

NEW MESONYCHIAN DENTITIONS FROM THE PALEOCENE AND EOCENE OF THE BIGHORN BASIN, WYOMING

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ABSTRACT

We figure and describe for the first time several exceptional mesonychian dental specimens from the late Paleocene-early Eocene Fort Union and Willwood formations of the Bighorn Basin, Wyoming. They include three new species of *Dissacus*, one of late Tiffanian and two of Wasatchian age, and several virtually complete dentitions of *D. praenuntius*. *Dissacus longaevus*, which is based on a nearly complete but poorly preserved dentary, lacks diagnostic traits, and is here considered a nomen dubium. Other specimens reported include well-preserved upper and lower dentitions of *Pachyaena gigantea*, the first nearly complete maxillary dentition of *P. gracilis*, and a new specimen of the very rare basal Wasatchian *Hapalodectes anthracinus*. Considerable variation in jaw depth and canine size among various mesonychians suggests that these animals may have been sexually dimorphic.

INTRODUCTION

The Mesonychia are an order of Paleogene land mammals distinctive for their cursorially specialized skeleton and peculiar dentition, which consists of laterally compressed, premolariform lower molars with tall protoconids and trenchant talonids, and simple tritubercular upper molars (e.g., Scott, 1888; Wortman, 1901-1902; Boule, 1903; Matthew, 1909, 1915, 1937; Szalay and Gould, 1966; Szalay, 1969; Thewissen, 1991; Zhou and Gingerich, 1991; Zhou et al., 1992; O'Leary and Rose, in press; Rose and O'Leary, in press). Mesonychia may have evolved from triisodontine arctocyonids (Matthew, 1937; Van Valen, 1978) and are believed to be close to the ancestry of cetaceans (Van Valen, 1966; Szalay, 1969; Thewissen et al., 1994). *Dissacus* and *Pachyaena* evidently had carnivorous diets which probably included hard objects (Szalay and Gould, 1966; O'Leary and Teaford, 1992), and it has been suggested that *Hapalodectes* was piscivorous (Szalay, 1969; Zhou and Gingerich, 1991), but the exact nature of mesonychian diets is still obscure.

Mesonychids and hapalodectids are among the rarest mammals in Paleogene Holarctic faunas; however, continuous collecting efforts in the Fort Union and Willwood formations of the Bighorn Basin over more than half a century (by G. L. Jepsen, E. L. Simons, P. D. Gingerich, T. M. Bown and K. D. Rose, and others) have produced many exceptional dental specimens of mesonychids which have until now remained undescribed. Here we report and illustrate the most important dentitions of *Dissacus*, *Pachyaena*, and *Hapalodectes* from the Tiffanian through the Wasatchian of the Clark's Fork and Bighorn basins, Wyoming. Willwood Formation localities in the southern Bighorn Basin and their stratigraphic levels are summarized by Bown et al. (1994).

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Abbreviations are as follows: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; USGS, Paleontology and Stratigraphy Branch, U.S. Geological Survey, Denver, Colorado; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM, Yale Peabody Museum, New Haven Connecticut; YPM-PU, Princeton University collection at Yale Peabody Museum, New Haven, Connecticut.

Photographs show original specimens in most cases, sometimes lightened with ammonium chloride. A few of the photographs are of epoxy casts of the original specimens.

SYSTEMATIC PALEONTOLOGY

Order Mesonychia Van Valen, 1969

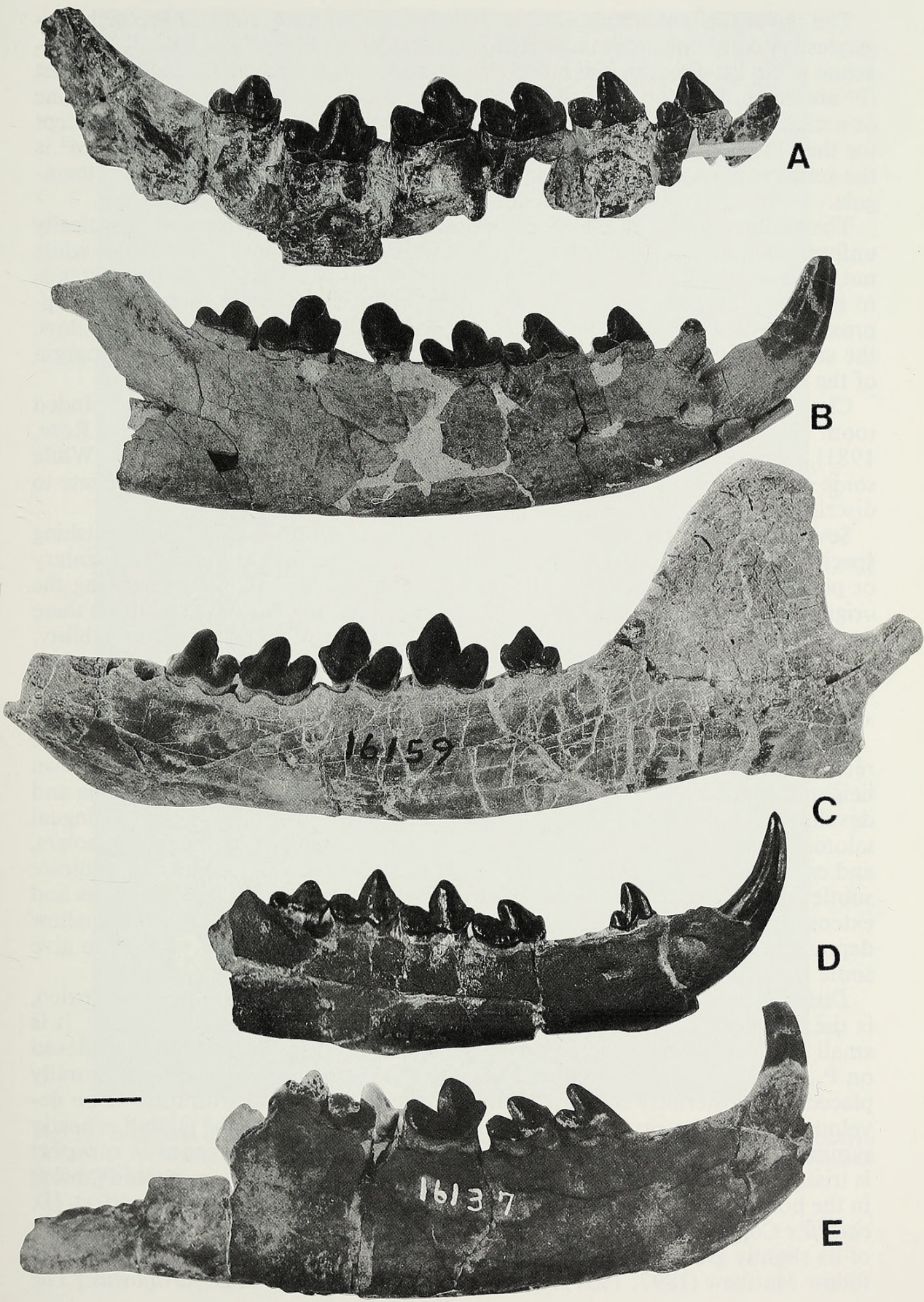
Family Mesonychidae Cope, 1875

Dissacus Cope, 1881

Dissacus is one of the oldest and most primitive mesonychids. Cope (1881) proposed the genus for mesonychids that differed from *Mesonyx* in retaining a metaconid on the lower molars. Matthew (1915, 1937) further distinguished *Dissacus* from other mesonychids by the presence of three upper and lower molars (M^3 being lost in some mesonychids), "well-developed" metaconids, and reduced paraconids "especially on P_4 and M_3 " (Matthew, 1915:85). At least ten species of the genus have been proposed from the Paleocene and Eocene of Europe, Asia, and North America (e.g., Lemoine, 1891; Matthew, 1915; Stehlin, 1926; Russell, 1964; Crusafont and Golpe, 1968; Szalay and McKenna, 1971; Zhou et al., 1973; Dashzeveg, 1976; Yan and Tang, 1976; Zhou and Qi, 1978; Godinot et al., 1987; Russell and Zhai, 1987).

Most previous accounts of *Dissacus* provided rather inadequate descriptions of the dentition; hence we present the following summary based on material we have examined. *Dissacus* has a small lower incisor region with three subequal incisors, and ovoid, somewhat laterally compressed and slightly recurved lower canines. P_1 is typically one-rooted (although Novacek et al. [1991] reported a two-rooted P_1 in *Dissacus* sp. from the early Eocene of Baja California) with a simple, low-crowned cusp and an indistinct heel. P_1 is the only postcanine tooth that is not trenchant. P_2 is two-rooted and, like P_1 , is separated from adjacent teeth by short diastemata. P_2 – M_3 are each characterized by a mesiodistally-oriented ridge joining the apices of the paraconid, protoconid, and hypoconid. The lower molar trigonids are dominated by the high protoconid, and have distinct metaconids, connate with the protoconid (positioned lingual and slightly mesial to the apex of the protoconid), and small basal paraconids at about the same height as the simple trenchant talonid. The main cusps are aligned just buccal to the midline of P_4 – M_3 . Relative size of M_1 and M_2 is variable, but M_3 is always the smallest and lowest crowned molar.

Fig. 1.—Lower dentitions of *Dissacus* in lateral view. A–C, *D. praenuntius*: A, YPM-PU 19597 (right P_1 – M_3); B, YPM-PU 18711 (right C– M_3); C, YPM-PU 16159, (left P_3 – M_3); D, *D. argenteus*, n. sp., YPM-PU 16135, holotype, (right C, P_2 , P_4 – M_3); E, *D. willwoodensis* n. sp., YPM-PU 16137, holotype (right P_3 – M_3 , C, and M_2 protoconid are from left side, superimposed in this view). Scale = 1 cm.



The upper teeth have the characteristic triangular mesonychid shape with parastyles (usually the larger) and metastyles present on P^4 – M^3 . On P^3 – M^3 , the paracone is the largest cusp, the protocone second, and the metacone is the smallest (P^3 and M^3 each have a vestigial posterobuccal cusp, which is either a metacone or a metastyle); there is no hypocone. The protocone on P^4 – M^3 is conical except for the flattened buccal surface demarcated by pre- and postprotocristae. M^3 is the smallest upper molar. M^{1-3} have variably developed pre-, post-, and ectocingula.

