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The Hapalodectinae and a Phylogeny of the Mesonychidae (Mammalia, Condylarthra)

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Hapalodectine mesonychids are relatively rare fossils of continental Eocene sediments of Asia and North America. Among the archaic placentals, these predominantly small condylarths represent one of the most unusual specializations toward an inferred carnivorous and piscivorous mode of life. Specimens of the subfamily were recorded, described, and discussed by Matthew (1909, 1915), Gazin (1962), Chow (1965), Szalay and Gould (1966), and Guthrie (1967). In addition to the description of previously unreported material both from the early Eocene of North America and the late Eocene of Central Asia, the systematics of this subfamily is reviewed here.

It is suggested that, in spite of the first occurrence of hapalodectines in the early Eocene, the subfamily was probably distinct from mesonychines prior to the middle Paleocene. A few subtle but probably important characters of hapalodectines may be more primitive than those of middle Paleocene mesonychines, such as *Dissacus*. One of these is the unreduced M_3 (longer than the preceding molars) in *Hapalodectes*. There appear to be three possibilities for the origin of the Hapalodectinae: (1) differentiation from early or middle Paleocene mesonychids, more primitive than known mesonychines; (2) derivation from Asiatic or

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North American (less likely than Asiatic) mesonychines during the Paleocene; or (3) *Hapalodectes* and their allies represent a distinct family derived from unknown sources. The last possibility does not appear to be probable at present.

As a result of a re-evaluation of the interrelationships of mesonychid genera, a tentative phylogeny, together with continental occurrences, is presented.

No functional analysis is detailed in this paper. Another work by me on the origin and evolution of the mesonychid feeding mechanism will be submitted elsewhere, in which pertinent functional considerations of the Hapalodectinae are treated.

I thank Dr. Glenn L. Jepsen, of Princeton University, for lending me several specimens. I am grateful to Drs. Bobb Schaeffer, Chairman of the Department of Vertebrate Paleontology, Malcolm C. McKenna, Frick Associate Curator, and Richard H. Tedford, Associate Curator, of the Department of Vertebrate Paleontology, the American Museum of Natural History, for the use of facilities to conduct this research.

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Figures 10–12 and 18 were drawn by Miss Biruta Akerbergs, and figure 19 was prepared by Mr. Raymond J. Gooris.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History

P.U., Princeton University

U.S.N.M., United States National Museum of the Smithsonian Institution

SYSTEMATICS

ORDER CONDYLARTHRA COPE, 1881

SUPERFAMILY MESONYCHOIDEA OSBORN, 1910

FAMILY MESONYCHIDAE COPE, 1875

SUBFAMILY HAPALODECTINAE SZALAY AND GOULD, 1966

Hapalodectinae SZALAY AND GOULD, 1966, p. 152.

INCLUDED GENERA: *Hapalodectes* Matthew (1909), and an unnamed new genus ("*Hapalodectes lushiensis*") in Chow (1965).

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

EMENDED DIAGNOSIS: Hapalodectines differ from mesonychines and andrewsarchines in their distinctly smaller size, in the greater transverse

constriction of the lower teeth, in the presence of a hypocone on the upper molars, and in having deep, vascularized embrasure pits between the lingual parts of the upper cheek teeth.

They differ from all known mesonychines in having M_3 the longest tooth of the lower molars.

HAPALODECTES MATTHEW, 1909

Hapalodectes MATTHEW, 1909, p. 498.

TYPE SPECIES: *Hapalodectes leptognathus* (Osborn and Wortman, 1892).

INCLUDED SPECIES: *Hapalodectes leptognathus* and *Hapalodectes serus*.

DISTRIBUTION: Same as for subfamily.¹

DIAGNOSIS: Same as for subfamily.

Hapalodectes leptognathus (Osborn and Wortman, 1892)

Matthew, 1909

Figures 1-12

?*Dissacus* (*Pachyaena*) *leptognathus* OSBORN AND WORTMAN, 1892, p. 112.

Hapalodectes leptognathus (OSBORN AND WORTMAN): MATTHEW, 1909, p. 498.

Hapalodectes compressus MATTHEW, 1909, p. 499.

HOLOTYPE: A.M.N.H. No. 78, fragment of right horizontal ramus with broken P_4 - M_1 and almost complete M_2 , from Gray Bull beds in 1891, Big Horn Basin, Wyoming.

HYPODigm: A.M.N.H. Nos. 78, 79, Gray Bull beds. A.M.N.H. Nos. 12781, 12782, 12783, P.U. Nos. 16181, 17698, 18161, Lysite beds. A.M.N.H. No. 14748, Lost Cabin beds. U.S.N.M. No. 22447, New Fork beds.

DISTRIBUTION: Wasatchian sediments of North America.

SPECIFIC DIAGNOSIS: Differs from the Asiatic *Hapalodectes serus* in retaining a vestigial metaconid and in having slightly larger teeth.

DESCRIPTION, INTERDEME AND INTRADEME VARIATION: As discussed below, the Gray Bull, Lysite, and Lost Cabin samples are not large enough for one to determine whether or not there is a meaningful difference in the relative depth of the dentaries of these samples. The horizontal ramus is deepest under M_2 and M_3 . On the medial side of the dentary there is a long horizontal groove, probably for the origin of the mylohyoid muscle. The ascending ramus is unknown. The long symphysis was loose. In all the specimens known there are two mental foramina,

¹ I wish to correct the mistake in Szalay and Gould (1966, p. 168, and table 10) that *Hapalodectes* occurs in Bridgerian rocks in North America. The known distribution is correctly stated in that paper on page 152.

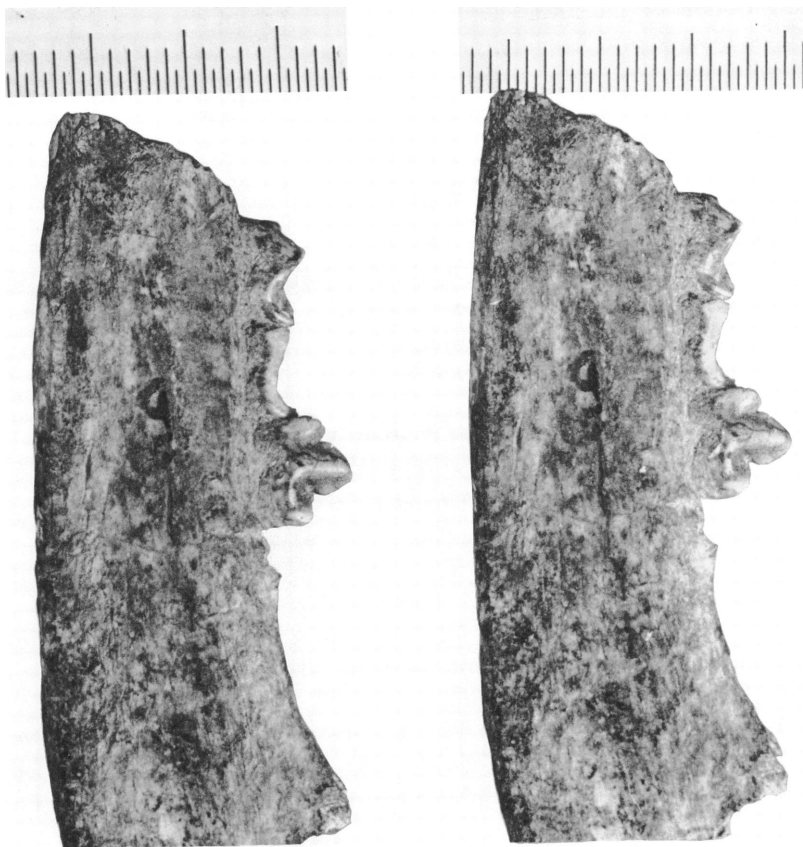


FIG. 1. *Hapalodectes leptognathus*, medial view of broken right dentary with P_4 - M_2 , holotype, A.M.N.H. No. 78, Gray Bull beds, Big Horn Basin, Wyoming.

under P_1 and under P_2 (or slightly posterior to P_2), respectively.

