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EARLY WASATCHIAN, EARLY EOCENE, OF NORTHWESTERN WYOMING**

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# NEW SPECIES OF *HAPALODECTES* (MAMMALIA, MESONYCHIA) FROM THE EARLY WASATCHIAN, EARLY EOCENE, OF NORTHWESTERN WYOMING

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XIAOYUAN ZHOU and PHILIP D. GINGERICH

*Abstract.*— A new species, *Hapalodectes anthracinus*, is described from the early Wasatchian land-mammal age of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. This is the earliest North American species of *Hapalodectes*, and it appears to be the earliest hapalodectid mesonychian known anywhere. *Hapalodectes anthracinus* resembles Asian *H. serus* and differs from Asian *H. hetangensis* and North American *H. leptognathus* in lacking a metaconid on lower molars. It differs from *H. serus* in having a more vertically erect protoconid and in being significantly smaller.

## INTRODUCTION

Hapalodectidae are an extinct family of piscivorous and carnivorous mammals of uncertain affinities. They are known from the early through middle Eocene of Asia and from the early Eocene of North America. New specimens described below may be the earliest record of this family. They also provide new evidence of faunal interchange between Asia and North America during the Eocene epoch.

The first specimen of *Hapalodectes*, a portion of a small right dentary with broken P<sub>4</sub>-M<sub>1</sub> and complete M<sub>2</sub> (American Museum of Natural History [AMNH] specimen no. 78), was collected in "Graybull beds" of the Bighorn Basin. It was described as *Dissacus (Pachyaena) leptognathus* by Osborn and Wortman (1892) and classified in Mesonychidae. Matthew (1909) moved this species to *Hapalodectes*, then a new genus of Mesonychidae, and described three other dentaries from the Lysite member of the Wind River Basin as *H. compressus*, which is now considered a synonym of *H. leptognathus* (Szalay and Gould, 1966). *Hapalodectes* from Asia was first reported by Matthew and Granger (1925), who described the new species *H. serus*. Szalay and Gould (1966) erected the new mesonychid subfamily Hapalodectinae.

Some finely preserved specimens of *Hapalodectes* from China were recently described by Ting and Li (1987). These include a complete skull and lower jaws (Institute of Vertebrate Paleontology and Paleoanthropology [IVPP] specimens V5253) and a partial rostrum (IVPP 5254) found in the early Eocene Lingcha Formation. Ting and Li (1987) raised Hapalodectinae to familial level, and suggested that relationships between Hapalodectidae and Mesonychidae are probably more distant than previously thought. The stratigraphic and geographic distribution of *Hapalodectes*, as now known, is summarized in Table 1.

TABLE 1—Stratigraphic and geographical distribution of *Hapalodectes*

Age	NORTH AMERICA (Gingerich, 1989, 1991)		ASIA (Qi, 1989; Li, pers. comm., 1990)	
MIDDLE EOCENE	Late		Irdir Manha	<i>H. serus</i>
	Bridgerian		Arshanto	<i>H. ?serus</i> (Qi, 1987)
EARLY EOCENE	Late	{Wa-7 Lostcabinian		
	Wasatchian	{Wa-6 Lysitean	<i>H. leptognathus</i>	Yuhuangdin
		{Wa-5 L. Graybullian		Lingcha
	Middle	{Wa-4 M. Graybullian	-----	-----
		{Wa-3 E. Graybullian		Wutu
	Early	{Wa-2 L. Sandcouleean		
	{Wa-1 M. Sandcouleean	<i>H. anthracinus</i>	Naran Bulak	
	{Wa-0 E. Sandcouleean			
PALEOCENE			Chijiang	? <i>Hapalodectes</i> sp. (Zhang et al., 1979)

## SYSTEMATIC PALEONTOLOGY

Hapalodectids share a number of dental features with mesonychids, including: premolariform lower cheek teeth, crested talonids, and protoconids the tallest and most prominent cusps on lower cheek teeth (Szalay and Gould, 1966). Hapalodectids differ from mesonychids in having lower cheek teeth highly compressed and transformed into trenchant blades, and they also differ from mesonychids in being smaller. In addition, a hypocone is present on upper molars of Hapalodectidae.