The dentary varies in depth and is gently convex ventrally, with a typically unfused mandibular symphysis (although in some specimens the dentaries, while not firmly coossified, are attached at the symphysis [see Fig. 7, 8]) which extends to the distal aspect of P_2 or P_3 . The mandibular condyle is cylindrical and approximately level with the tooth row (Fig. 1C, 6). The masseteric fossa is shallow, the angle of the mandible is neither enlarged nor inflected, and the distal margin of the coronoid process is straight.

Characters Matthew (1915) employed to distinguish species of *Dissacus* included tooth size, paraconid expression (now known to be somewhat variable; Rose, 1981), relative size of molars, and presence or absence of the M^3 metacone. While some of these traits may differ among species of *Dissacus*, they are inadequate to discriminate most species of the genus.

Several factors contribute to the difficulty of identifying and distinguishing species of *Dissacus*. Various type specimens were based on extremely fragmentary or poorly preserved material, often lacking diagnostic teeth, thus rendering the original definitions of some species either inadequate or obscure. In addition there was an unknown, but probably substantial, extent of intraspecific variability, perhaps due in part to sexual dimorphism and to relatively imprecise occlusion, as indicated by heavy apical tooth wear and rather irregular and poorly developed shearing facets.

Features that appear to be useful for distinguishing species of *Dissacus* include relative length of P_2 , retroflexion of P_{3-4} protoconids, relative size and crown height of M_1 and M_2 , relative reduction of M_3 , position of the cristid obliqua and development of a shallowly "basined" talonid on P_3 – M_1 , presence of lingual talonid cusps on P_4 – M_2 , presence and expression of cingula on the upper molars, and expression of metaconules on P^3 – M^3 . We use the term "basined" to indicate subtle widening of the talonid with buccal displacement of the cristid obliqua and extension of the postcristid lingually and slightly anteriorly, to enclose a shallow depression. A ratio of mesiodistal canine length to length of M_1 is used to give some indication of how the relative sizes of these teeth vary in *Dissacus*.

Dissacus navajovius, from the Torrejonian of the San Juan Basin, New Mexico, is the type species and the oldest and most primitive species of *Dissacus*. It is small and has tall, relatively upright protoconids on P_3 – M_3 (slightly retroflexed on P_{3-4}), and a relative unreduced M_3 . On P_3 – M_3 the cristid obliqua is centrally placed and posteriorly meets a subtle transverse postcristid with little or no development of accessory cusps lingual to the hypoconid. Thus the talonid is nearly symmetrical when viewed from the distal end (Fig. 3). P_2 (holotype of *D. carnifex*) is triangular with a straight mesial border, and P_3 has a variable paraconid (absent in the holotype of *D. navajovius*, rudimentary in the holotype of *D. carnifex*). [*D. carnifex* Cope, 1882, was initially distinguished from *D. navajovius* on the basis of its slightly greater size and the presence of a paraconid on P_3 . We tentatively follow Matthew (1897, 1937) in considering it a synonym of *D. navajovius*.] The



Fig. 2.—Dentitions of *Dissacus* in occlusal view, stereographs. A–B, *D. argenteus*, n. sp., holotype (YPM-PU 16135): A, right dentary with C, P₂, P₄–M₃; B, right M¹ (epoxy cast); C, *D. praenuntius* (YPM-PU 16159), left dentary with P₃–M₃. Scale = 1 cm.

C_1/M_1 ratio is approximately 0.74, associated with its gracile mandible. P^3 has a small but distinct lingual cusp and P^4 has a distinct metacone which is more separated from the paracone than in other species. A small metaconule is present on P^{3-4} but is not evident on the molars. Weak pre- and postcingula are present on M^{1-2} , and M^3 has a relatively wide buccal margin.

Dissacus argenteus, new species

Fig. 1D, 2A, B

Dissacus cf. *navajovius*, Rose, 1981:156–157.

Holotype.—YPM-PU 16135, dentaries with right C_1 , P_2 , P_4 – M_3 , and alveoli for $P_{1,3}$, left C_1 , P_4 – M_1 , C^1 , right M^1 , and associated fragments. Collected by A. C. Silberling, 1937.

Type Locality and Horizon.—Princeton Quarry, Sec. 21, T. 57 N., R. 100 W., Park County, Wyoming; late Paleocene (late Tiffanian, Ti-5 of Gingerich, 1983), upper Fort Union Formation.

Referred Specimens.—YPM-PU 13924 (RM'?) and three uncatalogued isolated teeth (lower pre-molar and molar, upper premolar) in the YPM-PU collection, all from Princeton Quarry (Rose, 1981).

Etmology.—Latin, of silver, for the Silver Coulee beds where the specimens were found.

Diagnosis.—About the size of *D. navajovius*, roughly 15% smaller than *D. praenuntius*. Differs from *D. praenuntius* in having a shorter P_2 with a convex (not flat) mesial border, and from *D. navajovius* in having a lower crowned P_4 with more retroflexed protoconid and longer talonid. Talonids of P_4 – M_1 incipiently basined. Differs from *D. europaeus* in being about 10% larger and lacking a metaconid on P_4 .

Description.—The nearly complete right dentary of YPM-PU 16135 is gracile and shallow, with a mental foramen located just below the diastema between P_2 and P_3 . The mandibular symphysis was unfused and extended distally to the back of P_2 .

The teeth in the holotype (YPM-PU 16135) are well preserved and relatively unworn. The lower canines are gracile (C_1/M_1 ratio = 0.71) with distinct, low vertical ridges in the enamel that run the height of the tooth on all sides. The one-rooted P_1 was set off by short diastemata, longer mesially than distally. P_2 has a tall, rather pointed anterior cusp with a long, convex mesial margin (as in *D. europaeus*; Russell, 1964:fig. 50) and a small centrally placed heel with a single cusp. The tooth appears to be higher crowned and the talonid slightly larger than in Russell's illustration of *D. europaeus*. P_3 , judging from the alveoli, was two-rooted with a larger distal root. P_4 has a more retroflexed protoconid than in *D. navajovius* (Fig. 3). Anterior and slightly lingual to it is a small, basal paraconid. The talonid is more than 40% the length of the tooth (compared with about 35% in *D. navajovius*), and a little longer than the molar talonids. It is wedge-shaped, steep labially, and slightly broader and less steeply sloping lingually. The mesio-distal ridge on P_4 is interrupted at the talonid notch and joins a short anterolingual cingulid at the paraconid.

The lower molars are generally similar to each other and to those in other *Dissacus* species. M_2 is slightly larger and has a higher protoconid than M_1 , and M_3 is smaller than the other molars but not significantly reduced over the size in *D. navajovius*. The talonid of M_1 , like that of P_4 , differs from that of *D. navajovius* in having a broader, slightly concave, and more gently sloping surface lingual to the cristid obliqua than buccal to it (Fig. 3). This is associated on M_1 with the presence of a rudimentary lingual cusp (entoconid?), not evident in the holotype of *D. navajovius*, and a faint trace of an entoconid can be detected on the M_2 of *D. argenteus*. M^1 does not appear to differ significantly from that of *D. navajovius*. See Tables 1 and 2 for measurements.

Discussion.—Rose (1981) allocated these specimens to *Dissacus* cf. *navajovius* but, as described above, they differ in several derived aspects from the latter species, and *D. argenteus* is substantially younger than *D. navajovius*. The new species closely resembles contemporaneous *D. europaeus*, but the latter is smaller (see illustrations in Russell, 1964, and Godinot et al., 1987), and has a metaconid on P_4 (Russell, 1964:226), a condition not seen in any North American *Dissacus*.

Table 1.—Measurements (mm) of lower teeth of mesonychids (left side, right side). L = maximum mesio-distal length; W = maximum width of trigonid; a = alveolus; r = root; and * = approximate.

Species	Specimen no.	CL	CW	P ₁ L	P ₁ W	P ₁ L	P ₁ W	P ₂ L	P ₂ W	M ₁ L	M ₁ W	M ₂ L	M ₂ W	M ₃ L	M ₃ W	Depth ¹
<i>D. navajovius</i>	AMNH 3356	—	—	—, 4.6	—, 3.0	—, 8.1r	—, 3.8r	—, 9.9	—, 4.6	—	—	—, 10.1	5.2, 5.1	—, 12.1	—, 4.6	—, 17.4
<i>D. carnifex</i>	AMNH 3361	—	—	—	—	—, 8.9	—, 4.3	—, 10*	—, 4.9	—	—	—, 12.0	—, 6.1	—, 12.8	—, 5.2	—
<i>D. argenteus</i> , n. sp.	YPM-PU 16135	9.4, 9.2	6.2, 7.1	4.4a, —	2.6a, —	—, 8.7	—, 4.9	—, 8.7a	—, 4.7a	—	—	—, 10.4	—, 6.1	—, 13.2	—, 4.9	18.1, 19.2
<i>D. praenuntius</i>	AMNH 16069	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>D. praenuntius</i>	YPM-PU 18711	11*, 12*	9*, 9*	—, 5.1	—, 4.3	9.9, 10.0	4.6, 4.7	13.5, 13.7	5.4, 5.6	—	—	—	—	—	—	—
<i>D. praenuntius</i>	YPM-PU 19597	12.2, —	9.8, —	—, 5.2	—, 3.6	11.7, 12.1	5.4, 5.4	14*, 13.9	—, 6.1	—	—	—	—	—	—	—
<i>D. praenuntius</i>	YPM-PU 13295	12*, 12*	10*, 9*	—, —	—, —	—, 10*	—, 7*	—, 13.5	—, 6.4	—	—	—	—	—	—	—
<i>D. praenuntius</i>	YPM-PU 16159	5.5a, —	8.2a, —	8*, —	7*, —	10*, —	6*, —	12.3, —	6.3, —	—	—	—	—	—	—	—
<i>D. longaeus</i>	AMNH 15732	9.3a, —	3.2a, —	—, —	—, —	—, —	—, —	—, —	—, —	—	—	—	—	—	—	—
<i>D. willwoodensis</i> , n. sp.	YPM-PU 16137	9.8, —	7.7, —	—, 6*	—, 5*	—, —	—, —	10.9, 10.9	4.4, —	—	—	—	—	—	—	—
<i>D. willwoodensis</i> , n. sp.	USGS 27635	9.4r, 9.1r	—, 5.7	—, 6.2a	—, 5.1a	—, 7.6	—, 4.2	10.8, —	4.9, —	—	—	—	—	—	—	—
<i>D. serior</i> , n. sp.	USGS 27612	—, —	—, —	—, 4.9	—, 3.6	—, —	—, —	—, —	—, —	—	—	—	—	—	—	—
<i>P. gigantea</i>	YPM 50000	34.2, 31.2	22.0, 22.2	—, 14*	—, 8*	—, 14*	—, 10.9	15.3, —	16.2, —	—	—	—	—	—	—	—
<i>H. anthracinus</i>	USGS 9628	—, —	—, —	—, —	—, —	—, —	—, —	—, —	—, —	—	—	—	—	—	—	—

