. NOS. 26661 AND 26662)

	Length	Width
Upper dentition		
P^1	—	—
P^2	16^a	11.8
P^3	24^a	20.2
P^4	30^a	30.4
M^1	31^a	34.0
M^2	26.8	27.9
P^1-P^3	82.3	
P^3-M^2	110.0	
P^4-M^2	87.1	
P^4-M^1	60.8	
M^1-M^2	56^a	
Lower dentition		
P_1	—	—
P_2	18.3	10.3
P_3	30^a	15.0
P_4	33.6	15.0
M_1	33^a	16^a
M_2	32^a	16.5
M_3	—	—
P_1-P_4	107.0	—
P_2-P_4	90.2	—
P_3-M_1	92^a	—
P_3-P_4	62.5	—
P_4-M_2	92.0	—
Upper dentition from posterior border of alveolus of canine to posterior border of M^2	165^a	—
P_1-M_3	200^a	—
P_1 to posterior border of mandibular condyle	335^a	—

^{a} Measurement approximate.

The relatively tall protoconids of *Mongolestes* lean posteriorly more on the premolars than do the homologous teeth of *Harpagolestes*.

Mongolestes clearly differs from *Mongolonyx* in the absence of M_3, in having a more arcuate mandible and tooth row and in having P_1 in the process of reduction.

Tooth formula: I_2^3, C_1^1, $P_4^{(3)}$, M_2^2.

Mongolestes hadrodens, new species

Plate 12, figure 2, plates 13, 14; text figure 3; table 3

TYPE: A.M.N.H. No. 26064, well-preserved right ramus with the canine and cheek teeth intact; somewhat crushed tooth-bearing portion of left ramus with cheek teeth present; fragments of left maxilla with P^2, P^3, and

M^{1-2}; left canine, all six upper incisors, and right P^4.

HYPODIGM: The type and A.M.N.H. No. 26065, greater part of left mandible with all teeth badly shattered and fragments of the right maxilla.

HORIZON AND LOCALITY: The type is from "Ulan Gochu" Formation, Jhama Obo, East Mesa, Shara Murun region. The referred specimen is from "Ulan Gochu" Formation, Twin Obo, East Mesa, Shara Murun region, Inner Mongolia.

DIAGNOSIS: Only known species of genus.

DESCRIPTION: The right mandible of the type is beautifully preserved. In general form and size this mandible is not unlike that of the Torrejonian *Dissacus saurognathus* from North America (see pl. 15). The angle, how-
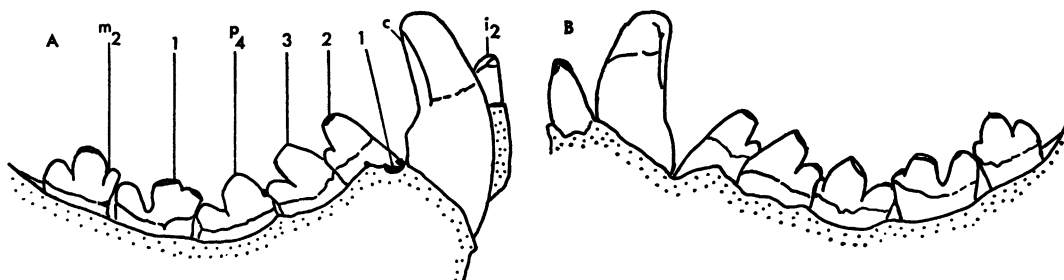
FIG. 3. *Mongolestes hadrodens*, new genus and new species, lower dentition. A. Buccal view. B. Lingual view.

ever, is much more inflected in *Mongolestes hadrodens* than in *D. saurognathus*, and the huge teeth of the Mongolian species are of entirely different relative size. The lower teeth of *Mongolestes* are probably larger in relation to the mandible than those of any other well-known mesonychid species (neither the mandible nor any of the lower teeth of *Andrewsarchus* are known). *Mongolonyx dolichognathus* has a longer mandible (see pl. 12, fig. 2), but the jaw is less deep and the individual teeth are smaller than those of *Mongolestes hadrodens*.

Lower Dentition: The first lower incisor is lost, as it is in *Harpagolestes*, and, of the two remaining ones, I_3 is larger than I_2. The canine is larger and more massive than that of *Harpagolestes uintensis* or that of *H. immanis*. There is heavy wear on the anterior and anterolabial tip of the tooth and very heavy wear on the posterior surface. The very small (probably non-functional) P_1 seems to have erupted labial to the anterior root of P_2. The second premolar is a relatively large tooth compared to that of *H. uintensis*, with a protoconid over twice the height of the incipient trenchant talonid. The whole tooth arches posteriorly. The third premolar is roughly the size of M_2, lacking a paraconid, as does the preceding P_2. The large protoconid of P_3 leans over the talonid. P_4, with a small paraconid, is the widest tooth in the mandible (see table 3), but the following M_1 is much longer. The long first molar bears marks of the heaviest wear in the entire lower cheek tooth row. The large paraconid, leaning forward, and the protoconid are badly worn. A wide transverse groove running between the protoconid and the talonid is deepened by heavy wear. The

talonid is more worn than that of any of the lower teeth. The square-heeled last molar, M_2, is set on the base of the ascending ramus, a condition not seen in primitive mesonychids. This feature, if we knew the ancestor of *Mongolestes*, could probably be correlated either with the shortening of the jaw or with the enlargement of individual teeth.

Upper Dentition: There is a gradual increase in size of the upper incisors, the third incisor being about twice as large as the second and more than twice the size of the first. There is an appreciable amount of wear on their crowns, mainly on the posterior and slightly lateral surfaces and on the root of I^3. The massive upper canine is heavily restored, but signs of heavy wear can be recognized on the anterolingual surface, the place of occlusal contact with the posterior surface of the lower canine. Only P^2, P^4, M^1, and M^2 are preserved. The second premolar is large and double rooted, but the crown is not preserved. The single right P^4 is preserved adequately for description (see pl. 14). The worn paracone is large, in the size range of the slightly posteriorly placed protocone. The protocone is the taller cusp, but the paracone extends farther down from the upper jaw. This is generally true of most mesonychid P^4's and molars. The worn metacone is well defined and not connate with the paracone. P^4 extends the fartherest down from the upper cheek tooth row (not including the canines). The first molar is the largest and widest tooth in the maxilla. A small anterior cusp (?parastyle) precedes the massive paracone. The large metacone is connate with the latter cusp. There is a posterior shelf behind the metacone. The last molar, M^2, situated above

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF *Mongolestes hadrodens*, NEW GENUS AND
NEW SPECIES (A.M.N.H. No. 26064)

	Length	Width	Depth
Upper dentition			
I^1	11.5	7.7	—
I^2	14.5	12.2	—
I^3	21.9	18[a]	—
C	38.3	27.8	—
P^1	—	—	—
P^2	21.5[a]	14.1	—
P^{3b}	24.9	14.2	—
P^4	27.6	30.2	—
M^1	30.5	33.0	—
M^2	27.2	28.8	—
P^4–M^2	80[a]	—	—
P^4–M^1	55.6	—	—
Lower dentition			
C	29.8	26.0	—
P^1	—	—	—
P^2	24.2	15.0	—
P^3	33.5[a]	18.5	—
P^4	37.0	18.2	—
M^1	40.4	16.9	—
M^2	33.3	16.4	—
P_1–M_2	160.5[a]	—	—
P_2–P_3	53.5	—	—
P_3–P_4	67.8	—	—
P_4–M_1	73.2	—	—
M_1–M_2	73.0	—	—
Right mandible from condyle to anterior border of symphysis	360[a]	—	—
Posterior border of condyle to posterior border of M_2	140[a]	—	—
Top of coronoid process to posteroventral border of angular process	150[a]	—	—
Mandible at posterior root of P_3	—	—	61[a,b]
Mandible at posterior root of P_4	—	—	60[a,c]
Mandible at posterior root of M_1	—	—	72[a,d]
Mandible at posterior root of M_2	—	—	89[a]
Partition of alveoli of roots of P_2 on superior and medial edge of mandible to ventralmost extent of symphysis	90[a,e]	—	—
Anterior border of masseteric fossa to ventralmost extent of symphysis	145[a,e]	—	—
Anterior border of masseteric fossa to posterior mental foramen	108[a,e]	—	—

[a] Measurement approximate.
[b] Approximately 80 mm. in A.M.N.H. No. 26065.
[c] Approximately 78.5 mm. in A.M.N.H. No. 26065.
[d] Approximately 79 mm. in A.M.N.H. No. 26065.
[e] Measurement taken on A.M.N.H. No. 26065, an old specimen.

M^1, is a tooth almost as wide as long. The paracone which is placed centrally on the labial side of the tooth occupies an area equal to that taken up by the protocone. The metacone is vestigial, connate with the reduced paracone.

DISCUSSION: The very large teeth of the arcuate tooth row and the nature of the mandibular symphysis are probably the most remarkable adaptations that can be inferred from the mandible of *Mongolestes hadrodens*. The unique character of the mandibular symphysis is accentuated in the mandible of A.M.N.H. 26065, the specimen representing an old individual of the species. The symphyseal surface is massive and exceptionally steep in relation to the horizontal ramus. It is not unlike the symphysis of the Mongolian oxyaenid *Sarkastodon* (A.M.N.H. No. 26641). The mandibular symphysis of *Dissacus*, *Pachyaena*, *Mongolonyx*, and *Harpagolestes* is also massive, but it is much less steep anteroposteriorly than that of *Mongolestes*. A comparison between the symphysis of *Mongolestes* and the symphyses of the above-listed mesonychid genera may be helped by an analogous contrast with those of some recent species. The degree of steepness of the symphysis in the mustelid *Taxidea* is similar to that of the mesonychids other than *Mongolestes*, the later having a symphysis not unlike that of *Hyaena crocuta* or that of *Felis lynx*. There is little doubt that the two types of symphyses reflect either divergent adaptations or different levels of the same adaptation in the mesonychid feeding mechanism. Possibly the steep symphysis and the very large blunt teeth represent a more accentuated crushing adaptation in *Mongolestes*. The relative position of the two mental foramina on the known mandibles of *Mongolestes*, the first under the anterior root of P_2 and the second below the anterior root of P_3, should not be regarded as taxonomically very significant.

HARPAGOLESTES WORTMAN, 1901

?Mesonyx SCOTT, 1888, p. 168.

TYPE: *Harpagolestes macrocephalus* Wortman, 1901.

KNOWN DISTRIBUTION: North America and eastern Asia during the middle and late Eocene and probably early Oligocene of Inner Mongolia.

REVISED DIAGNOSIS: Large to medium-sized mesonychids with a somewhat arcuate and deep lower jaw. M^2 is considerably wider than long, with a paracone subequal to the protocone.

Harpagolestes differs from *Dissacus* and *Pachyaena* in lacking M^3 and cingula on the upper teeth and in the absence of a metaconid on the trigonids.

Harpagolestes differs from *Mesonyx* in having a relatively deeper and wider skull. *Mesonyx* retains a metacone on the M^2, while in *Harpagolestes* it is almost completely vestigial or reduced. Homologous teeth are relatively wider in *Harpagolestes* than in *Mesonyx*. Teeth of *Harpagolestes* are often heavily worn, while those of *Mesonyx* rarely exhibit extreme wear. *Mesonyx* and *Synoplotherium* possessed highly specialized cursorial feet. When the size of most of the species belonging to *Harpagolestes* is considered, it is unlikely that these larger species were apt runners. Such a statement is based only on conjecture, since no feet of *Harpagolestes* are known.

At least one species of *Harpagolestes* (*H. macrocephalus*) has a humerus with an entepicondylar bridge, while *Synoploterium* lacks this structure and retains a small M^3. It should be emphasized here that *H. macrocephalus* is a poorly known species of the genus.

Harpagolestes differs from *Mongolonyx* in having a deeper, more arcuate lower jaw, canines not set so close to each other, and relatively smaller teeth.

Harpagolestes differs from *Mongolestes* in retaining M_3 and having relatively smaller teeth. The mandibular symphysis of *Harpagolestes* is much less steep anteroposteriorly than that of *Mongolestes*.

P^2 is lost in the type specimen of *H. macrocephalus* and, since that is the only specimen allocated to the taxon, the dental formula of the genus is problematical. Several specimens of *H. uintensis* show clear tendencies toward the reduction of P_1.

The dental formula can be given tentatively as follows: $I_2^3, C_1^1, P_{4}^{(?3)4}, M_3^2$.

REMARKS: Wortman gave his generic diagnosis as follows: "Internal cusps of inferior molars vestigial; external cusps of superior

molars equal; M_3^2, $PM_{4(?)}^3$," (Wortman, 1901–1902, vol. 12, p. 286). This diagnosis is inadequate for the genus as it is known today. The diagnostic characters are, moreover, insufficient and inadequate for the type species itself. Teeth of the type specimen are so badly worn that, judging the external cusps of the upper molars to be equal is unwarranted. The paracone and metacone are subequal on M^1 but certainly not on M^2 in the four better-known species (H. *macrocephalus*, H. *immanis*, H. *uintensis*, ?H. *orientalis*, new species). There is essentially one major labial cusp on M^3 of all the above-mentioned species, situated between one small anterior and one posterior stylar cusp.

The genus needs intensive study, and all specimens of all the species need careful re-examination. The above-cited characters are only an outline of the most important features of this holarctic genus.

Harpagolestes macrocephalus Wortman, 1901

Plate 16

TYPE: Y.P.M. No. 11901, incomplete skull and jaws, and a right humerus. The type specimen was collected in October, 1873, but the specimens were not catalogued until April 17, 1909.

HORIZON AND LOCALITY: Exact stratigraphic locality unknown. The type is from " . . . lower part of Bridger beds near the mouth of Smith's Fork." The horizon is designated in the catalogue as Bridger, in the vicinity of Millersville, Wyoming. Bridger localities are discussed in considerable detail by Wood (1934) and by Wheeler (1961).

DESCRIPTION: The diastema between P^1 and P^3 is about 3 cm. long. P^1 is rooted in a shallow alveolus and is strongly procumbent. P^3 is elongated anteroposteriorly, non-molariform. P^4–M^2 are so badly worn that the original cusp pattern is obliterated. M^1 is considerably larger than either P^4 or M^2.

The palate is narrowest at the level of the diastema. The infraorbital foramen opens and arches over P^3. There is a lateral depression from the infraorbital foramen to the diastema. The large posterior palatine foramen is anteromedial to the lingual root of M^1. The posterior border of the hard palate is rugose and heavily ridged. There is a distinct wide groove posteromedial to M^2. This structure is

homologous to the depressions on the palate of H. *uintensis* and ?H. *orientalis*. Postero-laterally, this groove seems to open from the area of the sphenopalatine foramen, indicating that it accommodated the palatine artery. There are several foramina in the anterior portion of the orbital depression, but it is impossible to determine the exact homologies of these structures.

The internal nares are separated by a median septum, the vomer; the palatine-pterygoid complex is arched over the pterygoid fossa.

Dorsally, the skull is badly broken and restored with plaster. The zygomatic arch, which lacks a postorbital process, is very wide in relation to the skull, particularly in relation to the narrow muzzle.

The lower jaw is restored to such a degree that most of the bone, of which very little remains, is completely covered with plaster. The last of the left cheek teeth in the mandible is very little worn, but the three preceding ones are worn down to the roots. The right lower canine is worn down to the dentine posterolaterally.

MEASUREMENTS (IN MM.) OF TYPE SKULL: Length of upper cheek teeth from posterior border of alveolus of canine to posterior border of M^2, 135; length of P^3–M^2, 85; length of P^4–M^2, 65; length of M^1–M^2, 42; length of P^3, 20; length of P^4, 20; length of M^1, 23; length of M^2, 18; width of M^1, 26.0; width of M^2, 21.5; length of lower cheek teeth, ?P_4–M_3, 83; length of last lower molar, 22.0; width of palate at diastema, 40.

Harpagolestes leotensis Peterson, 1931

TYPE: C.M. No. 11778, right ramus.

HORIZON AND LOCALITY: "Leota Ranch on Green River, six miles north and east of Ouray, Utah." Uinta Eocene, upper part of Horizon C.

SPECIFIC CHARACTERS (NOT A DIAGNOSIS): "P_1 vestigial or absent; shortening of the jaw between canine and P_2; canine of relatively greater diameter; heels of the cheek dentition of greater length compared with the type of H. *uintensis;* jaw slenderer than that of the specimen in the Carnegie Museum No. 2961, referred to H. *uintensis*" (Peterson, 1931, p. 337).

DIAGNOSTIC MEASUREMENTS (IN MM.):

The following measurements are from Peterson (1931): Length of P_2–M_3, 167.0; length of lower premolars, 87.0; length of lower molars, 80.0; length of P_2, 20.0; length of P_4, 30.0; length of M_1, 30.0; length of M_2, 26.0.

Harpagolestes uintensis (Scott, 1888)

Text figures 4, 5

Mesonyx (?) uintensis SCOTT, 1888, p. 168.
Mesonyx uintensis SCOTT, 1889, p. 471.

TYPE[1]: A.M.N.H. No. 1892, crushed skull, restored.

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[1] Scott never designated a type. Osborn (1895) referred to the skull of *M. uintensis* (A.M.N.H. No. 1892; designated as type in the present paper), most likely meaning to designate a type, although he made no formal statement. The skull (A.M.N.H. No. 1892) is cited as the type as it is exhibited in the American Museum, but the records do not indicate that it is. Osborn described the specimen in 1895 and gave additional measurements in 1924. Thorpe (1923) first referred the species to *Harpagolestes*. Matthew (1901), in a footnote, referred to a measurement of M_{1-3} of *Mesonyx*

REFERRED SPECIMEN: A.M.N.H. No. 1878, lower jaw with left and right canine, left P_{3-4}, right P_4–M_1.

HORIZON AND LOCALITY: Of the type, upper Eocene, Wagonhound Bend, White River, Uinta Basin, Utah. Of the referred specimen, middle beds (Horizon B of the Uinta Formation), Uinta Basin, Utah.

SPECIFIC CHARACTERS (NOT A DIAGNOSIS): Except for its large size, the skull is too fractured to offer good diagnostic characters. The unique dental features of the type specimen lie in the separation of the upper premolars. There is a diastema between P^1 and P^2 and between P^2 and P^3. The latter diastema is greater. These features may be a consequence of age and not diagnostic for the species. The zygomatic arch bears a postorbital process.

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uintensis as taken from the type specimen. This reference must be to the three lower molars of *Mesonyx (?)uintensis* mentioned by Scott (1888) which had never been formally designated as type.
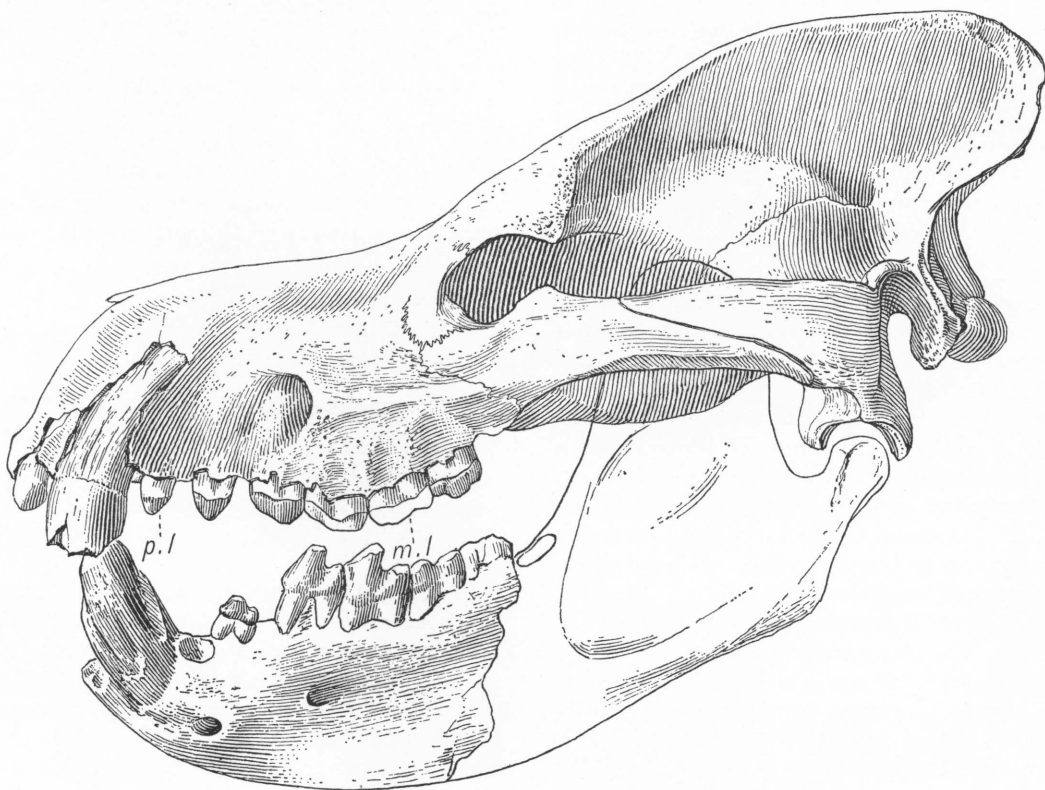
FIG. 4. Skull of *Harpagolestes uintensis*, type (A.M.N.H. No. 1892). The lower jaw is A.M.N.H. No. 1878. ×0.3.
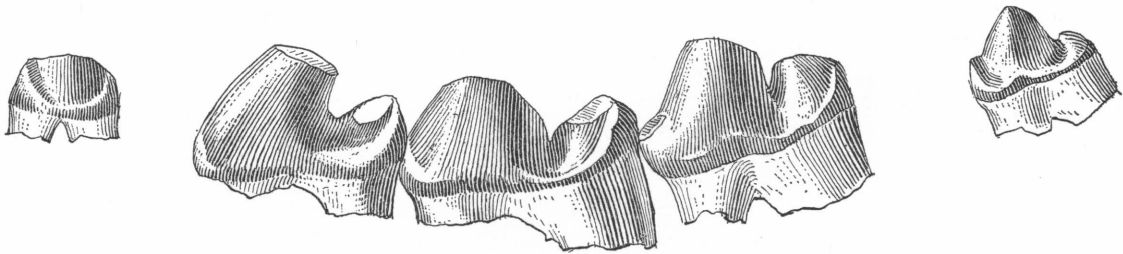
FIG. 5. Teeth on which Scott (1888) based the species *Mesonyx uintensis*, i.e., *Harpagolestes uintensis*. From right to left: M_3, M_1, P_4, and P_3. The tooth at the extreme left may not be that of a mesonychid. ×1.

