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Yale PEABODY MUSEUM OF NATURAL HISTORY

Postilla Number 193

**Two unusual specimens of
Helaletes in the
Yale Peabody Museum collections,
and some comments on the
ancestry of the Tapiridae
(Perissodactyla, Mammalia)**

Robert Milton Schoch

Abstract

A calvarium, mandible and partial skeleton
of *Helaletes nanus* and a partial upper den-
tition of *Helaletes intermedius*, both from
the middle Eocene (Bridgerian) of
Wyoming, are described and illustrated.
Previously unrecognized cursorial speciali-
zations in the hindlimb of *H. nanus* suggest
that it was not the direct ancestor of the
Tapiridae, as hypothesized by some earlier
workers. Alternatively, if *H. nanus* was the
true ancestor of the Tapiridae, an initial
tendency toward cursoriality in the hind-
limb was later reversed. Only four described
specimens are presently referred to *H.
intermedius*. Due to morphological dif-
ferences observed between these
specimens, it is unclear if they all pertain to
the same species-level taxon. As presently
constituted, the species *H. intermedius*,
might be better referred to a separate
genus from *Helaletes nanus*.

Introduction

The Yale Peabody Museum (YPM) is fortu-
nate to include among its vertebrate
paleontology collections two extremely
rare specimens of the Bridgerian (middle
Eocene) archaic tapiroid genus *Helaletes.*
These specimens are YPM 11807, the
holotype of *Helaletes boops* Marsh, 1872
[=*Helaletes nanus* (Marsh, 1871)], the
type species of the genus, and YPM 15233,
a partial upper dentition referable to
Helaletes intermedius (Osborn, Scott and
Speir, 1878).

YPM 11807 consists of an incomplete
skull, mandible and partial skeleton (Figs.
1–3); presently this is one of the most com-
plete specimens of *Helaletes nanus*
known. (Another fairly complete specimen
of *H. nanus* in the National Museum of
Natural History, Smithsonian Institution,
Washington, D.C., unfortunately was
mounted in plaster and placed on display
without being described.) Radinsky (1965a)
described the skeleton of the early Eocene
North American helaletid *Heptodon*, which
may represent a generalized ancestral
morphology both for *Helaletes* and for later
tapiroids. Radinsky (1965b) also described
the skeletal morphology of the late Eocene

Asian tapiroids *Lophialetes* and *Deperetella*. More recently, Reshetov (1977, 1979) described in much greater detail the osteology of *Lophialetes*. K.-H. Fischer (1964) described the osteology of the early to late Eocene European tapiroid *Lophiodon*. In this context a careful description of the osteology of *Helaletes* is important for a future synthesis of early tapiroid evolution. Although Peterson (1919, pp. 104–12) described the holotype of *Helaletes boops* in detail and gave a complete set of measurements, he presented only simple line drawings of selected parts of this specimen (Peterson, 1919; pl. 42, figs. 1–9; pl. 43, figs. 1–3). Therefore, I here supplement Peterson's (1919) descriptions and illustrations by photographically illustrating and briefly commenting on this specimen.

YPM 15233 (Fig. 4) is the second most complete specimen known of *Helaletes intermedius* and only the fourth specimen to be referred to this taxon. Moreover, this specimen bears a unique premolar morphology (see below). YPM 15233 was briefly described, but not illustrated, by Radinsky (1963a, pp. 50–51); here I thoroughly describe and illustrate this important specimen for the first time.

Study of these specimens suggests that *Helaletes nanus* bears cursorial specializations of the hindlimb not previously recognized. If *Helaletes nanus* is the direct ancestor of the Tapiridae, as suggested by Radinsky (1963a), then these cursorial adaptations were lost during later evolution toward the tapirid condition. Alternatively, these specializations may be viewed as autapomorphies of *Helaletes nanus* which would exclude it from the ancestry of the Tapiridae. *Helaletes intermedius* is a poorly known and poorly understood taxon. Specimens presently referred to *H. intermedius* may represent more than one species and there is also the possibility that *H. intermedius* should be referred to a genus distinct from *H. nanus*.

