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The Earliest *Hapalodectes* (Mesonychia, Mammalia) from the Paleocene of Mongolia

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Abstract—A lower jaw containing complete tooth rows of the earliest hapalodectid mesonychian, *Hapalodectes dux* sp. nov., is described from the Upper Paleocene of Tsagan-Khushu, Mongolia (Naran Bulak Formation, Zhigden Member). The new species is smaller than the Middle Eocene *H. serus* and larger than the Early Eocene *H. hetangensis*. The lower molars of *H. dux* have distinct metaconid, protocristid, rudimentary hypoconulid, and entoconid; M_2 and M_3 are equal in size. These characters suggest that *H. dux* is the most primitive species of the genus *Hapalodectes*.

INTRODUCTION

Hapalodectes Matthew, 1909 is the type genus of the Hapalodectidae, an Early Paleogene family of small specialized mesonychians (Mesonychia, or Acreodi) characterized by well-pronounced predatory adaptations in dental structure. The following four species have been assigned to the genus: *H. leptognathus* (Osborn et Wortman, 1892) and *H. anthracinus* Zhou et Gingerich, 1991 from the Lower Eocene of North America; *H. hetangensis* Ting et Li, 1987 from the Lower Eocene of China; and *H. serus* Matthew et Granger, 1925 from the Middle Eocene of China (Matthew and Granger, 1925; Szalay and Gould, 1966; Szalay, 1969; Ting and Li, 1987; Zhou and Gingerich, 1991; O'Leary and Rose, 1995). In addition, *Hapalodectes* sp. was discovered in the Lower Eocene of Mongolia (Dashzeveg, 1982) and *H. ? serus* was found in the Middle Eocene of China (Qi, 1987). *?Hapalodectes auctus* Matthew et Granger, 1925 from the Middle Eocene of China was referred to the genus *Mongoloryctes* Van Valen, 1966 (Didymoconidae) and *H. lushiensis* Chow, 1965 from the Late Eocene of China was referred to the genus *Lohoodon* Chow, Li, et Chang, 1978 (Mesonychidae). Late Paleocene *?Hapalodectes* sp. from China (Zhang et al., 1979) is currently treated as Mesonychidae (Ting and Li, 1987).

The second hapalodectid genus, *Hapalorestes* Gunnell et Gingerich, 1996, was discovered at the bottom of the Middle Eocene of North America. The only member of this genus, *H. lovei*, is more than twice as large as the largest species of *Hapalodectes*, *H. leptognathus* and *H. serus* (Gunnell and Gingerich, 1996). The Early Paleogene Asiatic genera *Plagiocristodon* Chow et Qi, 1979, *Metahapalodectes* Dashzeveg, 1976, and *Lohoodon* Chow et al., 1978 were originally placed in Hapalodectinae, but are currently assigned to Mesonychidae (Ting and Li, 1987; Ting, 1998; Meng et al., 1998).

Based on its unique dental structure, Szalay and Gould (1966) proposed ranking *Hapalodectes* as a sep-

arate subfamily of Mesonychidae. Ting and Li (1987) examined the skull structure of *H. hetangensis* and concluded that *Hapalodectes* should be regarded as a member of a separate family that is strongly distinct from Mesonychidae.

The type species *H. leptognathus* from the Middle–Late Wasatchian (zones Wa-4–Wa-7) is characterized by its relatively large size and the presence of rudimentary metaconids on the lower molars. The teeth of *H. serus* lack the metaconid. The most primitive structure of the lower molars occurs in the smallest species, the Asiatic *H. hetangensis* (Early Bumbanian, *Orientalophus* Zone), which is characterized by a distinct metaconid possessing a detached apex (Ting and Li, 1987, p. 166, fig. 4). The molars of *H. anthracinus* of comparable geological age (Early Wasatchian, Wa-1 Zone) had already lost the metaconid (Zhou and Gingerich, 1991; O'Leary and Rose, 1995). Consequently, the first adaptive radiation of the genus probably occurred as early as the Paleocene.