The palatine-pterygoid complex arches over the pterygoid fossa.

MEASUREMENTS (IN MM.): The following measurements were taken on the left side of the type (A.M.N.H. No. 1892): length of upper premolars and molars, approximately 145; length of P^1–P^4, approximately 104; length of P^4–M^2, 72.2; length of M^1–M^2, 48.5; length of M^2, 20.9; width of M^2, 25.7.

REMARKS: Scott based his description of *Mesonyx (?)uintensis* on fragments of incisors and canines, one upper and two lower premolars, three lower molars, and a mandibular fragment. He did not publish catalogue numbers or designate a type, as noted in the footnote. He mentioned that the specimens are portions of three individuals collected by the Princeton Expedition of 1886.

Harpagolestes immanis Matthew, 1909

Text figure 6; table 5

TYPE: A.M.N.H. No. 13143, incomplete skull and mandibles.

HORIZON AND LOCALITY: North side of Haystack Mountain, Washakie Basin, Wyoming. The exact locality of the type specimen was not recorded.

SPECIFIC CHARACTERS (NOT A DIAGNOSIS): The muzzle is relatively short in relation to the rest of the skull in this species. There are no diastemata between the upper cheek teeth. The canines are robust and procumbent. The postorbital process is lacking on the zygomatic arch. M_3 is reduced in size.

MEASUREMENTS (IN MM.): The following measurements are of the left mandible of the
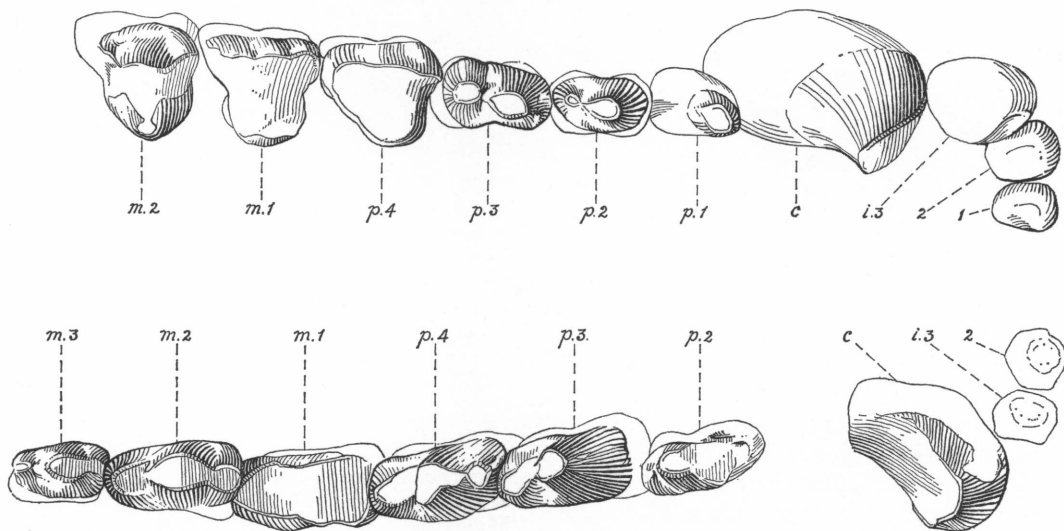
FIG. 6. *Harpagolestes immanis*, type (A.M.N.H. No. 13143).
From Matthew (1909, figs. 99, 100). ×3.5.

type (A.M.N.H. No. 13143): Length of premolars and molars, 163.0; anteroposterior diameter of canines at base of crown, 28.2; anteroposterior diameter of crown of P_2, 21.7; anteroposterior diameter of crown of P_3, 30.4; anteroposterior diameter of crown of P_4, 32.8; anteroposterior diameter of crown of M_1, 30.2; anteroposterior diameter of crown of M_2, 31.5; anteroposterior diameter of crown of M_3, 21.7; greatest transverse diameter of canines at base of crown, 19.3; width of P_2, 10.8; width of P_3, 15.1; width of P_4, 16.3; width of M_1, 15.8; width of M_2, 15.3; width of M_3, 11.0.

REMARKS: The diagnostic measurements of the type skull are given in table 5 in comparison with those of *?H. orientalis*, new species. The type skull is considerably restored, so that the diagnostic measurements are approximate. This species may very well be conspecific with *H. uintensis*. The teeth of the lower jaw are virtually identical with those of *H. uintensis*. The scarcity of specimens precludes further analysis.

Harpagolestes brevipes Thorpe, 1923

Harpagolestes breviceps (sic) PETERSON, 1931, p. 333.

TYPE: Y.P.M. No. 13098, fragmentary left mandible and right calcaneum.

HORIZON AND LOCALITY: Upper Eocene, White River, Uinta Basin, Utah. Specimens collected by Sam Smith from greenish white clay horizon. The exact locality of the type specimen was not recorded.

SPECIFIC CHARACTERS: "It (the jaw) exceeded the type of *H. uintensis* by about 30 per cent in the linear dimensions of the ramus. The characters of the teeth differ in no respects from those of *H. immanis*, except that P_3 has a small anterior tubercle near the base of the principal cusp" (Thorpe, 1923, pp. 219–220).

MEASUREMENTS (IN MM.): The following measurements are of the left mandible and calcaneum of the type (Y.P.M. No. 13098) from Thorpe (1923): length of premolars and first molar, 129.0; length of P_2, 23.0; length of P_3, 32.2; length of P_4, 36.0; length of alveoli of M_1, 37.0; depth of ramus below P_4, 52.0; length of calcaneum, 95.0.

REMARKS: The presence or absence of a small anterior tubercle on P_3 of one specimen is not likely to be diagnostic. There is a much greater degree of variation in the relative position of the tubercles on the upper cheek teeth of the two specimens of *?H. orientalis*, new species. At present, *H. brevipes* seems to be the largest species of the genus.

Harpagolestes koreanicus Shikama, 1943

Table 4

TYPE: The author designated three teeth as the holotype: "P_3 and P_4, anterior part of P^3 (?), all probably of left side" (Shikama, 1943, p. 9).

HORIZON AND LOCALITY: "Horizon: Main seam of Hosan coal mine, embedded in coaly shale in association with *Protitanotherium koreanicum*. Hosan coal bearing group; Upper Eocene" (Shikama, *loc. cit.*).

SPECIFIC CHARACTERS: From the figures and description of Shikama, none can be offered.

REMARKS: The tooth listed as P^3, as far as can be judged from Shikama's illustrations (figs. 1 and 2, p. 10), is very likely not P^3 but rather M^2, based on size relationships to the lower teeth. Therefore the main cusp of this fragment is a paracone, and not the protocone as Shikama indicated. It is unfortunate that a new species has been named on such insufficient and fragmentary evidence. The general size range of *H. koreanicus* may be very similar to that of *?H. orientalis*, new species.

?Harpagolestes orientalis, new species

Plates 17–19; text figure 7; table 5

TYPE: A.M.N.H. No. 26300, almost complete, slightly crushed and badly fractured skull, bearing left P^3–M^2 and right P^4–M^2; left femur.

HYPODIGM: The type and A.M.N.H. No.

TABLE 4

MEASUREMENTS (IN MILLIMETERS) OF THE HOLOTYPE OF *Harpagolestes koreanicus* (FROM SHIKAMA, 1943)

	P_3	P_4	$?P^3$
Maximum length	20.5	20.8	—
Maximum breadth	9.0	9.8	—
Height of main cusp	13.3	14.4	8.8
Height of posterior cusp	7.0	5.7	—

26301, a well-preserved, uncrushed anterior portion of a skull, bearing left P³–M² and right P³–M².

HORIZON AND LOCALITY: The hypodigm was collected during the 1928 Central Asiatic Expedition from the late Eocene Ulan Shireh beds at Chimney Butte, North Mesa, Shara Murun region, Inner Mongolia.

DIAGNOSIS: If the allocation of the new species is correct, then this is the best-known small species of the genus, and on the basis of size alone it can be easily differentiated from all other species that had been referred to *Harpagolestes*, with the exception of the poorly known *H. koreanicus*.

The size of skull is within the size range of *Mesonyx obtusidens*, although it is much more robust, the teeth of the new species being relatively much larger than those of *M. obtusidens*. The M² of the latter species bears a metacone connate with the paracone but still clearly distinct from it, while the homologous cusp of *?H. orientalis* is vestigial.

The new species differs from *Synoplotherium lanius* in the absence of the M³, but resembles the latter genus in the general appearance of the posterior region of the hard palate more than it resembles the same structure of *H. uintensis*.

The anterior half of the muzzle of the new species is the widest between the two upper canines as in *H. uintensis* (or *H. immanis*), although the muzzle itself is relatively more elongated in *?H. orientalis* than in *H. uintensis*.

DESCRIPTION: The type specimen represents a younger animal than A.M.N.H. No. 26301, judged from the degree of dental wear and the emergence of teeth from the alveoli. If the extent of wear often exhibited by mesonychid molars be considered, both specimens represent young adults.

Upper Dentition: The upper teeth of the two specimens of *?H. orientalis* are the best-preserved and least-worn teeth known for the genus *Harpagolestes*. The general pattern of the teeth is characteristically mesonychid. The dental formula is 3, 1, 4, 2. The alveoli for the incisors indicate lateral compression of I¹⁻² by the much larger I³, as can be observed in *H. immanis*. The configuration of the alveoli suggests that the incisors, like the canines, were procumbent. The single-rooted P¹ im-

mediately follows the canine and, in turn, is followed by the double-rooted P². P³ is double-rooted and elongated lengthwise, the crown bearing a paracone over the gap between the roots, as in *H. immanis*. The metacone is directly posterior to the paracone. As in *Mesonyx obtusidens* and *H. immanis*, there is an incipient style anterior to the paracone. There is a moderately steeply sloping shelf from the bases of the paracone and metacone, the slope dipping posteromedially and bearing no internal cusp. This condition is essentially like that in *H. immanis*. In *Dissacus* (see pl. 15) a broad shelf on P³ bears an internal cusp, transversely aligned with the paracone, indicating an incipient protocone. P⁴ has a rather centrally placed high paracone on the type, followed by a closely appressed, shorter metacone. Anterior to the paracone there is a well-developed parastyle. The protocone is almost subequal to the paracone, situated lingually to the latter. There is an interesting difference between P⁴ of the type and that of A.M.N.H. No. 26301. On the latter tooth, there is, in addition, a large metastyle posterior to the metacone. The somewhat worn tooth of A.M.N.H. No. 26301 seems to be bearing four cusps in a row. The molariform P⁴ of the type is similar to M¹ in all essential features. The M¹ bears a prominent parastyle. There is a groove on the labial wall and a shallower one on the lingual wall of M¹. These grooves separate the paracone superficially from the metacone. In P⁴ the metacone tends to be confluent with the paracone. The metastyle on M¹ of the type is less prominent than that of A.M.N.H. No. 26301, although this structure is incipient on the M¹ of both individuals. The protocone is prominent, separated from the paracone by a wider valley than on P⁴. M² is much more constricted anteroposteriorly than M¹. It has a large paracone, preceded by a distinct parastyle. There is no distinct metacone; this cusp is merged with the paracone. The valley between protocone and paracone is wider and the walls are less steep than on M¹. The widening of the valley between paracones and protocones of P⁴–M² results in an anteriorly constricted but gradually widening trough posteriorly. The buccal walls of the cheek teeth are essentially vertical, or perhaps tilted very slightly medially. (Owing to some degree

of crushing in both specimens, this statement cannot be made with certainty.)

The specimen of *H. immanis* has badly worn dentition, though it can be recognized that, despite its larger size, the essential dental morphology was probably very similar to that of the new species.

Skull: The anterior portion of the muzzle widens out as noted above. The premaxilla-maxilla suture can be seen at the anterior third of the alveolus for the canine. As well as can be discerned at this badly broken region of the skull, this suture comes behind the incisive (anterior-palatine) foramina to make contact with the suture from the opposite side, which would indicate that the incisive foramina were completely surrounded by the premaxillae, but that they were cannot be stated with certainty. Relatively large foramina surrounding the incisive foramina indicate a very high degree of vascularization, more than is seen in some fissiped carnivores. Grooves appear to extend from the incisive foramina to the alveoli for the first and second incisors.

The maxillary-palatine suture is transverse at the level of P^4 and turns backward at each of the single palatine foramina to the postero-lateral edge of the palate. The same situation is true in *H. uintensis*. Anterior to the incisura palatina there is a curious tear-shaped basin about the size of the protocone of the adjacent molar. Posteriorly and laterally, this basin is bordered by a single ridgelike thickening of the palatine, and medially by the medial limits of the palatine. This depression opens forward. Owing to the state of preservation, the presence or absence of a foramen in this basin cannot be determined. The palate of the type skull of *H. uintensis* shows the same structure. There is no sign of this structure in A.M.N.H. No. 26301, owing perhaps to the reconstruction of this area with plaster.

The palatines and pterygoids seem to be arching over the pterygoid fossa in the type and are widely separated in A.M.N.H. No. 26301. Both specimens are crushed, and the true condition of this region cannot be determined. Most likely, there was an incipient leaning over of the palatines and pterygoids, converging toward the condition seen in some hyaenodonts. *Harpagolestes immanis* has been restored to show the palatines and pterygoids arching over the pterygoid fossa, but the actual material of the fragmentary skull gives no indication of this condition.

Specimen A.M.N.H. No. 26301 shows a complete posterior separation of the nasal passage. The prominent median ridge of the vomer extends out to the presphenoid. The presphenoid and basisphenoid are exposed on the type, but the suture between them cannot be recognized. Traces of the vidian canal can be recognized on the type, running down on each side of the basisphenoid. On the right side, anteromedial to the medial limit of the glenoid fossa (the entire zygomatic arch is missing on this side), there is a distinct foramen with a grooved postero-external extension. This foramen, we believe, represents the posterior opening of the alisphenoid canal; the groove leads to the foramen ovale. The same condition is present in *Mesonyx obtusidens*. The type shows no extension of the pterygoids, but the latter join the alisphenoid-basisphenoid complex. Most likely, this ridge was the area of origin for a very large and strong internal pterygoid muscle which covered the alisphenoid canal (and foramen rotundum) and the grooved extension to the foramen ovale.

The zygomatic arch, which is preserved only on the left side of the type, lacks a post-orbital process. The jugal extends far back ventrally on the arch. The postglenoid process is much thicker and stronger than the anterior one. Dorsal and medial to the postglenoid process, the surface of the symphysis that binds the periotic and the squamosal is exposed. Behind the surface is the broken exposure of what must have been the lateral extension of the exoccipital.

The restored area of the supraoccipital on the type arches over the condyles, possibly exaggerated because of crushing.

The left side of the type skull is less badly crushed than the right. Medially, the maxilla extends back to the level of the posterior border of the orbit, a condition similar to that in *H. immanis*. The medio-anterior extension of the jugal is limited to the level of the anterior border of the orbit where it is in contact with the very large lacrimal. The lacrimal and anterior border of the orbit are dorsal to this contact. The anterior border of the orbit bears a lacrimal tuberosity. Medial and ven-

tral to this protuberance is the lacrimal fora-
men. The lacrimal extends all the way up to
the anterior dorsal border of the orbit and
forms the entire anterior border of the latter
by turning in medially about 2.5 cm. from the
postorbital process. This condition of the
lacrimal is paralleled in *H. immanis*, and the
same seems to be true for *Mesonyx obtusidens*.
If the figure of *Synoplotherium* (= *Dromo-
cyon*) *vorax* (Wortman, 1901) showing the
same feature is accurate, then this feature
may be a diagnostic mesonychid character.

On both sides of the type skull, at the junc-
tion of the lacrimals, frontals, and nasals,
there is a large hole due to damage, indicating
the probable extreme thinness of bone in the
ethmoid area of the skull. The nasals extend
far up between the frontals; the maxillae,
however, are limited in their extension by the
prominent lacrimals. The posteriorly broad-
ened nasals bar the contact of frontals and
maxillae (see text fig. 7). The large infra-
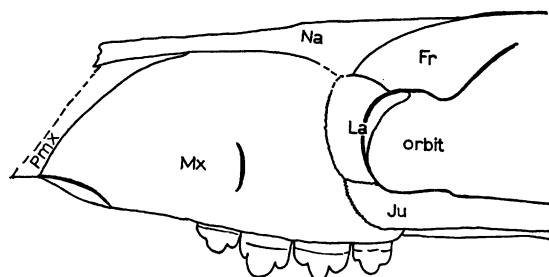orbital foramen opens above the contact of
P^3 and P^4.

FIG. 7. Schema of bones in the anterior half of
the skull of *?Harpagolestes orientalis*, new species
(A.M.N.H. No. 26300). See plate 17.
Abbreviations: Fr, frontal; Ju, jugal; La, lacri-
mal; Mx, maxilla; Pmx, premaxilla.

The sagittal crest is extremely prominent
and high. The greatest height, approximately
6 cm., is just medial to the lambdoidal crest.
The lambdoidal crest is very pronounced lat-
erally and extends down to the squamosal-
mastoid suture. The sutures between frontals
and parietals and between parietals and
squamosals cannot be recognized.

When the skull is viewed dorsally, a de-
pressed, shallow but pronounced basin can be
seen in the area of junction of the nasals and
frontals. The endocranial cavity is small.

Femur: The left femur of *?H. orientalis* is
very similar to that of *Mesonyx obtusidens*.
The latter, however, is much more slender, in
keeping with the general character of the
skulls.

In anterior view, the head of the femur
rests on a short and wide neck. Lateral to the
head is a prominent greater (or first) trochan-
ter, roughened for the attachment of M.
gluteus medius. Medially, on the posterior
portion below the head is the long, ridgelike,
lesser (or second) trochanter, probably serv-
ing for the insertion of iliac and psoas mus-
cles. The third trochanter is a very thick and
blunt ridge well down on the shaft, as is char-
acteristic of mesonychids. It is situated along
the external border of the femur, giving an
attachment area for a very large gluteus
maximus. There is a noticeable ridge parallel
to and between the lesser and third trochan-
ters, somewhat closer to the former. This
ridge is probably the place of insertion of M.
capsularis. The distal end of the femur is
wide and robust. Proximal to the border of
the trochlea for the patella, there is a deep
groove, 5 cm. long, obviously the result of
crushing. The trochlea is wide and rather
medially placed.

Medially, the head bears a very large de-
pression for the ligamentum teres. The lesser
trochanter is clearly visible extending down
one-third of the length of the shaft. The me-
dial supracondyloid ridge is prominent, in-
dicating the insertion for a strong M. semi-
tendinosus. Distal and anterior to the
supracondyloid ridge is a depression for the
internal lateral ligament. A distinct groove
runs along the folded-up medial edge of the
internal condyle.