The canine is relatively large and slender; it is known only in A.M.N.H. No. 14748 (fig. 6). The crown of P_1 is not known. It appears that this tooth was in many cases double-rooted. However, it cannot be established at present whether the two-rooted or the one-rooted condition of P_1 was more prevalent. On the right dentary of P.U. No. 17698 (from Lysite beds) and on A.M.N.H. No. 14748 (from Lost Cabin beds) there is a shallow alveolus, anterior to the large one, for the anterior root of P_1 .

In contrast to P_1 , which, judged from the alveoli, was procumbent, the double-rooted P_2 (known only in A.M.N.H. No. 14748) stood erect

in the dentary. The protoconid of this tooth points slightly posteriorly, whereas that of P_1 was probably inclined anteriorly. The crown of P_3 is unknown, but, judged from the size of the alveoli, it was the same size as P_2 , or slightly larger.



FIG. 2. *Hapalodectes leptognathus*, lateral view of broken right dentary with P_4 - M_2 , holotype, A.M.N.H. No. 78, Gray Bull beds, Big Horn Basin, Wyoming.

Complete specimens of P_4 are not known. It is clear from A.M.N.H. No. 14748 (Lost Cabin) and A.M.N.H. No. 78 (Gray Bull), however, that there was no well-developed paraconid, but only an incipient nubbin representing this cusp. P_4 is posteriorly inclined.

There are small diastemata between P_1 and P_2 , and between P_2 and P_3 .

M_1 is the smallest, and M_3 the largest, of the lower molar series. This size relationship is best displayed on P.U. No. 16181, but it can also be recognized from the size relationship of the alveoli of other speci-

mens. Although M_2 and M_3 bear a vestigial metaconid on all known specimens, the chipped protoconid of M_1 of P.U. No. 16181 may not

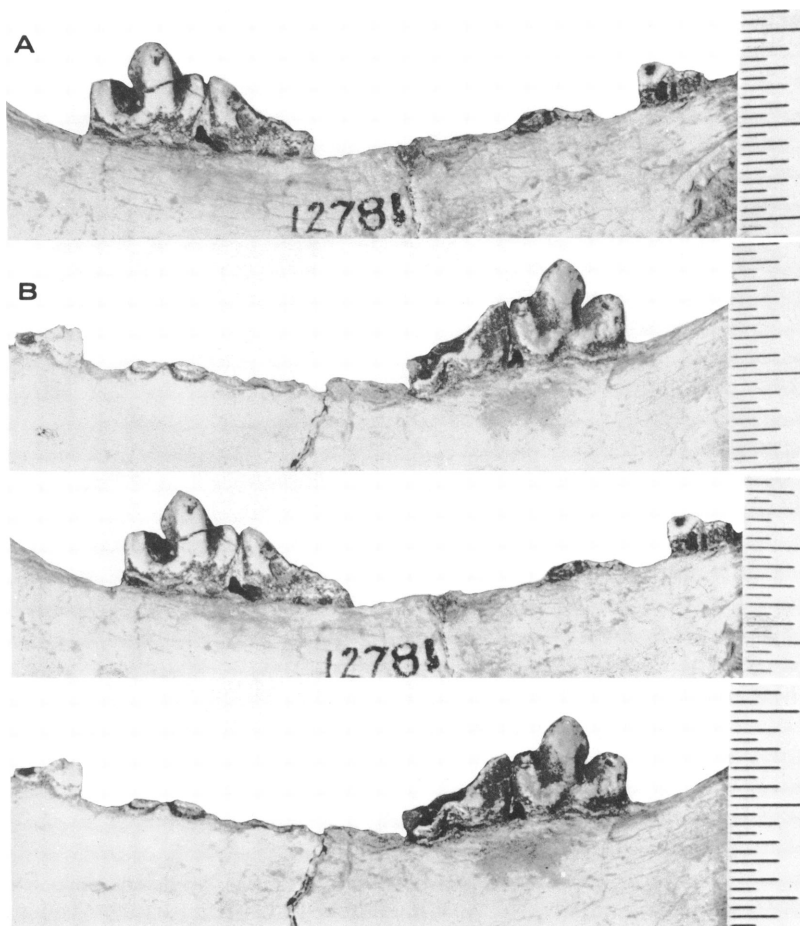


FIG. 3. *Hapalodectes leptognathus*, left dentary fragment with M_3 (type of "*Hapalodectes compressus*"), A.M.N.H. No. 12781, Wind River Formation. A. Lingual view. B. Buccal view.

have a metaconid. Because this specimen is broken on the anterior medial surface of the protoconid, it cannot be determined with certainty whether the vestigial metaconid was present or not.

In general, the molars are transversely narrow, with a dominant protoconid, small paraconid, vestigial metaconid, and the trenchant remnant

of a talonid that probably represents the cristid obliqua of less-advanced ancestry. There are well-defined re-entrant grooves¹ on the anterior face of the paraconids.

The only remains of the upper dentition or part of the skull of this species is P.U. No. 17698 from Lysite beds, a left maxilla fragment with the alveoli of P⁴ and M¹, and the somewhat broken last two molars, M² and M³. Guthrie (1967), who identified the specimen, published a rough drawing of it. I have thoroughly cleaned the specimen with acetic acid solution and an Airdent machine, and present a brief description below.

M² is the largest of the molars, with a large paracone, a distinctly smaller metacone, and a small but distinct metastyle, or at least a cuspule corresponding in position to the metastyle. The anterior part of the molar is broken off, but there is little doubt that there was a large parastyle (or a cusp corresponding to it in position) on this tooth. The buccal half of M³, although smaller than M², is essentially like that of the preceding tooth, with the large parastyle intact. The lingual half of M² is square, with the protocone broken off, and with a large hypocone. Although the apex of the protocone is broken, the cusp probably pointed in an anterobuccal direction. There is no trace of a paraconule or metaconule; the tooth is badly worn in these areas because of the propalinal action of the lower molars across the upper ones. This wear surface anterolingual to the paracone on M² is roughly triangular and is deeply etched into the tooth. A similar wear surface was present on M³, although much of the lingual part of the molar is missing. The lingual root of M¹ is larger than either of the buccal roots, whereas the lingual and posterobuccal roots of P⁴ are approximately the same size. One of the most striking peculiarities of the maxilla fragment is the deep embrasure pits thoroughly traversed with foramina (presumably for vessels of the circulatory system). The embrasure pit between P⁴ and M¹ is smaller than that between P⁴ and P³, possibly because either P³ lacked a protocone or this cusp on that tooth was very small. These

¹ The re-entrant grooves on the lower molars of *Hapalodectes* clearly indicate the importance of having the teeth form a straight, and not a crooked, tooth row. These grooves, apparently for the purpose of guiding teeth into their correct occlusal position, as well as adding to the resistance of the tooth against lateral and medial forces during mastication, occur also in triconodont mammals (Bob H. Slaughter, personal communication) as well as in hyaenodontids, such as *Hyaenodon* (James S. Mellett, personal communication). It is impressive that the selective forces responsible for the evolution of mesonychid "shear" were stringent enough to produce *de novo* mechanical means of insuring occlusion in hapalodectines.