A remarkable confirmation of this assumption is the finding of Late Paleocene *Hapalodectes* from Mongolia described below. The specimen came from the Zhigden Member of the Naran Bulak Formation of the Tsagan-Khushu locality (collected by V.Yu. Reshetov in 1987). The Zhigden Member is dated at the end of the Late Paleocene, and the fauna is assigned to the Gashatan Asian Land Mammal Age (Badamgarav and Reshetov, 1985; Ting, 1998).

SYSTEMATIC PALEONTOLOGY

Order Mesonychia Matthew, 1909

Family Hapalodectidae Szalay et Gould, 1966

Genus *Hapalodectes* Matthew, 1909

Hapalodectes dux Lopatin, sp. nov.

Etymology. From Latin *dux* (leader).

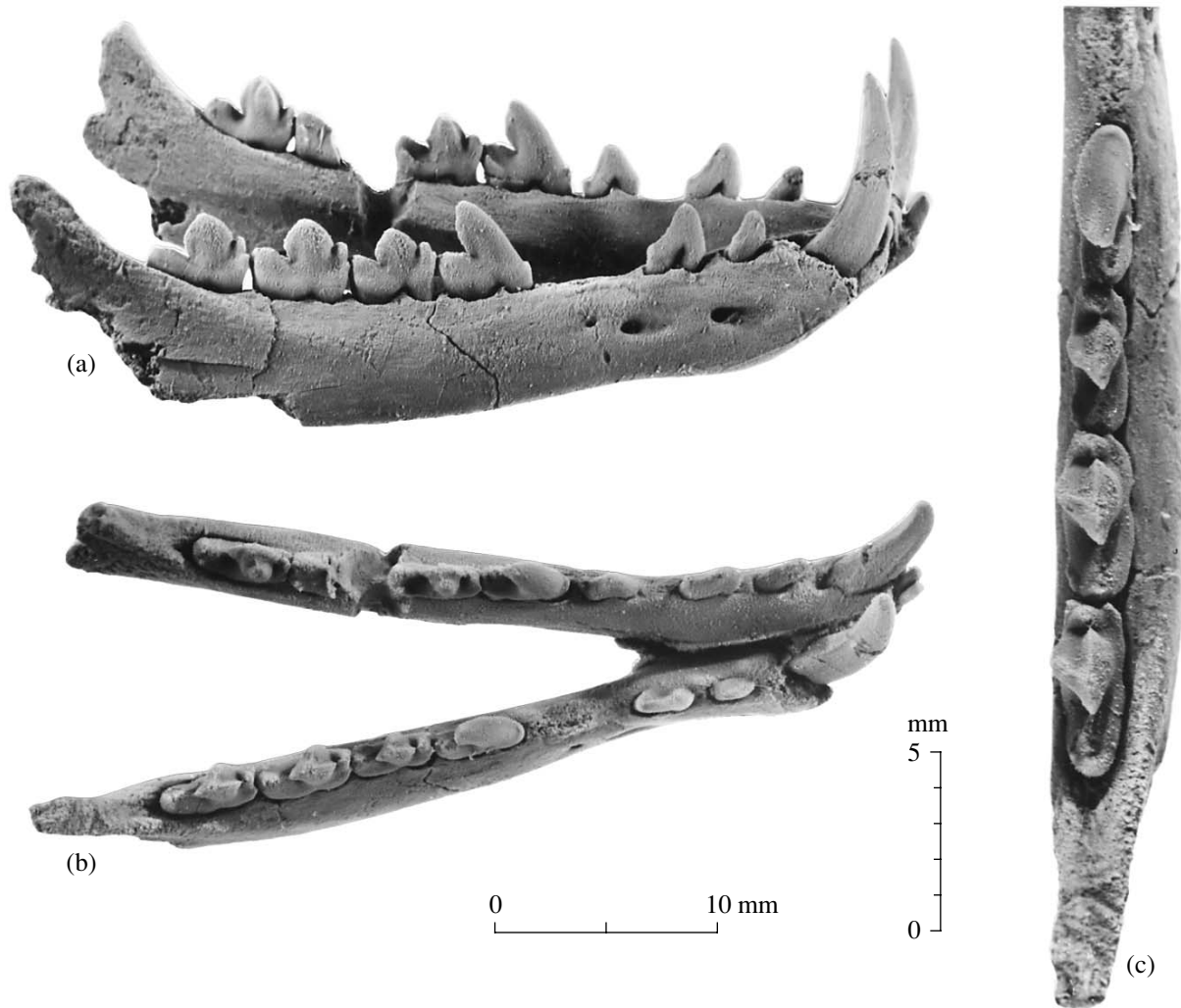


Fig. 1. *Hapalodectes dux* sp. nov., holotype, PIN, no. 3104/371, lower jaw: (a) right lateral view; (b) occlusal view; and (c) right P_4 – M_3 , occlusal view.