Order CONDYLARTHRA Cope, 1881

Suborder MESONYCHIA Van Valen, 1969

Family HAPALODECTIDAE (Szalay and Gould) Ting and Li, 1987

*Hapalodectes* Mathew, 1909

*Hapalodectes anthracinus*, new species

Fig. 1

*Holotype*.—UM 87491, isolated right M<sub>2</sub>.

*Type locality*.—UM Locality MP-3 in the Willwood Formation, SW 1/4, Section 20, T54N, R100W, in the Bighorn Basin, Park Co., Wyoming.

*Age and distribution*.—Early Eocene (early Wasatchian land-mammal age) of northwestern Wyoming.

*Hypodigm*.—Holotype; and UM 80833, a left mandible with P<sub>4</sub>-M<sub>1</sub> from UM locality SC-4 in the Willwood Formation of the Clarks Fork Basin, Wyoming.

*Etymology*.—Latin *anthracinus*, coal-black, in reference to the black color of the type specimen.

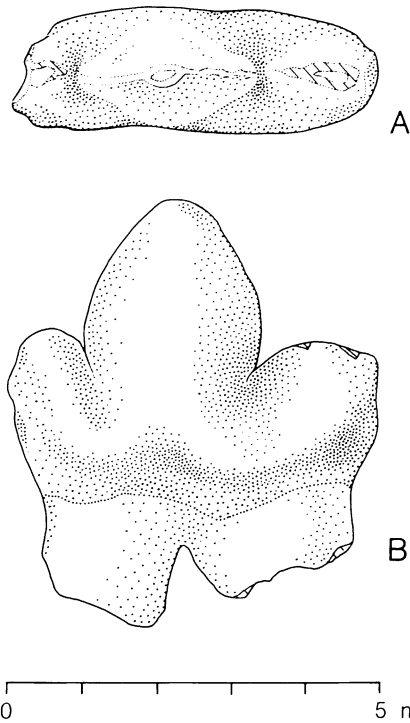


FIG. 1— Right lower molar ( $M_2$ ) of *Hapalodectes anthracinus*, UM 87491 (holotype) from McCullough Peaks locality MP-3. A, occlusal view. B, lingual view. Note absence of metaconid.

*Diagnosis.*—Differs from North American *H. leptognathus* in having lower molars 15-16% shorter and lacking a metaconid. Differs from Asian *H. serus* in having lower molars about 11-12% shorter, with a more vertically erect and relatively higher protoconid.

*Description.*—The holotype of *Hapalodectes anthracinus* from the northern Bighorn Basin is a well-preserved  $M_2$ , with a narrow laterally-compressed crown and a well-defined re-entrant groove on the anterior surface of the tooth (Fig. 1). The latter was considered by Ting and Li (1987) as a typical character for molars of *Hapalodectes*. The protoconid is large and sectorial, with no trace of an accessory metaconid cusp. There is a small basal cusp (paraconid) anterior to the protoconid, and a larger trenchant talonid cusp (hypoconid) posterior to the protoconid.

The referred specimen from the Clarks Fork Basin is a left dentary with two broken teeth,  $P_4$ - $M_1$ .  $M_1$  is small (Table 2), the protoconid is broken so that it is impossible to know whether a metaconid was present or not; the talonid of  $M_1$  in this specimen also lacks the rudimentary cusplule lingual to the hypoconid found in other *Hapalodectes*. There is a clear re-entrant groove on the anterior surface of the tooth.  $P_4$  has a small paraconid, resembling that of *H. leptognathus* but differing from *H. hetangensis* which does not have a paraconid on  $P_4$ . In *H. anthracinus*,  $P_4$  is larger than  $M_1$ , the same is true for *H. hetangensis* and *H. leptognathus* (Table 2).