Species	P ₄ L	P ₄ W	M ₁ L	M ₁ W	M ₂ L	M ₂ W	M ₃ L	M ₃ W	Depth ¹
<i>D. navajovius</i>	11.0, 11.3	4.7, 4.7	11.1, —	4.5, —	12.1, —	5.2, 5.1	—, 10.1	—, 4.6	—, 17.4
<i>D. carnifex</i>	—, 12.7	—, 5.4	—, —	—, —	—, 12.8	—, 6.1	—, 12.0	—, 5.2	—, —
<i>D. argenteus</i> , n. sp.	12.8, 13.1	5.4, 5.5	13.1, 12.9	5.6, 5.5	—, 13.2	—, 6.1	—, 10.4	—, 4.9	18.1, 19.2
<i>D. praenuntius</i>	14.5, —	6.9, —	—, —	—, —	—, —	—, —	—, —	—, —	—, —
<i>D. praenuntius</i>	14.7, 14.4	6.0, 5.8	14.7, —	6*, —	14.3, 14.2	7.1, 7.0	—, 11.2	—, 6.0	27.7, 27.3
<i>D. praenuntius</i>	—, 15.2	—, 6.3	—, 14.9	—, 6.9	16.1, 16.0	7.7, 7.5	13.6, 13.2	6.1, 6.1	29.9, —
<i>D. praenuntius</i>	—, 15.1	—, 6.2	—, 14.9	—, 6.3	—, 15.8	—, 7.1	—, 12.0	—, 5.6	—, —
<i>D. praenuntius</i>	13.4, —	6.4, —	14.5, —	6.9, —	14.8, —	7.4, —	10.5, —	5.8, —	24.2, —
<i>D. longaeus</i>	—, —	—, —	12.4, —	6.1, —	12.5, —	6.6, —	10.8, —	6.1, —	34.7, —
<i>D. willwoodensis</i> , n. sp.	11.1, —	4.8, 5.0	12.8, 12.8	6.0, 5.9	12.4, —	6.0, —	7.2, 7.2	3.8, 3.8	24.0, 22.6
<i>D. willwoodensis</i> , n. sp.	11.7, —	5.2, —	—, 11.5	—, 5.8	—, 11.6	—, 5.8	—, 8.6r	—, 3.8r	20.3, 19.8
<i>D. serior</i> , n. sp.	—, —	—, —	—, —	—, —	13.7, —	6.1, —	11.5, —	5.0, —	33*, —
<i>P. gigantea</i>	21.3, 21.3	17.2, 16.8	24.5, —	16.7, —	—, 28.4	—, 17.3	—, —	—, —	79.4, —
<i>H. anthracinus</i>	—, —	—, —	4.05, —	1.45, —	4.70, —	1.60, —	—, —	—, —	—, —

¹Depth of dentary under M₁.

Table 2.—Measurements (mm) of upper teeth of mesonychids (left side, right side). *L* = maximum mesio-distal length; *W* = maximum width of trigonid; *a* = alveolus; *r* = root; and * = approximate.

Species	Specimen no.	CL	CW	P ² L	P ² W	P ³ L	P ³ W
<i>D. navajovius</i>	AMNH 3360	—, —	—, —	—, —	—, —	11.0, —	6.7, —
<i>D. argenteus</i>	YPM-PU 16135	—, —	—, —	—, —	—, —	—, —	—, —
<i>D. praenuntius</i>	AMNH 16069	—, —	—, —	—, —	—, —	—, —	—, —
<i>D. praenuntius</i>	YPM-PU 13295	—, —	—, —	—, 12.0	—, 5.3	—, 13.2	—, 7.2
<i>D. willwoodensis</i>	USGS 27635	—, —	—, —	—, —	—, —	—, 10.3	—, 5.8
<i>P. gigantea</i>	YPM 50000	—, —	—, —	—, —	—, —	—, 22.5	—, 19.2
<i>P. gigantea</i>	YPM 23333	—, —	—, —	—, —	—, —	20.4, —	16.4, —
<i>P. gracilis</i>	USGS 7185	14.2, —	10.7, —	10.5, —	5.4, —	13.5, —	8.0, —

Dissacus praenuntius Matthew, 1915

Fig. 1A–C, 2C, 4, 5A–C

Referred Specimens.—YPM-PU 13295 (right dentary with P₂–M₃, and right P²–M³ and left P⁴–M²); YPM-PU 16159 (left dentary with P₃–M₃); YPM-PU 18711 (left dentary with P₂–M₃, and right dentary with C₁–M₃, miscellaneous upper teeth and right humerus); YPM-PU 19597 (left dentary with C₁–M₃, and right dentary with P₁–M₃, miscellaneous upper teeth and bone fragments); all specimens found by field parties working with G. L. Jepsen. Simpson (1937:fig. 5) illustrated the two complete teeth of the holotype; see Rose (1981) and Gingerich (1989) for other specimens of *D. praenuntius*.

Localities and Horizons.—YPM-PU 16159: NE¼, Sec. 3, T. 56 N., R. 100 W., Park County, Wyoming; late Paleocene (latest Tiffanian, Ti6? of Archibald et al., 1987), upper Fort Union Formation. YPM-PU 13295: Little Sand Coulee Basin; YPM-PU 18711: SE¼, Sec. 20, T. 56 N., R. 101 W. (Cf3 of Gingerich, 1983; Archibald et al., 1987); YPM-PU 19597: SW¼, Sec. 32, T. 57 N., R. 101 W. (Cf2 of Gingerich, 1983; Archibald et al., 1987); all Park County, Wyoming; latest Paleocene (Clarkforkian), lower Willwood Formation.

Description.—The mandibular symphysis (YPM-PU 16159) extends to the distal aspect of P₃ (18.6 mm long), and the canines have the typical shape and simple enamel. The C₁/M₁ ratio (YPM-PU 19597 = 0.82, YPM-PU 18711 = 0.79, YPM-PU 13295 = 0.81) indicates that these specimens were relatively gracile. P₁ is one-rooted and simple as in other *Dissacus*. P₂ is two-rooted and elongate with virtually no paraconid development. The P₂ protoconid is a tall, triangular, slightly retroflexed blade with straight mesial and distal borders and a small heel. P₃ is similarly shaped with a slightly larger protoconid (as tall as or taller than P₄), a relatively longer talonid, and a rudimentary paraconid. The talonid is a relatively symmetrical blade with little development of a postcristid (as in *D. navajovius*, but in contrast to *D. willwoodensis*, n. sp.).

P₄ has the most distinctly retroflexed protoconid of the premolars, but much less retroflexed than in *D. willwoodensis*. The talonid is longer than on P₃ but shorter than on M₁ and is not basined. The cristid obliqua on P₄–M₂ is more buccally situated, giving the talonid a more gently sloping lingual face than in *D. navajovius*. M₂ is slightly larger than M₁, but has a slightly narrower talonid. The isolated molar talonid preserved in the holotype shows the degree of lingual broadening and asymmetry typical of M₁. Remolarization of the talonids, however, is variable; YPM-PU 13295, 19597, and 16159 have incipient entoconid(?) formation on the talonids of M₁ and M₂, whereas YPM-PU 18711 has crenate (scalloped) posterointernal cingula on M₂₋₃, but no discrete entoconids.

P² is an elongate two-rooted tooth; it has one pointed cusp with a gently concave distal margin and no lingual lobe. P³ has a tall paracone, small styler cusps (the metastyle being the larger of the two) and an incipient lingual cusp. P⁴ has the most projecting paracone of the cheek teeth, a much lower, connate metacone, a well-developed protocone, and apparently no metaconule. The molars generally resemble those of *D. navajovius* except for being slightly larger.

These specimens display some interesting variations. YPM-PU 18711 has distinctive delicately crenulated enamel on the cheek teeth, while other specimens have this feature to a lesser degree. YPM-PU 16159, the only Tiffanian specimen of this species, differs from the others in several features, including a less retroflexed, higher crowned P₄, and a shorter and broader M₃ with a shorter talonid and a taller, more distinct paraconid. See Tables 1 and 2 for measurements.