Holotype. PIN, no. 3104/371, lower jaw with complete tooth rows; South Mongolia, Tsagan-Khushu; Upper Paleocene, Naran Bulak Formation, Zhigden Member.

Description (Figs. 1 and 2). The lower jaw is deformed, the rami are isolated at the symphysis and slightly displaced from each other in the vertical and horizontal planes. The ascending ramus is broken off. The tooth rows are well preserved; on the left side, the I_3 crown and the trigonid of M_2 are broken off.

The species is a medium-sized member of the genus, and the reconstructed skull is approximately 65 mm long. The mandibular body is narrow. The angle between the jaw rami is approximately 25° . The ascending ramus only gently slopes at the base. The masseteric fossa is superficial. The horizontal ramus is low and narrow (the maximum depth is under M_3), and relatively strongly curved lingually at the interval between P_2 and P_3 . On the lingual surface of the hori-

zontal ramus, there is a wide longitudinal groove (probably for the attachment of the mylohyoideus muscle), extending from the P_3 level to the level of the posterior edge of M_2 . The symphysis is long and weak and reaches the level of the posterior edge of P_2 . There are three mental foramina; the anterior foramen is located under the interval between P_1 and P_2 , the middle foramen is under the interval between P_2 and P_3 , and the posterior foramen is under the middle of P_3 or under the interval between P_3 and P_4 . An additional small foramen is on the anterior side of each jaw ramus under I_2 .

The dental formula of the lower jaw is $I_3C_1P_4M_3$. The incisors are located near the anterior base of the canines and form an arch projecting weakly anteriorly. $I_1 < I_2 > I_3$. The crowns are small, chisel-shaped, and lacking heels; the anterior surface is convex; the posterior surface is flattened.

The canine is relatively large, narrow, and long. It curves strongly and is transversely slightly com-

