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NEW HAPALODECTID *HAPALORESTES LOVEI* (MAMMALIA, MESONYCHIA) FROM THE EARLY MIDDLE EOCENE OF NORTHWESTERN WYOMING

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Abstract—A new mesonychian, *Hapalorestes lovei*, is described on the basis of three associated teeth from the Bridgerian (early middle Eocene) Aycross Formation of the southern Absaroka Range in northwestern Wyoming. These show the anteroposteriorly long and buccolingually broad lingual shelf for the protocone on upper molars, and the buccolingually compressed and sharply sectorial crowns of lower cheek teeth with lanceolate or diamond-shaped protoconids characteristic of hapalodectids. Tooth size and estimated body size (ca. 8 kg) indicate that *H. lovei* is intermediate in size and partially fills a long-standing gap between the size distributions of hapalodectids and mesonychids. *H. lovei* is interpreted as being part of an as yet poorly sampled upland fauna.

INTRODUCTION

There is great interest in the morphological diversity and evolutionary history of mammalian Mesonychia, a subgroup of archaic ungulates that is usually classified, following Van Valen (1969, 1978), within the order Condylarthra. Alternatively, this subgroup is sometimes classified as an order by itself (e.g., Order Acreodi following McKenna, 1975; or Order Mesonychia of others). Interest in Mesonychia is due in part to their unusual dental morphology and in part to their postulated ancestral relationship to archaeocete cetaceans (Van Valen, 1966; Gingerich et al., 1983; Thewissen, 1994; Zhou, 1995; Gingerich and Uhen, 1997). Mesonychia includes two, three, or possibly four families: Mesonychidae, Hapalodectidae, Andrewsarchidae(?), and Wyolestidae(?). These were all ranked as subfamilies until discovery of a well preserved skull of *Hapalodectes* (Ting and Li, 1987), which prompted Ting and Li to raise Hapalodectinae to family level. Cetaceans are usually thought to have originated from Mesonychidae, but Szalay (1969) suggested Hapalodectidae as the stem group.

Several new mesonychid species have been described in recent years from the early Eocene of the Bighorn Basin in northwestern Wyoming (Zhou and Gingerich, 1991; O'Leary and Rose, 1995). These are all referred to long-known genera of Hapalodectidae or Mesonychidae, which are easily distinguished from each other on the basis of size and dental morphology. Hapalodectids, as a rule, are small and have sharply sectorial premolars and molars, while mesonychids, as a rule, are larger and have blunter crushing teeth (Zhou, 1995). Here we describe a new hapalodectid that overlaps species of the small mesonychid *Dissacus* in size.

However, the new form is clearly hapalodectid because of its distinctively buccolingually-compressed and sharply-sectorial lower cheek teeth.

ABBREVIATIONS

Institutional abbreviations used here are as follows:

- AMNH — American Museum of Natural History, New York
 UM — Museum of Paleontology, University of Michigan, Ann Arbor
 USGS — U.S. Geological Survey, Denver (now being transferred to USNM)
 USNM — U.S. National Museum, Washington

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA
 Order CONDYLARTHRA Cope, 1881
 Suborder MESONYCHIA Van Valen, 1969
 Family HAPALODECTIDAE Szalay and Gould, 1966

Hapalorestes lovei, new genus and species
 Figs. 1, 2B

Holotype.—UM 102686, little-worn left M^2 , right P_4 and M_2 (Fig. 1). Teeth of the type specimen were found together by C. G. Childress on June 26, 1996.

Type locality.—Flattop Quarry, USGS locality D-1033 of Bown (1982) in NE¼, NW¼, NE¼, Section 12, T43N, R101W, Hot Springs County, Wyoming. The specimen was found at UTM coordinates 667.862 km E and 4,842.047 km N (UTM gridzone 12T).

Diagnosis.—*Hapalorestes* is intermediate in size between typical hapalodectids as represented by *Hapalodectes* and typical mesonychids as represented by contemporary *Mesonyx* (Fig. 2). It is larger but otherwise most similar to *Hapalodectes*. It differs from *Hapalodectes* in the following features. In the upper dentition M^2 is more robust, with a basally inflated paracone and metacone. The metacone is positioned more lingually and not on the buccal margin of the tooth. The metastylar region is better developed, with a relatively broader metastylar shelf. The metastylar cusp is more anteriorly placed and not at the posterior-most edge of the tooth.