Systematic Paleontology

CLASS Mammalia Linnaeus, 1758
ORDER Perissodactyla Owen, 1848
SUBORDER Ceratomorpha Wood, 1937
SUPERFAMILY Tapiroidea Burnett, 1830 (Gill, 1872)
FAMILY Helaletidae Osborn, 1892 in Osborn and Wortman, 1892
GENUS *Helaletes* Marsh, 1872
Helaletes nanus (Marsh, 1871)
(Figs. 1–3)

Referred Specimen

YPM 11807, holotype of *Helaletes boops* Marsh, 1872, calvarium with right C^1–M^3, alveoli or roots, or both, for right I^{1-3} (Fig. 1A–C; when Peterson, 1919, described this specimen it included the crowns of right I^{1-3} which have since been lost); fragments of mandible including the symphyseal region, right dentary with P_4–M_3 and roots of P_{2-3}, and left dentary fragment with P_4, M_1, M_3 and roots of M_2 (Fig. 1D–F); fragments of several cervical, a thoracic(?) and four lumbar vertebrae; anterior part of the sacrum (Fig. 2I, J); glenoid area of left scapula (Fig. 2A, B); distal end of left humerus (Fig. 2C–F); parts of left ulna and radius (Fig. 2F, G); left magnum (broken) and heads of metacarpals III, IV and V (Fig. 3C, D); right ilium and acetabular part of pelvis (Fig. 2J, K); proximal and distal ends of right tibia (Fig. 2O; 3A, B); proximal end of left tibia; distal end of right fibula (Fig. 3A, B); right astragalus (Fig. 3A, B); right calcaneum, right navicular (broken: Fig. 3A, B); right and left cuboids (Fig. 3A, B); proximal and distal ends of right metatarsals II, III, and IV (Fig. 3A, B); three proximal phalanges of the pes (Fig. 3A, B); median phalanx of the pes; distal phalanx of the pes (Fig. 3A, B); and other skeletal fragments.