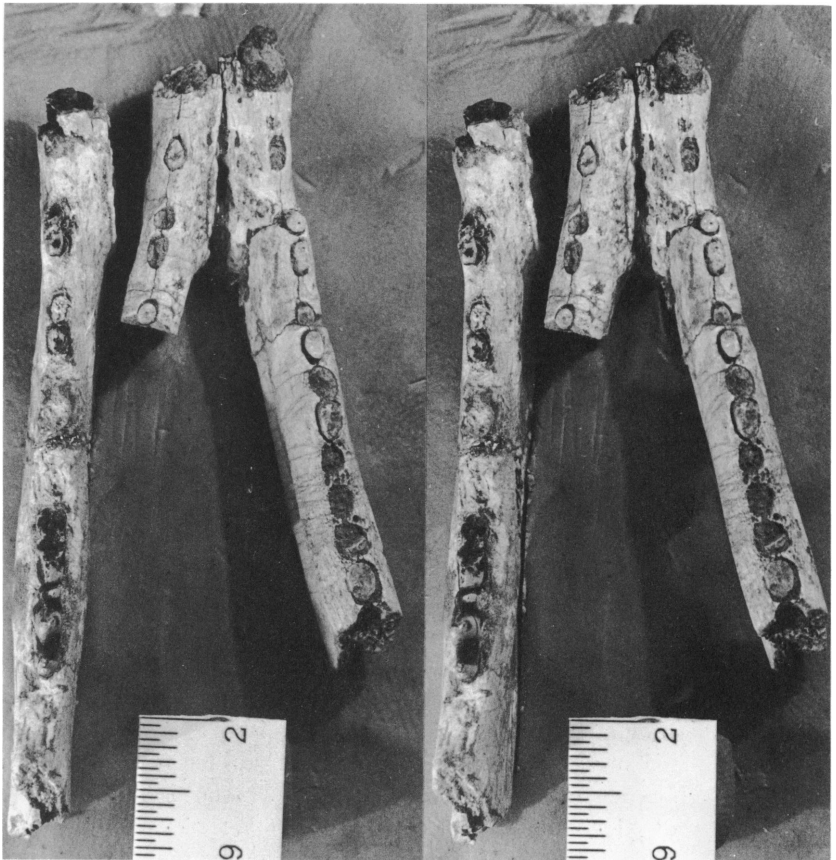


FIG. 4. *Hapalodectes leptognathus*, left dentary with M_2 - M_3 , A.M.N.H. No. 12781, and part of lower jaw with roots of teeth, P.U. No. 17698, Lysite Member of the Wind River Formation.

embrasure pits are apparently limited both anteriorly and posteriorly by the lingual halves of the cheek teeth. The zygomatic arch originates lateral to M^2 and begins to descend posteroventrally at the level of the metacone of M^2 . The preserved part of the zygoma is partly split off as a result of either preburial or postburial damage. Any attempt to clean out this crack and refit the two parts might result in serious damage to this unique specimen.

As a point of interest it must be added that the broken tip of the protoconid of M_3 was removed from the embrasure pit posterior to M^2 while the fossil was being cleaned.

The palatal view of *Hapalodectes leptognathus* (fig. 12) was based on P.U. No. 17698. In addition to the skull fragment, the tooth-bearing part of the right dentary from the canine to M₃ and the anterior part of the left dentary are also present. I superimposed the lower tooth row (fig. 11, reconstructed from various dentitions) on the drawing of the known upper teeth and added the missing anterior part in correct

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND MANDIBLES
OF *Hapalodectes leptognathus*

	P ₄		M ₁		M ₂		M ₃		Depth	Depth
	L	W	L	W	L	W	L	W	Below M ₂	Below M ₃
A.M.N.H. No. 78 ^a	5.6	1.9	5.2	—	5.8	2.3	—	—	11.75	13.00
A.M.N.H. No. 79 ^a	—	—	—	—	—	—	—	—	11.4	12.2
A.M.N.H. No. 1278 ^b	—	—	—	—	—	—	6.15	2.3	10.35	11.65
A.M.N.H. No. 1278 ^b	—	—	—	—	5.5	1.9	—	—	10.4	11.6
A.M.N.H. No. 1278 ^b	—	—	—	—	—	—	6.0	2.45	—	—
P.U. No. 16181 ^b	—	—	—	—	—	—	7.00	2.25	12.55	13.10
P.U. No. 17698 ^b	—	—	—	—	—	—	—	—	11.00	—
A.M.N.H. No. 14748 ^c	4.7	1.7	5.8	2.0	5.9	2.1	—	—	8.5	—

^a From Gray Bull beds.
^b From Lysite beds.
^c From Lost Cabin beds.

proportions. Because the symphyseal parts of both dentaries are preserved in P.U. No. 17698, it is possible to give the accurate distances between the lower teeth on opposite sides at any one point on the lower tooth row. Consequently, from the occlusal relationship of these lower cheek teeth with the upper ones, the width of the palate at any point can be determined and reconstructed.

DISCUSSION: There are no meaningful morphological, size, or proportional differences among the meager samples of *Hapalodectes* from the Gray Bull, Lysite, and Lost Cabin beds. I believe that the distinctions made by Matthew (1909) based on jaw depth differences and the relative compression of molars, which were subsequently used by Gazin (1962), break down when applied to samples rather than to individual specimens. P.U. No. 16181 is a dentary fragment with teeth, collected from Lysite beds as was A.M.N.H. No. 12781, the type of "*Hapalodectes compressus*." The mandible of P.U. No. 16181 is as deep as that of the type of *Hapalodectes leptognathus*, from Gray Bull beds. The dentary of

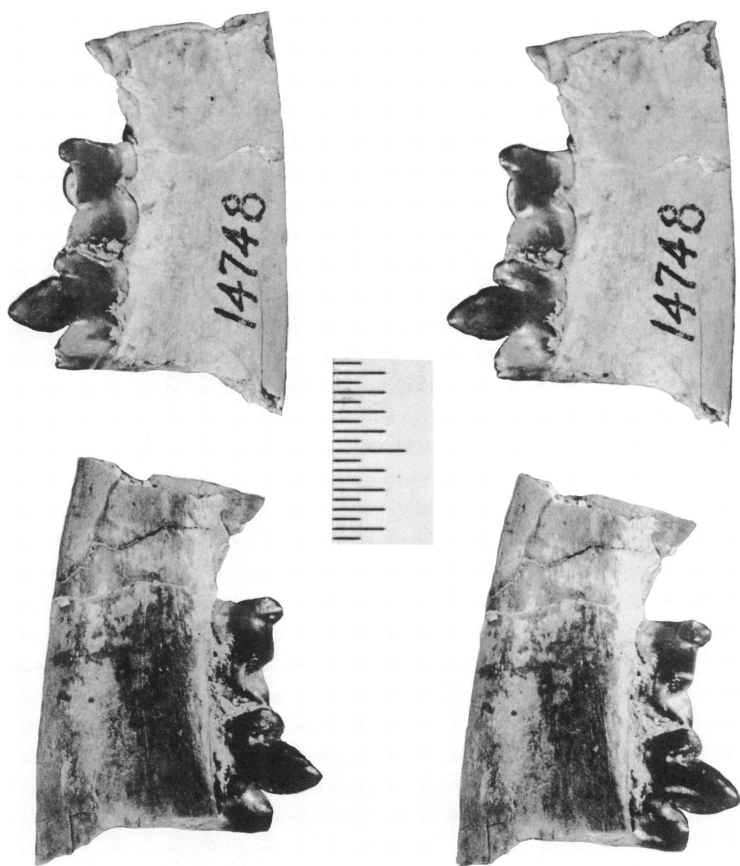


FIG. 5. *Hapalodectes leptognathus*, right dentary fragment with M_{1-2} , A.M.N.H. No. 14748, Lost Cabin beds, Wind River Basin, Wyoming. Above: Lateral view. Below: Medial view.