In the lower dentition P_4 has a protoconid shaped like the protoconids of molars; the protoconid is anteroposteriorly elongated and lanceolate or diamond-shaped rather than being anteroposteriorly shorter, broader, and more pillar-like. The protoconid on P_4 does not slope posteriorly as it does in *Hapalodectes* but rather is oriented vertically like the molar protoconids. The anterior basal cusp is larger and more robust. The crown of M_2 is a little broader buccolingually at its base than that of *Hapalodectes*. The preparacristid is longer and more curving. Viewed from the side, the preprotocristid and postprotocristid are almost straight and form a right angle rather than being curved and forming an acute angle.

Referred specimens.—None.

Age and distribution.—*Hapalorestes lovei* is known only from the Aycross Formation in the southern Absaroka Range bordering the Bighorn Basin of northwestern Wyoming. It is part of a Bridgerian land-mammal age fauna (early middle Eocene) and falls within biochron Br-2 within the Bridgerian.

Etymology.—*Hapalo*, delicate, and *orestes*, mountaineer (Gr., masc.); parallels *Hapalodectes* in acknowledging the delicate form of preserved teeth, while also alluding to a probable habitus in or bordering mountains. Species is named for Dr. David Love, native of Wyoming and

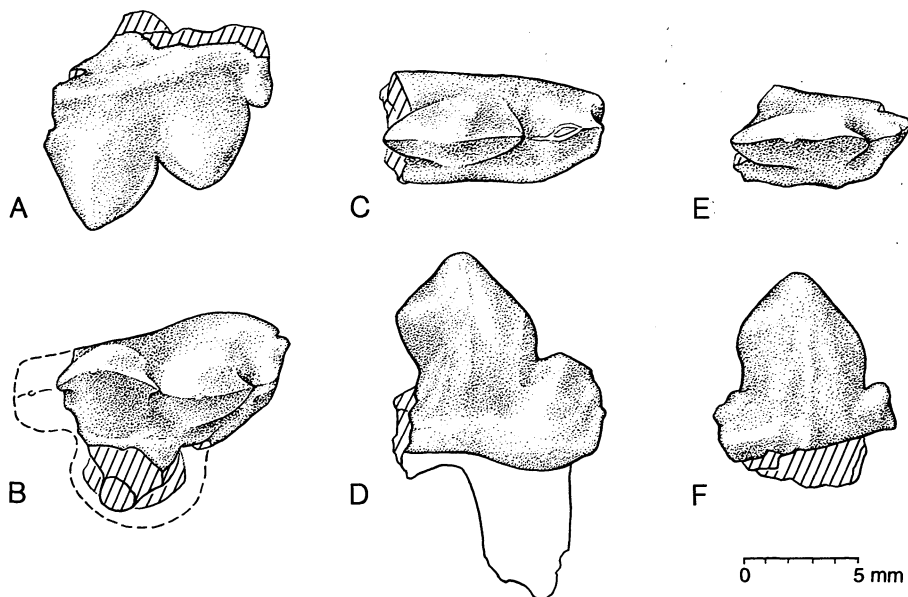


FIG. 1—Little-worn upper and lower cheek teeth of early middle Eocene *Hapalorestes lovei*, UM 102686 (holotype), from Flattop Quarry in the Aycross Formation of the southern Absaroka Range, Wyoming. A-B, left M^2 in buccal and occlusal views. C-D, right M_2 in occlusal and buccal views. E-F, right P_4 in occlusal and buccal views. Note the anteroposteriorly long protocone shelf on the lingual side of M^2 (dashed line in B surrounding preserved dentine core of tooth; presence of a distinct hypocone cannot be determined). Note also buccolingually compressed crowns of P_4 and M_2 (shown in E and C), metaconid near the apex of the protoconid on M_2 (in C), and anteroposteriorly-expanded but buccolingually-narrow lanceolate or diamond-shaped protoconids on lower cheek teeth (in D and F).

geologist of the Absaroka Mountains. Love is famous for ranging through the Absarokas in modern times as we imagine *Hapalorestes* did in the Eocene.