Horizon and Locality

Middle Eocene (Bridgerian)-aged strata of the Bridger Formation, Grizzly Buttes,
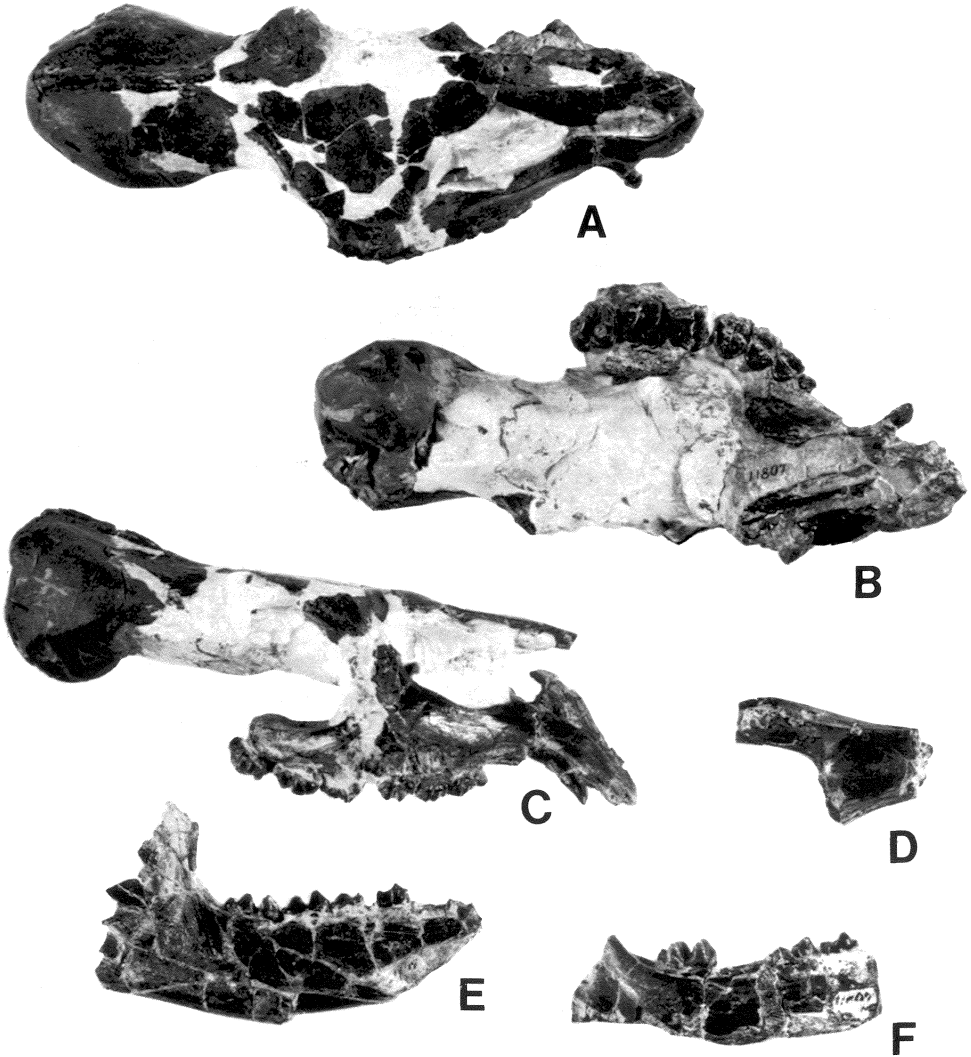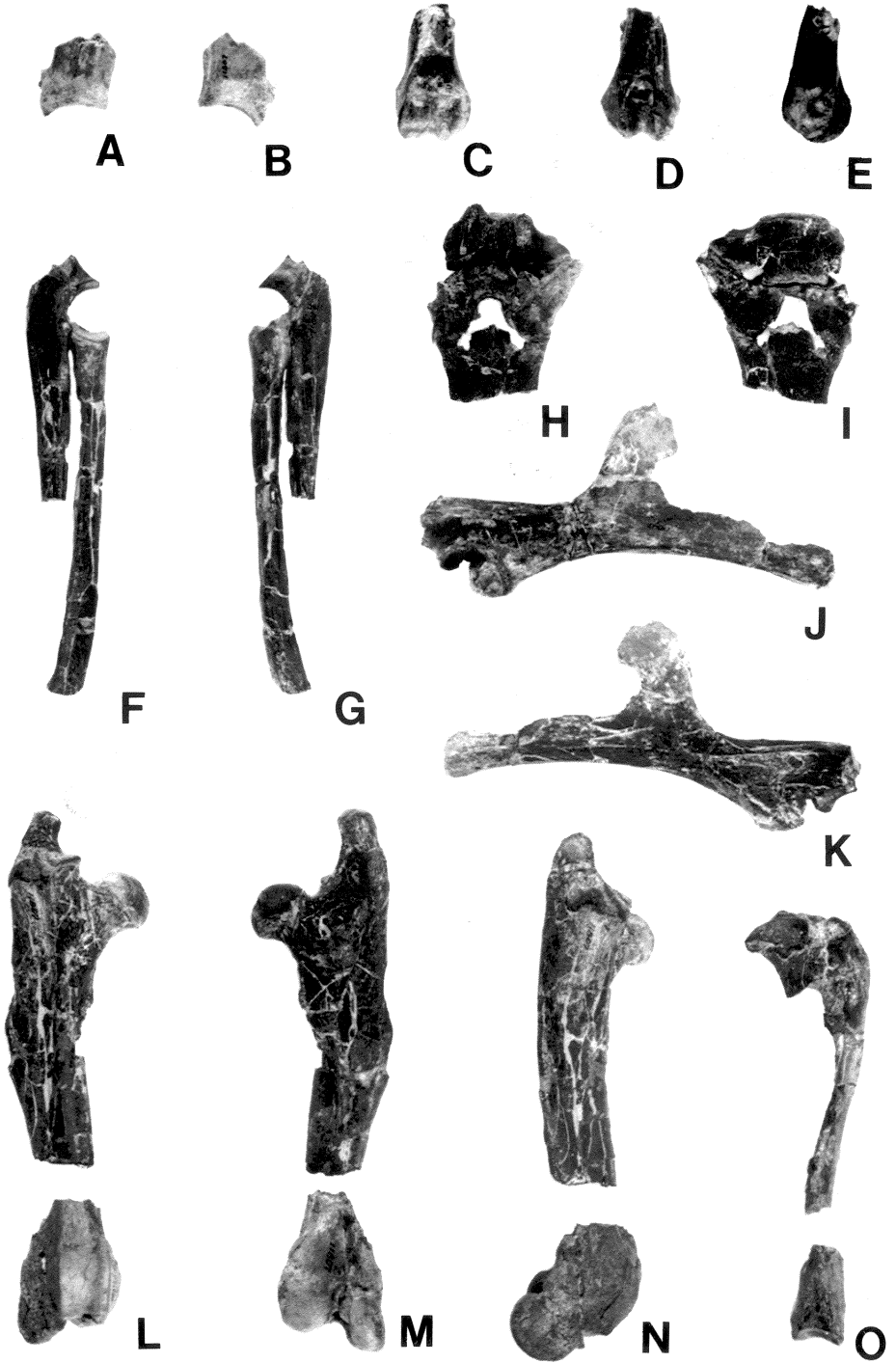
Fig. 1
Holotype of *Helaletes boops* (= *Helaletes
nanus*), YPM 11807: *A*) dorsal view of
calvarium, x 2/3; *B*) ventral view of calvarium,
x 2/3; *C*) right lateral view of calvarium, x 2/3;
D) occlusal view of symphyseal region of
mandible, x 1; *E*) labial view of right dentary,
x 2/3; *F*) lingual view of left dentary, x 2/3.