P.U. No. 18161, from Lysite beds, is also comparable in depth with that of the Gray Bull holotype.

Samples of homologous teeth are scarce. It cannot be demonstrated that differences either in jaw depth or in the relative compression of the molars are consistent with the stratigraphic provenance of the specimens. The only taxonomic decision that can be made from the known samples of the North American *Hapalodectes* is to unite the specimens under one species. The recognized differences can be explained by sexual dimorphism, or by normal variation resulting from age, or simply by intraspecific variability.

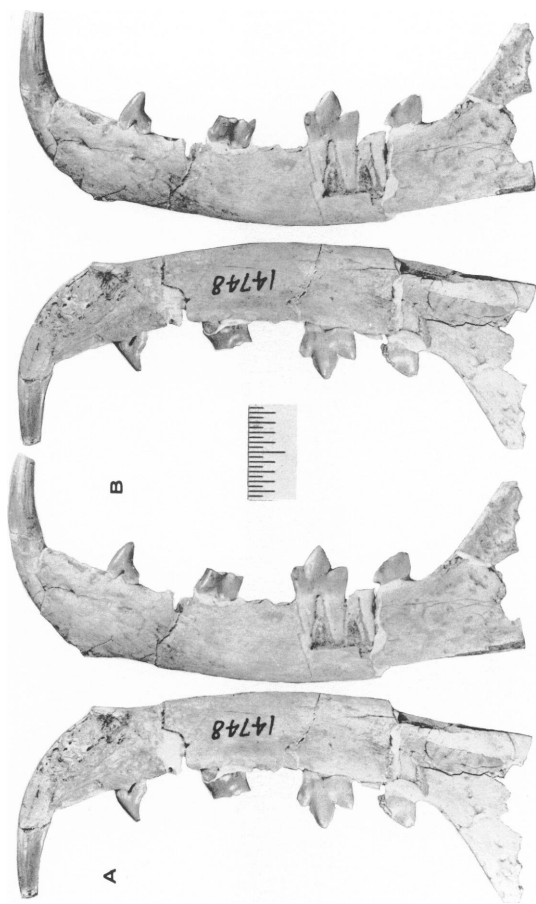


FIG. 6. *Hapalodectes leptognathus*, left dentary fragment with C, P₂, P₄, M₂, and talonid of M₃, A.M.N.H. No. 14748, Lost Cabin beds, Wind River Basin, Wyoming. A. Medial view. B. Lateral view.

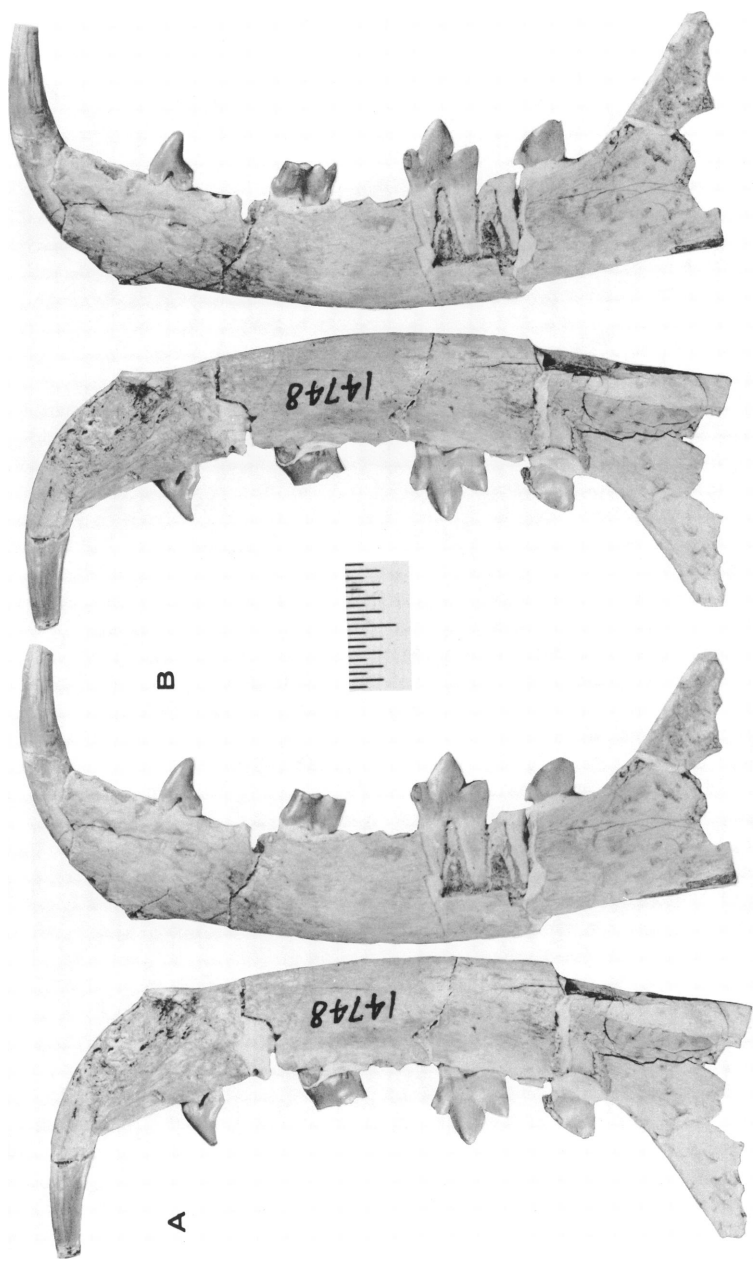


FIG. 6. *Hapalodectes leptognathus*, left dentary fragment with C, P₂, P₄, M₂, and talonid of M₃. A.M.N.H. No. 14748, Lost Cabin beds, Wind River Basin, Wyoming. A. Medial view. B. Lateral view.

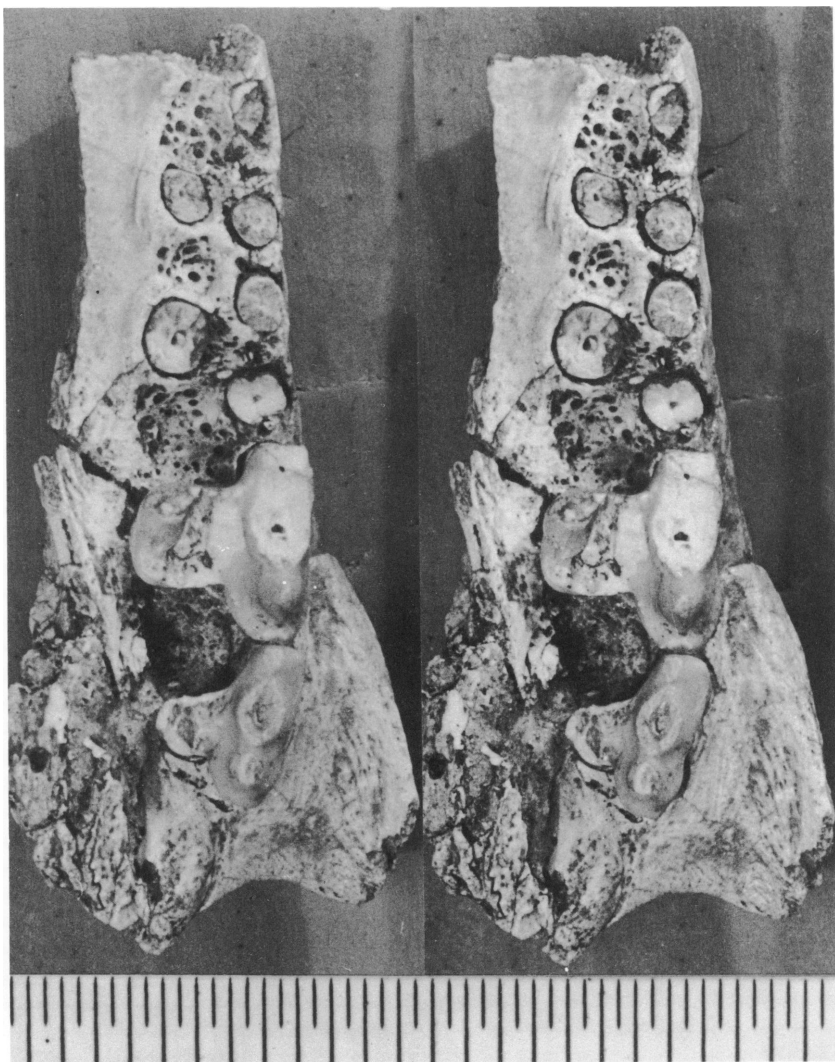


FIG. 7. *Hapalodectes leptognathus*, occlusal view of right maxilla fragment with M²⁻³, P.U. No. 17698, Lysite Member, Wind River Formation.