Description.—UM 102686 includes substantial parts of the crowns of left M^2 , right P_4 , and right M_2 . M^2 is broken anteriorly and lingually. The paracone is approximately twice the height of the metacone. Both the paracone and metacone are basally inflated and bluntly cusped. The paracone is positioned at the buccal margin of the tooth, while the metacone is placed more lingually such that a relatively well-developed sloping stylar shelf extends posterobuccally from the base of the metacone. The crown of M^2 is expanded posteriorly into a moderate metastylar shelf with a small bluntly-rounded metastylar cusp. The metastylar cusp is positioned directly behind the metacone, separated from the posterior margin of that cusp by a narrow valley. The postparacrista and premetacrista are buccolingually compressed, forming sharp cutting surfaces separated from each other by a narrow valley. The preparacrista and postmetacrista are more smoothly rounded and not as sharply defined. Although broken, it appears that the protocone was positioned directly lingual to the base of the paracone. The lingual shelf supporting the protocone is expanded like that of *Hapalodectes*, as evidenced by a well preserved surface of dentine, but this shelf appears to have been relatively shorter anteroposteriorly than that of *Hapalodectes*, and there may not have been a distinct hypocone (which is very small in *Hapalodectes* in any case). M^2 , as preserved, measures 10.3 mm in length and 8.1 mm in width across the dentine exposed on the lingual shelf, and we estimate that the crown, when complete, measured 12.5 mm in length and 8.9 mm in width.

P_4 is broken posterior to the protoconid. The protoconid is tall and lanceolate or diamond-shaped as in the lower molar described below. The pre- and postprotocristids are sharply defined, with the postprotocristid being buccolingually broader and more robust. The preprotocristid is steeply sloping, with a sharply defined cutting surface formed along the lower two-thirds of its height. The postprotocristid is more gently sloping, with a more curved cutting surface that turns slightly anteriorly (viewed from the side) along its lower extent. There is a small, low, but well developed, anterior basal paraconid. This cusp is separated from the anterior base of the protoconid by a sharply defined notch. The enamel along the buccal surface of the protoconid is slightly rugose. P_4 , as preserved, measures 7.5 mm in length and 4.2 mm in width, and we estimate that the crown, when intact, measured 9.1 mm in length and 4.2 mm in width.

The M_2 is broken posteriorly behind the protoconid. The protoconid is high, with distinct and sharply defined pre- and postprotocristids. The preprotocristid slopes steeply away from the apex of the protoconid and then turns directly downward to form a vertical cutting surface posterior to the paraconid. The postprotocristid slopes more gently away from the apex and then turns abruptly anteriorly (much more so than on P_4), defining a distinct posterior projection of the posterior flank of the protoconid. In buccal view the crown of the protoconid has the distinctive lanceolate or diamond shape characteristic of *Hapalodectes*. The preprotocristid and postprotocristid are almost straight and form a right angle (as in Asian *Hapalodectes serus*) rather than curved and forming a more acute angle (as in North American *Hapalodectes leptognathus*). There is a very small metaconid cuspule closely appressed to the protoconid. A swelling of enamel on the lingual side of the protoconid curves slightly anteriorly and forms a strong vertical pillar. The paraconid is low (approximately half the height of the protoconid), with a relatively long, curving, sharply-defined preparacristid. In anterior view, the preparacristid bifurcates into buccal and lingual branches that enclose a reentrant groove for the hypoconid of the preceding tooth (in this case M_1) as in *Hapalodectes* and in contrast to *Mesonyx*. The postparacristid is short and straight, joining the preprotocristid to form a narrow valley that separates the protoconid from the paraconid. There is a very weak buccal cingulid present and, as in P_4 , the enamel along the buccal surface of the protoconid is slightly rugose. M_2 , as preserved, measures 9.3 mm in length and 4.8 mm in width, and we estimate that the crown, when intact, measured 12.8 mm in length and 4.8 mm in width.

DISCUSSION

Hapalorestes lovei is known only from a single specimen preserving parts of three cheek teeth. M^2 is intermediate in size but otherwise resembles upper molars of *Hapalodectes* more than it does *Mesonyx* (Fig. 2). Lower teeth are buccolingually compressed and sharply sectorial, with a distinctively lanceolate or diamond-shaped protoconid. M_2 has a reentrant groove in the anterior base of the crown. Taken together, these characteristics indicate that *Hapalorestes* is a hapalodectid rather than a mesonychid. *Hapalorestes lovei* differs from some similar-sized Asian mesonychids in having a reentrant groove on the front of the one known lower molar. *Lohoodon lushiensis* (Zhou et al., 1973) and *Metahapalodectes makhchinus* (Dashzeveg, 1976) were first described as hapalodectines, but Ting and Li (1987) suggest that both are mesonychids and not really hapalodectids.