Bridger Basin, Wyoming. Collected by G. G. Lobdell, Jr., Yale Scientific Expedition, August, 1871.

Description and Discussion

Helaletes boops is the type species of *Helaletes*. Although provisionally regarded as specifically distinct by Peterson (1919) and Troxell (1922), *H. boops* was synonymized with *Lophiodon nanus* Marsh, 1871 by Radinsky (1963a) who presents a complete justification and discussion of this synonymy. Radinsky (1963a) also upheld the validity of *Helaletes* as a genus of tapiroids distinct from the genus *Lophiodon*. The preserved dentition of YPM 11807 has been adequately described and illustrated by Peterson (1919, pl. 43, figs. 2, 3) and Radinsky (1963a, pl. 2, fig. 2). As noted above, Peterson (1919) has described the skeleton of YPM 11807 and the following discussion is intended as a supplement to his description.

Skull

The calvarium of *Helaletes* (Fig. 1A–C) is most notable for its greatly expanded, deep, posteriorly rounded nasal incision which extends to a point over P^{3-4}. Similarly, a large nasal incision is seen in

other tapiroids such as the Eocene-Oligocene helaletid *Colodon* (Radinsky, 1963a), in *Protapirus* and *Tapirus* (Hatcher, 1896) and in *Lophialetes* (Radinsky, 1965b; Reshetov, 1977, 1979). This is a significant advance over the condition seen in *Heptodon* (Radinsky, 1965a), but note that retraction of the nasal incision has appeared independently in several ceratomorph lineages (cf. Radinsky, 1966a, 1967a, 1969; Wall, 1980; Lucas, Schoch and Manning, 1981). The nasal region of *Helaletes* differs from those of the above-mentioned tapiroid genera. In *Helaletes* the nasal incision appears to be relatively larger and deeper than in *Heptodon,* and the nasals are reduced to transversely narrow bones which have lost contact with the premaxillae. However, unlike the condition seen in *Colodon, Lophialetes* and the Tapiridae, in *Helaletes* the nasals extend to the anterior tip of the skull (Radinsky, 1963a, p. 89: the anterior tips of the nasals are broken off and missing in YPM 11807). Radinsky (1963a) described a large, shallow, vertical groove on the ascending portion of the maxilla of *Helaletes;* YPM 11807 has been damaged in this area and this groove is not clearly discernable.

The symphysis of the mandible (Fig. 1D) is solidly fused, but is relatively short and shallow, and there is a long diastema between C_1 and P_2 (P_1 is absent in *Helaletes*). The body of the mandible (Fig. 1E, 1F) is moderately deep and the ventral edge is anteroposteriorly convex.

Axial Skeleton

Only a few vertebral fragments (listed above) are preserved with YPM 11807 and they do not appear to differ from the corresponding elements of *Heptodon* described by Radinsky (1965a). Only the three anterior centra of the sacrum (Fig. 2H, 2I) are preserved. Unfortunately the sacrum is missing from the specimen of *Heptodon posticus* described by Radinsky (1965a) and thus there is no ready comparison for the sacrum of *H. nanus.*