Viewed posteriorly, the digital fossa is
transversely elongated. Distal and lateral to
the third trochanter, proximal to the external
condyle, the series of large tuberosities are
for the origin of the lateral head of M. gas-
trocnemius. Medial and proximal to the
inner condyle, the posterior rough facet of
the medial supracondyloid ridge marks the
origin of the strong medial head of the M.
gastrocnemius. The depression between the
two ridges was occupied by a widely inserting
M. semimembranosus. The intercondyloid
notch is deep, leading into an intercondyloid
groove. In the latter, depressions for the an-

TABLE 5

MEASUREMENTS (IN MILLIMETERS) OF TWO SKULLS AND A FEMUR OF *?Harpagolestes orientalis*, NEW SPECIES, AND THE TYPE SKULL OF *Harpagolestes immanis*

	?H. orientalis		H. immanis
	A.M.N.H. No. 26300	A.M.N.H. No. 26301	A.M.N.H. No. 13143
Upper dentition			
Total length from posterior border of alveolus for canine to posterior border of M^2			
Left side	106.7	103.7	146.3
Right side	103.5	106.3	141.8
Total length of P^3–M^2, left side, inclusive	75.5	78.4	101.1
Total length of P^4–M^2, left side, inclusive	58.2	61.9	74.3
P^4–M^1, left side, inclusive	41.8	44.2	50.0
M^1–M^2, left side, inclusive	38.3	40.8	47.1
Length			
Left P^3	20.0	19.4	26.0
Left P^4	19.7	21.2	25.2
Left M^1	21.7	22.9	23.7
Left M^2	16.6	18.7	21.7
Width			
Left P^3	11.6	11.8	18.3
Left P^4	19.4	20.6	24.5
Left M^1	21.4	21.5	26.2
Left M^2	19.3	19.7	27.9
Skull[a]			
Total length from anterior border of premaxilla to posterior margin of sagittal crest	320[b]	—	460[b]
Least width of palate between P^1's	42.0	46.4	—
Least width of palate between anterior roots of P^3's	33.2	41.8	—
Width between roots of M^1's	45.1	56.1	—
Width between roots of M^2's	53.8	63.3	—
Distance between incisive foramina and posterior border of internal nares	122.1	118.8	—
Greatest length of nasals	155[b]	—	230[b]
Width across postorbital process of frontal	109.0	—	—
Femur			
Length	280[b]	—	—
Greatest width of shaft at distal border of third trochanter	36.3	—	—
Anteroposterior diameter of head	35.0	—	—
Ratios			
Length of P^3/width of P^3	1.72	1.64	1.42
Length of P^4/width of P^4	1.02	1.03	1.03
Length of M^1/width of M^1	1.01	1.06	0.90
Length of M^2/width of M^2	0.86	0.93	0.69
Length of P^3–M^1/least distance between preglenoid process and posterior margin of M^2	0.99	—	0.73

[a] Not many measurements are useful because of the badly crushed condition of the specimens.
[b] Measurement approximate.

terior and posterior cruciate ligaments can be seen clearly.

In lateral aspect, on the distal extremity of the femur, the outer tuberosity is prominent. There are two distinct depressions to the rear, the more proximal for the external lateral ligament, the more distal for the origin of M. popliteus. A groove distal to the latter depression serves as origin of the M. extensor digitorum longus.

DISCUSSION: Generic delineation on the basis of dental characters alone is an extremely difficult and often impossible task for many species of the Mesonychidae. The generic allocation of the new species is based partially on the general character of the skull (the similarity of the posterior portion of the hard palate of ?H. orientalis to that of Synoplotherium lanius has been noted) but mainly on the general morphology of the upper cheek teeth. No part of the lower dentition is known, so the evidence that allocation to Harpagolestes is certain is far from complete. New specimens of this species, which very probably will be found if collecting continues in Inner Mongolia, may alter its present generic status. Features of the P⁴ and molars of ?H. orientalis are as similar to those of Mesonyx obtusidens as to those of any species of Harpagolestes. Mesonyx, however, is contrasted to the latter genus by its much lighter build and evident cursorial adaptation. Mesonyx was most likely an active predator or was at least as different from Harpagolestes in its mode of life as Lycaon (Cape hunting dog) is from Hyaena.

The genotype, H. macrocephalus, is very unlike the genus as now recognized. The presence of a pronounced diastema where P² was missing and the somewhat narrower character of the anterior half of the skull well separate this Bridgerian species from the other species referred to this genus. We find greater similarity among ?H. orientalis, H. immanis, and H. uintensis than between any of these and H. macrocephalus. If we had feet of the various species of Harpagolestes, then, in accordance with Matthew's view on the importance of locomotory adaptations, this genus might be thoroughly re-evaluated.

Harpagolestes has been characterized throughout the literature as a genus of gigantic animals. Allocation of the Mongolian species may alter this character of the taxon. The skulls of ?H. orientalis are large, but not gigantic; they are about the size of the skull of Mesonyx obtusidens, but they are much more robust than the relatively light cranium of that species.

The slightly curved shaft of the moderately robust femur is characteristic of all mesonychids and also of the Oxyaenidae (Denison, 1938). Denison noted (1938, p. 231) that the patellar trochlea in the Carnivora (sensu Matthew) is comparatively narrow and long, as well as deeply grooved, with a small patella in cursorial animals. The trochlea is broader, more shallowly grooved and shorter, with a wide, robust, and relatively long patella in ambulatory types. Concerning the biomechanics involved, Denison remarked: "The extensor of the tibia, and quadriceps femoris, which has its insertion on the patella and whose pull is extended to the tibia by the ligamentum patellae, is a more slender muscle with a faster action at poorer leverage in the cursorial types; it is a larger muscle with a stronger but slower action in ambulatory types. The range of motion of the tendon or patella over the trochlea is also much greater in cursorial forms" (Denison, 1938, p. 231). ?Harpagolestes orientalis, on these criteria, cannot be definitely placed in either category. The nature of the trochlea is intermediate. It is wide and shallow, but also long enough not to preclude a running habit. The tendon or patella could have a range wide enough over the trochlea further to imply running ability. Cursorial or ambulatory habits of mesonychids may be correlates of bulk rather than generic characters (which are recognized on the bases of skull and tooth morphology). ?Harpagolestes orientalis, which is intermediate in bulk between the light, cursorial Mesonyx obtusidens and the large ambulatory H. uintensis and H. immanis, seems to possess characteristics of the femur that are intermediate between those of cursorial and those of ambulatory forms.

The relative position and orientation of the head of the femur indicate that the hind limbs were well under the body. ?Harpagolestes orientalis was probably a carrion-feeding scavenger, not a pursuer of evasive, fast game, despite its ability to run.

Dissacus-LIKE MESONYCHID FROM THE TANYA BEDS OF SOUTH CHINA

Young and Chow (1963), in a brief note on Cretaceous and Paleocene vertebrate horizons of north Kwantung, reported the skull fragments and upper cheek teeth of a mesonychid from the Tanya beds of Nanyung Basin. Young and Chow thought that the specimen resembled the Torrejonian *Dissacus*. Our skepticism about the correct allocation of the Tanya mesonychid must be expressed until illustrations of the specimens are published. Generic allocation of mesonychids without available specimens for comparison is a task full of uncertainties. Young and Chow also reported skulls and skeletons of a pantolambdid-like pantodont from the same beds that yielded the mesonychid.

tooth. Judged from Gromova's line drawings and description, the animal is certainly not *Mesonyx*, but *Pachyaena*. The broad anterior, posterior, and labial cingula on the upper teeth of the illustrated specimen convey without any doubt the *Pachyaena* affinities. Figure 11 of Gromova's paper shows a complete absence of M^3 on the broad shelf posterior to M^2. If this condition is representative of the species and not that of an immature animal (from the degree of wear, the badly worn lower tooth could not have been associated with the figured maxilla), then "*Mesonyx obtusidens*" is most likely a new species of *Pachyaena*. (Figure 8 of the present paper attempts to show some of the outstanding differences between the upper teeth of *Mesonyx* and those of *Pachyaena*.)
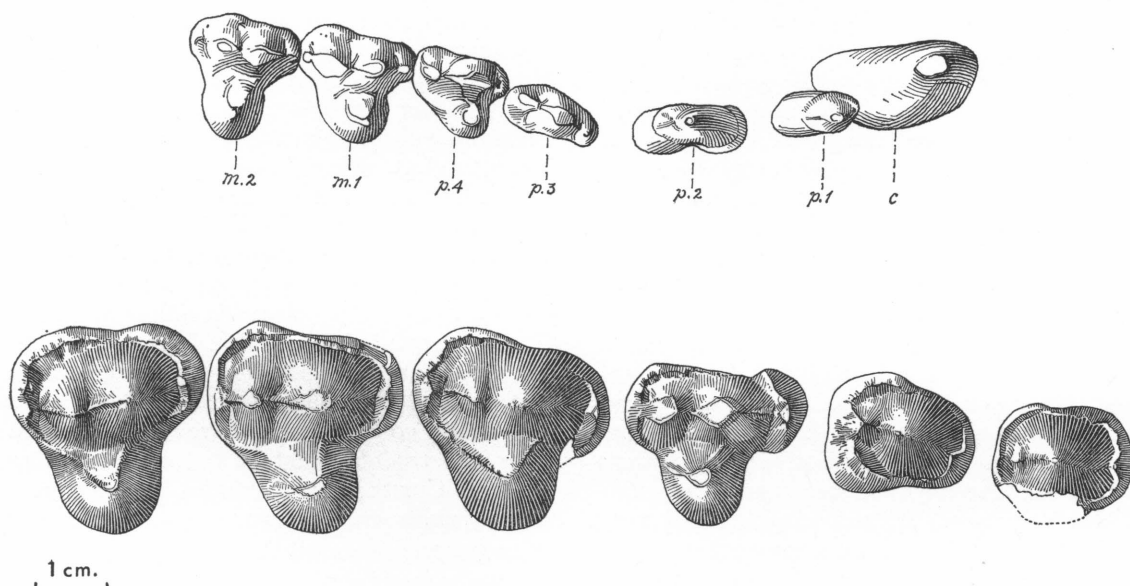
FIG. 8. *Above:* Upper cheek teeth of *Mesonyx obtusidens* (A.M.N.H. No. 12643). From Matthew (1909, fig. 94). *Below:* Isolated teeth of *Pachyaena gigantea*, from left to right: M^3, M^2, M^1, P^4, P^3, and P^2. The scale serves for the whole figure.

"*Mesonyx obtusidens*" FROM THE NARAN BULAK BEDS OF MONGOLIA

Gromova (1952) reported and described specimens, which she called *Mesonyx obtusidens*, from the Naran Bulak beds of Mongolia. She illustrated a left maxilla with slightly worn P^4–M^2 and a badly fractured mandibular fragment with a heavily worn $?M_2$ as the only unbroken and recognizable

?SUBFAMILY MESONYCHINAE

GANDAKASIA DEHM AND OETTINGEN-SPIELBERG, 1958

TYPE: *Gandakasia potens* Dehm and Oettingen-Spielberg, 1958.

KNOWN DISTRIBUTION: Middle Eocene of southwestern Asia; lower Chharat Series of Pakistan.

DIAGNOSIS (TRANSLATED FROM ORIGINAL):
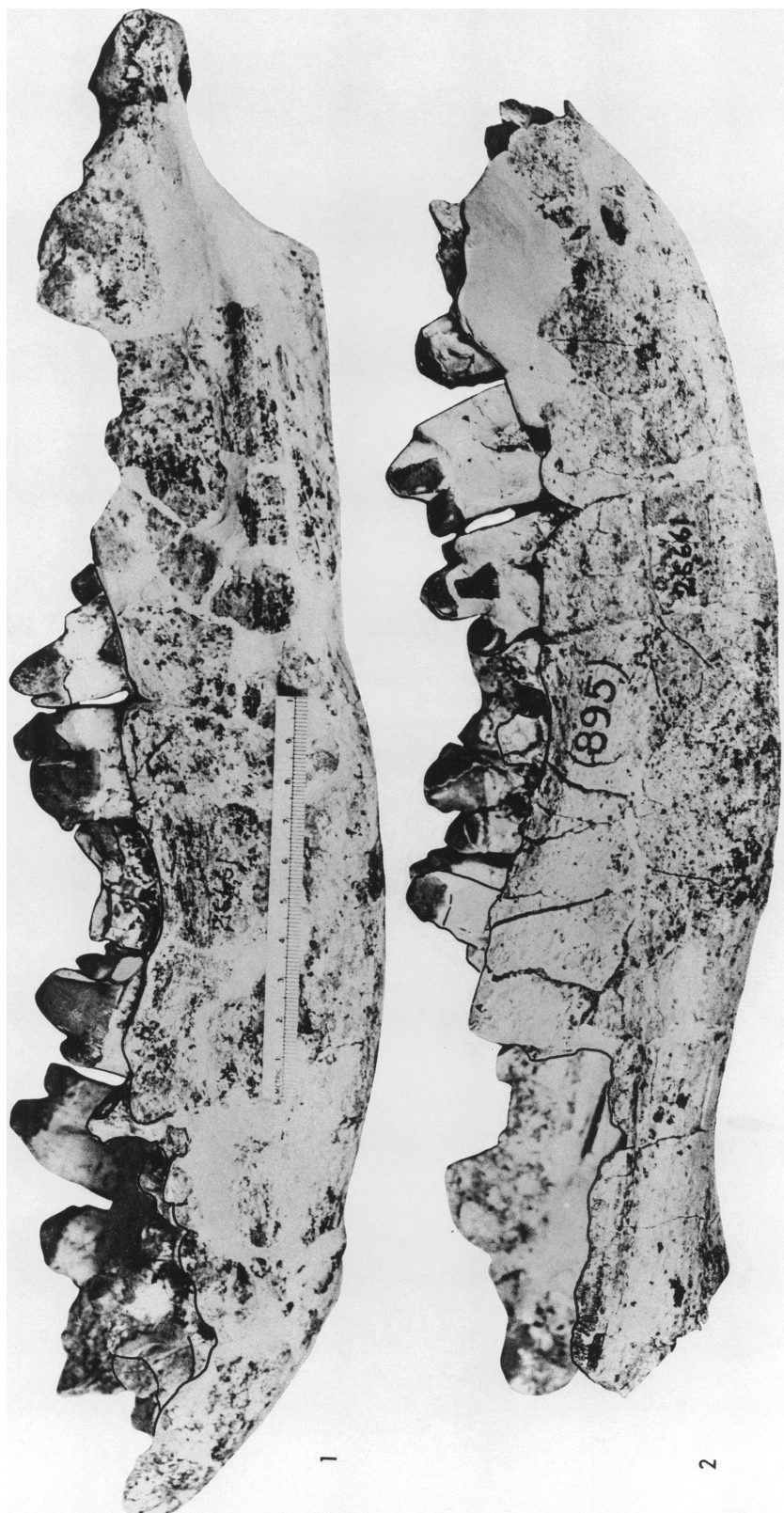
Mongolonyx dolichognathus, new genus and new species, type (A.M.N.H. No. 26661).   1. Lateral view of the left ramus.   2. Lateral view of right ramus
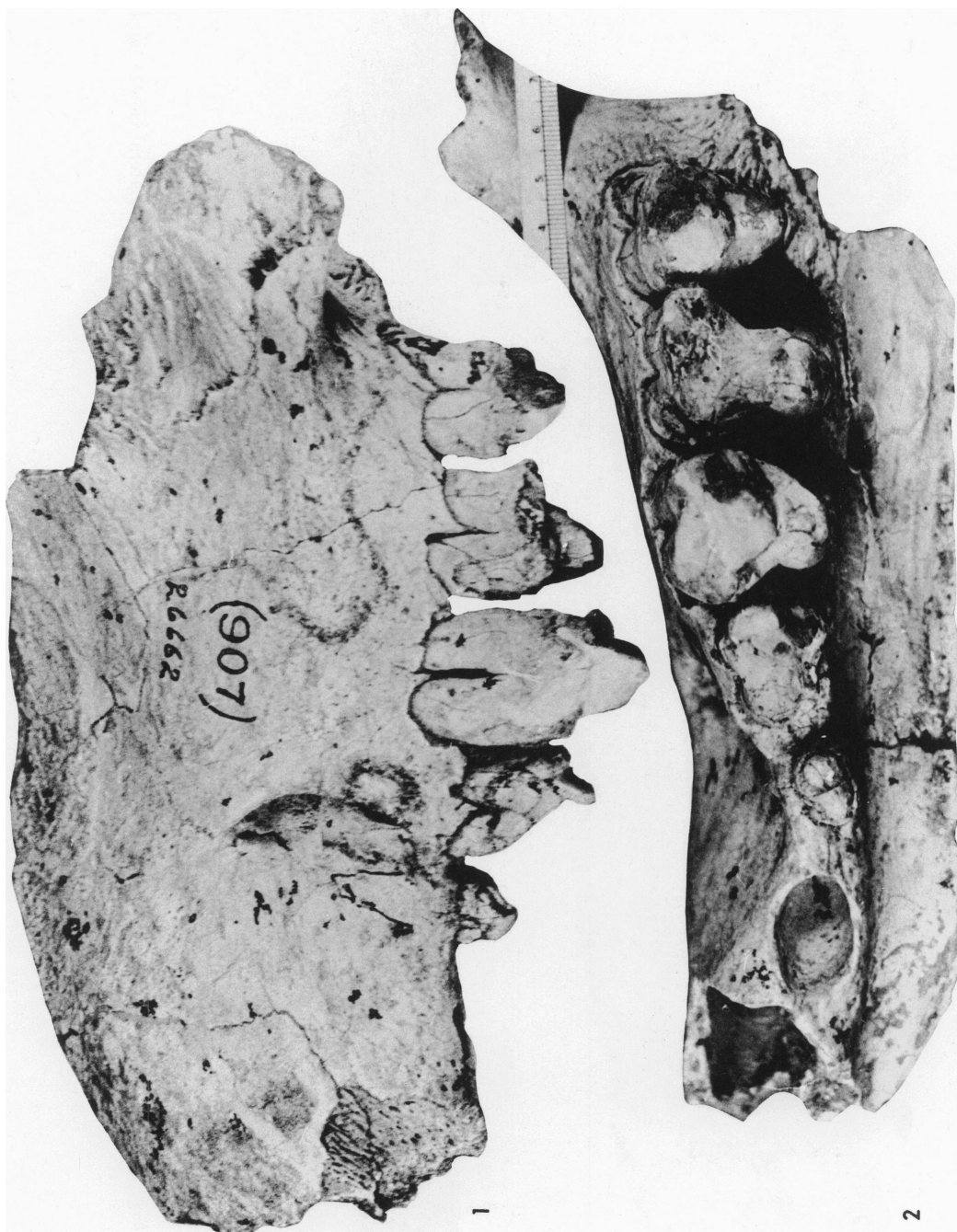
Mongoloryx dolichognathus, new genus and new species (A.M.N.H. No. 26662), left maxilla. 1. Lateral view. 2. Ventral view
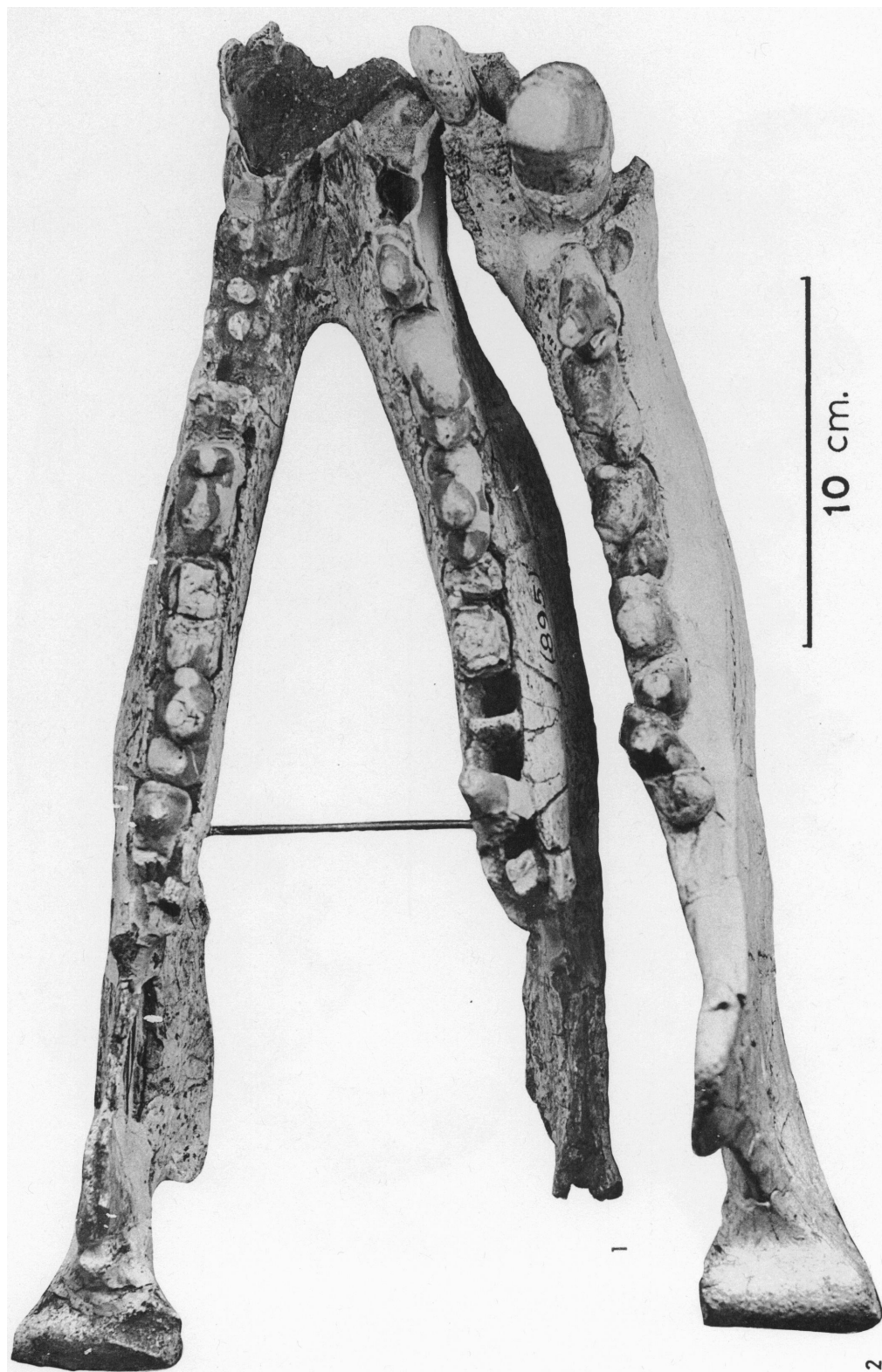
1. *Mongolonyx dolichognathus*, type (A.M.N.H. No. 26661), occlusal view.   2. *Mongolestes hadrodens*, right ramus of type (A.M.N.H. No. 26064), occlusal view
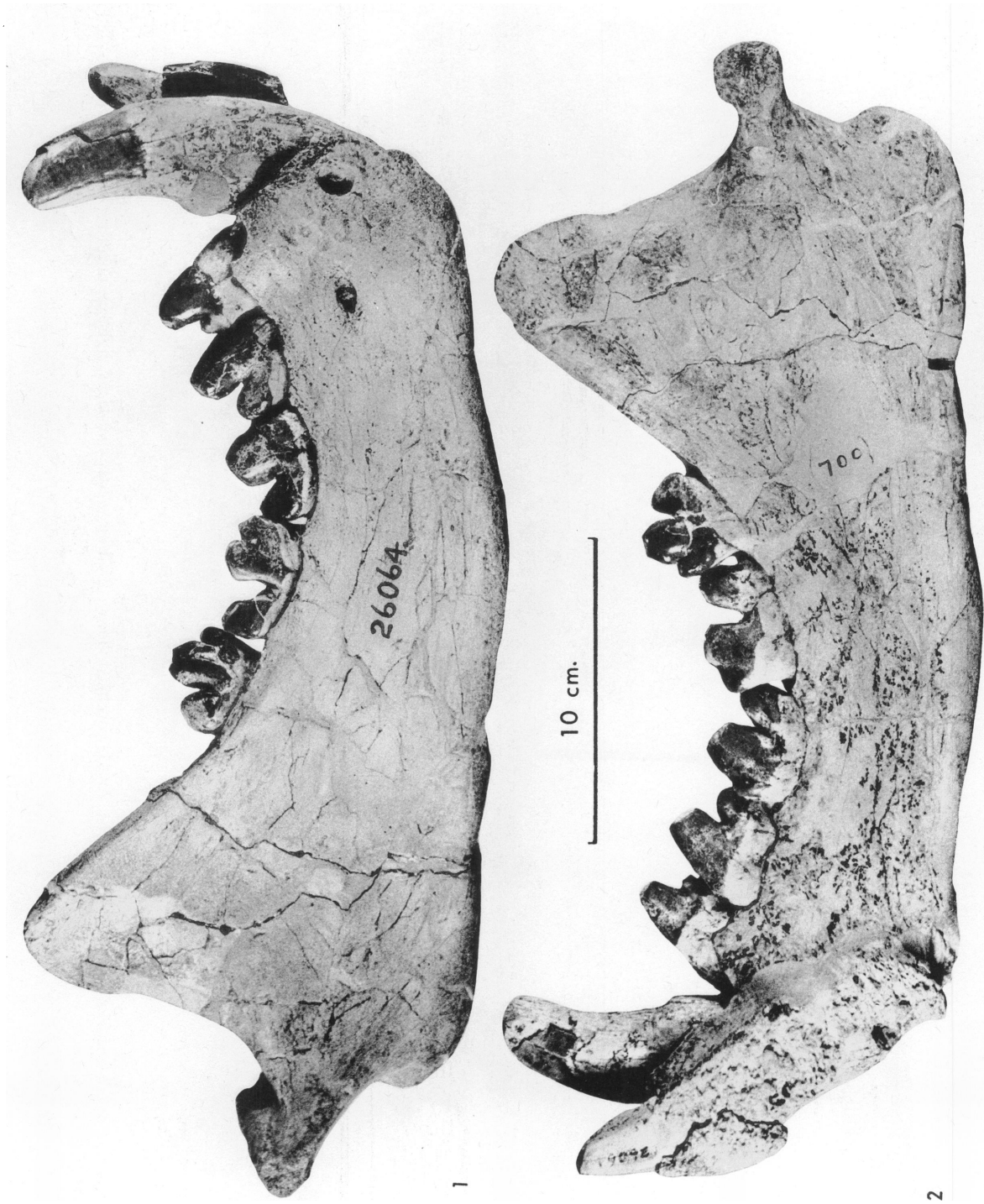
Mongolestes hadrodens, new genus and new species, right mandible of type (A.M.N.H. No. 26064). 1. Lateral view. 2. Medial view
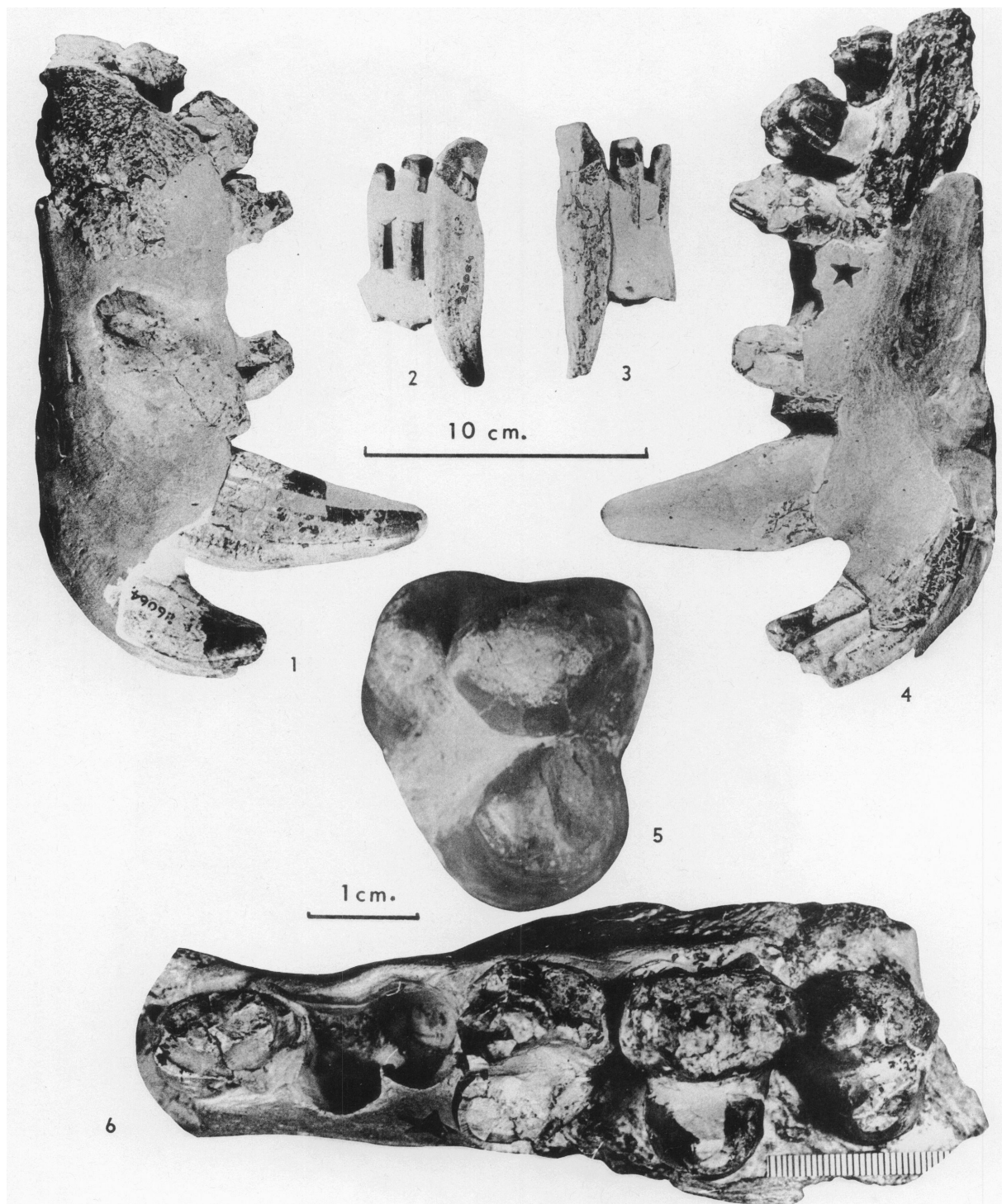
Upper teeth of *Mongolestes hadrodens*, new genus and new species, type (A.M.N.H. No. 26064). 1. Left upper teeth, buccal view. 2. Three right upper incisors, anterior view. 3. Three right upper incisors, posterior view. I^1 is the largest of the upper incisors. 4. Left upper teeth, lingual view. 5. Right P^4, occlusal view. 6. Left upper teeth, from left to right, ?P^3, P^4, M^1, and M^2, occlusal view. P^4 and ?P^3 are attached by plaster to the posterior fragment of maxilla