Quantitative prediction of body mass in mesonychians requires special care because of the unusually-narrow shape of their lower molars. Zhou (1995) investigated this problem and found that tooth size and body size in mesonychids scales like that in felid Carnivora. He developed an equation for Mesonychidae relating body-mass-estimated-from-postcranial-skeletal-dimensions to M_2 size in order be able to predict body mass from M_2 size. Zhou's prediction equation is $Y = 1.327 \cdot X - 3.355$, where X is $\ln M_2 L \times W$ in mm^2 and Y is \ln weight in kg. We have extended this to predict the body masses of *Hapalodectes leptognathus*

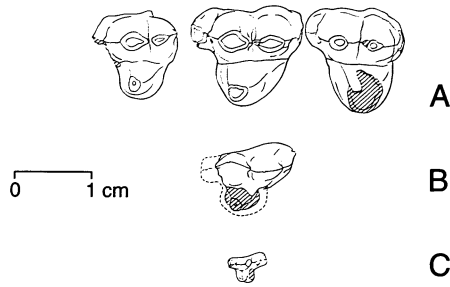


FIG. 2.—Comparison of the sizes and shapes of upper cheek teeth of three middle Eocene mesonychids, all drawn to the same scale and shown natural size. A, left P^4 - M^2 of *Mesonyx obtusidens*, USGS 1988 from the Aycross Formation of the southern Absaroka Range, Wyoming. B, left M^2 of *Hapalorestes lovei*, UM 102686 (holotype), from the Aycross Formation of the southern Absaroka Range, Wyoming. C, left M^1 of *Hapalodectes serus*, AMNH 80802, from the Irдин Manha Svita of Mongolia (Asian *Hapalodectes serus* is very similar in size to North American *Hapalodectes leptognathus*). Note the intermediacy of *Hapalorestes lovei* between *Mesonyx* and *Hapalodectes* in size, and its greater similarity to *Hapalodectes* in molar shape.

and *H. serus* using M_2 measurements in Zhou and Gingerich (1991), and the body mass of *Hapalorestes lovei* using measurements given above. We estimate that *H. leptognathus* and *H. serus* weighed 0.7 to 1.1 kg, with a mean of about 0.9 kg, while *H. lovei* is estimated to have weighed about 8 kg. For comparison, Zhou (1995) estimated that *Mesonyx obtusidens* weighed 22 to 32 kg with a mean of 28 kg. *H. lovei* is intermediate in size and partially fills a long-standing gap between the size distributions of North American hapalodectids and mesonychids.

The type specimen of *Hapalorestes lovei* is the second mesonychid specimen reported from the Aycross Formation in the Absaroka Range of western Wyoming. Bown (1982) described three teeth of *Mesonyx* sp., cf. *M. obtusidens*, USGS 1988 (illustrated here in Fig. 2A) from his locality D-1057. We have examined these and affirm that they belong to *Mesonyx obtusidens* (see Matthew, 1909). As Bown noted, they are similar in size to upper cheek teeth of Bridgerian-age *M. obtusidens* from southwestern Wyoming. In addition, there is no interproximal facet on the back of M^2 , indicating that there was no M^3 , which is an *M. obtusidens* characteristic. Eaton (1982) reported mesonychid tooth fragments from his locality V-78001 in the Blue Point marker bed but this is stratigraphically higher than strata he regarded as equivalent to the Aycross Formation (we have not studied these).

Hapalorestes lovei is part of a small faunal sample from Flattop Quarry that includes taxa rarely found elsewhere (e.g., a possible multituberculate, the anaptomorphine primate *Gazinius amplus*, and the hyaenodontid creodont *Proviverroides piercei*). Discovery of *H. lovei* supports the idea that taxa living on the flanks of intermontane basins are part of an upland fauna that will never be adequately known if sampling is confined to richly fossiliferous basin deposits (Black, 1967; Bown, 1982; Gunnell et al., 1992; Gunnell, 1995). On present evidence, *Hapalorestes lovei* appears to have been a 'gracile mountaineer' that rarely ventured into basin lowlands.

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