Table 2.—*Extended.*

P ⁴ L	P ⁴ W	M ¹ L	M ¹ W	M ² L	M ² W	M ³ L	M ³ W
11.2, 11.4	8.2, 8.8	12.0, 12.8	10.4, 10.6	12.4, 12.9	12.2, 12.4	7.8, —	7.4, —
—, —	—, —	—, 13.1	—, 10.6	—, —	—, —	—, —	—, —
—, —	—, —	13.9, —	10.8, —	—, —	—, —	—, —	—, —
12.8, 12.7	9.7, 9.3	15.1, 14.9	12.2, 12.0	—, 14.4	—, 14.1	—, 8.2	—, 8.7
—, 10.1	—, 7.9	11.7r, 12.2	10.6r, 10.4	10.7, 10.8	10.8, 10.5	—, 7.1	—, 7.8
—, 26.2	—, 29.0	—, 27.8	—, 29.0	—, 27.5	—, 29.8	—, 19.0	—, 20.7
22.8, —	25.5, —	26.0, —	24.8, —	—, —	—, —	—, —	—, —
16.0, 15.7	12.6, 13.1	18.5, 18.5	16.3, 16.3	17.8, 17.2	17.6, 17.7	—, 11.8	—, 13.8

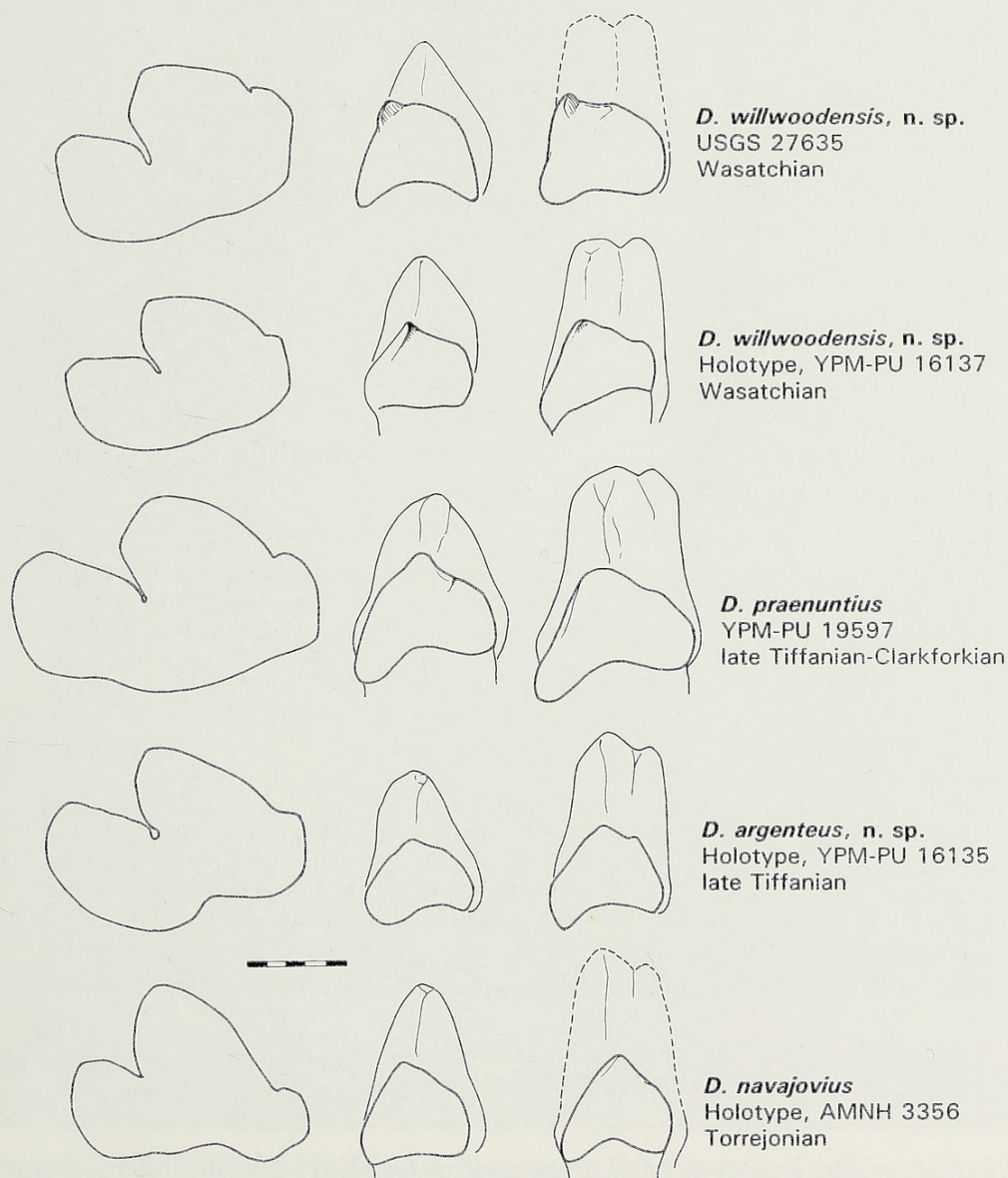


Fig. 3.—Lower teeth of *Dissacus*. Left column, lateral view of right P₄; middle column, distal view of left P₄; right column, distal view of left M₁. Solid lines are based on complete teeth or restorations from the opposite side of the same specimen. Dotted lines are restored from closely related forms. Scale = 5 mm.



Fig. 4.—Lower dentitions of *Dissacus praenuntius* in occlusal view, stereographs. A, YPM-PU 18711 (right C–M₃); B, YPM-PU 19597 (right P₁–M₃). Scale = 1 cm.

Discussion. — The holotype of *D. praenuntius* (AMNH 16069, left P₄, fragments of right M₁ and left and right M₂s, left M¹, and fragmentary postcrania: Matthew, 1915; Simpson, 1937), from the latest Clarkforkian of the Willwood Formation provides very limited information about this species. The Princeton specimens add considerable new data on dental anatomy and its variability in this species.



Fig. 5.—Dentitions of *Dissacus* in occlusal view, stereographs. A–C, *D. praenuntius*: A, YPM-PU 13295 (right P²–M³); B, holotype (epoxy casts), AMNH 16069, left P₄ and M₂ (mesial fragment), and right M₁ (talonid) and M₂ (trigonid); C, holotype (epoxy cast), AMNH 16069, left M¹; D, “*D. longaevus*,” holotype, AMNH 15732, left dentary with incomplete P₄, M_{1–3} (epoxy cast). Scale = 1 cm.

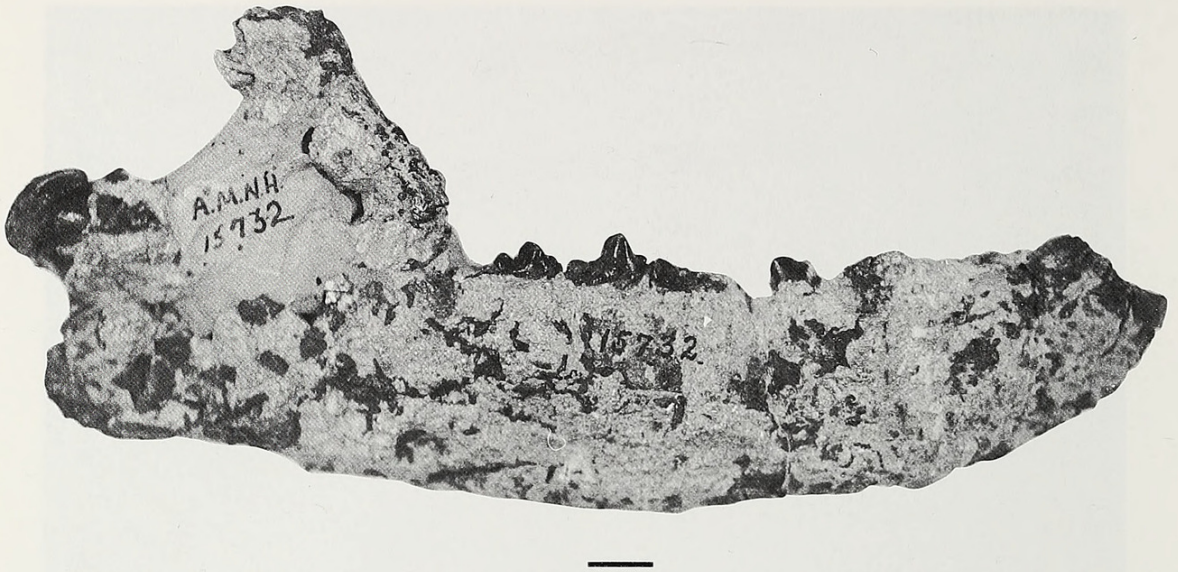


Fig. 6.—Medial view of holotype of “*D. longaevus*” (AMNH 15732). Scale = 1 cm.

Dissacus praenuntius has larger cheek teeth than any other North American species of *Dissacus*. Nonetheless, the depth of the dentary in these specimens, while greater than in *D. navajovius* and *D. argenteus*, is less than that of the holotype of *D. longaevus*, which has smaller teeth. Derived features of this species (relative to *D. navajovius*) include increased size, broader talonids (often with a rudimentary entoconid), and slightly retroflexed protoconids on P_3 and P_4 .

Dissacus willwoodensis, new species

Fig. 1E, 7, 8

Holotype.—YPM-PU 16137, mandible with left C_1 , P_3 (broken), P_4 – M_3 , P_1 alveolus, P_2 root; right P_3 – M_1 , M_2 (talonid), M_3 , P_1 alveolus, P_2 root; and associated fragments. Collected by Austin Van Houten, 1938.

Referred Specimen.—USGS 27635 (mandible with right I_1 – I_3 roots, fragmentary P_2 – M_2 ; fragmentary left P_3 – M_1 , and roots or alveoli of most other teeth from both sides; and right maxilla with fragmentary P^3 – M^3 ; and left M^1 – M^2 roots).

Localities and Horizon.—Holotype: “7 miles southwest of Basin, Gray Bull”; USGS 27635: USGS locality D-1211?, Sand Draw area, north of Emblem; both from early Eocene (early Wasatchian), lower Willwood Formation, Bighorn Basin, Wyoming.

Etymology.—From the Willwood Formation.

Diagnosis.—About the size of *D. navajovius* and *D. argenteus*, roughly 20% smaller than *D. praenuntius*. Differing from these species in having more strongly retroflexed P_3 and P_4 , and more basined talonids on P_3 – M_1 , each with more buccally situated cristid obliqua and stronger postcristid with two small cusps lingual to the hypoconid (especially on M_1 , faintly seen on M_2). Small, sharp crest descends the distal wall of the talonid at the junction of the cristid obliqua and the postcristid of P_3 – M_1 .

Description.—The incisor roots in USGS 27635 indicate that all three incisors were small, subequal in size (I_1 the smallest and most laterally compressed), and oval in cross section with the long axis



Fig. 7.—*Dissacus willwoodensis*, n. sp., holotype, YPM-PU 16137, mandible in occlusal view, stereograph (left C, left and right P_3 – M_3). Scale = 1 cm

oriented approximately labiolingually. I_2 is positioned more posteriorly than the other incisors (a configuration also observed in *Pachyaena gigantea*, USNM 14915), and I_3 is set close to the canine.