10 c m.

1

2

METRIC 1

3
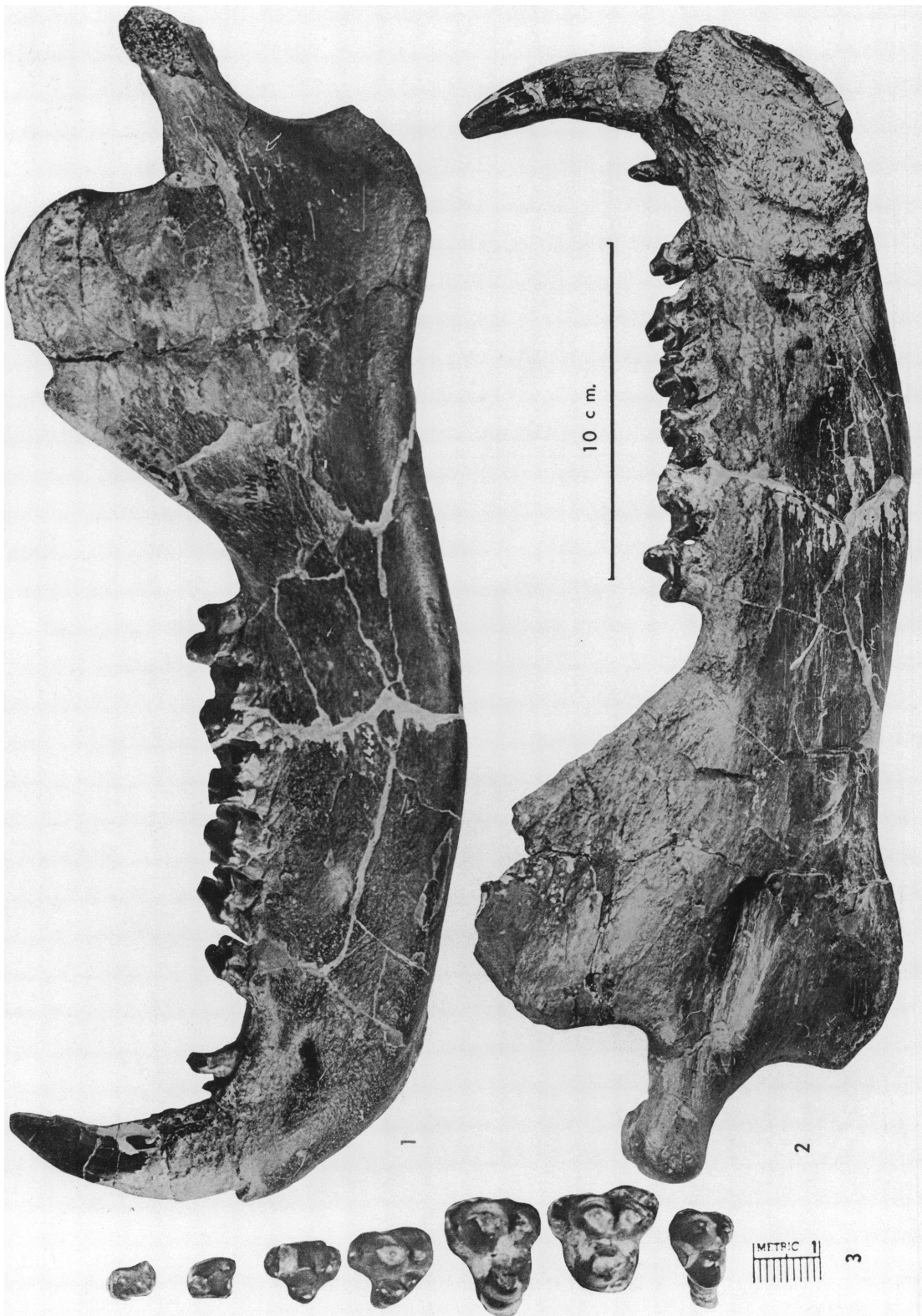
1, 2. Left mandible of *Dissacus saurognathus* (A.M.N.H. No. 2454).   1. Lateral view.   2. Median view.   3. Occlusal view of the upper premolars and molars of *Dissacus saurognathus* (A.M.N.H. No. 776)