◀ **Fig. 2**

Holotype of *Helaletes boops* (= *Helaletes nanus*), YPM 11807: *A*) lateral view of glenoid area of left scapula; *B*) medial view of glenoid area of left scapula; *C*) anterior view of distal end of left humerus; *D*) posterior view of distal end of left humerus; *E*) medial view of distal end of left humerus; *F*) medial view of left ulna and radius; *G*) lateral view of left ulna and radius; *H*) dorsal view of sacrum; *I*) ventral view of sacrum; *J*) lateral view of right ilium; *K*) medial view of right ilium; *L*) anterior view of right femur; *M*) posterior view of right femur; *N*) lateral view of right femur; *O*) lateral view of right tibia. All x 1/2.
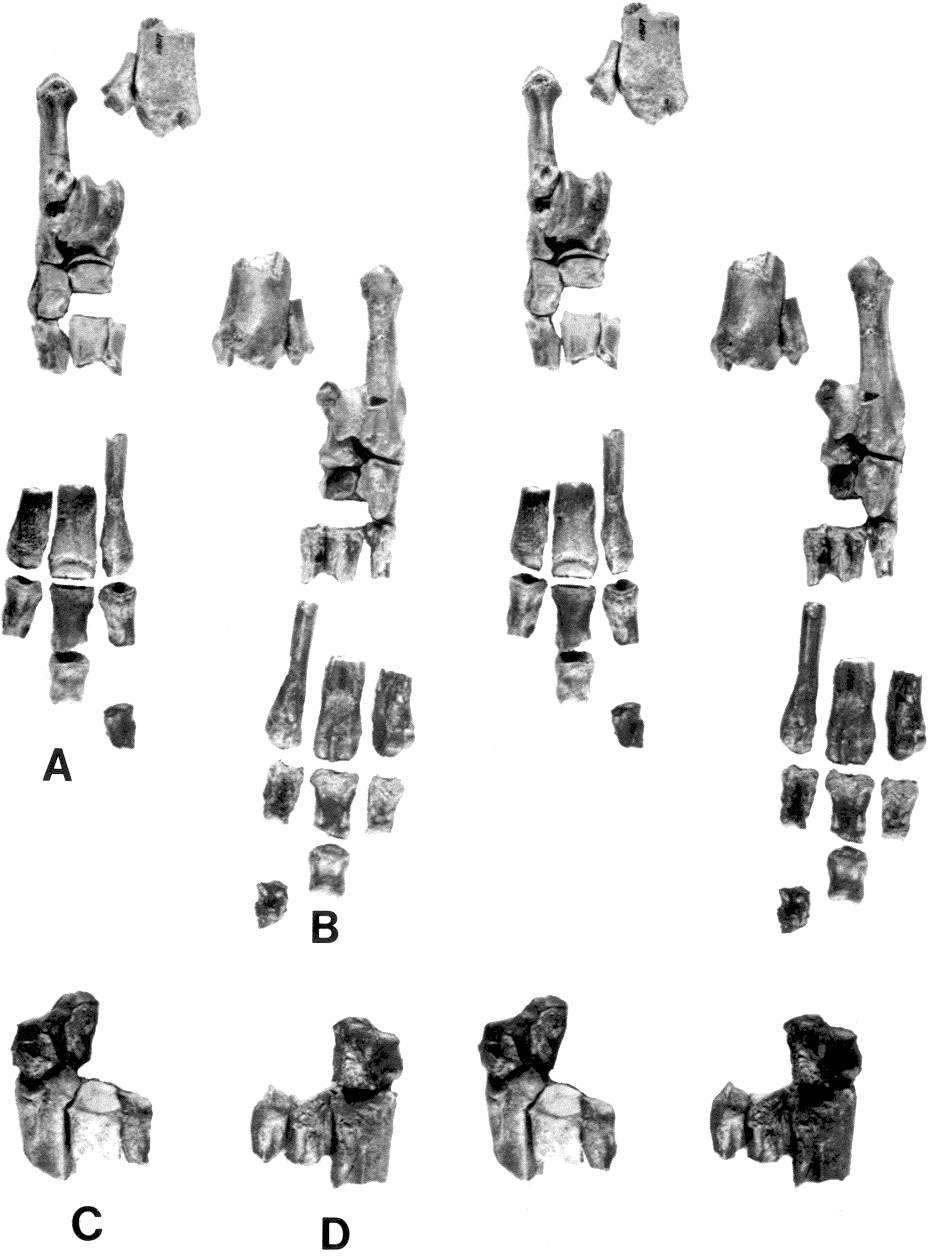
Limbs

The parts preserved of the fore- and hind-limbs of YPM 11807 (Figs. 2A–G, J–O; 3: see Peterson, 1919, for a thorough description) are much closer in overall morphology to the corresponding elements of *Heptodon* (Radinsky, 1965a) than to any other known tapiroid. This is to be expected in light of the close relationship between these two forms (Radinsky, 1963a). What little is known of the forelimb (Fig. 2A–G) and manus (Fig. 3C, D) of *H. nanus* is extremely similar to the forelimb and manus of *Heptodon posticus,* and need not be further described here. Major points of departure between the skeletons of *H. nanus* and *H. posticus* are seen in the hindlimb, as follows: 1) although broken, the ilium of *H. nanus* appears to be relatively longer than the ilium of *Heptodon;* 2) the greater trochanter of the femur appears to be much higher and better developed in *Helaletes* (cf. Fig. 2L with Osborn, 1929, fig. 676A, a complete femur of *Heptodon calciculus:* the femur of *Heptodon posticus* described by Radinsky, 1965a, fig. 15, is missing the top of the greater trochanter, but based on the smaller dimensions of its base it too had a smaller greater trochanter than *Helaletes nanus*); 3) the trochlea of the astragalus of YPM 11807 is relatively high and narrow, more like that of *Heptodon calciculus* (Radinsky, 1965a) and *Lophialetes expeditus* (Radinsky, 1965b;