In addition to the conspicuous absence of *Plagiomene*, *Plesiadapis*, *Ectoganus*, *Dissacus*, *Palaeonictis*, *Meniscotherium*, *Probathyopsis*, and *Homogalax* from the Four Mile fauna noted by McKenna (1960), *Hapalodectes* is also missing from this well-sampled fauna.

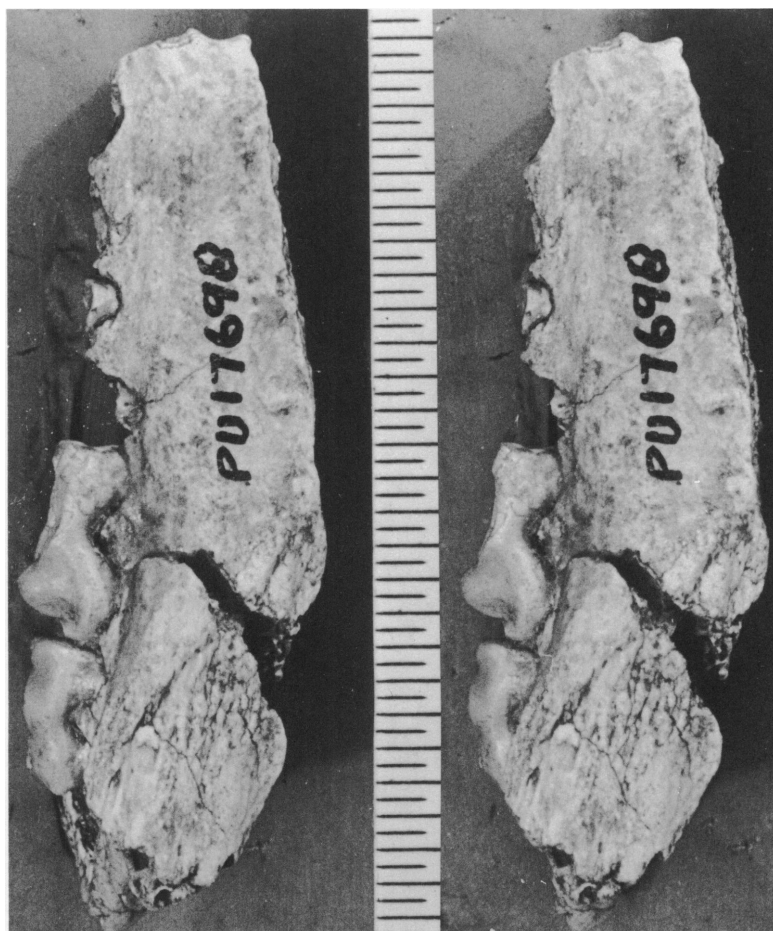


FIG. 8. *Hapalodectes leptognathus*, buccal view of left maxilla fragment with M^{2-3} , P.U. No. 17698, Lysite Member, Wind River Formation.

Hapalodectes serus Matthew and Granger, 1925

Figures 13–18

Hapalodectes serus MATTHEW AND GRANGER, 1925, p. 3.

The holotype of this Asiatic species was studied by Szalay and Gould (1966, pp. 153–154). *Hapalodectes serus* is clearly distinct from the North American *Hapalodectes*. The absence of a metaconid from the lower molars of *H. serus* is an advanced feature compared with those of the North American *Hapalodectes* which still retain a vestigial metaconid.

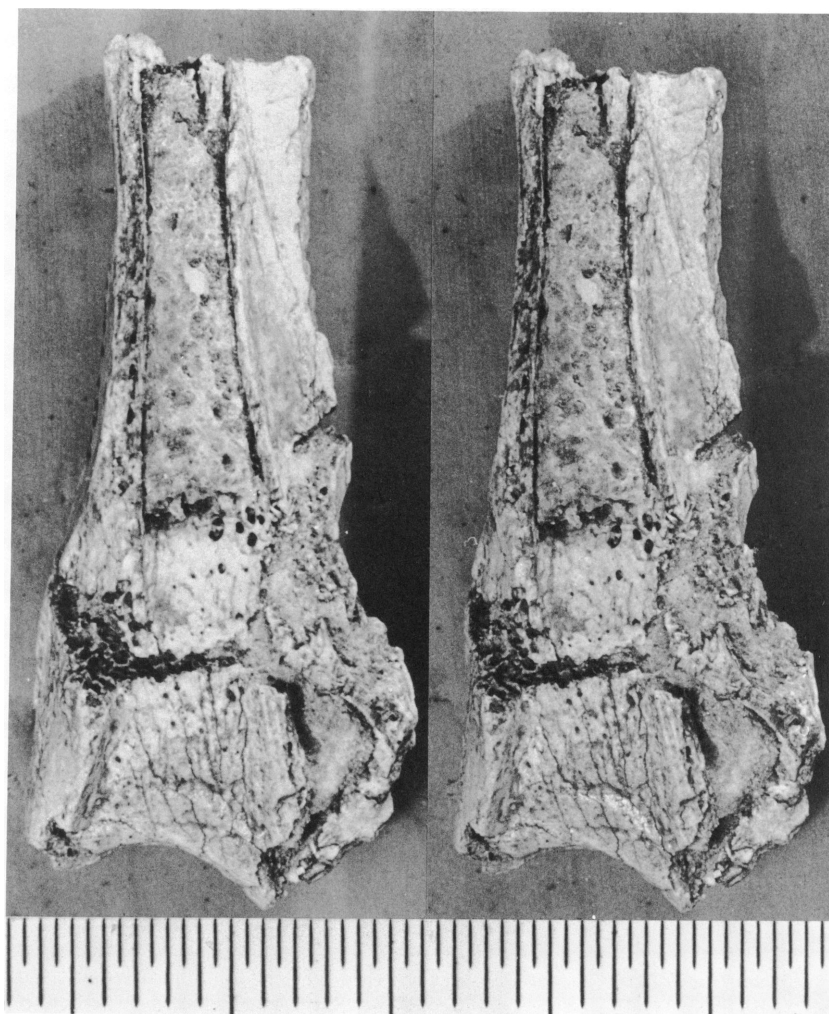


FIG. 9. *Hapalodectes leptognathus*, dorsal view of left maxilla fragment, P.U. No. 17698, Lysite Member, Wind River Formation.

The lingual and buccal profiles of the only known lower molar, the type (a right M_2), and the general morphology of the referred Asiatic upper molar are too similar to those of the North American form to warrant separation on the generic level. If anything, the new material of *Hapalodectes serus* identified by me and described below only strengthens the generic allocation of the species.