P_2 is preserved, though incomplete, only in USGS 27635. It has a rudimentary paraconid, and is short and apparently had a convex mesial border, as in *D. argenteus* and *D. europaeus*, in contrast to the more elongate, triangular P_2 of *D. praenuntius* and “*D. carnifex*.”

P_3 and P_4 have diminutive paraconids, smaller and lower on P_3 , and low-crowned protoconids that are more strongly retroflexed than in other species of *Dissacus* (Fig. 3). In addition, these teeth are somewhat rotated in the jaw, accentuating the degree of retroflexion, with the result that the paracristid is oriented almost horizontally. The talonid of P_4 is about as long as in *D. argenteus* (about 40% of total tooth length). M_1 and M_2 are almost equal in size, M_1 being slightly larger (longer, wider, and slightly taller), in contrast to *D. navajovius*, *D. argenteus*, and *D. praenuntius*. The talonids of M_{1-2} have strong postcristids with two poorly defined cusps lingual to the hypoconid. These cusps (distinct

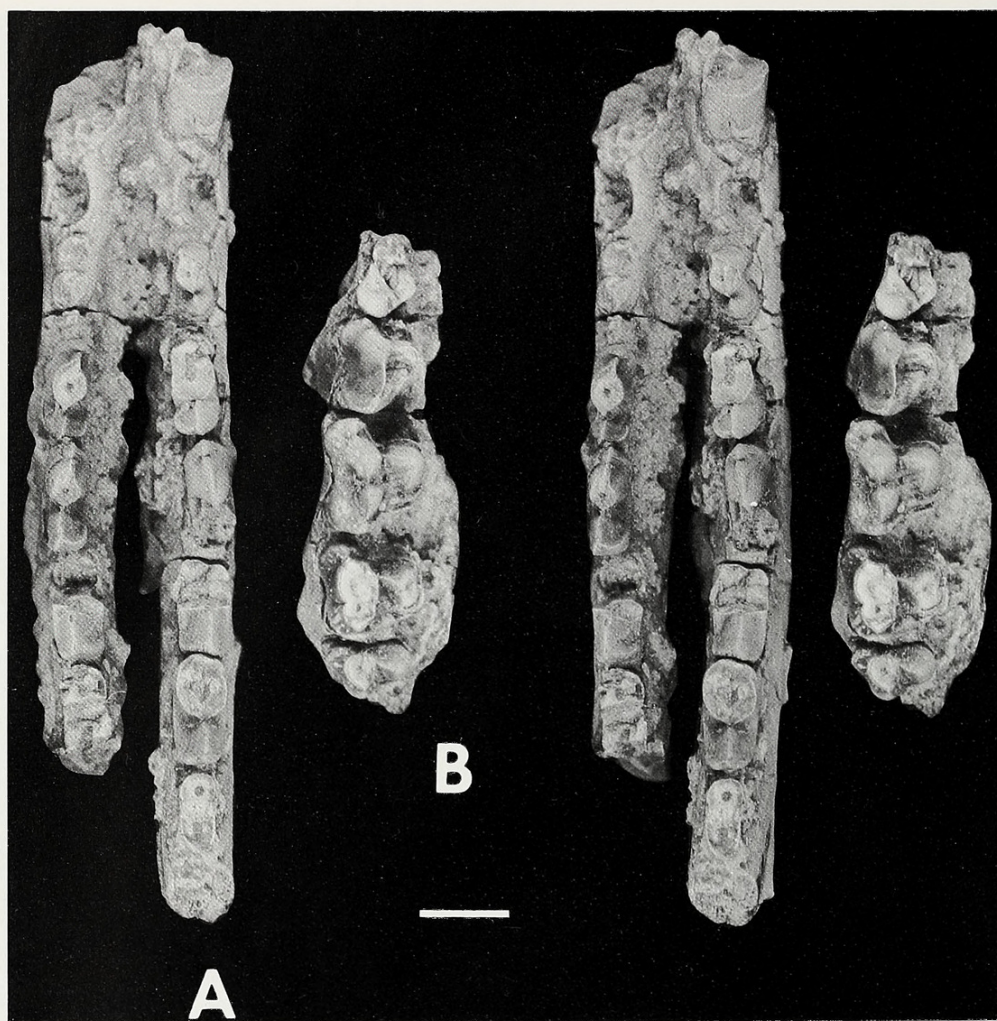


Fig. 8.—*Dissacus willwoodensis*, n. sp., USGS 27635, occlusal view, stereographs. A, mandible with much of lower dentition, crowns incomplete; B, maxilla with right P^3 – M^3 . Scale = 1 cm.

hypoconulid and weaker entoconid?) are better developed on M_1 ; the more lingual one is very weak on M_2 . M_3 is greatly reduced in YPM-PU 16137, narrower and only about two-thirds as long as in *D. argenteus*. Although the roots present in USGS 27635 appear to have supported a larger M_3 , expansion of the base of the tooth in the holotype suggests that the crown of M_3 may not have been significantly larger in the referred specimen. M_3 generally resembles the other molars in shape but is lower crowned and has a much shorter, unbasined talonid lacking lingual cusps.

P^3 has a small lingual lobe, as in *D. navajovius*, larger than that in *D. praenuntius*. Distinct parastyles and metastyles are present on P^3 – M^3 . P^4 had a prominent protocone (broken away), and small cuspules on its mesial and distal borders, representing traces of pre- and postcingula (much better developed on M^1 – M^2). Because the crown is broken, it is impossible to ascertain if a metacone was present; however, a faint swelling of the postparacrista suggests the presence of a small metacone connate with the paracone, as in *D. praenuntius* (compare Fig. 5A and 8). A small metaconule is also present on P^4 . The molars are generally similar to those of *D. navajovius* but have more reduced buccal cingula, much stronger pre- and postcingula (weakly continuous lingually on M^1), and stronger metaconules. M^1 has less columnar cusps and M^3 has a relatively shorter buccal margin than in *D. navajovius*. The C_1/M_1 ratio is 0.80 in USGS 27635 and 0.75 in YPM-PU 16137, indicating relatively gracile canines. See Tables 1 and 2 for measurements.

Discussion.—*Dissacus willwoodensis* is a rare early Eocene species differing from earlier North American *Dissacus* in derived aspects of lower premolar structure,

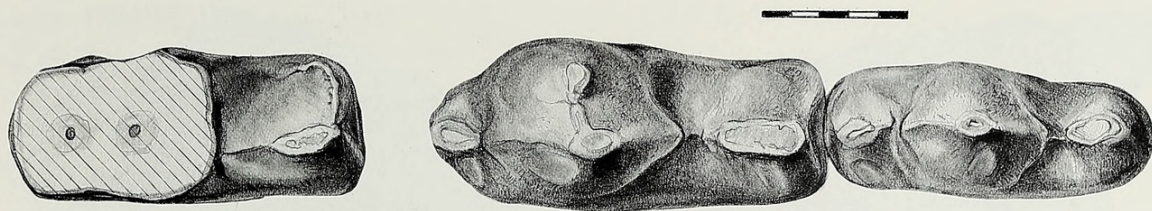


Fig. 9.—*Dissacus serior*, n. sp., holotype, USGS 27612, occlusal view, left P₄ (incomplete), M₂, and M₃. Scale = 5 mm.

talonid morphology of M₁, and M₃ reduction. Ironically, the advanced traits of this species include molarization of the talonids of P₃–M₁, an apparent reversal of the general trend towards simplification of the lower cheek teeth in mesonychids.

Dissacus magushanensis Yan and Tang, 1976, from the late Paleocene of China, was based on a dentary fragment with two incomplete teeth originally identified as M₂₋₃, but more likely either P₄–M₁ or M₁₋₂. These teeth closely approach *D. willwoodensis* in talonid structure but are smaller, and the trigonids differ slightly. The premolar protoconids are not preserved in the holotype, hence degree of retroflexion cannot be established. *Dissacus indigenus* from the late Paleocene of Naran Bulak, Mongolia (Dashzeveg, 1976:fig. 1, 2), seems to have a relatively longer, narrower P₄ with a less basined talonid than in *D. willwoodensis* or *D. argenteus*.

The dimensions of P₄–M₂ in the new specimens are similar to those of the holotype and only described specimen of *D. longaevus* (AMNH 15732, Fig. 5D, 6; Matthew, 1915) and it is possible that all belong to the same species. M₃ in AMNH 15732, however, while having the reduced talonid characteristic of *D. willwoodensis*, is otherwise similar in size to that of *D. argenteus*. This may not be of much significance because the dimensions of third molars are known to be highly variable (Gingerich, 1974; Gingerich and Winkler, 1979). The holotype of *D. longaevus* further differs from the specimens described here in having a much larger canine (C₁/M₁ = approximately 1.6 in AMNH 15732 in contrast to 0.75–0.80 in *D. willwoodensis*) and a much deeper, more massive dentary—differences which suggest the possibility of sexual dimorphism (e.g., Kurtén, 1966, 1969; Harvey et al., 1978; Van Valkenburgh and Ruff, 1987; Wright, 1993). Complicating the situation is the fact that the exact provenance is not known for any of these specimens, although all appear to be from the lower Willwood Formation (see also Gingerich, 1989). Upon close examination, many of the characters that readily distinguish *D. willwoodensis* from *D. navajovius*, *D. argenteus*, and *D. praenuntius*, such as retroflexed, low-crowned P₃ and P₄ and specialization of the talonids of P₃–M₁, are either ambiguous or not preserved in the holotype of *D. longaevus*. For these reasons we regard *D. longaevus* as a nomen dubium.

Dissacus serior, new species

Fig. 9

Holotype.—USGS 27612, left dentary fragments containing M₂, M₃, and parts of P₄–M₁, isolated right P₁, and associated fragments; only known specimen. Collected by K. D. Rose, 1992.

Type Locality.—USGS locality D-1754, 511-m level of the Willwood Formation, early Eocene (later Wasatchian, Wa-6 of Gingerich, 1983), Bighorn Basin, Wyoming.