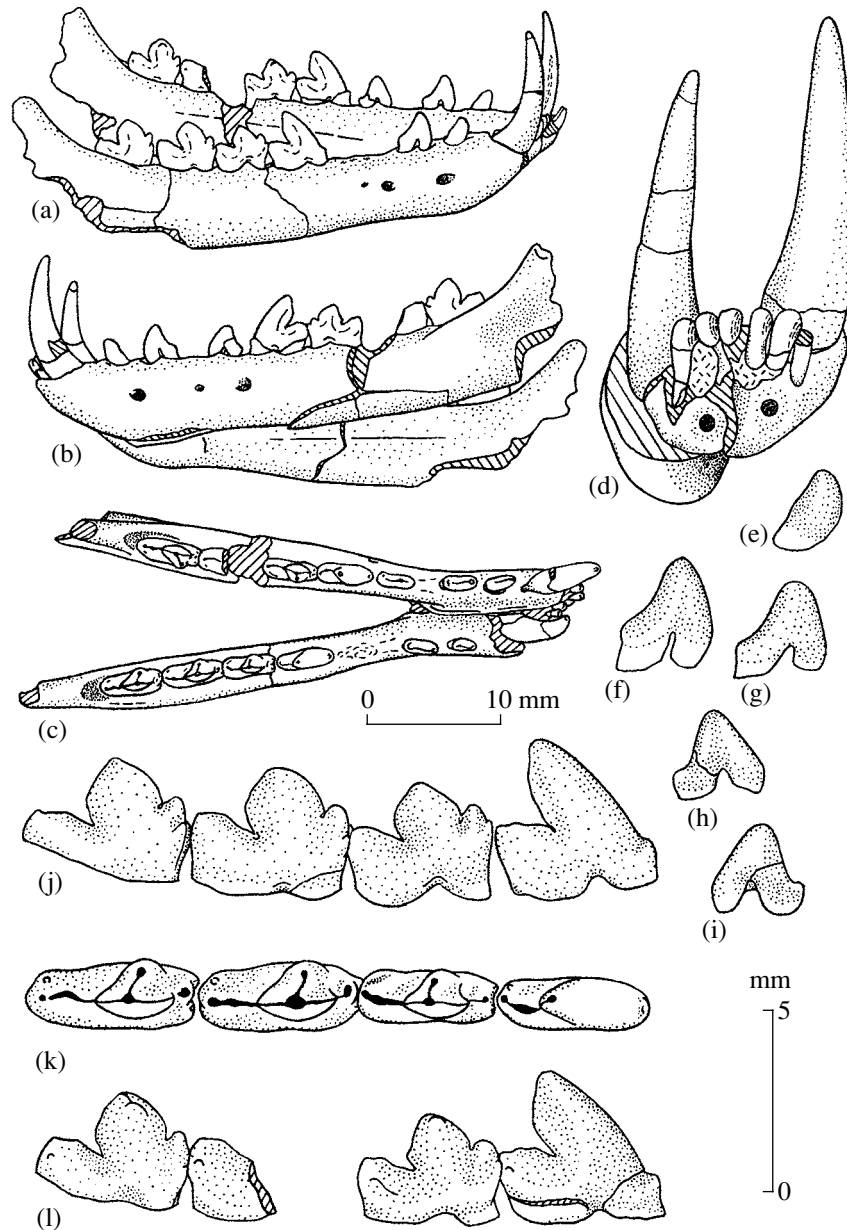


Fig. 2. *Hapalodectes dux* sp. nov., holotype, PIN, no. 3104/371, lower jaw: (a) right and (b) left lateral views, (c) occlusal view; (d) incisors and canines, front view; (e) right P_1 , labial view; (f) right P_2 , labial view; (g) left P_2 , lingual view; (h, i) left P_3 : (h) lingual and (i) labial views; (j, k) right P_4 – M_3 : (j) labial and (k) occlusal views; and (l) left P_4 – M_3 , lingual view.

pressed. The posterior crest is weak. The canine is weakly inclined anteriorly at the base, as are the incisors. Behind the canine, the upper part of its alveolus extends posteriorly and looks like a small, narrow superficial fossa. The canine and premolars (except for P_4 , adjoining M_1) are separated from each other by intervals, the longest of which is between P_2 and P_3 .

P_1 is small and single-rooted; the crown is strongly compressed transversely and weakly inclined anteriorly. P_2 is substantially larger than P_1 and double-rooted. The protoconid is inclined somewhat anteriorly; the apex is on a level with the anterior root, and

the anterior slope is very abrupt. The heel is short and bears a small cusplule at the posterior edge. P_3 is similar to P_2 in shape and size but differs by a better developed posterior cusp, the position of the protoconid apex above the middle of the tooth, and, consequently, by a more gentle anterior slope. It is only slightly lower than P_2 .

P_4 is semimolariform, relatively large and high, and substantially higher than the molars. It bears an extremely small anterior basal cusp, a rudimentary paraconid; a stout protoconid that is strongly inclined posteriorly; and a narrow trenchant talonid possessing two cusps, i.e., the hypoconid located in the middle of

Table 1. Cheek teeth measurements

Tooth	P ₁		P ₂		P ₃	P ₄		M ₁		M ₂	M ₃	
	sin	dex	sin	dex	sin	sin	dex	sin	dex	dex	sin	dex
Length	1.7	1.7	2.55	2.5	2.6	4.2	4.2	4.1	4.0	4.5	4.4	4.5
Width	0.9	0.95	1.05	1.0	1.05	1.5	1.5	1.4	1.5	1.65	1.65	1.65
Height	2.0	2.1	2.8	3.0	2.5	4.2	4.4	3.2	3.3	3.5	3.2	3.4

the shearing crest and a very small hypoconulid located at the posterior edge of the talonid. Substantially below the shearing crest, the posterolingual side of the talonid bears a weak prominence, a rudimentary entoconid. There is a well-pronounced notch between the protoconid and the talonid.