*Discussion.*—The holotype  $M_2$  is very similar to the type specimen of *H. serus* (Matthew and Granger, 1925; Szalay and Gould, 1966), except that the new specimen has a relatively higher, more vertically erect protoconid, and it is 11-12% shorter anteroposteriorly (Table 2). The new specimen is older geologically and it is remote geographically from *H. serus* (Table 1). *Hapalodectes anthracinus* does not have the metaconid on lower molars characteristic of *H. leptognathus* and *H. hetangensis*. The talonid of *H. anthracinus* lacks a rudimentary cusplule (vestigial entoconid?) lingual to the hypoconid, which is present in *H. hetangensis* and

TABLE 2—Measurements of teeth of *Hapalodectes* species. Length (L), width (W), and height (H) are maximum crown dimensions (H measured on buccal side of tooth). All measurements in mm.

Specimen	P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>		
	L	W	H	L	W	H	L	W	H	L	W	H
<i>Hapalodectes anthracinus</i>												
UM 80833	5.34	1.70	--	4.14	1.70	--	--	--	--	--	--	--
UM 87491 (holotype)	--	--	--	--	--	--	4.88	1.60	4.19	--	--	--
<i>Hapalodectes leptognathus</i>												
AMNH 78 (holotype)	5.64	1.87	--	5.09	--	--	5.76	2.33	4.93	--	--	--
AMNH 12781 (type <i>H. compressus</i> )	--	--	--	--	--	--	--	2.08	--	6.02	2.12	5.05
AMNH 12782	5.52	--	--	4.83	--	--	5.40	1.81	--	--	--	--
AMNH 12783	--	--	--	--	1.80	--	6.01	2.10	--	--	--	--
AMNH 14748 (left)	4.97	1.60	--	4.88	--	--	5.81	1.97	4.99	6.37	1.88	--
	[P <sub>2</sub> =	3.25	1.24	-- ]								
AMNH 14748 (right)	--	--	--	--	--	--	5.64	1.95	--	6.00	1.96	5.86
AMNH 39299	5.60	--	--	--	--	--	--	--	--	5.90	1.84	--
AMNH 39300 (left)	--	--	--	--	--	--	5.80	2.12	--	--	2.24	--
AMNH 39300 (right)	5.61	1.80	--	4.96	--	--	5.59	1.96	--	--	--	--
UM 82513	--	--	--	--	1.60	--	--	1.96	4.92	--	--	--
<i>Hapalodectes serus</i>												
AMNH 20172	--	--	--	--	--	--	5.51	2.05	4.48	--	--	--
<i>Hapalodectes hetangensis</i>												
IVPP V5253 (r, Li and Ting, 1987)	3.7	0.7	--	3.3	1.0	--	3.4	1.1	--	3.1	--	--
IVPP V5253 (left)	--	--	--	3.0	1.1	--	3.1	1.1	--	--	--	--
? <i>Hapalodectes</i> sp.												
IVPP V5038 (Zhang et al., 1978)	[P <sub>3</sub> =	7.0	2.8	-- ]								

some specimens of *H. leptognathus*. The new species is smaller than *H. leptognathus*, but larger than *H. hetangensis*.

The new materials are from zones Wa-1 and Wa-2 (or middle and late Sandcouleean) of the Wasatchian early Eocene (Table 1). The faunal list for the type locality, UM locality MP-3 in the northern Bighorn Basin, is as follows: *Palaeoryctes* sp., *Ignacius graybullianus*, *Cantius ralstoni* or *C. mckennai*, *Esthonyx spatularius*, *Hyopsodus loomisi*, *Ectocion osbornianus*, *Phenacodus* sp., *Hapalodectes anthracinus* n. sp., *Miacis* sp., *Diacodexis metsiacus*, *Hyracotherium grangeri*, and *Coryphodon* sp. The associated fauna indicates that the holotype came from zone Wa-1 or Wa-2, probably the latter. The referred specimen from the Clarks Fork Basin is definitely from zone Wa-1. The new species is earlier than all known *H. leptognathus*, the earliest record of which is middle or late Graybullian (if AMNH 78 and 79 are Graybullian in age, their white color indicates that they are from the upper part of the Graybull beds).