Skull of *Harpagolestes macrocephalus*, type (Y.P.M. No. 11901).   1. Ventral view.   2. Lateral view
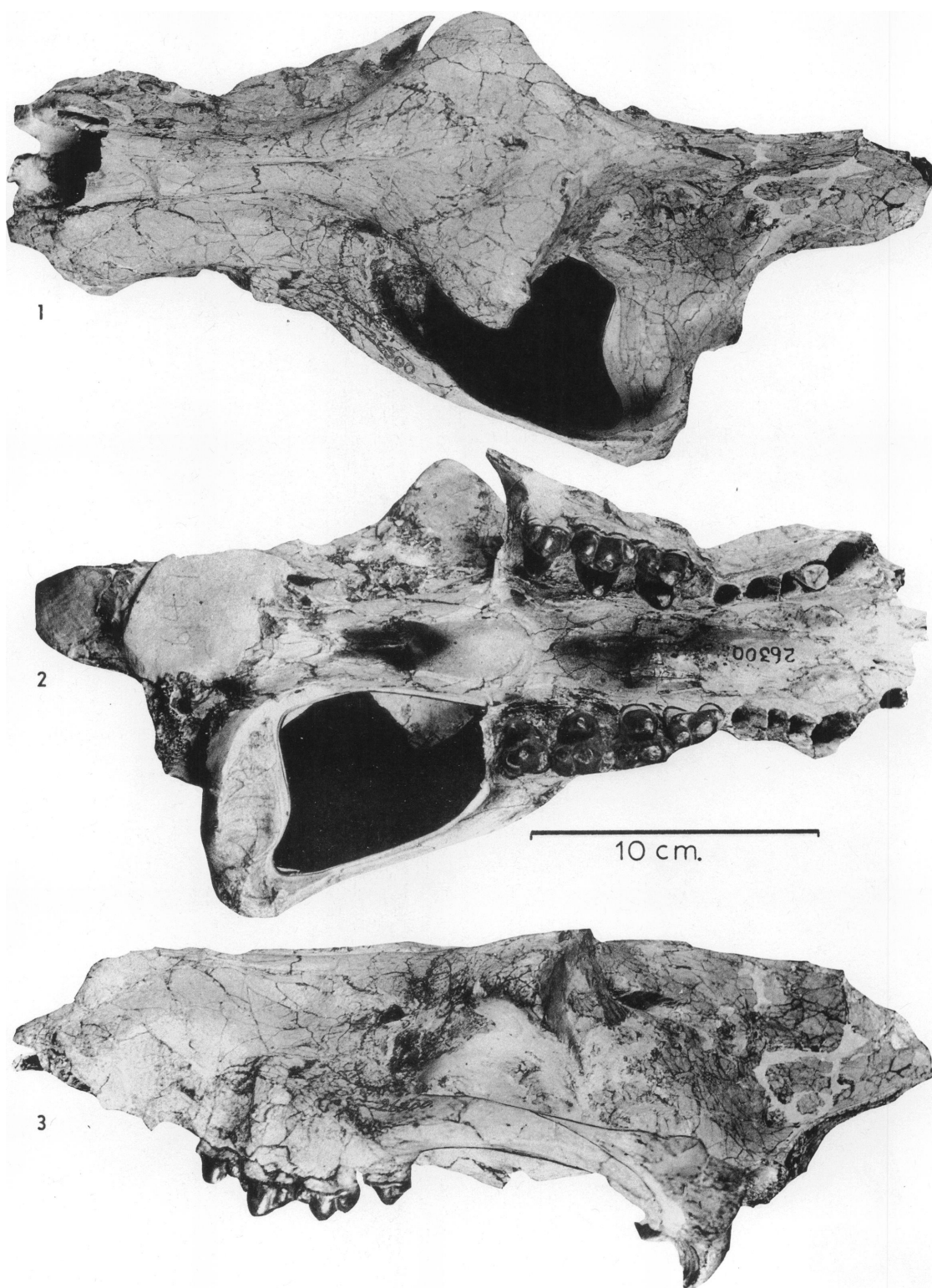
Skull of *?Harpagolestes orientalis*, new species, type (A.M.N.H. No. 26300). 1. Dorsal view. 2. Ventral view. 3. Lateral view
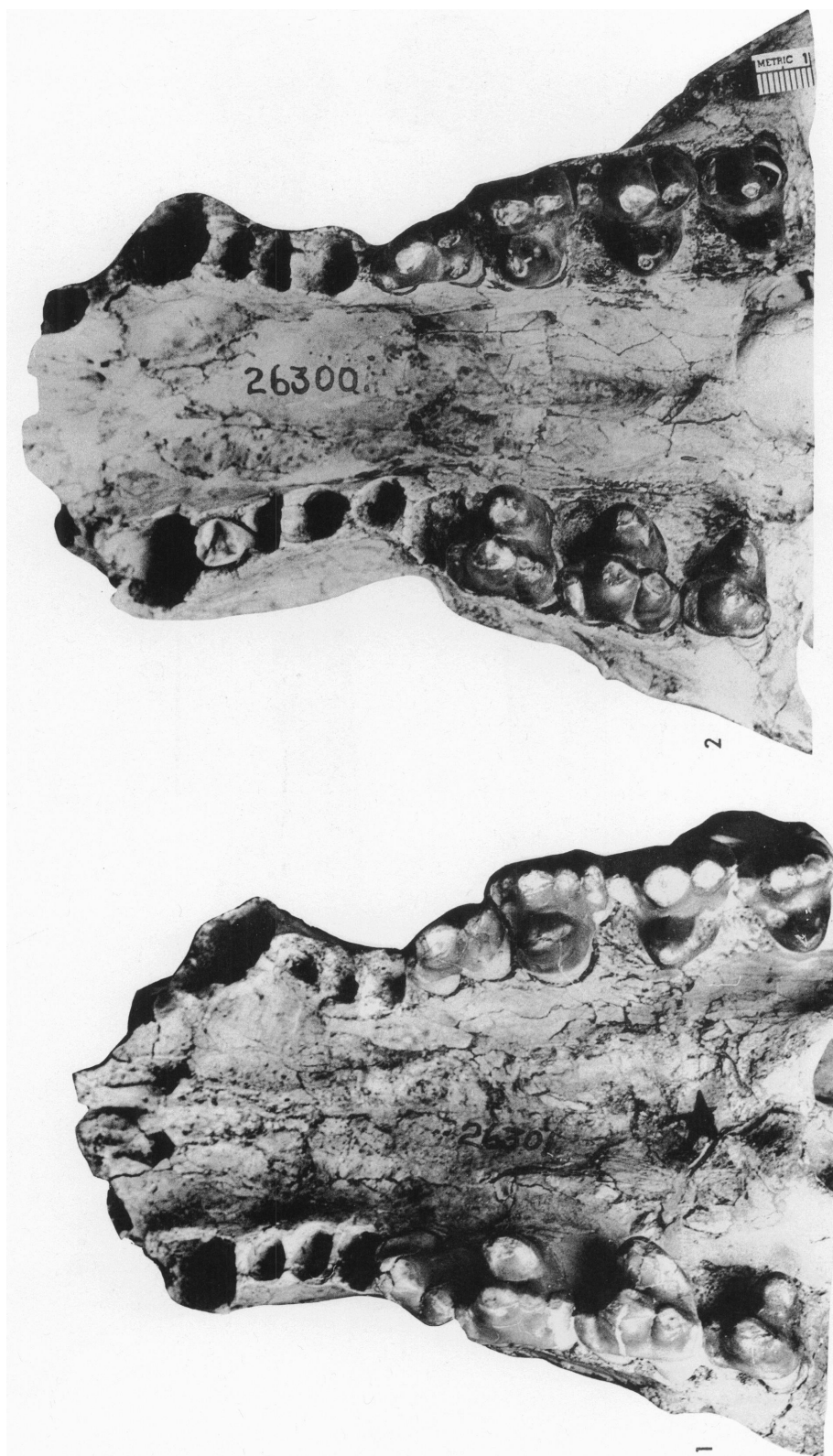
Anterior portions of the two known skulls of *?Harpagolestes orientalis*, new species, ventral views.   1. A.M.N.H. No. 26301.   2. A.M.N.H. No. 26300
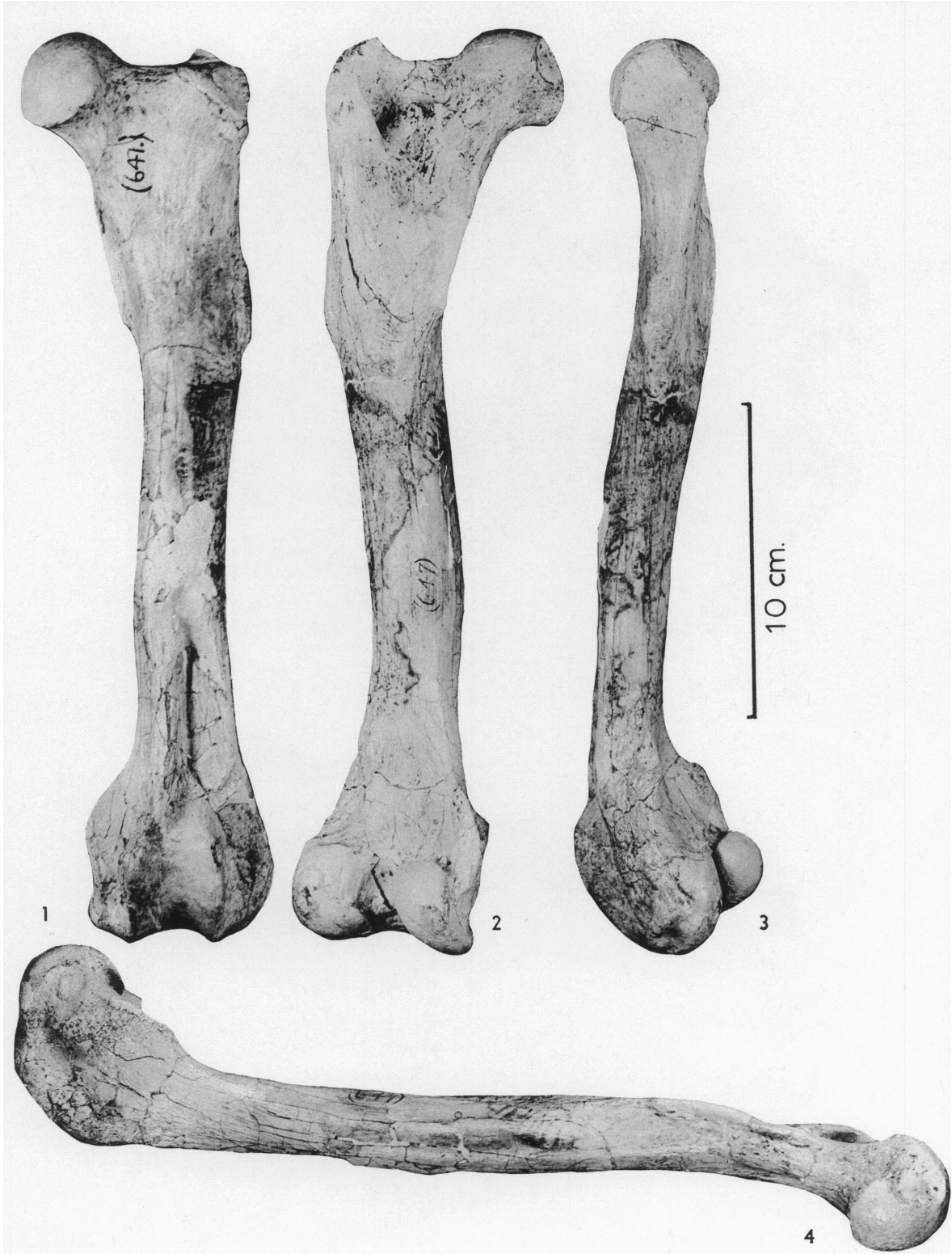
Femur of *?Harpagolestes orientalis*, new species (A.M.N.H. No. 26300). 1. Anterior view. 2. Posterior view. 3. Lateral view. 4. Medial view
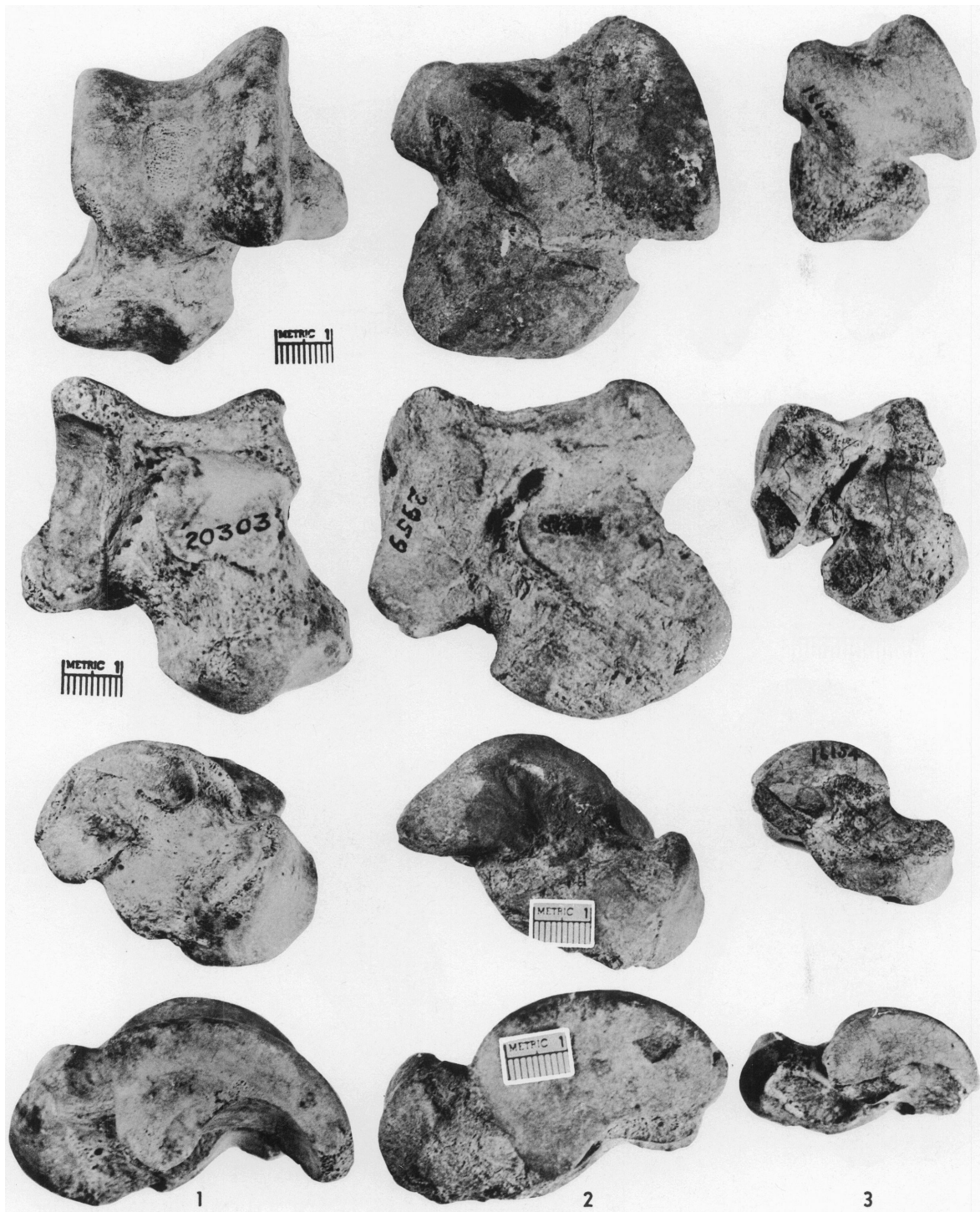
Dorsal, ventral, medial, and lateral views (from top to bottom) of astragali. 1. *Olsenia mira*, type (A.M.N.H. No. 20303). 2. *Pachyaena gigantea* (A.M.N.H. No. 2959). 3. *Pachyaena ossifraga* (A.M.N.H. No. 16154). The scale is identical for each of the four views of the three astragali
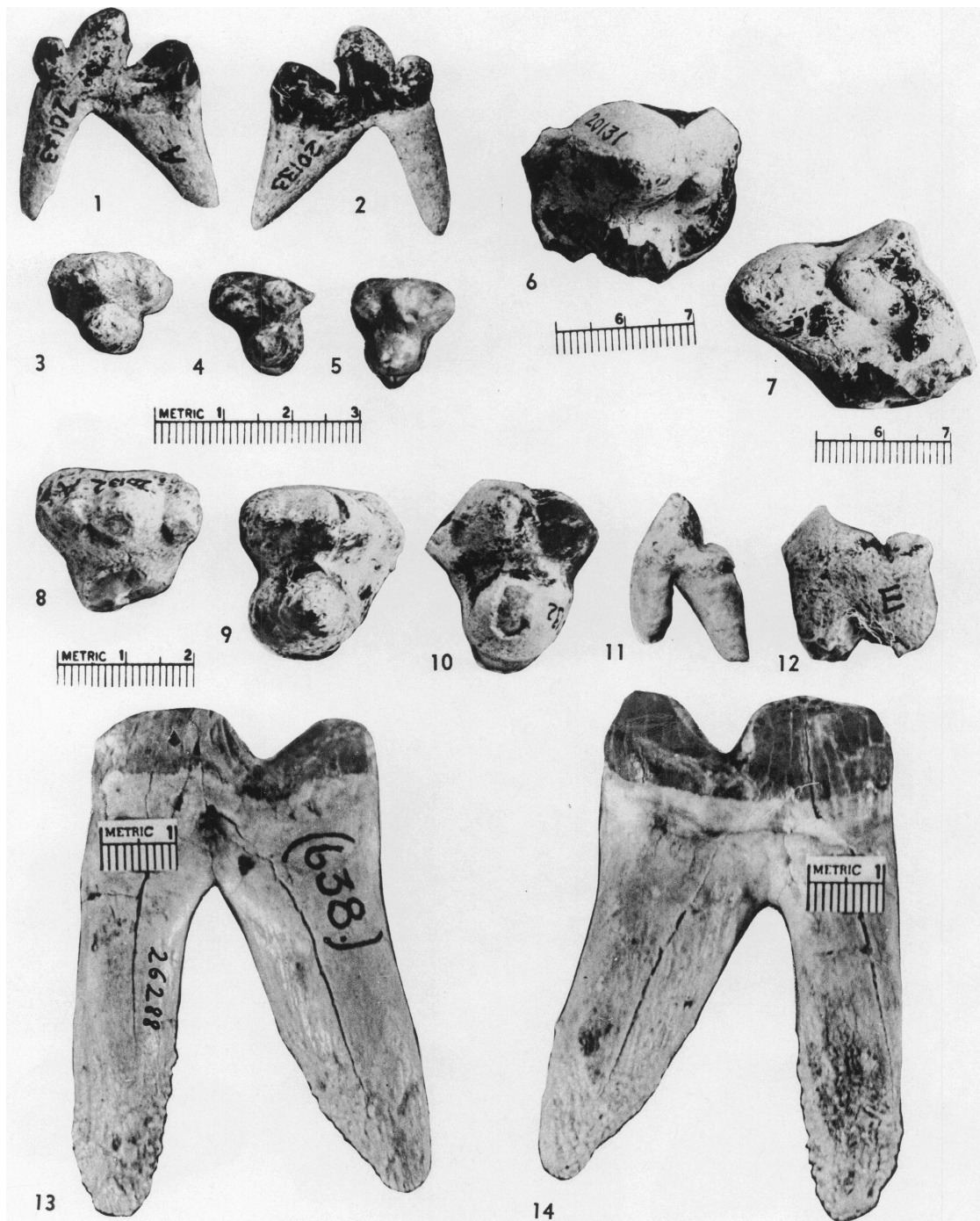
Unallocated mesonychid teeth. 1, 2. Lingual and buccal views of A.M.N.H. No. 20133A, posterior lower cheek tooth; Irdin Manha beds. 3, 4. A.M.N.H. Nos. 20133B and 20133C, right upper cheek teeth; Irdin Manha beds. 5. A.M.N.H. No. 26303, right upper cheek tooth; Ulan Shireh beds. 6, 7. Occlusal and posterior views of A.M.N.H. No. 20131, a fragmentary left upper cheek tooth; Irdin Manha beds. 8–12. A.M.N.H. Nos. 20132A, 20132B, 20132C, 20132D, and 20132E; Irdin Manha beds. 13, 14. Lingual and buccal views of A.M.N.H. No. 26288, a very large right lower cheek tooth; Ulan Shireh beds

"Large creodonts of the Mesonychidae-Mesonychinae; M_2 with very large protoconid, strongly reduced paraconid, deep groove in the anterior slope of the protoconid, almost without metaconid; lower molars of almost equal length; a high isolated protocone is assumed for the upper molars" (Dehm and Oettingen-Spielberg, 1958, p. 11). Configuration of the protocone is inferred from wear patterns of the lower molars; no upper teeth are known.

Gandakasia potens Dehm and Oettingen-Spielberg, 1958

TYPE: S.M. No. II.4, left lower jaw with one-half of M_1, a complete M_2, and a presumably associated M_3.

HORIZON AND LOCALITY: Middle Eocene beds of the lower Chharat Series in northwest Pakistan; Ganda Kas north of Basal, Pakistan, locality 18.

DIAGNOSIS: Only known species of the genus.

REMARKS: Additional material includes a right P_4 lacking the anterior third, scraps of three other premolars, and fragments of lower jaw.

Pilgrim (1940) described some mesonychid material (unallocated) from the lower Khirthar beds of Pakistan, a presumed correlate of the *Planorbis* fresh-water beds of the lower Chharat Series. A left maxilla with roots of P^4–M^2 and a fragment of the innominate bone were found. Since these roots indicate a large protocone and size range near that of *Gandakasia*, and because the geologic correlation is nearly exact, Dehm and Oettingen-Spielberg suggest that these previously unallocated fragments may belong to their genus.

MEASUREMENTS (IN MM.): The measurements given in the original description for the type and associated material of *Gandakasia* are: estimated length of M_1, 29; width of M_1, 12; length of M_2, 38.0; width of M_2, 12.5; estimated length of M_3, 32; width of M_3, 11.6; worn height of M_2, 18.0; height of talonid of M_2, 7.5; height of talonid of M_3, 8; depth of jaw under M_1–M_2, 17; unworn height of P_4, 30; estimated length of P_4, not less than 35; width of P_4, 11.9.

In addition, from a comparison with mesonychid genera in which the length of M_2

and the length of the skull are known for the same individual, Dehm and Oettingen-Spielberg estimated a skull length of 47 cm. for *Gandakasia*. Among mesonychids, the size of individual teeth relative to that of the mandible and skull varies tremendously. Any extrapolation to skull size and thence to the size of the animal must be viewed with extreme caution.

ICHTHYOLESTES Dehm and Oettingen-Spielberg, 1958

TYPE: *Ichthyolestes pinfoldi* Dehm and Oettingen-Spielberg, 1958.

KNOWN DISTRIBUTION: Middle Eocene of southwestern Asia; lower Chharat Series of Pakistan.

DIAGNOSIS (TRANSLATED FROM ORIGINAL): "Middle sized creodonts of the Mesonychidae-Mesonychinae, last and next to last upper molar with pointed cone-shaped, isolated protocone; labial cusps on next to last molar nearly united; only a single labial cusp on the last molar: all labial cusps with sharp anterior and posterior borders; cingulum weakly developed" (Dehm and Oettingen-Spielberg, 1958, p. 15).

Ichthyolestes pinfoldi Dehm and Oettingen-Spielberg, 1958

TYPE: S.M. No. 1956 II.7, fragment of left upper jaw with an alveolus of M^1, a newly erupted M^2 missing, the labial border of, and an unerupted, M^3. No unambiguously associated material was found.

HORIZON AND LOCALITY: Middle Eocene beds of the lower Chharat Series in northwest Pakistan; Ganda Kas north of Basal, Pakistan, locality 21.

DIAGNOSIS: Only known species of the genus.

REMARKS: This material is morphologically quite distinct from all other known mesonychids. The distinguishing sharp protocone is so separated from the labial cusps that, on M^3, the angle between the lingual wall of the labial cusp and the labial wall of the protocone approaches 90 degrees. Dehm and Oettingen-Spielberg (1958, p. 16) concluded that "we are dealing here with a previously unknown sidebranch." They believed that the tooth structure is "suited less for cutting and crushing than for the retention of slippery prey, like fish."

MEASUREMENTS (IN MM.): The following measurements were given in the original description: length of M², 14.6; width of M², 13; length of M³, 13.5; width of M³, 13.2; height of protocone on M², 8.5; height of protocone on M³, 8.5; height of labial cusp on M³, 11.2; length of alveolus, M¹, 10; width of alveolus, M¹, 9; length of M¹–M³, approximately 40.

OLSENIA MATTHEW AND GRANGER, 1925

Plate 20, figure 1; text figure 9

Matthew and Granger (1925) described a new genus from the "Shara Murun Eocene" of Mongolia on the basis of three astragali (type specimen of *Olsenia mira:* left and right astragalus, A.M.N.H. No. 20303). An upper premolar (A.M.N.H. No. 20319) " . . . of mesonychid type, recalling in its size and proportions the fourth premolar of *Dissacus* and *Pachyaena*" (p. 4), was also collected on the same stratigraphic level as *Olsenia*. We cannot find this rather important tooth in the collection.

It is unfortunate that a new genus was erected on the basis of the specimens listed above. The astragali could very easily belong to any of several genera discussed or newly described in this paper. Mesonychid foot bones are found rarely in comparison to the finding of teeth and jaws, and consequently differences among the feet of various species and genera are almost completely unknown. Future workers will do well to ignore the generic distinction of *Olsenia mira*, which may be considered a *nomen dubium*.

On plate 20 the left astragalus of *Olsenia mira* is illustrated, as well as the similar-sized left astragalus of *Pachyaena gigantea* and that of the smaller *P. ossifraga*. The truly significant differences of the astragalus of *Olsenia mira* from that of *Pachyaena gigantea* seem to be the deeper tibial trochlea, a much longer and pronouncedly more concave astragalocalcaneal facet, a very noticeable dorsoventral flattening of the posterior half of the medial portion of the bone between the tibial trochlea and the astragalocalcaneal facet, and the lack of the astragalar foramen.

The deepened tibial trochlea and the lost astragalar foramen point to a more cursorial mesonychid than does the plantigrade or semiplantigrade astragalus of *Pachyaena gigantea*.

HAPALODECTINAE, NEW SUBFAMILY

INCLUDED GENERA: *Hapalodectes* Matthew, 1909.

KNOWN DISTRIBUTION: Early Eocene of North America and late Eocene of Asia.

DIAGNOSIS (BASED ON *Hapalodectes*): Small mesonychids with lower cheek teeth highly compressed, transformed into trenchant blades; a vestigial metaconid may or may not be present on lingual wall of protoconid. Second upper molar with hypocone subequal to protocone; M³ small but metacone not vestigial.

HAPALODECTES MATTHEW, 1909

Text figure 10

TYPE: *?Dissacus* (*Pachyaena*) *leptognathus* Osborn and Wortman, 1892.
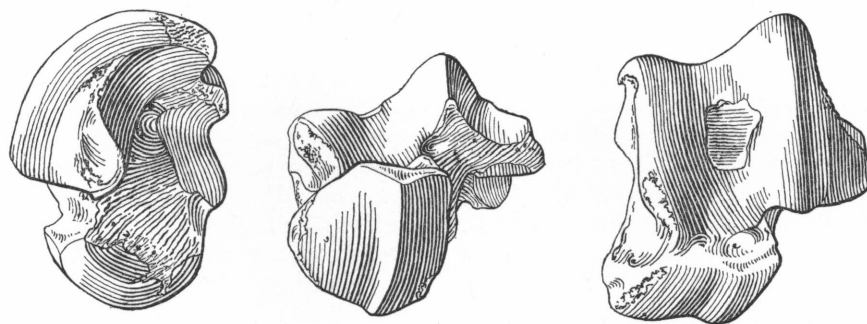
INCLUDED SPECIES: *Hapalodectes lepto-*

FIG. 9. Lateral, distal, and dorsal views of the left astragalus of *Olsenia mira*, type (A.M.N.H. No. 20303). From Matthew and Granger (1925a, fig. 3). ×0.7.

gnathus (Osborn and Wortman, 1892); *H. compressus* Matthew (1909); *H. serus* Matthew and Granger (1925b). (*Hapalodectes auctus* is not a mesonychid.)

KNOWN DISTRIBUTION: Same as for subfamily.

DIAGNOSIS: Same as for subfamily.

Hapalodectes serus Matthew and Granger, 1925b

Text figure 10

TYPE: A.M.N.H. No. 20172, lower cheek tooth, molar or posterior premolar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Irdin Manha beds around Telegraph Line Camp of the 1923 Central Asiatic Expedition of the American Museum of Natural History, Inner Mongolia.