The molars are similar in structure. M₁ is substantially shorter than M₂ (or M₃), and M₂ and M₃ are equal in length. The protoconid is the most massive and highest cusp, characterized by peculiar lanceolate outlines of the labial side. The preprotocristid and postprotocristid are stout and positioned almost at right angles to each other. At the base, the protoconid closely adjoins a relatively small but distinct metaconid with a detached apex; the latter is displaced somewhat anteriorly in relation to the apex of the protoconid. The apices of the protoconid and metaconid are connected by a weak protocristid. On M₂ and M₃, the metaconid is developed to a greater extent than on M₁, i.e., it is larger, better detached, and more strongly displaced anteriorly. The protoconid–metaconid region is isolated from the paraconid and talonid by deep notches. The paraconid is as massive as the metaconid (it is somewhat larger on M₁). There are two small additional cusps at the base of the paraconid on the anterolabial and anterolingual sides. A well developed reentrant groove extends between them on the anterior surface of the crown. The posterior projection of the talonid of the preceding tooth enters the groove. This structure provides functional unity of the P₄–M₃ row and, hence, gives the teeth an increased resistance to lateral loading as a food object is cut. As in P₄, the stout shearing crest of the talonid includes the hypoconid and a reduced hypoconulid. The entoconid is rudimentary and appears as a tiny cuspule on M₂ and M₃; on M₁, it is a weak expansion that substantially extends anteriorly like a narrow cingulid.

Measurements, mm. Length of tooth rows: I₁–M₃, 34.0; C–M₃, 33.0; and P₄–M₃, 18.0.

Incisor measurements, length × width, (sin) left and (dex) right: I₁, 0.6 × 0.65 (sin and dex); I₂, 0.65 × 0.65 (sin) and 0.7 × 0.65 (dex); and I₃, 0.55 × 0.52 (dex).

Canine measurements: straight line labial length, 8.9 (sin) and 9.0 (dex); diameters at the base, 2.6 × 1.75 (sin) and 2.5 × 1.7 (dex).

Cheek teeth measurements are shown in Table 1.

The depth of the horizontal ramus under P₁–P₂ is 5.5; under P₃, 5.0–5.1; under P₄, 5.5; under M₁–M₂, 5.7;

and under M₃, 6.0. Thickness at P₃ is 2.3; at P₄, 2.8; at M₁, 3.0; at M₂, 3.2; and at M₃, 3.0.

The jaw width in the symphysis at P₁ is approximately 6.0; at the talonids of M₃, it is approximately 14.0.

Comparison. The new species is clearly distinguished from other species of the genus by the ratio of molar measurements (Table 2), especially by the equal lengths of M₂ and M₃ (in *H. anthracinus* and *H. leptognathus*, M₃ is strongly increased; in *H. hetangensis*, it is reduced). The presence of a rudimentary paraconid on P₄ distinguishes *H. dux* from *H. hetangensis*. A well developed metaconid on M₁–M₃ distinguishes it from *H. leptognathus*, *H. serus*, and *H. anthracinus*. The new species is approximately 1.3 times larger than *H. hetangensis*, but substantially smaller than *H. serus* and *H. leptognathus* (Table 2).

Remarks. Since the specimen is well preserved, the complete formula of the lower teeth of Hapalodectidae is established with certainty for the first time, I₃C₁P₄M₃. Previously, the number of incisors in *Hapalodectes* was not known, although Ting and Li (1987) proposed that there were three pairs.

In the right jaw ramus, P₃ and its alveoli are absent; however, there is surface roughness and small superficial depressions in their place, i.e., obvious traces of overgrown alveoli. A radiographic examination has shown the presence of the P₃ alveoli inside the bone. They are filled with porous bone tissue and completely overgrown not only in the dorsal part but also in the ventral part, since they are isolated from the mandibular canal. The abnormal absence of teeth is frequently observed in Recent mammals (Miles and Grigson, 1990; Vilà *et al.*, 1993) and was also recorded in fossil mammals (Wilson, 1955; Palmqvist *et al.*, 1999). This is caused by genetic (for example, oligodonty and anodonty; expressed as the absence of tooth primordia) or mechanical factors (loss of a damaged or diseased tooth and subsequent alveolus overgrowth). In the latter case, as a tooth is lost, its alveoli are filled by porous bony tissue and completely obliterated externally in the course of reossification (Vilà *et al.*, 1993; Palmqvist *et al.*, 1999), as in *H. dux*. Consequently, the absence of the right P₃ alveoli observed in the holotype of *H. dux* is caused by overgrowth after the loss of the tooth during the animal's life rather than by a genetic anomaly.