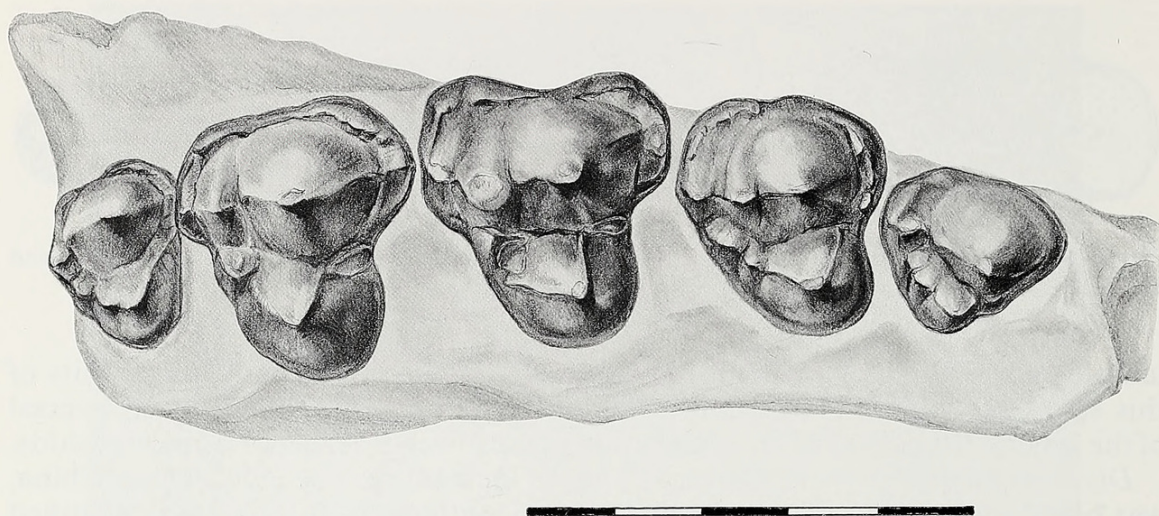


Fig. 10.—*Pachyaena gigantea* (YPM 50000), right maxilla with P^3 – M^3 , occlusal view. Scale = 5 cm.

Etymology.—Latin, occurring late.

Diagnosis.—Differs from all other species of *Dissacus* in having an enlarged paraconid and no metaconid on M_3 . Slightly larger than *D. navajovius*, *D. argenteus*, and *D. willwoodensis*, and smaller than *D. praenuntius*.

Description.— P_1 is simple with a small posterior cuspule as in other *Dissacus*. The other teeth are all from the left side, the two fragmentary teeth in serial succession and the two complete teeth in separate fragments. The more anterior and more complete of the fragmentary teeth is identified as P_4 because of its basined talonid with well-developed postcristid; however, it is possible that it is P_3 . Assuming it is P_4 , the larger complete molar must be M_2 . Moreover, this molar resembles M_2 in *D. willwoodensis* and *D. argenteus* in having a less basined, narrower talonid than P_4 . The tooth identified as M_3 is shorter and narrower than M_2 and has an interstitial facet anteriorly (indicating contact with another tooth) but not posteriorly. It has a much larger paraconid than in M_3 of other *Dissacus*; furthermore, there is no metaconid, only a slight swelling of the lingual side of the protoconid. Although this tooth is superficially premolariform, it cannot be a premolar because the paraconid is much larger and the talonid much less developed than in P_{3-4} of other *Dissacus* (not to mention the lack of a posterior interstitial facet). The dentary fragments are deeper than in *D. willwoodensis* and shallower than in the holotype of "*D. longaevus*." See Tables 1 and 2 for measurements.

Discussion.—*Dissacus serior* is notable for its high stratigraphic occurrence, evidently several hundred meters above the occurrence of *D. willwoodensis*. It is the latest occurring *Dissacus* in North America. Nonetheless, its M_3 is about as long as in *D. argenteus* (much larger than in *D. willwoodensis*) but otherwise more specialized than in all other *Dissacus* in having a much more prominent paraconid and in lacking a metaconid.

Development of a metaconid on the lower molars has been considered a significant taxonomic character in mesonychids, used to distinguish genera. Matthew (1915, 1937) recognized the presence of a metaconid on the lower molars as a diagnostic character of *Dissacus*, while Van Valen (1978, 1980) separated *Ankalagon* partly on the basis of loss of the metaconid on M_1 . *Pachyaena* typically has no metaconids or only vestigial traces of a metaconid. Apart from M_3 , the teeth of *D. serior* do not differ markedly from those of other *Dissacus*; hence, we retain it in that genus.



Fig. 11.—*Pachyaena gigantea* (YPM 50000), right rostral fragment, with P³–M³, lateral view. Canine is completely reconstructed. Scale = 5 cm.

Pachyaena, Cope, 1874

Pachyaena gigantea Osborn and Wortman, 1892

Fig. 10–12

Referred Specimens.—YPM 23333 (left P³–M¹) and YPM 50000 (fragmentary right rostral aspect of skull with P³–M³, and mandible with left C₁, P₁ alveolus, P₃–M₁, right C₁, P₁ alveolus, P₂, P₄, base of M₁, M₂). Parts of YPM 50000 have been reconstructed in plaster, including the mandibular symphysis, both M₃s, C¹, and parts of some other teeth. Collected by field crews working with E. L. Simons.

Localities and Horizons.—YPM 23333: YPM locality 131, 344–348-m level of Willwood Formation; YPM 50000, YPM locality 149, 360-m level of Willwood Formation; both early Eocene (early Wasatchian, Wa-4 of Gingerich, 1983), Big-horn Basin, Wyoming.

Description.—Skull: The nasal is wide caudally and, although incomplete, partly preserves the long nasomaxillary suture. The lacrimomaxillary suture and the facial extent of the lacrimal are difficult to discern due to breakage and crushing, but the lacrimal appears to form most of the anterior margin of the orbit and to have a large pars facialis as in other mesonychids (the primitive eutherian condition,



Fig. 12.—*Pachyaena gigantea* (YPM 50000), mandible, right lateral view with right C, P₂, P₄, M₁ (base), M₂; other right teeth are reconstructed (see text for details). Also visible are left C and P₂. Scale = 5 cm.

according to Novacek, 1986). The orbital rim is marked by a distinct lacrimal tubercle (derived according to Novacek, 1986) located just lateral and slightly dorsal to a pair of elliptical lacrimal foramina, each about 6 mm in dorsoventral diameter. These openings, which are positioned fully within the rim of the orbit, presumably housed the lacrimal sac, leading into the nasolacrimal duct. The orbit is broken along its inferior aspect at what seems to be approximately the junction with the jugal. The premaxilla is partially preserved including an incomplete incisor alveolus, and forms a thin wedge extending caudally between the nasal and the maxilla to just above the infraorbital foramen.

Mandible: Plaster applied at the mandibular symphysis makes it difficult to discern its size, orientation, and whether or not it was ossified as in some *Pachyaena* specimens; but it seems to have extended to below P₃ as in USNM 14915 (O'Leary and Rose, in press:fig. 2A). In USNM 14915 the symphysis is clearly unfused, but the specimen is subadult. The massive dentaries of YPM 50000 are convex inferiorly, shallowing slightly towards the rostrum. The body is deepest under M₁, and the medial surface of each dentary is gently excavated from the distal end of the symphysis to M₃. The angle of the mandible is relatively large and flares medially. A small mental foramen is located under P₃. The coronoid process is well developed and the masseteric fossa is well defined. The condyle is cylindrical and located approximately at or below the level of the tooth row, as in carnivores generally. The right mandibular condyle and both coronoid processes have rugose borders, and the M³ is not fully erupted, features indicating that this animal, too, was subadult.

Dentition: The well-preserved maxillary dental series of YPM 50000 differs from previous illustrations and descriptions of this species (Osborn and Wortman, 1892:fig 12; Szalay and Gould, 1966:fig. 8), in part because some of the original associated teeth were apparently assigned to the wrong loci. Most different are P⁴ and M³. "P⁴" in the holotype is probably a deciduous tooth, as suggested by Osborn and Wortman (1892) and Matthew (1915). Osborn and Wortman's "M³" (apparently not the same tooth as in Szalay and Gould's fig. 8) appears to be misidentified and is more similar to P⁴ in the specimens described here. In addition, Matthew's (1901:fig. 13) illustration of *P. gigantea* shows three teeth identified as M¹–M³ which are probably P⁴–M².

P³–M³ in YPM 50000 are each dominated by a large, swollen conical paracone which is the highest cusp. P³ is a small, triangular tooth with a relatively wide buccal margin and a slightly retroflexed paracone. A rudimentary posterobuccal cingulum gives rise to a low metastyle just posterior to the paracone. Lingual and slightly posterior to the paracone is a small, low protocone, followed by a scalloped postprotocrista bearing two cusps and running to the metastyle. P⁴ has a tall paracone, a rudimentary metacone, and a protocone about half the height of the paracone and positioned directly lingual to it. The buccal margin of the tooth is wide and is marked by a small parastyle and a crenate posterobuccal cingulum ending in a distinct metastyle, which is larger than that of the molars and is situated well in from the buccal margin and just posterior to the metacone. The protocone has a flat

buccal face demarcated by the pre- and postprotocristae, the latter bearing two cusps similar to those of P^3 . YPM 23333 is similar but about 10% smaller, has a smaller protocone on P^3 , and has smooth, not scalloped, postprotocristae on P^3 – P^4 . In size and P^3 structure, this specimen is closer to the holotype.

M^1 of YPM 50000 is the largest tooth and has a well-developed protocone that is almost the size and height of the paracone. The metacone is bigger than in any other tooth but still smaller and lower than the other main cusps. Both paracone and metacone are moderately worn exposing dentine. An ectocingulum runs the entire length of the buccal aspect of the tooth, which has a noticeable ectoflexus and is wider and more crenate at the anterior and posterior margins. It gives rise to a prominent parastyle (preserved in YPM 23333, broken in YPM 50000) and a distinct metastyle just posterior to the metacone. The posterobuccal surface of the protocone is flat and oriented more posteriorly than in P^4 . The preprotocrista is short and runs directly buccally, whereas the postprotocrista is longer and runs almost directly posteriorly to the base of a small, low metaconule, largely worn away in these specimens. M^2 is slightly smaller than M^1 , and has a smaller metacone, no pronounced ectoflexus, and more rounded antero- and posterobuccal margins. The ectocingulum is more pronounced at the midbuccal margin than in M^1 and, as in the other molars, extends lingually beyond the styler cusps, which are slightly smaller than on M^1 . There is a distinct metaconule at the buccal end of the postprotocrista. M^3 is unworn and incompletely erupted, but it is clearly much smaller than the other molars and about the size of P^3 . The ectocingulum gives rise to a small parastyle anteriorly where it joins the crenate preprotocrista; posteriorly it runs to a low cusp (metacone or metastyle) behind the paracone. The protocone is faintly divided at its apex and the postprotocrista is scalloped and bears one low cusp (metaconule?).