DISCUSSION: In 1892, Osborn and Wortman considered the newly described species, *Dissacus leptognathus*, from Wasatch beds, a *Dissacus-Pachyaena* intergrade and expressed this opinion by referring to the species as *?Dissacus (Pachyaena) leptognathus*. (The type of this species, A.M.N.H. No. 78, most of the right mandible, contained P_4, a broken M_1, and the well-preserved M_2.) Matthew in his 1909 monograph erected the genus, based on the latter species (not noting Wortman's junior authorship). In the same monograph he also described a new species from the Wind River Formation, *Hapalodectes compressus*, based on a left lower jaw (A.M.N.H. No. 12781). The species from

Mongolia was characterized by Matthew and Granger (1925b, p. 3) as follows: "Cusps high and sharply compressed, the principal cusp (protoncoid) showing no trace of metaconid; the heel large, sharply crested in the characteristic mesonychid style, a minute anterior basal cusp (paraconid). Length of tooth 5.6 millimeters, smaller than either of the described American species."

"*?Hapalodectes auctus*" described on the basis of an upper molar by Matthew and Granger (1925b) from the same beds in which *H. serus* was found is not a mesonychid as its authors had already suspected. Van Valen (1966) has erected a new didymaconid genus based on the specimen.

It seems unlikely that the somewhat more slender jaw and supposedly more slender teeth of *H. compressus* are specifically different from those of *H. leptognathus*. It is difficult to refer the single type tooth from Mongolia (A.M.N.H. No. 20172) to a species different from that (or those) found in the lower Eocene beds of North America.

The absence of a vestigial metaconid on the type of *H. serus* is not convincing evidence of its specific distinction. Owing to the great similarity of the serial lower cheek teeth of *Hapalodectes*, the type specimen of *H. serus* cannot be homologized with certainty, hence its proper allocation is accordingly difficult. Its size difference from the American species seems insignificant, despite the remark of Matthew and Granger that *H. serus* is " . . . smaller than either of the de-
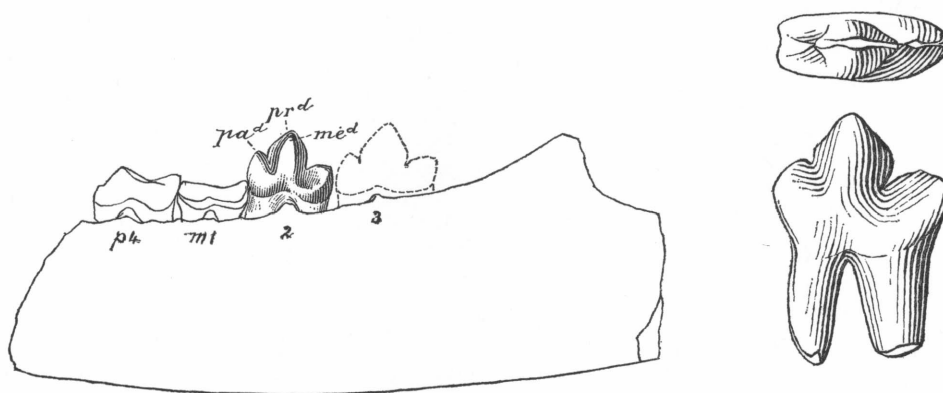

FIG. 10. *Left: Hapalodectes leptognathus*, type (A.M.N.H. No. 78). From Osborn and Wortman (1892, fig. 10). ×2. *Right: Hapalodectes serus*, type (A.M.N.H. No. 20172). From Matthew and Granger (1925b, fig. 1). ×4.1.

scribed American species." On the other hand, because of the meager sample of the Mongolian species and because of the uncertain transcontinental correlation between North America and Asia, *H. serus* cannot be synonymized with an American taxon.

The only upper teeth known of *Hapalodectes* are described by Guthrie (MS) from the Lysite member of the Wind River Formation of Wyoming. The second upper molar of one of the specimens of *Hapalodectes* figured by Guthrie shows a hypocone subequal and posterior to the protocone. *Hapalodectes* is, at present, the only known genus of the Mesonychidae that has a hypocone.

ANDREWSARCHINAE, NEW SUBFAMILY

INCLUDED GENUS: *Andrewsarchus* Osborn, 1924.

KNOWN DISTRIBUTION: Late Eocene of Asia.

DIAGNOSIS (BASED ON *Andrewsarchus*): Large mesonychids with complete placental tooth formula; upper incisors arranged in semicircle in front of canines; second upper incisor enlarged almost to same size as canine, second and third premolars elongate, single-cusped, deceptively entelodont-like; P⁴ uniquely premolariform in having only one very large cusp, presumably the paracone; protocone is merely vestigial on this tooth. Muzzle greatly elongate; sagittal crest much reduced compared to presumably ancestral mesonychine condition.

ANDREWSARCHUS OSBORN, 1924

TYPE: *Andrewsarchus mongoliensis* Osborn, 1924.

KNOWN DISTRIBUTION: Same as for subfamily.

DIAGNOSIS: Same as for subfamily.

Andrewsarchus mongoliensis Osborn, 1924

Table 6

TYPE: A.M.N.H. No. 20135, slightly crushed skull with right I¹, I², P³, M¹, M², M³, and left P², P³, P⁴, M¹, M² preserved.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Irdin Manha beds around Telegraph Line Camp of the 1923 Central Asiatic Expedition of the American Museum of Natural History (2 miles north of the line, according to the field notes, which are available for inspection in the American Museum), Inner Mongolia.

DIAGNOSIS: Only known species of the genus.

DENTITION: In Osborn's (1924) paper the description of the dentition is somewhat less than adequate. His description is in telegraph style and does not mention all observable details. For this reason, as well as for the sake of a more coherent picture of the Asiatic genera of mesonychids, the upper dentition and the palate are redescribed in as much detail as the preservation of the type specimen permits.

The long and narrow hard palate is slightly more constricted than in life at the level of P² and P³ because of postmortem crushing. The incisors are placed in a semicircular configuration in front of the canines, a feature characteristic also of entelodonts. The first and second upper incisors are relatively small, but the large I² is only slightly smaller than the canines (the size of the latter is inferred from the diameter of the alveoli). Osborn claimed that the canines were (p. 3) " . . . of enormous size." They are not. The canines are very reduced in size in proportion to the whole dentition and to the whole skull. Both *Mongolonyx dolichognathus* and *Mongolestes hadrodens*, with skulls approximately half of the size of the cranium of *Andrewsarchus mongoliensis*, had upper canines almost as large as those of the last-named species. The first premolar, judged from the size of the alveolus, was single-rooted and about the size of the I³. P² is single-cusped; the crown is shaped like an anteroposteriorly constricted cone, resting on widely spread and firmly anchoring double roots. Each of the roots is thickened midway between its extremity and the crown. The third premolar is a much wider tooth; its crown, although relatively wider, is not unlike that of P². The crown of P³ culminates in an apex on the anterior half of the tooth. The posterior root splits to give rise to a third root (the only known mesonychid P³ with three roots) more lingual than the one it separated from. As in P², the roots are thick but widely spread and separate immediately under the crowns. There is no tendency in *A. mongoliensis* for the roots to be confluent and to have a dentine platform under the crowns, an adaptive feature to pro-

long the functional life of the tooth after the abrasion of the crown in some species of mesonychids which probably lived on very hard food (e.g., bone). On P⁴ the paracone dominates the entire surface of the crown. Approximately one-third of this cusp is worn down to an even, horizontal surface. The protocone is only a very small lingual vestige. The enamel is wrinkled, and there is a slight buccal cingulum. M¹ is the smallest of the molars; its orientation is peculiar. The tooth seems to have been, figuratively speaking, twisted anteriorly, the portion bearing the protocone being more anterior than is usually seen in mesonychid molars. The first molars reflect the same condition on both sides of the skull. The crown of this unusually seated tooth is totally worn off; the resulting wear facet is more or less horizontal. The second molar is the widest cheek tooth. It is heavily worn, but its wear facet differs significantly from that of M¹. Transversely from the buccal border of the second molar, the wear becomes more and more extensive lingually. This sloping wear pattern results in the complete wear of the crown of the type specimen inferior to the lingual root, while the buccal portion of the tooth is worn, but not so extensively as the lingual portion. The third molar is relatively unworn. The

TABLE 6

MEASUREMENTS (TO THE NEAREST MILLIMETER) OF THE UPPER DENTITION OF *Andrewsarchus mongoliensis* (A.M.N.H. No. 20135)

	Length	Width
Right I¹	18	24
Right I²	32	26
Alveolus for I³	24	—
Alveolus for C	45	37
Right P¹	21	17
Left P²	43	23
Right P³	57	27
Right P⁴	42	40
Left M¹	34	45
Left M²	44	62
Right M³	47	66
P⁴–M¹	90	—
P⁴–M²	130	—
P⁴–M³	170	—
M¹–M³	120	—
M²–M³	98	—

wrinkled crown, although most probably a secondary acquistion, is reminiscent of that of some condylarths (also of suids and other omnivorous forms). The apices of the protocone and paracone are worn, but not so as to obscure the crown. The paracone is only slightly larger than the protocone, but the metacone is only a vestigial nubbin. The last molar, which bears confluent anterior and buccal cingula, is characteristically rounded off at its posterobuccal corner.

CONVERGENT FEATURES OF *Andrewsarchus* AND ENTELODONTS

Osborn (1924) briefly referred to the convergent features of *Andrewsarchus* and entelodonts. He pointed out that the cranial and facial proportions in the giant mesonychid are strikingly similar to those of *Entelodon* and *Dinohyus* (p. 1) " . . . doubtless because of similar omnivorous feeding habits." In addition to Osborn's remarks, it is of interest here to point out some additional similarities of and differences between *Andrewsarchus* and entelodonts that can be inferred from the skull. The portion of the muzzle anterior to the canines is very similar. Both in entelodonts and in *Andrewsarchus* the incisors are arranged in the premaxilla in a semicircular pattern. The P¹ is usually double rooted in entelodonts but single rooted in *Andrewsarchus* and the known mesonychids. The second and third upper premolars of *Andrewsarchus*, were they known only as isolated teeth, would certainly be allocated to the Entelodontidae. Both in *Andrewsarchus* and entelodonts the first and second upper molars are much more heavily worn than either P⁴ or M³.

Andrewsarchus is probably the most aberrant genus in the family Mesonychidae. As is strongly suggested above, its feeding mechanism was much more entelodont than mesonychid-like. Below, we briefly point out the cranial characters of *Andrewsarchus* that diverge from those of the rest of the Mesonychidae. The sagittal crest (and very probably the temporalis muscle) are much reduced and the glenoid fossa is more flattened, with a less-developed preglenoid process and postglenoid process. These characters alone, since we lack any knowledge about the mandible, might indicate a weakened bite in *Andrewsar-*

chus, as compared to the majority of mesony-chids. The heavily wrinkled crowns of the cheek teeth suggest an ominvorous diet also. The functional significance of the reduced canine and enlarged I^2 is not clear. It can mean either a reduction of the canine function or a shift anteriorly of the area of caninization. These two explanations appear to be mutually exclusive, but they may not be.

Osborn (1924) reconstructed height and other size measurements of *Andrewsarchus*, based on the proportions of *Mesonyx*. Such a conjecture seems unjustified, since the entelodont-like mesonychid giant is certainly very different from other mesonychids in habitus and consequently probably also unlike in body proportions. If a size estimate must be made of *Andrewsarchus*, then body proportions of entelododonts would be more profitable to follow than those of other mesonychids.

SYNOPTIC CLASSIFICATION OF THE SUPERFAMILY MESONYCHOIDEA OSBORN, 1910

Order Condylarthra Cope, 1881
 Superfamily Mesonychoidea Osborn, 1910
  Family Mesonychidae Cope, 1875
   Subfamily Mesonychinae Wortman, 1901
    Dissacus Cope, 1881
    Pachyaena Cope, 1874
    Synoplotherium Cope, 1872 (= *Dromocyon* Marsh, 1876)
    Mesonyx Cope, 1872
    Harpagolestes Wortman, 1901
    Hessolestes Peterson, 1931
    Mongolonyx, new genus
    Mongolestes, new genus
   ?Subfamily Mesonychinae
    Gandakasia Dehm and Oettingen-Spielberg, 1958
    Ichthyolestes Dehm and Oettingen-Spielberg, 1958
   Subfamily Hapalodectinae, new subfamily
    Hapalodectes Matthew, 1909
   Subfamily Andrewsarchinae, new subfamily
    Andrewsarchus Osborn, 1924
 ?Superfamily Mesonychoidea, incertae sedis[1]
    Microclaenodon Scott, 1892

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[1] Van Valen (1966) considered *Apterodon* a mesonychid. The senior author, after having thoroughly examined and compared the excellent specimens of skulls and dentition of this genus from the Fayum of Egypt, has no reasonable doubts left that *Apterodon* is a hyaenodontid and not a mesonychid.

UNALLOCATED ASIATIC MESONYCHIDAE

Plate 21; table 7

Collecting around the Telegraph Line Camp of the Central Asiatic Expedition in 1923 yielded relatively abundant mesonychid fossils. In addition to *Andrewsarchus* and *Hapalodectes* there are, in our estimation, at least three more species of mesonychids represented by isolated teeth from an area of a few square miles surrounding Telegraph Line Camp. All these specimens are supposedly from the Irdin Manha beds.

Five teeth are labeled and catalogued under A.M.N.H. No. 20132. Matthew and Granger (1925b, p. 1) reported the following on the five specimens united under the above number: "Mesonychid, gen. indet. One species, No. 20132, is of about the size of *Harpagolestes uintensis* of the Uinta, but we are unable to determine the molar formula and it cannot be even provisionally assigned to any genus." The teeth in this sample are as follows: A slightly worn left P_2 (A.M.N.H. No. 20132D) and a right ?P_3 (A.M.N.H. No. 20132E). The second lower premolar is not worn and displays a tall, posteriorly leaning protoconid. ?P_3 is badly worn, but the incipient character of the tiny paraconid is recognizable. One of the three upper molars of A.M.N.H. No. 20132 is a well-worn right, possibly first, molar (A.M.N.H. No. 20132A), somewhat reminiscent of *Harpagolestes*. The protocone is broken off; the metacone is about half of the size of the connate paracone. The remaining two upper cheek teeth (A.M.N.H. Nos. 20132B and 20132C) undoubtedly belonged to the same species and likely to the same individual animal. The two teeth are P^4 and M^1 from the left side, neither showing any signs of wear, although the extremely narrow root canals indicate an adult individual. The cutting ridges characterizing *Pachyaena* are present, but cingula are missing. On the P^4 (A.M.N.H. No. 20132B) the cusps anterior and posterior to the large paracone are small and equal in size. The protocone has the accentuated cutting edges of *Pachyaena*, one on the buccally facing slope and the other on the posterior slope of the protocone. The M^1 (A.M.N.H. No. 20132C), with a larger metacone and a paracone less tall than those

of the P⁴, has cutting ridges (in addition to those found on the protocone) on both the paracone and metacone.

A very large broken P⁴ (A.M.N.H. No. 20131) was also collected from the Irdin Manha beds surrounding Telegraph Line Camp. The broken tooth displays striking *Pachyaena*-like features. A ridge runs antero-posteriorly on the tall paracone (the paracone is approximately 20 mm. high), and an unmistakable posterior cingulum is evident posterior to the incipient metacone. The enamel of the tooth is completely smooth, unlike that of *Andrewsarchus;* hence the specimen cannot be allocated to that genus. The broken P⁴ is at least twice as large as A.M.N.H. Nos. 20132B and 20132C, and it also bears a cingulum which the latter lack; hence on the basis of dental characters it cannot be either conspecific or congeneric with *Andrewsarchus*.

Three more teeth are catalogued under A.M.N.H. No. 20133 from the Telegraph Line Camp area. Matthew and Granger (1925b, p. 1) commented on them as follows: "Mesonychid, gen. indet. A second, smaller species, about the size of *Synoplotherium lanius*, is likewise represented by isolated teeth, No. 20133, and cannot be placed in any one of the mesonychid genera." The two upper teeth A.M.H.H. Nos. 20133B and 20133C are close to those of either *Mesonyx* or *Dissacus*. A.M.N.H. No. 20133B is probably a right M¹ or P⁴ with a large paracone. The anterolabial portion of A.M.N.H. No. 20133C (RM²) is broken, and the roots are missing. A.M.N.H. No. 20133A is an unusually long, slightly worn M₁ or P₄. The tiny lingual bump on the protoconid is a vestige of the metaconid (this feature does not necessarily mean that the specimen should be allocated to *Pachyaena*; specimens of *Dissacus* may have a reduced metaconid). The trenchant heel of the tooth is as long as the total length of the paraconid and protoconid. The protoconid is only slightly higher than the highest point on the talonid. The roots split almost immediately under the enamel line, the posterior root being triangular in its medial and lateral aspects. Although this tooth may be of a highly carnivorous mesonychid, the possibility that it is a milk tooth cannot be dismissed.

In addition to the two skulls of *?Harpago-* *lestes orientalis*, several specimens are known from the Ulan Shireh beds at Chimney Butte, North Mesa, Shara Murun region. A.M.H.N. No. 26288 is an exceptionally large, badly worn right lower cheek tooth, wider although not longer than most other known mesonychid lower premolars or molars. The roots are long and massive; the length of the anterior root from the lower limit of the enamel to the tip of the root is well over 50 mm. The inferior third of the roots is covered with bony protuberances and thickenings, a likely adaptation for strengthening the tooth in the mandible.

There are two more small mesonychid teeth (considerably smaller than those of *?Harpagolestes orientalis*) from Chimney Butte. The somewhat broken upper molar (A.M.N.H. No. 26303A) almost certainly belonged to the same species as did A.M.N.H. No. 20133C from the Irdin Manha beds (close to either *Dissacus* or *Mesonyx*). The very badly fractured lower cheek tooth (A.M.N.H. No. 26303B) also probably belonged to the same species as the upper molar.

Three upper cheek teeth from the beds correlated with the Ulan Gochu Formation at Twin Obo, East Mesa, Shara Murun region, do not belong to *Mongolestes hadrodens*. The three separate teeth (A.M.N.H. No. 26267)

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF
TEETH OF UNALLOCATED ASIATIC
MESONYCHID SPECIMENS

	Length	Width
"Irdin Manha" Beds		
A.M.N.H. No. 20132A, upper	26.2	—
A.M.N.H. No. 20132B, upper	24.9	25.4
A.M.N.H. No. 20132C, upper	27.4	25.7
A.M.N.H. No. 20132D, lower	15.7	8.0
A.M.N.H. No. 20132E, lower	22.0	13.5
A.M.N.H. No. 20133A, lower	24.5	8.5
A.M.N.H. No. 20133B, upper	18.0	15.1
A.M.N.H. No. 20133C, upper	—	14.1
Ulan Shireh Formation		
A.M.N.H. No. 26288, lower	38.5	20.0
A.M.N.H. No. 26303, upper	15.7	15.0
Ulan Gochu Formation		
A.M.N.H. No. 26267A, upper	22.0	23.0
A.M.N.H. No. 26267B, upper	26.4	24.6
A.M.N.H. No. 26267C, upper	18.8	23.4

represent the same species. A.M.N.H. No. 26267A is a completely worn left molar (?M¹). The largest of the three teeth (A.M.N.H. No. 26267B) is highly unusual in having the protocone lingual to the cusp preceding the paracone. On all the known mesonychid cheek teeth that we examined the protocone is invariably lingual (not anterolingual or posterolingual) to the paracone. The protocone is heavily worn anterobucally,

and this wear facet is confluent with the anterolingual wear of the cusp anterior to the paracone (?parastyle). The remaining M² (A.M.N.H. No. 26267C) is of the same type as the homologous tooth of *Harpagolestes*. The molar is much wider than long, with a paracone only slightly larger than the protocone. The preparacone and postparacone area is small. In conclusion, A.M.N.H. No. 26267 may be allocated to cf. *Harpagolestes*.

ADDENDUM

While this paper was in press, three new species of mesonychids were reported by Chow (1965) from the Honan Eocene of China.

Chow based the new genus *Honanodon* on *Honanodon hebetis* from the Yuanchü Formation (lower fossil zone, upper part of Upper Eocene). This species is very poorly known, more so than many of the unallocated specimens described and illustrated in the present paper. The type consists of an upper tooth and less than half of a lower one. An additional lower tooth is figured with the type specimen, but there is no reference to it in the text.

Honanodon macrodontus is described from the Lushi Formation (lower Upper Eocene) based on a single isolated upper tooth. If the illustration of the type specimen is accurate, then the figure given for the length of the tooth corresponds to the width, and vice versa.

The type upper teeth of *H. hebetis* and *H. macrodontus* are identified by Chow as both representing ?M². Both teeth, however, are probably P⁴'s and not molars. It is possi-

ble that the specimens are molar teeth, in which case they would seem to represent a possibly *Pachyaena*-derived genus in which the cingula were completely lost and the reduced metacone characteristic of *Pachyaena* progressed to an extreme condition, not seen among any mesonychid known previously to *Honanodon*. It seems more probable, however, that the upper teeth figured represent *Harpagolestes*- or *Mongolestes*-like P⁴'s. The protocone is relatively more anterior to the paracone of P⁴ of *Mesonyx* than on the upper teeth described by Chow. If the two upper teeth are homologous, whatever their correct homology may be, then Chow is probably correct in placing both species in the same genus.