*H. anthracinus* appeared much earlier than *H. serus*, which appeared in late Bridgerian-equivalent time, with a possible occurrence in early Bridgerian-equivalent time (Qi, 1987). *H. hetangensis* comes from the Lingcha Formation, Hengdong County, Hunan, China. The Lingcha Formation was considered to be Cuisian or Sparnacian (Li et al., 1979). Later, Li and Ting (1983) considered the Lingcha Formation and Wutu Formation as Wasatchian equivalents. Russell and Zhai (1987) gave an upper limit for the Lingcha fauna as Cuisian and considered that they can be approximately correlated with Yuhuangding Formation, etc. Li (personal communication, 1990) prefers to put it in the way that is shown in Table 1, where the Lingcha Formation might be younger than the Wutu Formation, and both are possibly correlated with the Graybullian. As *H. anthracinus* appeared early in the Wasatchian, by the middle Sand-

couleean, this new species is probably the earliest record of *Hapalodectes*, and it may be as much as a million years older than *H. hetangensis*.

*Hapalodectes leptognathus* (Osborn and Wortman, 1892)

UM 82513 is from UM locality MP-6, of late Graybullian age, in the northern Bighorn Basin. This specimen has two broken teeth, a talonid of left  $M_1$  and a trigonid of left  $M_2$ . There is a clear re-entrant groove on the anterior surface of the trigonid of  $M_2$ , and a metaconid is present. *H. leptognathus* ranges from middle or late Graybullian to Lostcabinian in age, spanning about half of Wasatchian time.

#### DISCUSSION

*Hapalodectes anthracinus* is probably the earliest record of *Hapalodectes* known anywhere, and it provides additional evidence of faunal interchange between Asia and North America during early Eocene time. However, *Hapalodectes* species are always rare faunal elements, and we can as yet say little about their true temporal range or geographic dispersal.

*Hapalodectes serus* is found in Irudin Manha beds of Asia, which is probably late Bridgerian-equivalent in age (Qi, 1987); *H. ?serus* (Qi, 1987) is represented by a broken lower jaw with broken teeth from Arshanto beds, probably early Bridgerian-equivalent in age (Table 1). The absence of a metaconid on the lower molars is considered to be a derived character (Szalay, 1969a; Ting and Li, 1987), therefore *Hapalodectes anthracinus* might be closer to *H. serus* than it is to *H. hetangensis* and to *H. leptognathus*. The new species and *H. serus* may represent one lineage, without a metaconid on lower molars at least from the beginning of Eocene. This explanation favors a faunal interchange between North America and Asia during early to middle Eocene time. If this is one lineage, it exhibits some trend toward larger size.

*Lohoodon* (Chow et al., 1978), *Plagiocristodon* (Chow and Qi, 1978), *Metahapalodectes* (Dashzeveg, 1976), and *?Hapalodectes* (Zheng et al., 1979) are considered members of Mesonychidae, not Hapalodectidae, because they all lack a re-entrant groove on the anterior surface of lower molars (Ting and Li, 1987). Thus Hapalodectidae includes only one genus, *Hapalodectes*, with four species: *H. anthracinus*, *H. hetangensis*, *H. leptognathus*, and *H. serus*, ranging from early Wasatchian to Bridgerian-equivalent in age. It is worth noting that *?Hapalodectes* (Zheng et al., 1979) is represented by a possible  $P_3$  with a length of 7.0 mm (Table 2). Ting and Li (1987) considered that it is better to refer the tooth to *?Dissacus*, but the size is very small for *Dissacus* so we still list the specimen as a possible Paleocene hapalodectid (Table 1).

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