The left C_1 has a honing facet extending half the height of the distolateral aspect of the tooth, produced by occlusion with the upper canine. P_{2-4} are progressively larger and have high, slightly retroflexed protoconids, and distinct talonid heels. P_4 has a well-developed paraconid, more lingually positioned than in the molars, which is joined to a buccolingually oriented anterolingual cingulum. M_1 has no metaconid; M_2 , however, has a small ridge that represents a vestigial metaconid. Presence of this vestige seems to be variable in *Pachyaena* (it is present on M_2 of YPM 50000 and on both M_{1-2} of AMNH 2959). A small cuspsule arises from the postcristid at the lingual base of the talonid of M_1 and there is a re-entrant groove at the distal margin. The re-entrant groove is more pronounced in M_2 . Well-developed shearing facets are present on the paraconid of M_1 and on the protoconids of M_{1-2} , but the teeth do not show the heavy cusp tip wear typical of many mesonychid specimens. The enamel surface of the cheek teeth is delicately rugose. See Tables 1 and 2 for measurements.

Discussion.—As far as can be determined, the features of the cranial fragment do not differ greatly from those described in other advanced mesonychids such as *Mesonyx*, *Dromocyon*, or *Harpagolestes* (Scott, 1888; Wortman, 1901; Szalay and Gould 1966).

Matthew (1915) distinguished the subspecies *Pachyaena gigantea ponderosa* from *P. gigantea* proper on the basis of its larger size (about 10% larger) and smaller M^3 . In view of the very small sample size of *P. gigantea* it is unclear whether such a small size difference is sufficient to distinguish taxa of similar age and occurrence. Furthermore, there is no reliable evidence that M^3 was unreduced in *P. gigantea*. The claim of unreduced third molars in *P. gigantea* (e.g., Matthew, 1915) apparently was based on erroneous identification of M^3 (see Osborn and Wortman, 1892:fig. 12; Szalay and Gould, 1966:fig. 8). M^3 is small, however, in both YPM 50000 and the holotype of *P. gigantea ponderosa*, which are similar in size. In addition, P^{3-4} exhibit considerable variation of the protocones and postprotocristae. YPM 23333 and the holotype of *P. gigantea* (Osborn and Wortman, 1892:fig. 12) have a rudimentary protocone and little development of the postprotocrista on P^3 , whereas in YPM 50000 there is a strong protocone and a cuspsate postprotocrista. P^4 in YPM 50000 (and in the holotype of *P. gigantea ponderosa*, to judge from Matthew, 1915:fig. 85) also has a well-developed, cuspsate postprotocrista in contrast to YPM 23333. The original criteria used to separate *P. gigantea ponderosa* from *P. gigantea* proper are not particularly persuasive; however, the premolar characteristics described here, when better known, may

substantiate the presence of two species of large *Pachyaena* in the Willwood Formation. For this present, however, we retain these specimens in *P. gigantea*.

Pachyaena gigantea is a very rare constituent of Wasatchian faunas and is known from very few specimens (probably less than 20). Several of the more complete specimens, including YPM 50000, AMNH 2959, AMNH 15227 and USNM 14915, are subadult.

Pachyaena gracilis Matthew, 1915

Fig. 13

Referred Specimen.—USGS 7185 (maxillary fragments with left P²–M³, right P⁴–M³, and isolated left I¹–I²(?), C¹. Collected by K. C. Beard, 1985.

Locality and Horizon.—USGS locality D-1640, 140-m level, lower Willwood Formation, early Eocene (early Wasatchian, Wa-2 of Gingerich, 1983), Bighorn Basin, Wyoming.

Description.—The incisors are small, simple, conical and gently recurved. The larger of the two (I²?) has a broader base, whereas the smaller incisor is somewhat laterally compressed. Their tips are only slightly blunted, exhibiting little wear. The slender canine is oval in cross section with the long axis oriented mesiodistally, and is approximately four times as tall as the largest incisor. It is gently recurved and has a narrow honing facet that is a little over half the length of the crown.

P² is a simple, two-rooted, premolariform tooth that is mesiodistally elongate with a tall, gently retroflexed anterior cusp, and a weakly developed posterior cusp. P³, also two-rooted, is expanded posteriorly, with a trace of a posterolingual cingulum which gives rise to a weak cusplule at its anterior end and runs to a larger posteromedian cusp. From the latter, a low crest runs directly buccally. P⁴ is molariform with a large paracone, a much smaller and closely appressed metacone, and a protocone intermediate in size. P⁴–M³ are marked by distinct crenate ectocingula, weak or interrupted near the middle of each tooth. The ectocingula end in small parastyles on M¹⁻² (weaker on P⁴ and M³) and small metastyles on P⁴–M². The paracone and protocone are approximately equal in size on M¹ although the protocone is not as tall, and the metacone is less closely appressed to the paracone on M¹ and M² than on P⁴. The small metaconule is variably developed on P⁴–M³, weakest on P⁴ and strongest on M². M¹ and M² are approximately the same size, while M³ is decidedly smaller (smaller than P⁴) and has a very reduced posterobuccal cusp (metacone?). See Table 2 for measurements.

Discussion.—Although some fragmentary upper teeth of *P. gracilis* have been reported (Matthew, 1915), the upper dentition of this species has never been illustrated or described. Compared to *P. gigantea*, the metacones are stronger and more separated from the paracones, and the ectocingula and metaconules of *P. gracilis* are weaker. P³ shows strikingly less development of a lingual cusp in *P. gracilis* (and *P. ossifraga* Cope, 1884:plate 28a) than in *P. gigantea*.

Family Hapalodectidae (Szalay and Gould, 1966) Ting and Li, 1987

Hapalodectes anthracinus Zhou and Gingerich, 1991

Fig. 14

Referred Specimen.—USGS 9628 (left M₁–M₂, right M₃ fragment).

Locality.—University of Wyoming locality V-73086, 61-m level, lower Willwood Formation, early Eocene (early Wasatchian, Wa-1 of Gingerich, 1983), Bighorn Basin, Wyoming.

Remarks.—This specimen is allocated to *Hapalodectes anthracinus* on the basis of the tall, upright protoconids, the absence of metaconids on the lower molars, and its small size (Table 1; see Zhou and Gingerich, 1991). If the teeth are correctly identified, M₃ was the largest molar, as in other hapalodectids (Szalay, 1969), and has a deep re-entrant groove on the mesial aspect of the paraconid to receive the talonid of M₂. The only other North American species, *H. leptognathus*, is larger

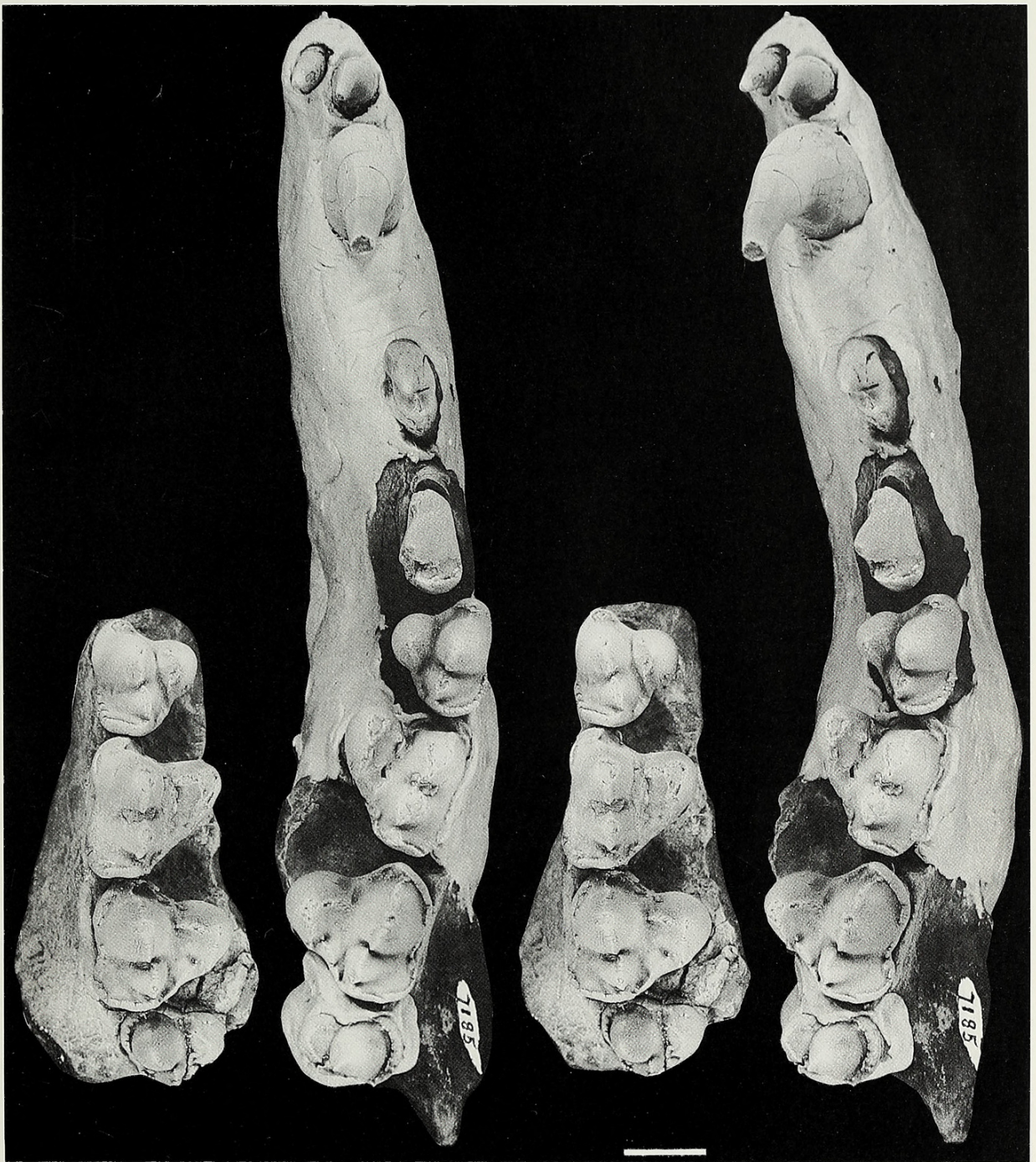


Fig. 13.—Upper dentition of *Pachyaena gracilis* (USGS 7185), occlusal view, stereographs; right P⁴–M³, and left I¹–I²?, C, P²–M³. Scale = 5 cm.