The third new mesonychid described was *Hapalodectes lushiensis* from the same locality as *Honanodon macrodontus*. *Hapalodectes lushiensis* is certainly a hapalodectine, and, if the line drawing of the type ?M₃, the only referred specimen, is accurate, then this species warrants generic separation from the North American and Mongolian *Hapalodectes*.

ADAPTATIONS IN MESONYCHIDS

FEEDING ADAPTATIONS

IT HAS BEEN MORE OR LESS accepted fact in the literature dealing with mesonychids that the mandibular musculature of these mammals was weak. Boule (1903) and Matthew (*in* Matthew and Granger, 1915), among others, referred to various genera of mesonychids in general as weak jawed, weakly biting, and so on, independently stating that mesonychids could hardly crush bones as a staple diet. Matthew (*in* Matthew and Granger, 1915, p. 85) wrote about the diet of these animals: "The mesonychid teeth may perhaps have been adapted to crushing freshwater mollusks or some similar food that could involve a great deal of the cusps without entailing any great strength of jaw. They certainly are not suited either for bone crushing or flesh cutting, nor do they appear suitable for omnivorous or frugivorous habits; they are neither pig-like nor bear-like, and the hoof-like claws are not consonant with digging nor the snout with rooting habits."

It is most unlikely that among the impressive variety of mesonychids, from the *Hapalodectes*-sized species to the giant *Andrewsarchus*, the same type of food procuring or the same diet prevailed. If we consider features such as the strength and depth of the mandible in many genera, the solid symphysis, the powerful mandibular condyles to resist the stresses of a powerful bite, the enormous sagittal crest, it is almost imperative to conclude that, in general, mesonychids possessed a very strong mandibular musculature. The opinions of previous workers, that mesonychids had a weak jaw musculature, were based on the deceptive shallowness of the masseteric fossa. Disregard for the other more important features depicting the strength of the bite, such as those listed above, resulted in the serious misconception of the mesonychid feeding mechanism.[1] The zygomaticomandibularis muscle, originating from the internal surface of the zygomatic arch, occupied the masseteric fossa. Although this muscle is well developed in the

[1] In a separate paper (in preparation), the senior author will treat the jaw mechanics and dental adaptations involved in the mesonychid feeding mechanism.

Carnivora, it can be correlated with an increase in the lateral shift of the mandible (Sicher, 1944) rather than with the absolute strength of the bite. The presence of a very large and consequently very powerful temporalis muscle (which inserted farther forward on the mandible than does that of fissiped carnivores), the primary factor in a strong bite, can be inferred from the exceptionally high sagittal crests (except in *Andrewsarchus*). The strong and thick posterior border of the hard palate and the inflected angle of the mesonychid mandible strongly suggest an unusually large internal pterygoid. The above-cited examples seem sufficient to indicate the presence of powerful jaw musculature and a strong bite in the majority of known mesonychid species.

The mesonychid dental characters are present in the earliest known genus, *Dissacus*, from the Torrejonian of North America. The major changes (which are not many) from the *Dissacus*-level involve the gradual reduction of the metaconid, accentuation of various cingula on the upper cheek teeth (e.g., *Pachyaena*), development of a large hypocone in *Hapalodectes*, the premolarization of the lower molars, and the molarization of the last upper premolar. In many genera the ability of cheek teeth to endure excessive wear on their roots after the crowns have been abraded off is remarkable. The earliest mesonychids must have been carnivorous mammals: the premolarized lower molars and the trenchant talonids did not evolve for crushing and heavy wear alone. Notwithstanding, the ability to endure excessive wear by having solid and closely packed roots below the fairly brachyodont teeth was a crucial adaptive feature in many genera.

Although Matthew called the mesonychids Acreodi, since they lacked any kind of apparent carnassial function, we believe that many genera have evolved a morphogenetic field primarily concerned with powerful crushing and chewing. More than one line of evidence points to this belief. The area of concentrated usage of the tooth row has slightly fluctuated in the family, probably according to the length of the tooth row. It

did not depend on any particular occlusal pair as carnassial function did in oxyaenids, hyaenodontids, or fissiped carnivores. The presence or absence of M^3 may have had an effect on the shifting of the area of most intense crushing function. The determining factor of the area of most effective crushing was probably the greatest torque that could be developed on a particular tooth in the lower jaw. The slightly worn dentition of various species provides the first line of evidence for special bone-crushing adaptations. In *Dissacus saurognathus* (A.M.N.H. No. 2454) the second and first lower molars are the most heavily worn teeth, while premolars of the same mandible show relatively little wear. In *Mongolonyx dolichognathus* (A.M.N.H. No. 26661) and *Harpagolestes uintensis* the first lower molar is the most heavily worn tooth. In *Mongolestes hadrodens* M_1 is the longest cheek tooth, and considerably worn down, while the preceding teeth have wear only on the posterosuperior surfaces of the large protoconids (see pl. 11).

It can be observed that on skulls (those of *?Harpagolestes orientalis*) or well-preserved maxillae (such as the maxilla of *Mongolonyx*) the P^4 and M^1 invariably extend farther down than any of the other upper cheek teeth. These P^4's and M^1's are also usually more worn than the remaining teeth.

The right ramus of *Mongolestes hadrodens* (A.M.N.H. No. 26064) is uncrushed, and it well shows the strongly arcuate tooth row. The dental arc is similar in the well-known species of *Harpagolestes*. The arcuate lower dentition and the "sagging" posterior cheek teeth obviously complement each other's function. In genera such as *Harpagolestes* and *Mongolestes* the proposed mortar-pestle relationship of the lower and upper teeth (the "crushers" M_1 or M_2 or both; P^4 and M^1) was augmented, as noted above, by the arcuate lower tooth row. A large and heavy bone would fit easily into the space between M_1 and M_2. The high and massive posteriorly leaning protoconids would prevent the slipping of the bone forward while the upper "crushers" were breaking it up into digestible pieces.[1] Several genera, such as *Synoplo-*

therium, *Harpagolestes*, and *Mongolestes*, may have been specialized carrion feeders, the excessive wear exhibited on the teeth of these forms being due to a staple diet of marrow-rich long bones. Mention must be made of the large and apparently functional canines and incisors in relation to the carrion-feeding habitus. The usually broad anterior region of the muzzle, the heavily worn incisors, could probably actively tear off and crack bones (e.g., snap off ribs to be chewed) of a decaying carcass. The very vertical-oblique symphysis of *Mongolestes* is probably an adaptation to strengthen the anterior region of the muzzle. Without our attempting an exhaustive explanation of adaptation to a very hard diet, it must be repeated that not all genera were omnivores or carrion feeders.

In *Dissacus*, *Mesonyx*, or *Hapalodectes* (all of which can be regarded as carnivorous along with several other species) the features noted in the above discussion are not accentuated. The long and slender lower teeth of *Hapalodectes* are certainly those of a carnivorous mammal. Its active predatory mode of feeding, to our knowledge, has never been questioned.

Wear facets which can be regarded as shear facets are present on both the upper and lower molars of *Mesonyx* and *Pachyaena gracilis* and on the only lower cheek tooth of *Hapalodectes serus*. In text figure 11 an attempt is made to illustrate schematically these various facets found on several specimens of the taxa noted in this paragraph. Specimens that illustrate shearing between the cheek teeth are very few, and the facets are highly variable among individual teeth. In general, very inefficient shearing took place between the lingual slopes of the paracone and metacone and the labial wall of the talonids and the paraconids of the following tooth. Occasionally there is detectable shear on the anterolingual slope of the paracone against the posterolabial wall of the protoconid. On some rare specimens there are paired shear facets on the labial wall of the protoconid caused by the paracone and meta-

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[1] The teeth in a lower jaw of *Hyaena* [A.M.N.H.(M.) No. 20810] are completely worn down; the exposed pulp cavity is covered with secondary dentine formed in the

lifetime of the animal. The pattern of the excessive wear on the lower cheek teeth of this carrion-feeding fissiped, with the exception of M_1, is strikingly similar to the wear patterns seen on heavily worn mesonychid teeth.

cone of an upper tooth. It is doubtful that shear between upper and lower molars of mesonychids played an important part in mastication, with the possible exception of *Hapalodectes*.
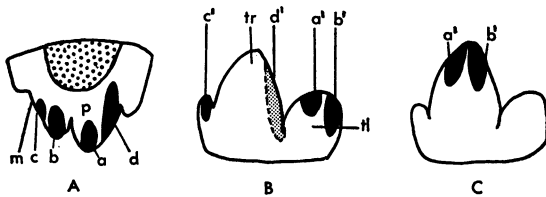

FIG. 11. Schema of shear facets of mesonychid cheek teeth. A. Upper molar, lingual view. B. Lower molar, labial view. C. Lower molar, labial view. The heavily stippled area in A represents the plane where the protocone bearing the lingual half of the upper tooth was cut off for a clear exposure of the lingual shear facets on the paracone and metacone. The shear facets are labeled a, a', b, b', c, c', and d, d'. The lightly stippled area (d') is inferred from the corresponding heavy wear (d) of several upper teeth. The letters p, m, tr, and tl indicate the paracone, metacone, trigonid, and talonid, respectively.

The roots of the lower teeth in *Hapalodectes* have a tendency to part immediately under the crown, in contrast to the teeth of the genera exhibiting habitual heavy wear. The latter maintain a thick dentine layer below the enamel-covered portion of the crown, undoubtedly for prolonged wear after the abrading of the enamel-covered crown (see pl. 21, figs. 13, 14; A.M.N.H. No. 26288). Lack of the latter adaptation in a mesonychid species may mean adaptation to a softer diet than that of the suggested bone-crushing species.

The possible significance of the length/width ratios of lower cheek teeth to differentiate carnivorous species from omnivorous ones occurred to the senior author, and consequent observations and ratio comparisons of homologous teeth of species that show excessive wear to those that do not confirmed his belief that, in general, relatively wider teeth may indicate a less carnivorous adaptation in the dentition.

A quantitative treatment of the data by the junior author is presented below. It may be appropriate to note here the relative size differences of teeth to the size of the mandible in various species. The size of the mandible of *Dissacus saurognathus* and *Mongolestes hadrodens* is roughly the same, although the cheek teeth of the latter genus are strikingly larger. This variation of proportion between teeth and mandible (also the skull) should greatly caution anyone against extrapolating to the size of a mesonychid known either from isolated teeth or jaw fragments.

When only the lower jaw of a mesonychid is known, wear on the whole surface of M_3 will be indicative of the presence of M^3. On the other hand, as Matthew noted (1909, p. 492), referring to *Mesonyx* and *Harpagolestes*, little wear or absence of it on the third lower molar will be due to the absence of M^3 (providing, of course, that the specimen in question shows heavy wear on the teeth preceding M_3).

LOCOMOTOR ADAPTATIONS

The new Asiatic material described in this paper supplies us with very little evidence pertaining to locomotory adaptations of the family. The manus and pes of early mesonychids were, according to Matthew (1909, p. 486), " . . . tetradactyl, the first digit a vestigial nodule. In *Dissacus saurognathus* they were probably pentadactyl; the hallux, in any event, was complete, but of reduced size; the manus, as articulated by Osborn and Earle, is pentadactyl with large mc. I and mc. V much reduced. This construction, if correct, would preclude our regarding this species as ancestral to the later Mesonychidae, and would be a very exceptional character. In *D. navajovius* the digits are unknown, but the foot was evidently much more slender and compressed, to judge from the characters of the tarsals." As Matthew (1909) pointed out, the deeply fissured ungual phalanges are more similar to those of the Condylarthra than to those of the Carnivora.

CORRELATION OF SIZE AND SHAPE IN MESONYCHID LOWER CHEEK TEETH

In an assessment of the probable mode of feeding for the various mesonychid genera, considerations of absolute size might be important, for members of the family, which range from tiny *Hapalodectes* to large *Andrewsarchus*, display the greatest range in size of

any mammalian group of known or probable predatory habits. Thus, while smaller forms seem to have been active cursorial predators, the sheer bulk of *Andrewsarchus* and some of the other giants probably precluded such a mode of life.

Variations in the length/width ratio of lower cheek teeth might serve as an index for inferences regarding feeding habits. A decreasing ratio with increasing size may indicate change of adaptive level, as the long, sharp cheek tooth of an active carnivore is transformed to the broad, blunt, crushing tooth of an omnivore or carrion feeder.

We therefore made measurements, and gathered information from the literature, on the lower cheek teeth of as many mesonychid species as possible. We took 53 of the 60 pairs of measurements; the remaining seven are

from Matthew (1909), Matthew and Granger (1915), Peterson (1931), and Shikama (1943). Data sufficient for significant results were compiled for P_3–M_2 and are presented in table 8. The data can be sorted rather neatly into three classes of tooth size. The first group, containing only *Hapalodectes*, is sharply set off from the remaining two in comprising teeth that rarely exceed one-third of the length of the smallest representative of the next group. The average length/width ratio is at a group maximum for each tooth measured, thus justifying the etymology of the generic name, the "slender biter," which was given by Matthew (1909, p. 498) "in allusion to the slender and highly compressed teeth." An active predatory mode of feeding has never been questioned.

The distinction in size between the teeth of
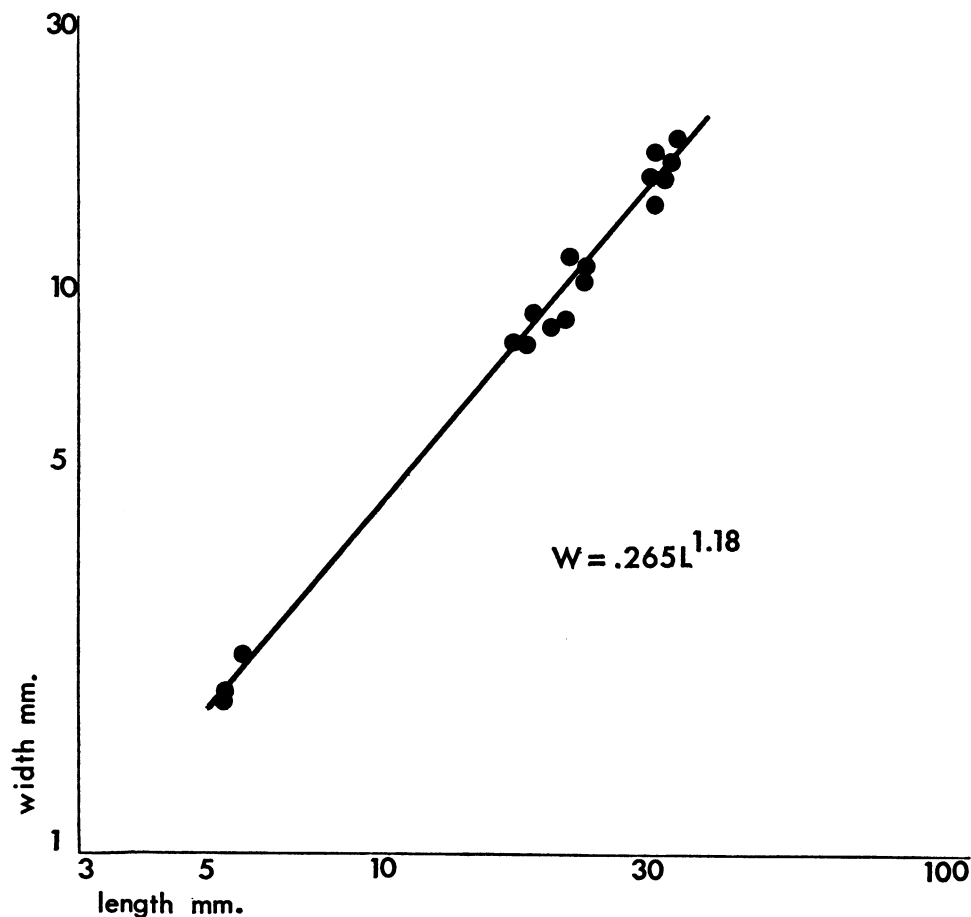

$$W = .265L^{1.18}$$

FIG. 12. Calculated reduced-major-axis fit for the correlation of length and width in M_2 of various mesonychid species. Note the natural division of measurements into three size classes. Log-log scales.

group 2 and those of group 3 is equally unam-
biguous, for with each tooth the gap in length
between the largest specimen of group 2 and
the smallest of group 3 is larger than the total
observed range of lengths within group 2 (see
text fig. 12).

Group 2 includes mesonychids of moderate
tooth size: *Dissacus saurognathus*, *Dissacus*
sp., *Pachyaena gracilis*, *Pachyaena ossifraga*,
Mesonyx spp., *Hessolestes ultimus*, and *"Har-
pagolestes" koreanicus*. As established from
data independent of dentition, these may
represent, for the most part, active cursorial
carnivores. The average length/width ratios
for the four teeth measured show a surprising
similarity, ranging from 2.21 for M_1 to 2.27
for P_3.

Data for large mesonychid teeth are gath-
ered in group 3 (*Mongolestes hadrodens*, *Mon-
golonyx dolichognathus*, *Pachyaena gigantea*,
Pachyaena ponderosa, *Harpagolestes uintensis*,
Harpagolestes immanis). Many of these forms
may have been carrion feeders or omnivores.
The average length/width ratios are consis-
tently the lowest among the three size groups,
ranging from 1.89 for P_4 to 2.03 for M_1.

Increasing relative tooth width is thus
strongly correlated with increase in tooth size
in mesonychids. Although we assume a gen-
eral correspondence between bulk and adap-
tive level, no causal inference is offered.
Adaptive increase in size might have necessi-
tated a shift away from active predation, but,
on the other hand, radiation into carrion
feeding or omnivore niches might have pro-
vided a primary impetus for bulk increase.

The observed change of tooth proportions
with tooth size could occur in two ways. At
one extreme, increments of length and width
are added in a constant ratio to each other,
and change in proportions is dependent upon
initial size. This mode of change in propor-
tions can be depicted as a linear regression
which does not pass through the origin. Add-
ing successive increments of 2 mm. in length
and 1 mm. in width to a 1-mm. cube, for
example, will rapidly result in a length/width
change in proportions from 1/1 to nearly 2/1.
(A regression constructed from increments of
two units to the x dimension for each one unit
to the y dimension, but passing through the
origin, maintains constant proportions.) Al-
ternatively, simple allometry may occur. If it

does, the arithmetic plot is curvilinear
(straight line in log-log plot, as in text fig. 12),
and change in proportions is effected largely
by the greater geometric increase of width
versus length.

The logarithmic correlation coefficient
(0.995) for M_2 is much higher than the arith-
metic (0.982), indicating, although not prov-
ing, that the simple allometry formula may be
preferable to a linear regression. The reduced-
major-axis fit (see Imbrie, 1956) gives values:

$$W = 0.265L^{1.18}.$$

The simple allometric formula actually
takes into account both modes of change in
proportions. The exponent (1.18) expresses
the geometric increase of width versus length,
whereas the coefficient (0.265) is complexly
related to initial tooth size at the onset of
allomorphosis. (The coefficient is not, as
many have held, a direct measure of inherent
or initial size. The statement that it equals
the value of y at an x value of one unit in the
measurement system employed should be
considered merely as a convenience for calcu-
lation, for the coefficient is part of a relation-
ship that is valid only over a certain interval
which, since units are generally chosen to be
much smaller than objects measured, usually
does not include an x of 1. Extrapolation of
the empirical allometric relationship to un-
observed sizes is unwarranted. In this case,
since no mesonychid is known, and it seems
unlikely that one ever existed, with an M_2
only 1 mm. in length, the statement that such
a hypothetical animal would have an M_2
0.265 mm. wide is unjustified.)

Thus, the combined effects of initial tooth
size and geometric increase of width versus
length produce a change in length/width
proportions from nearly 3/1 to less than 2/1
in the size interval over which the computed
allometric regression is valid.

Although the data presented in table 8 are
averages for teeth measured within a size
class, we note that further support for our
contention that a high length/width ratio
may indicate active predation is gained from
considering intraclass data. Thus, within size
group 2, the length/width ratio for *Dissacus
saurognathus* ranges from 1.94 for M_1 to 2.09
for P_3, whereas similar values for *Pachyaena
gracilis* run from 2.36 for M_1 to 2.68 for P_4,

and various teeth of *Mesonyx* exhibit length/width values of 2.15 to 2.42. *Dissacus saurognathus* was probably pentadactyl and plantigrade (Matthew, 1909) with short, stout, spreading feet (Wortman, 1901–1902, vol. 12,

p. 286), whereas *Mesonyx* and the smaller *Pachaena* species were tetradactyl, digitigrade, and "remarkably specialized for cursorial habits" (Scott, 1944, p. 216).