Gunnell and Gingerich (1996) estimated the body weight of hapalodectids using the formula proposed by

Table 2. Comparisons of measurements and structure of P₄-M₃ in *Hapalodectes*; the data on previously described species are given after Ting and Li (1987), Zhou and Gingerich (1991), and O'Leary and Rose (1995)

Parameter	<i>H. dux</i>	<i>H. hetangensis</i>	<i>H. anthracinus</i>	<i>H. leptognathus</i>	<i>H. serus</i>
P ₄ length, mm	4.2	3.7	5.34	4.97–5.64	?
M ₁ length, mm	4.0–4.1	3.0–3.3	4.05–4.14	4.83–5.09	?
M ₂ length, mm	4.5	3.1–3.4	4.7–4.88	5.4–6.01	5.51
M ₃ length, mm	4.4–4.5	3.1	?, > M ₂	5.9–6.37	?*
M ₁ /P ₄ , %	95–98	81–89	76–77.5	87.5–98	?
M ₂ /M ₁ , %	110–112.5	103	116–118	112–119	?
M ₃ /M ₂ , %	98–100	91	?, > 100	106–110	?**
Formula	P ₄ ≈ M ₁ < M ₂ = M ₃	P ₄ > M ₁ ≈ M ₂ > M ₃	P ₄ ≫ M ₁ ≪ M ₂ < M ₃	P ₄ > M ₁ ≪ M ₂ < M ₃	?
Paraconid of P ₄	+	–	+	+	?
Metaconid of M ₁ -M ₃	+	+	–	+–	–
Entoconid of M ₁ -M ₃	+	+	–	+–	–

* Isolated M₃, described by Dashzeveg (1976) from the Irdyn Manha locality (Inner Mongolia, China) as a tooth belonging to *H. serus*, extremely large, 14.5 mm long, 6.5 mm wide, and about 12 mm high; judging by the structure, belongs neither to this species nor to the family Hapalodectidae.

** M₂ of *Hapalodectes? serus* from the Arshanto Fauna (Middle Eocene of China), incompletely preserved, reconstructed tooth is about 5.3 mm long (Qi, 1987); judging by the alveoli, M₂ > M₃; however, the form cannot be assigned to *H. serus* with certainty because of poor preservation.

Zhou, $Y = 1.327 \cdot X - 3.355$, where $X = \ln(L \times B)$ (L is M₂ length, B is M₂ width, mm) and $Y = \ln W$ (weight, kg). They estimated that *Hapalodectes leptognathus* and *H. serus* weighed 0.7 to 1.1 kg (on average, 0.9 kg) and *Hapalodectes lovei* weighed approximately 8 kg. I applied this formula to the other species of *Hapalodectes* and was able to estimate that *H. dux* and *H. anthracinus* weighed approximately 0.5 kg, and *H. hetangensis* weighed approximately 0.2 kg.

The narrow cutting lower molars and long, narrow canines of *Hapalodectes* allow one to propose that this was an active highly-specialized predator (Szalay and Gould, 1966; Szalay, 1969). The structure of the postcranial skeleton suggests terrestrial locomotion, but limited adaptations to running (Zhou and Beard, 1993; O'Leary, 1998). Recent Carnivora in the 0.1–0.5 kg weight range include the mustelids *Mustela* and *Poecilictis*. The 0.5–1.0 kg weight range includes the procyonids *Bassariscus* and *Bassaricyon*, and many small mustelids and viverrids (Strel'nikov, 1970).

M a t e r i a l. Holotype.

DISCUSSION

Hapalodectes dux is the earliest known member of the genus and the family. This find extends the lower boundary of the time distribution of Hapalodectidae to the Late Paleocene and give evidence for their Asian origin.

The analysis of tooth characters (Table 2) shows that *H. dux* is the most primitive known species of *Hapalodectes*. Primitive molar features of *H. dux* include (1) equal measurements of M₂ and M₃; (2) a well-pro-

nounced metaconid bearing the protocristid; (3) relatively large additional cusps in front of the paraconid; and (4) the presence of rudimentary cuspules of the talonid, hypoconulid, and entoconid. The relatively small size and the presence of a rudimentary paraconid on P₄ are probably plesiomorphic features of the genus.