and has vestigial metaconids (Szalay, 1969). *Hapalodectes hetangensis*, from the early Eocene of China, is smaller than *H. anthracinus* and further differs in having distinct molar metaconids (Ting and Li, 1987). *Hapalodectes anthracinus* closely resembles *H. serus* from the middle Eocene of Asia. Both have no metaconids, and *H. serus* is only slightly larger, even less so if its holotype is M₃ rather than

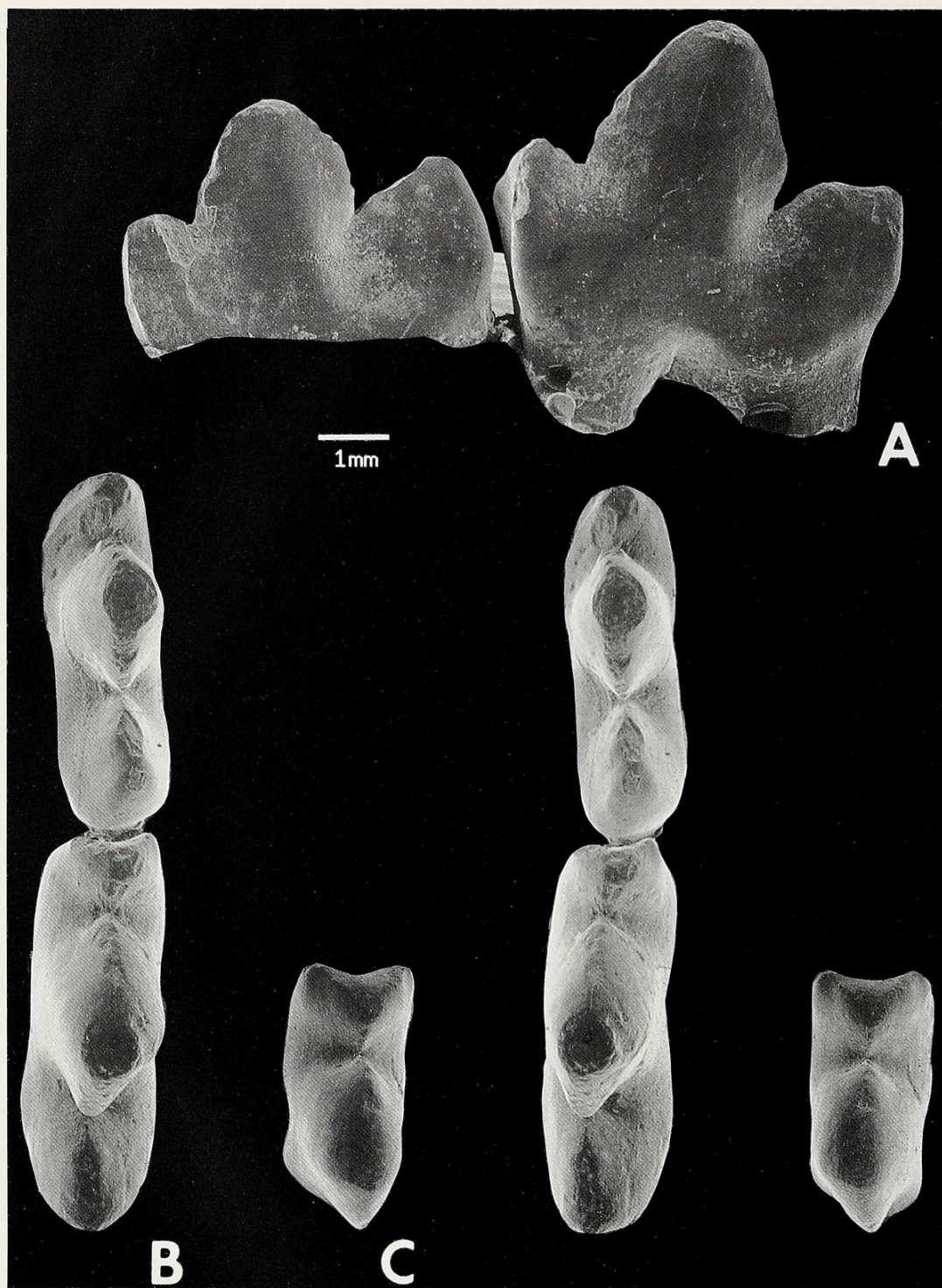


Fig. 14.—SEM photographs of *Hapalodectes anthracinus* (USGS 9628). A, left M_1 – M_2 , lateral view; B, left M_1 – M_2 , occlusal view, stereographs; C, right M_3 , occlusal view, stereographs. Scale = 1 mm.

M_2 . In view of the geographical and temporal separation of these two species, however, we tentatively retain both as valid. This is only the third known specimen of this very rare mesonychian and is the best preserved. See Table 1 for measurements.

DISCUSSION AND CONCLUSIONS

The late Paleocene–early Eocene dentitions described above exhibit a rather impressive range of morphological variation, both interspecific and intraspecific, and substantially expand what is known of mesonychian dental anatomy from this interval. Available specimens indicate the presence of three new species of *Dissacus*, one from late Tiffanian strata and two from the Wasatchian, doubling the number of North American species of the genus.

Torrejonian *D. navajovius* is a plausible stem group for all currently known North American species of *Dissacus*, and there is nothing to preclude it from being directly ancestral to the new Tiffanian species, *D. argenteus*, which has a more retroflexed P_4 protoconid and slightly basined P_4 – M_1 talonids. Wasatchian *D. willwoodensis*, n. sp., further accentuates these features. *Dissacus navajovius* may also have given rise to late Tiffanian–Clarkforkian *D. praenuntius*, which shows somewhat similar specializations but is larger than the other North American species. The later Wasatchian *Dissacus serior*, n. sp., is unique among *Dissacus* in having lost the metaconid on M_3 .

Samples of *D. praenuntius* and *D. willwoodensis* described here each exhibit minor morphologic variations (e.g., differences in overall tooth size, relative M_3 size, and jaw depth) but, in the absence of more compelling evidence, these are considered intraspecific variations. The range of cheek tooth size in other *Dissacus* samples also suggests substantial intraspecific variability or, possibly, the presence of more than one species in some faunas. *Dissacus carnifex*, from the same strata as *D. navajovius* (Torrejonian of the San Juan Basin), was initially considered distinct because of slightly larger size, a deeper jaw, and the presence of a paraconid on P_3 (Cope, 1882, 1884). Matthew (1897), who contested the size difference and reported the existence of specimens intermediate between the two species, concluded that they were synonymous. Our measurements indicate that the holotype of *D. carnifex* is, in fact, roughly 10% larger than the type of *D. navajovius*, especially in P_4 and M_3 dimensions, but whether this difference would justify recognition of two species is equivocal. The dentary of the holotype of *D. carnifex* is about 50% deeper than that of *D. navajovius*, which is not incompatible with an interpretation of sexual dimorphism rather than different species.

There is additional evidence suggesting sexual dimorphism in mesonychians. As discussed earlier, the holotype of Wasatchian “*D. longaevus*” has cheek teeth of similar size to those of contemporaneous *D. willwoodensis*, together with a much larger canine alveolus and a deep, robust dentary—characters consistent with its being a male of the new species. It differs from *D. willwoodensis*, however, in having a relatively larger M_3 and a less basined M_1 talonid. These characters are not likely to be sexually dimorphic, but whether they are of specific distinction is unknown. The specimen lacks several key diagnostic characters, thus preventing an adequate assessment of its affinities. Variation in jaw depth and tooth compression in *Hapalodectes* has also been suggested to result from sexual dimorphism or intraspecific variability (Szalay, 1969). By contrast, Zhou et al. (1992) interpreted the supposed lack of sexual dimorphism in *Pachyaena* as indicating that these animals were solitary scavengers; but such an inference may be premature. Sample sizes of mesonychians, especially *Pachyaena*, are probably too small to allow confident resolution of whether or not they were sexually dimorphic.

The contrast in dentary depth in *D. longaevus* and *D. willwoodensis*, despite similar-sized teeth, indicates that tooth size and jaw depth are not necessarily

directly related in species of *Dissacus*. Szalay and Gould (1966) also observed that jaw size and tooth size are not always correlated in mesonychids, noting that *Mongolestes hadrodens* has a dentary comparable in size to that of *Ankalagon saurognathus* but much larger cheek teeth.

The exact provenance is unknown for most previously described specimens of *Pachyaena*, but the upper dentition of *P. gracilis* reported here is older than all *P. gigantea* for which stratigraphic data exist. Its smaller size and more distinct metacones, especially on P^4 , appear to be primitive relative to *P. gigantea*. In comparison, P^4 in *Dissacus* has a well-separated metacone in primitive species (*D. navajovius*) but a connate paracone-metacone in more derived species (*D. praenuntius*, *D. willwoodensis*). *Pachyaena* specimens described here show variations in the expression of the protocone of P^3 and the postprotocristae of P^{3-4} , but the polarities of these characters are unclear.

Hapalodectes anthracinus is the oldest known hapalodectid and one of the smallest. In contrast to *H. hetangensis* (early Eocene of China), the most primitive hapalodectid, *H. anthracinus* is relatively derived in having lost the metaconids on the lower molars.

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