TABLE 8

CORRELATION OF RATIO OF LENGTH TO WIDTH WITH SIZE OF TOOTH (MEASUREMENTS IN
MILLIMETERS) IN MESONYCHID LOWER DENTITION

Size Class	P_3			P_4			M_1			M_2		
	OR_x	N	$\overline{L/W}$	OR_x	N	$\overline{L/W}$	OR_x	N	$\overline{L/W}$	OR_x	N	$\overline{L/W}$
1	—	0	—	5.9	2	3.10	4.8– 5.3	3	3.24	5.4– 5.9	3	2.72
2	15.9–17.9	5	2.27	17.1–21.1	7	2.24	17.9–20.8	6	2.21	17.6–24.0	8	2.25
3	25.0–32.8	6	1.94	26.7–37.5	7	1.89	29.2–40.0	7	2.03	30.8–35.0	6	1.99

N is the number of specimens.
OR_x is the observed range of lengths for teeth in a given size class.
$\overline{L/W}$ is the average length/width ratio for teeth in a given size class.

PHYLOGENY AND EVOLUTION OF THE MESONYCHOIDEA

MATTHEW, THE GREATEST STUDENT of creodonts, considered the mesonychids "a peculiar aberrant group of the Creodonta, apparently very early differentiated from the main stock" (1937, p. 89). According to Simpson (1945), the Mesonychoidea arose from an arctocyonid stock (the triisodontines) independently and at about the same time as the other two great carnivore groups (the superfamily Oxyaenoidea and the suborder Fissipeda). Van Valen (1966) included the Mesonychidae (and the Arctocyonidae) in the Condylarthra. His main argument for doing so stems from the triisodont origin of mesonychids (recognized by Matthew) and the consequent polyphyly of the Carnivora, at least at the subfamily level, if the mesonychids are retained in the latter order. We also believe that the allocation of the mesonychids to the Condylarthra is correct.[1]

Although we find general agreement for the derivation of the Mesonychoidea from an arctocyonid condylarth near the triisodont line, the tracing of lineages within the group has barely been attempted. Boule (1903) proposed a major lineage from *Dissacus* through *Pachyaena* to *Mesonyx* based primarily on the gradual loss of the metaconid. The supposed *Dissacus-Pachyaena* intergrade described by Osborn and Wortman (1892, p. 112) was later made the type of *Hapalodectes* by Matthew (1909, pp. 498–499). In the same monograph, Matthew proposed two major groups:

whether even these phyla represent direct lines of descent; the relations of the species of *Dissacus* to their successors in the Wasatch being not at all certain." Now that we have become aware of a surprising mesonychid diversity in the late Eocene and early Oligocene of Asia, any phylogeny that we may be tempted to suggest would be badly plagued by our ignorance of Asiatic Paleocene and early Eocene faunas. It is likely that the major phyletic advances in the Mesonychidae took place in Asia, and the North American species may be taxa that originated from unknown Asiatic ancestors.

Sound phylogenetic conclusions cannot be drawn profitably; however, most of the genera can be arranged to form various adaptive levels,[2] based on their inferred habitus. Viewing mesonychid evolution in terms of adaptive levels facilitates understanding and allows an appreciation of the morphologically somewhat conservative but, we believe, adaptively divergent Mesonychidae. The following brief discussions of various adaptive levels do not imply that there were any phyletic connections between various taxa.

CARNIVORE LEVEL: The earliest known mesonychids from the Torrejonian, Tiffanian, Clarkforkian, and Wasatchian of North America, the species of *Dissacus*, represented an undoubtedly more carnivorous grade than their triisodontine ancestors. The premolarization of the lower molars and the relatively efficient, sharp, and trenchant teeth can be

Dissacus saurognathus → *Pachyaena gigantea* → *Harpagolestes*
Dissacus navajovius → *Pachyaena ossifraga* → *Synoplotherium*
└─────────────→ *Pachyaena intermedia* → *Mesonyx*

Matthew was aware of the doubtful nature of his proposed phylogeny, and he repeatedly emphasized it (p. 487): "It is very doubtful

[1] Mac Intyre (1966) pointed out that Cope's original order Creodonta consisted of miacids, oxyaenids, and hyaenodontids. He followed Schlosser and others in removing the miacids from the Creodonta and associating them with the later fissiped families, but did not abandon the name "Creodonta" as applied to an order containing the Oxyaenidae, the Hyaenodontidae, and their close relatives.

interpreted only as increasing adaptations to a carnivorous habitus. The cheek teeth in *Dissacus* were relatively small, and the canine was large and pointed and followed by a diastema. In *Dissacus saurognathus* the foot was already showing tendencies toward a cursorial tetradactyl condition (Matthew,

[2] The term "adaptive level" is preferred here to the concept of grade, since grades tend to imply progressive changes in the character complexes of a group.

1909). As Matthew noted, the hallux, although present, was reduced in size, and the fifth metacarpal was also reduced. In *Dissacus navajovius*, a smaller species of the genus, the foot seems to have been slender and compressed (more than in *D. saurognathus*) as shown by the tarsals (Matthew, 1909).

ADVANCED CARNIVORE LEVEL: *Mesonyx obtusidens* was probably an advanced carnivore. The metaconids of the lower molars became completely reduced, which made the lower teeth more trenchant. The foot was tetradactyl, indicating a digitigrade animal, undoubtedly an active runner and probably a pursuer of fast prey. According to Wortman (1901–1902, vol. 12, p. 286), *Mesonyx* and *Synoplotherium* (the latter not a carnivorous form in our judgment, for reasons noted below) " . . . developed a limb structure almost equaling, if not actually surpassing, that of the modern dogs in point of specialization for a running habit." In demonstrating the digitigrade gait of *Mesonyx obtusidens*, Scott (1888) noted that the almost perfect interlocking of metacarpals is excelled in modern carnivores only by cats. *Hapalodectes* has even more elongate and cutting lower teeth than those seen in *Mesonyx*. Both *Hapalodectes* and *Ichthyolestes* (the latter known from upper teeth only) were considered possible fish eaters by their original

describers, Matthew (1909) and Dehm and Oettingen-Spielberg (1958), respectively. *Pachyaena gracilis*, judged from its dentition, was a much more carnivorously adapted form than the remaining species allocated to this genus (*P. ponderosa*, for example). The genus *Pachyaena* seems to show a recognizable adaptive radiation among its species.

OMNIVORE-CARNIVORE LEVEL: A noticeable and peculiar phenomenon on the teeth of *Pachyaena* is the consistent absence of heavy wear, so characteristic of *Harpagolestes*, for example. All known teeth of *Pachyaena ponderosa*, *P. gigantea*, and cf. *Pachyaena* from Irdin Manha (A.M.N.H. No. 20131) [Gromova's (1952) "*Mesonyx obtusidens*" from the Naran Bulak beds of Inner Mongolia is a juvenile *Pachaena*] are either slightly worn or not worn at all. On the cheek teeth of *Pachyaena*, especially on the upper ones, there are distinct, very pronounced cutting edges, similar to those found in *Dissacus* but accentuated. The cutting ridges not only run in an anteroposterior direction on the buccal cusps of the upper teeth and on the protoconids, but they are also quite prominent and more or less transverse on the buccal and posterobuccal slope of the protocones.[1] These features suggest that such large mesonychids as *P. ponderosa* and *P. gigantea* were omnivorous

[1] There are very slight transverse ridges on the protocones of *Dissacus* and *Mesonyx*.

TABLE 9

VARIOUS ADAPTIVE LEVELS OF THE MESONYCHIDAE (NO PHYLETIC RELATIONSHIPS IMPLIED)

Carnivore Level	Advanced Carnivore Level	Omnivore-Carnivore Level	Omnivore Level	Bone-crushing Level
Teeth relatively small; pes and manus evolving in direction of tetradactyly. Example: *Dissacus*	Lower teeth elongate, cutting; some known species with tetradactyl foot adapted for fast running. Length/ width ratio of lower cheek teeth high. Examples: *Hapalodectes, Ichthyolestes, Mesonyx, Pachyaena gracilis*	Teeth with cingula and cutting edges, usually large. Examples: *Pachyaena ponderosa, P. gigantea*	Sagittal crest reduced; teeth with cingula; enamel on crowns of cheek teeth heavily wrinkled. Example: *Andrewsarchus* (lower teeth unknown)	Powerful jaw musculature; teeth relatively large, consistently exhibiting heavy wear even after crown abraded off, remaining roots serving as functional teeth. Examples: *Harpagolestes, Synoplotherium, Mongolestes, Mongolonyx*

and also actively preyed to some degree. *Pachyaena* teeth are prominently piercing and cutting compared to those of *Harpagolestes* and *Mongolestes;* also the dentition of *Pachyaena* is never worn to such a degree as to allow an inference of carrion feeding or active bone crushing.

OMNIVORE LEVEL: There is not much doubt that *Andrewsarchus* was the most omnivorously adapted genus of all the known mesonychids. Many features adapted to a highly omnivorous niche, as inferred from the type skull, are discussed in the section dealing with *Andrewsarchus*.

BONE-CRUSHING LEVEL: Genera consistently showing extensive wear on the dentition (*Synoplotherium* and *Harpagolestes*, but probably not all species of the latter taxon)

and taxa known from specimens that bear signs of incipient wear, indicating a hard diet (*Mongolestes* and perhaps *Mongolonyx*), were very probably carrion-feeding, bone-consuming mammals. Although they were undoubtedly poorly adapted to cut meat or tendons with their blunt teeth, they were, we believe, well adapted for feeding on the abundant carcasses of large herbivores of the early Tertiary of North America and Asia. The bone-crushing, carrion-feeding adaptation is discussed in some detail in the section dealing with feeding adaptations.

Table 9 is a summary of the various adaptive levels of certain mesonychid taxa proposed in this paper, with no attempt to place the poorly known species of the family into any of the defined levels.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION
OF THE MESONYCHIDAE

THE MESONYCHIDAE are almost exclusively a holarctic family, known only from Asia, Europe, and North America. The earliest known representative, *Dissacus*, is known from various Torrejonian, Tiffanian, Clarkforkian, and Wasatchian localities in North America, and from the Cernaysian, Sparnacian, and Lutetian faunas of Europe (see table 10). The oldest known Asiatic mesonychid was reported by Young and Chow (1963) from the Tanya beds of Nanyung Basin of south China. If the tentative allocation of these authors is correct, namely, that this mammal resembles *Dissacus* (there are neither descriptions nor illustrations in their publication), then we have at the beginning of the Tertiary in North America, Europe, and Asia similar stocks of primitive mesonychids (providing also that the Paleocene age of the Tanya beds given by Young and Chow is correct). Other than Young and Chow's (1963) report, virtually nothing is known of the mammal faunas of Asia during Paleocene times, a blank of approximately 10,000,000 years in the mammalian history of the Asian continent. Besides *Dissacus* in the Wasatchian faunas of North America, *Pachyaena* and *Hapalodectes* appear in the Eocene for the first time. In the European Lutetian fauna (a well-established age equivalent of the Bridgerian assemblage) *Dissacus* seems to be the last survivor of the Mesonychidae of Europe. If the Naran Bulak beds (not formally described) of southern Mongolia are early Eocene in age (Gromova, 1952), then the second oldest known mesonychid from Asia is a species of *Pachyaena* (see discussion of "*Mesonyx obtusidens*" on p. 150).

During Bridgerian times in North America three more genera besides *Hapalodectes* occur: *Synoplotherium*, *Mesonyx*, and *Harpagolestes*. Our present knowledge of middle Eocene fossil mammals of Asia is extremely poor; there is not a single well-known mammalian fauna from that time interval. *Ichthyolestes* and *Gandakasia* from the Gandakas fauna of Pakistan (supposedly middle Eocene in age according to Dehm and Oettingen-Spielberg,

1958) are not known from elsewhere. The lower Chharat Series of Pakistan, where the Gandakas fauna was discovered, is a supposed correlate of the lower Khirthar Beds in the same country. From the latter strata Pilgrim (1940) reported a mesonychid, but because of the poor preservation of the specimen he could not refer it to any taxon.

Only *Harpagolestes* is known for certain from the Uintan assemblage of North America. *Hessolestes*, from the type Duschesnean mammal fauna, seems to be the last survivor of the family on the North American continent. Shikama (1943) allocated several mesonychid teeth from Korea to a new species of *Harpagolestes* (the "wastebasket" genus for most of the poorly known and scrappy material of Eocene mesonychids). The supposedly early late Eocene Irdin Manha Formation of Inner Mongolia yielded the type skull of *Andrewsarchus mongoliensis*; specimens of *Mongolonyx*, new genus; a single tooth of *Hapalodectes*; scraps of a form very close to *Mesonyx*; a fragment of tooth indicating a very large species of cf. *Pachyaena* (or a derivative of *Pachyaena*); and a mesonychid of indeterminate genus. From the Ulan Shireh Formation (very likely the same age as the Irdin Manha Formation) was collected the type skull of *?Harpagolestes orientalis*. Although, on the basis of the upper dentition, this new species can be referred to *Harpagolestes*, our ignorance of the lower dentition and certain features of the palate would make definite generic allocation questionable. The Ulan Shireh beds also yielded some mesonychid teeth probably conspecific with those indicated as cf. *Mesonyx* from the Irdin Manha beds (see table 11). In our opinion, this fact reinforces the equivalence in age of the Irdin Manha and Ulan Shireh formations, as was suggested by Radinsky (1964). A very large, heavily worn mesonychid lower cheek tooth from the Ulan Shireh beds cannot be allocated to any well-known taxon.

Olsenia was described as a new genus by Matthew and Granger (1925a), based on several astragali from the Shara Murun Formation of Inner Mongolia. Although we

TABLE 10

TEMPORAL RANGES OF NORTH AMERICAN AND EUROPEAN MESONYCHID GENERA

Epoch	North America	Europe
Early Oligocene	*Hessolestes*	—
Late Eocene	*Harpagolestes* *?Mesonyx*	—
Middle Eocene	*Hapalodectes* *Mesonyx* *Synoplotherium* *Harpagolestes*	*Dissacus*
Early Eocene	*Dissacus* *Pachyaena* *Hapalodectes*	*Dissacus* *Pachyaena*
Late Paleocene	*Dissacus*	*Dissacus*
Middle Paleocene	*Dissacus*	—

believe that the generic distinction of this mesonychid should be ignored (see above discussion of *Olsenia*), the specimens undoubtedly indicate the presence of a medium to large mesonychid during Shara Murun time.

The type specimen of *Mongolestes hadrodens*, new genus and new species, was collected from the "Ulan Gochu" Formation (not the type strata of the latter formation). We also describe in this paper teeth of an animal very close to *Harpagolestes* (cf. *Harpagolestes* in table 11) from the same beds.

After a brief review of the temporal and geographic ranges of the known mesonychid genera the following two questions arise: Do the presently known stratigraphic and geographic ranges and the relative taxonomic abundance on the three holarctic continents suggest a center of origin for the Mesonychidae? Can we infer times of migrations for members of the family along holarctic dispersal routes? As noted, the earliest record of the family in North America does not necessarily mean that the family originated on this continent. On the other hand, the almost total ignorance of Asiatic Paleocene mammals[1] should not allow us to extrapolate an

abundance of mesonychid taxa to account for the well-known diversity of the family that began only with Irdin Manha and Ulan Shireh times. There is no convincing evidence, therefore, about the origin of the Mesonychidae, either in North America or in Asia. The abundance of various condylarths in North America during early Paleocene times would be meaningful in this regard only if the mammal assemblages of equivalent age of Asia were known.

In order to answer the question of dispersal in geologic time for the family, we would have to know the missing Asiatic mammal record in the Paleocene and most of the Eocene, and it would also be imperative to place the taxonomy of all known mesonychid forms on a much firmer basis than has been done in the past. The only statement that can be made concerns the migration of *Dissacus* during late Paleocene and probably early Eocene

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[1] The Gashato local fauna of the Gashato Formation is a very poorly known assemblage. The age of the fauna is supposed to be late Paleocene, mainly because

of the presence of *Prodinoceras*, a form very similar to the North American Tiffanian and Clarkforkian uintatheres. Van Valen (1966) suggested a possibly early Eocene age owing to the presence of *Sarcodon*, which was classified by him as a palaeoryctid. Kowalski (personal communication) maintains that the Gashato and Naran Bulak local faunas are synchronous, whatever the relative age of the two faunas may be in relation to other known mammalian assemblages. The presence of *Pachyaena* strongly supports an early Eocene age for the Naran Bulak mammal assemblage.

TABLE 11

Temporal Ranges and Synopsis of Asiatic Mesonychids

?Late Eocene (later fauna)	*Mongolestes* (this paper) Cf. *Harpagolestes* (this paper)	"Ulan Gochu" Formation, Mongolia	
	Mesonychid (*"Olsenia"*)	Shara Murun Formation, Mongolia (Matthew and Granger, 1925)	
?Late Eocene (earlier fauna)	Korea ?*"Harpagolestes" koreanicus* (Shikama, 1943)	Irdin Manha Formation, Mongolia *Andrewsarchus* (Osborn, 1924) *Hapalodectes* (Matthew and Granger, 1925) Mesonychid, gen. indet. (this paper) Cf. very large *Pachyaena* (this paper) Cf. *Mesonyx* (this paper) *Mongolonyx* (this paper)[a]	Ulan Shireh Formation, Mongolia ?*Harpagolestes orientalis* (this paper) Very large mesonychid, gen. indet. (this paper) Cf. *Mesonyx* (this paper)
?Middle Eocene	Lower Chharat Series, Pakistan *Gandakasia* Dehm and Oettingen-Spielberg, 1958 *Ichthyolestes* Dehm and Oettingen-Spielberg, 1958	Lower Khirthar Beds, Pakistan ?Mesonychid (Pilgrim, 1940)	
?Early Eocene	Naran Bulak Beds, Mongolia *Pachyaena* (*"Mesonyx obtusidens"* Gromova, 1952)		
?Paleocene	South China, Nanyung Basin *Dissacus*-like mesonychid reported by Young and Chow (1963)		

[a] Not from the type Irdin Manha.

times between North America and Europe and Asia, and also that of *Pachyaena* in early Eocene time between the first two continents. At present it is very likely that the Mesonychidae became extinct in Europe by the end of Lutetian time.

The relatively well-known early Tertiary beds of North America have yielded not more than seven genera of mesonychids, while, in our estimation, the presence of at least 10 genera has been ascertained from the poorly known strata of Asia (see table 11). Despite our meager knowledge of early Tertiary Asiatic mammals, the greater abundance of mesonychid genera in Asia compared with the fewer number in North America is highly significant.

SUMMARY

THE SUBFAMILY Mesonychinae is rediagnosed. Two new genera and species are described: *Mongolonyx dolichognathus* from the "Irdin Manha" beds and *Mongolestes hadrodens* from the "Ulan Gochu" Formation of Inner Mongolia. *Harpagolestes* was probably represented in Asia. *?Harpagolestes orientalis*, new species, is described, and the published literature and most of the known specimens of this probably holarctic genus are re-evaluated. This is not, however, a substitute for a systematic revision of *Harpagolestes*. "*Mesonyx obtusidens*," reported by Gromova (1952), from the Naran Bulak beds of Mongolia, is a species of *Pachyaena*. *Olsenia*, a mesonychid described by Matthew and Granger (1925a) based solely on astragali, is not comparable to most of the known genera because of the scarcity of associations between mesonychid teeth and foot bones. The name "*Olsenia*" is suggested to be a *nomen dubium*. A new subfamily, the Hapalodectinae, is erected and is based on *Hapalodectes*. "*Hapalodectes auctus*," described by Matthew and Granger (1925b), is not a mesonychid but a didymaconid. A new subfamily, the Andrewsarchinae, is diagnosed and is based on *Andrewsarchus*. Several unallocated Asiatic mesonychids are described.

Studying the feeding mechanism of mesonychids led to a re-examination of the previous ideas of Boule, Matthew, and others, who maintained that the Mesonychidae had a very weak jaw musculature and that therefore these mammals could not fill a carnivore or scavenger niche. On the basis of the present studies, it seems very probable that mesonychids had a powerful mandibular musculature. The variation of the length/width ratio of homologous lower cheek teeth of various species of mesonychids might serve as an index to feeding habit. A relatively long lower cheek tooth suggests a carnivorous habit, while a relatively transverse, blunt lower tooth may indicate an omnivorous or scavenging habit.

The Mesonychoidea, in agreement with the action of Van Valen (1966), are transferred from the Carnivora to the Condylarthra. No sound phylogenetic conclusions can be offered for the evolution within the Mesonychidae. The known diversity of mesonychids in the late Eocene and early Oligocene of Asia, and our ignorance of the Asiatic Paleocene and early and middle Eocene faunas would badly mar any proposed phylogeny. As a heuristic alternative, the arrangement of the known mesonychid genera to form several adaptive levels may partially clarify mesonychid diversity. In this paper the following five adaptive levels are suggested without implying any phyletic relationship between the various levels: carnivore level, advanced carnivore level, omnivore-carnivore level, omnivore level, bone-crushing level.

This study of Asiatic mesonychids revealed a previously unsuspected diversity of genera among the Asiatic forms in comparison to European and North American taxa. The presence of at least 10 genera is ascertained from the poorly known Asiatic strata in comparison to the seven known genera of mesonychids from the relatively well-known early Tertiary of North America and Europe. For a summary of the known worldwide temporal and geographic distribution of the Mesonychidae, see tables 10 and 11.

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