An increase in the measurements of M₃ in relation to those of M₂ is observed in *H. leptognathus* and is associated with a general increase in size. On the contrary, in a very small *H. hetangensis*, M₃ is shorter than M₂. The identical size of two posterior molars is probably a primitive condition of *Hapalodectes*; an increase or reduction of M₃ is probably associated with changes in general body size.

The metaconid is well pronounced in *H. hetangensis*; strongly reduced (occasionally absent) in *H. leptognathus*, and absent in *H. anthracinus* and *H. serus*. Additional cuspsules ahead of the paraconid are well developed in *H. hetangensis*. In the other species, they look like crests of bifurcate preparacristids. In addition to *H. dux*, a rudimentary entoconid is present in *H. hetangensis* and, occasionally, in *H. leptognathus*. A residual hypoconulid occurs in *H. hetangensis*. A rudimentary paraconid on P₄ is developed in all species, except for *H. hetangensis* (P₄ of *H. serus* was not found).

Thus, *H. dux* is a plesiomorphic taxon in relation to all Eocene species of *Hapalodectes* and may be their common ancestor. However, the existence of at least three species of *Hapalodectes* of various extent of morphological advantage (*H. hetangensis* in Asia and *H. anthracinus* and *H. leptognathus* in North America) in the Early Eocene requires explanation.

H. hetangensis is almost as primitive as *H. dux*, and is distinguished by its small size, reduced M_3 , and the absence of a paraconid on P_4 . It is reasonable to consider this form as a miniaturized descendant of *H. dux*.

In North America, the most probable descendant of *H. dux* is the relatively large *H. leptognathus* characterized by the rudimentary metaconid and entoconid of the lower molars. The earlier *H. anthracinus* (presumably contemporary with *H. hetangensis* and only a little later than *H. dux*) had already lost the metaconid and entoconid on the teeth. Therefore, it should be related to a species that was more advanced with reference to the reduction of these cusps. Consequently, *H. anthracinus* should be excluded from the presumable descendants of *H. dux* and assigned to a hypothetical lineage that deviated as a result of an earlier adaptive radiation.

However, Beard (1998) proposed that in the commonly accepted scheme of correlation between Asian and North American Early Paleogene Land Mammal Ages (Dashzeveg, 1982; Ting, 1998; Wang *et al.*, 1998), the ages of the Gashatan and Bumbanian are strongly underestimated (Gashatan = Clarkforkian and Bumbanian = Wasatchian). Beard compared the Gashatan to the second half of the Tiffanian and the beginning of the Clarkforkian (Late Paleocene) and correlated the Bumbanian with the Late Clarkforkian and Early Wasatchian (the end of the Paleocene and the beginning of the Eocene). If this is the case, *H. dux* and *H. hetangensis* become earlier in relation to *H. anthracinus* and *H. leptognathus*; this agrees with the substantially more primitive dental structure in these forms and removes the above contradiction. Thus, one can propose that *H. anthracinus*, *H. leptognathus*, and *H. hetangensis* are descendants of *H. dux* but belong to different evolutionary lineages.

The simplified dental structure of *H. serus* indicates that it may be a descendant of the *H. anthracinus* lineage. On the other hand, it is not inconceivable that, in the Middle Eocene, the Asian forms of *Hapalodectes* independently reached the same level of specialization as the North American *H. anthracinus* did in the Early Eocene.

Mesonychians are considered to be the closest relatives of whales (Van Valen, 1966; Luo and Gingerich, 1999). McKenna and Bell (1997) have united the Mesonychia (Acrodi) and the Cetacea in the order Cete. It is suggested that the Cetacea deviated from the Mesonychia in the Early Eocene, approximately 54–55 Ma ago (Bajpai and Gingerich, 1998). Szalay (1969) believed that *Hapalodectes* and primitive whales are very close to their common ancestor. However, the cranial and dental structures of the earliest known Archaeoceti and Mesonychia show a closer affinity of the land ancestor of whales to the Mesonychidae than to the Hapalodectidae (Luo and Gingerich, 1999).

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