A.M.N.H. No. 80802, a left maxilla fragment with broken P^4 and complete M^1 , was collected by the Central Asiatic Expeditions of the American Museum of Natural History in 1930. It was found in the Camp Margetts area, in "Irdin Manha" beds. These strata, however, cannot be correlated with the type Irdin Manha Formation on a lithological basis (see Radinsky, 1964, remarks on the stratigraphical problems involved). It is possible that these beds at Camp Margetts may represent the Arshanto Formation rather than the Irdin Manha Formation. Type Arshanto beds underlie the type Irdin Manha Formation at Telegraph Line Camp.

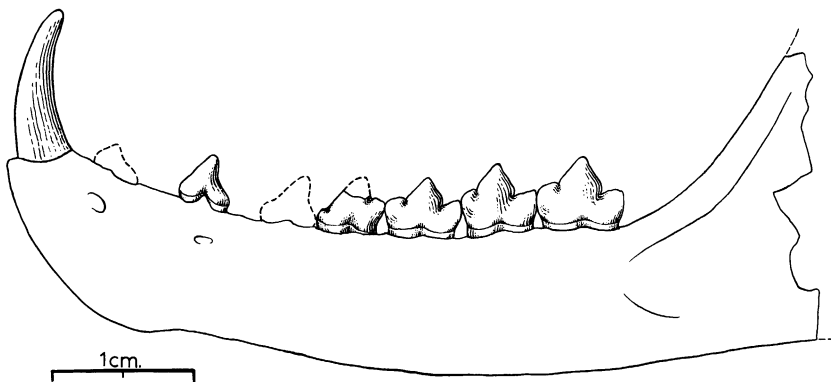


FIG. 10. *Hapalodectes leptognathus*, reconstruction of left horizontal ramus in lateral view, based on A.M.N.H. Nos. 12781 and 14748, and P.U. No. 17698.

Although A.M.N.H. No. 80802 was not recovered from the type beds of the Irdin Manha Formation (unlike A.M.N.H. No. 20172, the holotype of *Hapalodectes serus*, which was collected from the type sediments), there is no reason to suspect that the maxilla fragment represents a different species. The construction of M^1 of A.M.N.H. No. 80802 is essentially the same as that of the upper molars of the North American *Hapalodectes leptognathus*. The outline of the Asiatic M^1 is quite similar to the outline of M^1 inferred from the alveoli on P.U. No. 17698, the maxilla fragment of *Hapalodectes leptognathus*. On the first molar of the Asiatic species the lingual and buccal parts are well differentiated. Of the transversely constricted buccal cusps the paracone is by far the largest. The characteristic hypocone is of the same form and proportion as in *Hapalodectes leptognathus*. Judged from the broken outline of P^4 , this tooth was smaller than M^1 and also of somewhat

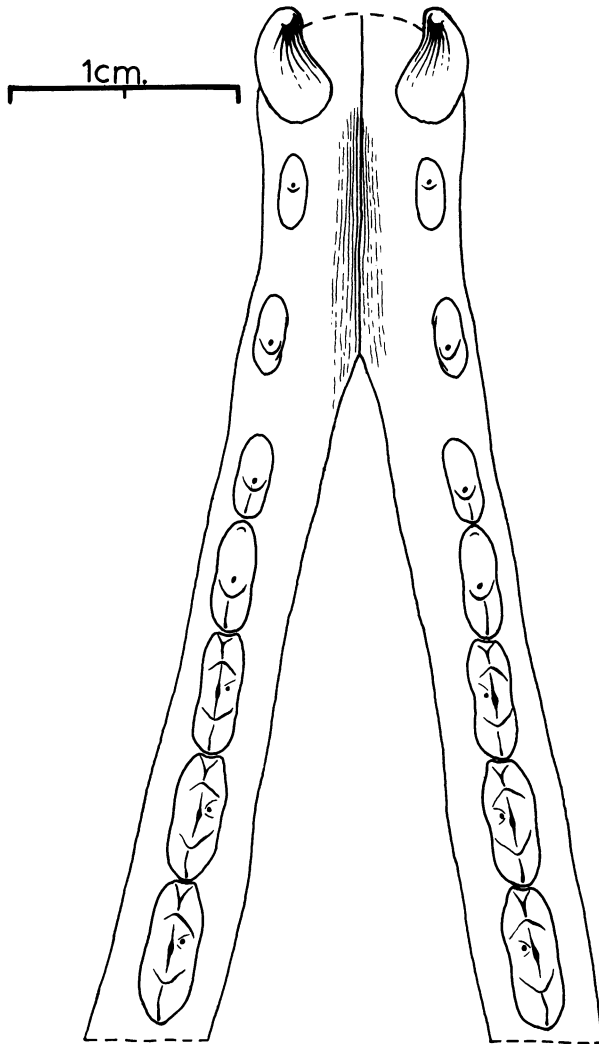


FIG. 11. *Hapalodectes leptognathus*, reconstruction of the lower dentition in occlusal view.

different proportions. The constricted, anterobuccal part of the fourth upper premolar appears to be distinctly longer than the posterobuccal segment of this tooth. The same can be inferred from the alveoli of P⁴ of *Hapalodectes leptognathus* (P.U. No. 17698).

A.M.N.H. No. 26164, from Chimney Butte Quarry, Chimney Buttes,

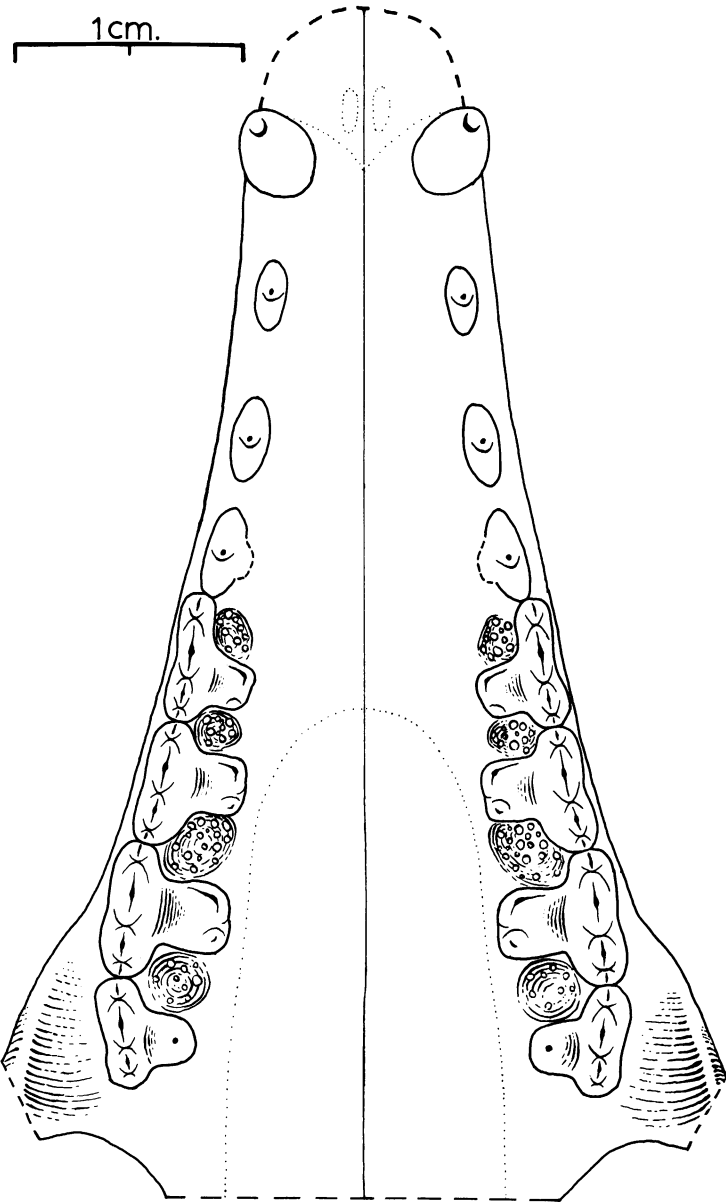


FIG. 12. *Hapalodectes leptognathus*, reconstruction of the palate and upper dentition. For explanation, see page 9.

North Mesa, Shara Murun Region, Ulan Shireh Formation (type sediments), is referred to *Hapalodectes serus* with a query. The specimen (figs. 15, 16) is an edentulous horizontal ramus of the left dentary. From the posterior border of the canine alveolus to the inferred posterior border of M_3 it is 41 mm. long. Among the features that strongly indicate that it may belong to *Hapalodectes* (or is very closely related to it) are the medial mylohyoid groove, the shape and proportions of

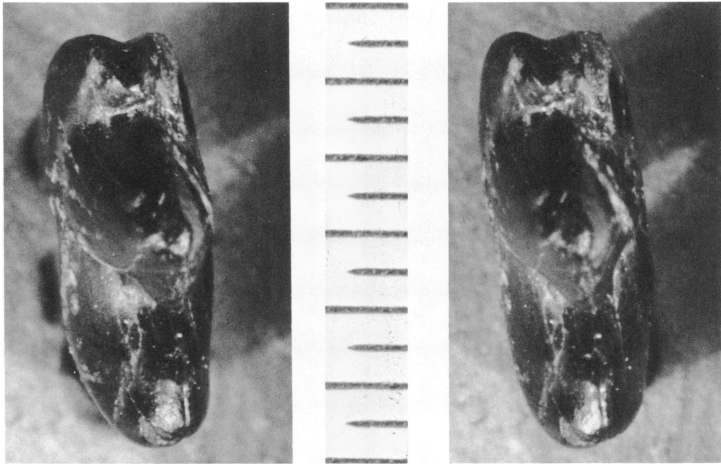


FIG. 13. *Hapalodectes serus*, occlusal view of right M_2 , holotype, A.M.N.H. No. 20172, Irдин Manha beds, Telegraph Line Camp of 1923 Central Asiatic Expeditions, Inner Mongolia.

the alveoli, the manner of canine implantation (exactly as in A.M.N.H. No. 12781, fig. 3), and the number and position of the mental foramina. This specimen from type Ulan Shireh beds is very likely *Hapalodectes serus*, although it has yet to be proved by dental association.

UNNAMED NEW GENUS FROM THE LOWER UPPER EOCENE LUSHI FORMATION OF CHINA

Hapalodectes lushiensis CHOW, 1965, p. 288.

Szalay and Gould (1966, p. 158), in an addendum to their paper, noted that Chow's (1965) species of *Hapalodectes*, *H. lushiensis*, warranted generic separation from the North American and Central Asiatic *Hapalodectes*. Although it is not my task to name a new genus on the basis of illustrations and the description of Chow, it may be useful to list the generic differences that I believe exist between Chow's species



FIG. 14. *Hapalodectes serus*, right M₂, holotype, A.M.N.H. No. 20172, Irdin Manha beds, Telegraph Line Camp of 1923 Central Asiatic Expeditions, Inner Mongolia. *Above*: Buccal view. *Below*: Lingual view.



FIG. 15. ?*Hapalodectes serus*, lateral view of edentulous horizontal ramus of left dentary, A.M.N.H. No. 26164, Ulan Shireh beds, Chimney Butte Quarry of 1928 Central Asiatic Expeditions, North Mesa, Shara Murun Region, Inner Mongolia.

and *Hapalodectes*. These diagnostic differences are as follows: The protoconid is relatively longer anteroposteriorly than in *Hapalodectes*



FIG. 16. *?Hapalodectes serus*, medial view of edentulous horizontal ramus of left dentary, A.M.N.H. No. 26164, Ulan Shireh beds, Chimney Butte Quarry of 1928 Central Asiatic Expeditions, North Mesa, Shara Murun Region, Inner Mongolia.

leptognathus or in *H. serus*. The notch that separates the protoconid from the talonid is a large gap, whereas in *Hapalodectes* it is merely a tight

opening between these moieties of the lower molars. This latter character was also noted by Chow. As a result of the enlarged protoconid the paraconid may be relatively smaller in the relatively large Lushi species than in known *Hapalodectes*.

SYSTEMATIC POSITION OF THE HAPALODECTINAE

Although the first hapalodectines appeared in early Wasatchian rocks in North America, it seems quite possible that the Hapalodectinae were already differentiated prior to the middle Paleocene Torrejonian occurrence of mesonychines. There are a few, but important, clues.

In all species of the earliest and most primitive known mesonychine, *Dissacus*, M_3 is already quite reduced, and further reduction or loss of M_3 characterizes almost all later mesonychines known to me. In *Hapalodectes* the third lower molar is unreduced, and furthermore it is the longest of the lower cheek teeth. At present it is impossible to determine whether the long M_3 of *Hapalodectes* is an advanced character or represents the primitive mesonychid condition. The triisodontine *Eoconodon* has a slightly reduced lower third molar, and the enigmatic, poorly known, near-mesonychid *Microclaenodon* seems to have an elongated, anteroposteriorly unreduced M_3 (see also footnote on p. 25).

The large and deep, thoroughly vascularized embrasure pits in the palate of *Hapalodectes* are unique specializations among mesonychids.¹ The presence of a broad, low hypocone is also the only such development among known forms of the family.

Although the two known, valid species of *Hapalodectes* are the smallest of the mesonychids, the Lushi genus from China, if it is a hapalodectine, as I believe, indicates that the Hapalodectinae contained not exclusively small species. Whereas the two species of *Hapalodectes* appear to have been in the size range of a living *Bassariscus astutus* (*Hapalodectes* probably had a relatively larger head), the Lushi genus shows a tooth about the size of a lower carnassial of *Urocyon cinereoargenteus*. The latter comparison, again, has the probable complication that hapalodectines had a relatively larger head than most modern mammals.

Needless to say, any speculations or conclusions on the phylogenetic ties of the Hapalodectinae closely concern mesonychid origins. If mesonychids originated from North American triisodontines, then

¹ Embrasure pits similar to those in *Hapalodectes* characterize the primitive genera of archeocete whales. The possible meaning of this similarity, as well as the feeding mechanism of archeocete whales, is treated elsewhere.

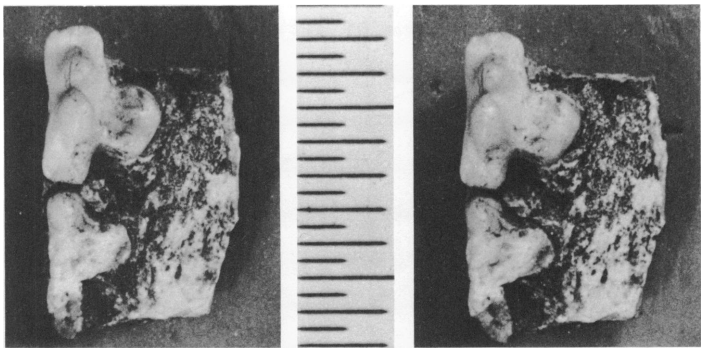


FIG. 17. *Hapalodectes serus*, occlusal view of left maxilla fragment with broken P⁴ and M¹, A.M.N.H. No. 80802, “Irdin Manha” beds around Camp Margetts of the 1930 Central Asiatic Expeditions, Inner Mongolia.

mesonychines (*sensu* Szalay and Gould, 1966), *Dissacus* in particular, in most respects represent the most primitive stage of the mesonychid

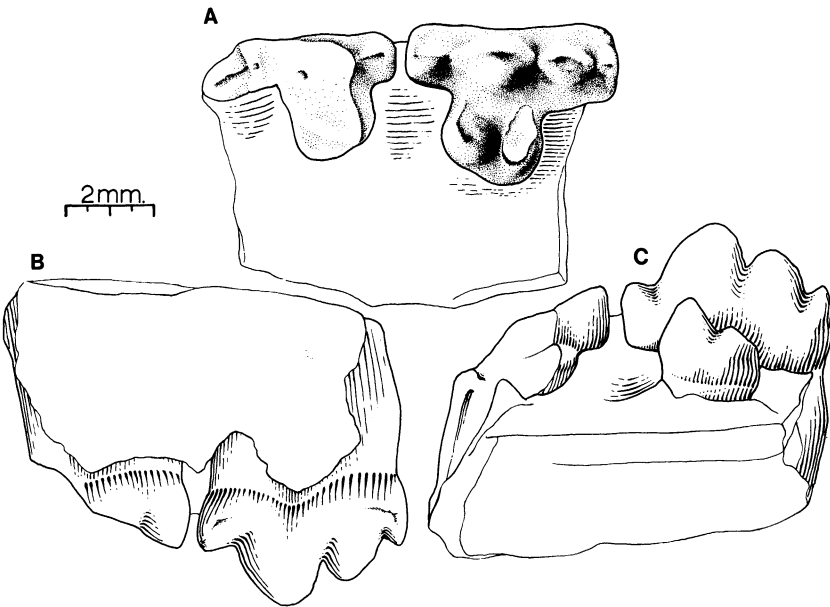


FIG. 18. *Hapalodectes serus*, left maxilla fragment with M¹ and broken P⁴, A.M.N.H. No. 80802, “Irdin Manha” beds around Camp Margetts of the 1930 Central Asiatic Expeditions, Inner Mongolia. A. Occlusal view. B. Buccal view. C. Lingual view.

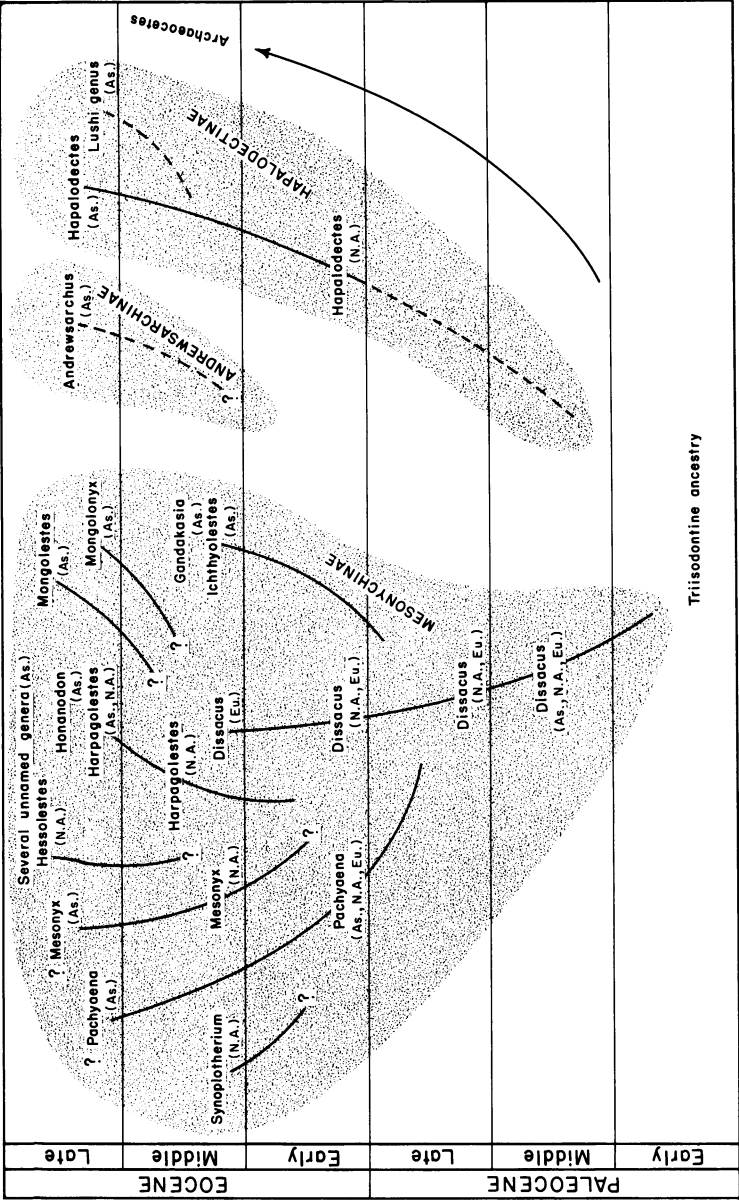


FIG. 19. Tentative phylogeny and known geographical and geological occurrence of the genera of three mesonychid subfamilies. The geological time scale on the chart is not proportional to the actual time involved. Abbreviations: As., Asia; Eu., Europe; N.A., North America.

level of organization. If triisodontine origins eventually become confirmed, and if *Dissacus* is a stem-genus, then we have at least two alternatives as to hapalodectine affinities, and possibly three.

The most likely possibility is that hapalodectines derived from either early or middle Paleocene mesonychids, species more primitive than known mesonychines. Such derivation probably occurred in Asia, where hapalodectines may have already been distinct during the Paleocene. The second, and at the present less likely, possibility is that mesonychines, such as the known North American and Asiatic (see Young and Chow, 1963) *Dissacus*, were ancestors of hapalodectines. A third possibility, that the Hapalodectinae represent a distinct family derived from unknown ancestry, does not appear probable.

Several problems should be noted concerning the fine points of mesonychid origins. The holarctic mesonychid radiation (Szalay and Gould, 1966), the virtual lack of collected Paleocene mammal records of Asia, the Asiatic presence of triisodontine-like forms, such as *Paratriisodon* (Chow, 1959),¹ for example, and the *Dissacus*-like fossils reported from the ?Paleocene of China (Young and Chow, 1963) are important facts to consider. These make it probable that unknown stocks of Asiatic arctocyonids, probably triisodontines or merely a group structurally parallel to the North American subfamily, gave rise to mesonychids in Asia, less likely in North America, and least likely in Europe.

I believe either that the approximately equal-sized *Andrewsarchus* and *Paratriisodon* were parallel developments from Asiatic stocks of triisodontine-like arctocyonids; or that *Andrewsarchus* converged toward *Paratriisodon* from a mesonychine ancestry. Unfortunately no lower teeth of *Andrewsarchus* are known or recognized, and the upper teeth in the type skull are too worn for detailed comparison. It should be noted, however, that wear on the upper teeth of *Andrewsarchus* is unlike that on the upper cheek teeth of mesonychines. Also, the third upper molar of *Andrewsarchus* is relatively unreduced, whereas known mesonychine genera, which would be considered as possible ancestors of the late

¹The gigantic *Paratriisodon honanensis* (Chow, 1959) was described from the late Eocene Lushi Formation of Honan Province. The same formation also yielded the mesonychid *Honanodon macrodontus* and a new genus of hapalodectines, named *Hapalodectes lushiensis* by Chow (1965). Figures of isolated teeth on plate 1 of Chow's 1959 paper clearly show that *Paratriisodon* had paraconules and metaconules on the upper molars. Figure 5a on plate 1 in Chow's paper indicates that the hypoconid is the largest of the talonid cusps and that the entoconid and hypoconulid are greatly reduced. M_3 of *Paratriisodon* is clearly the largest tooth of the lower molars.

Eocene condylarth giant, have reduced or eliminated the third upper molar. The sporadic facts of the Asian record are tantalizing, but adequate only for speculation, not for conclusions.

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