Reshetov, 1979) than that of *Heptodon posticus* (Radinsky, 1965a), *Lophiodon tapirotherium?* (K.-H. Fischer, 1964) and *Tapirus pinchaque* (Radinsky, 1965a); and 4) the medial crest of the trochlea of YPM 11807 is slightly longer than the lateral crest of the trochlea, whereas the reverse is the case in the specimen of *Heptodon posticus* described by Radinsky (1965a). Peterson (1919, p. 111) stated that there is "no evidence of facets for metatarsals I or V" in YPM 11807; however, although not preserved in YPM 11807, a vestigial metatarsal I was present in *Helaletes* as in *Heptodon* and many other perissodactyls (Radinsky, 1963b).

Functional Significance of the Differences between the Skeletons of *Heptodon* and *Helaletes*

The most striking difference observed between the skulls of *Heptodon* and *Helaletes* is the greatly retracted nasal incision of the latter genus. However, as Radinsky (1963a, p. 89) noted, "extension of the nasals to tip of snout [in *Helaletes*] seems to preclude development of a lengthy proboscis" like that seen in *Tapirus* and other tapirids. Rather the large nasal incision of *Helaletes* may have been to accommodate enlarged nasal diverticula.

As described above, several significant differences are observed between the hindlimbs of *Heptodon* and *Helaletes.* All of the features in which the hindlimb of *Helaletes* differs from that of *Heptodon* are modifications toward a more cursorial condition. Particularly notable are the relatively longer ilium and much higher greater trochanter of the femur in *Helaletes nanus,* both classic cursorial adaptations (cf. Gregory, 1912; Osborn, 1929; Smith and Savage, 1956, on mammalian limb morphology and function).

◀ **Fig. 3**
Holotype of *Helaletes boops* (= *Helaletes nanus*), YPM 11807. *A*) stereophotographic pair, dorsal view of right pes, distal ends or right tibia and fibula, x 1/2; *B*) stereophotographic pair, ventral view of right pes, distal ends of right tibia and fibula, x 1/2; *C*) stereophotographic pair, dorsal view of left manus, x 1; *D*) stereophotographic pair, ventral view of left manus, x 1.

Helaletes intermedius (Osborn, Scott and Speir, 1878)
(Fig. 4)

Referred Specimen

YPM 15233, occipital region of skull pre-
serving posterior tip of sagittal crest and
right occipital condyle; right maxilla with
P^2–M^3 (Fig. 4: crowns of all teeth damaged
except for M^3); and left maxilla with P^2–M^3
(crowns of all teeth damaged).

Horizon and Locality

Collected by B. D. Smith, probably from
middle Eocene (Bridgerian)-aged
strata of the Bridger Formation, Bridger
Basin, Wyoming in August, 1872
(see Radinsky, 1963a, p. 50).

Description and Discussion

YPM 15233 is a poorly preserved
specimen. The preserved bone material of
the occiput and maxillae are weathered,
discolored and show what appear to be
numerous rootlet traces. The teeth are only
moderately worn, but except for the right
M^3 all are damaged to various degrees. The
labial faces of left P^2–M^2 are sheared off
and missing, making it impossible to even
measure the lengths and widths of these
teeth. Virtually the complete crown of the
left M^3 is missing. The teeth of the right
maxilla have suffered less damage (Fig. 4).
Both the labial and lingual faces of P^2 are
missing. The posterolabial corner, including
the entire metacone, is missing from P^3.
The lingual face of P^4, including the
protocone-hypocone, has been sheared off.
The anterolabial corner, bearing the
parastyle, is missing from M^1. The antero-
labial corner, bearing part of the parastyle,
and the tip of the protocone are missing
from M^2. M^3 is the only complete tooth. The
enamel of the teeth of YPM 15233 is slightly
rugose where unworn, and is deep blue-
gray in color mottled with white corrosion.
Because of this mottling, the teeth of YPM
15233 do not photograph well and I decid-
ed that it was best to illustrate them by a
detailed line drawing (Fig. 4).

In preserved parts of the skull (occiput,
maxillae and teeth), YPM 15233 is com-
parable in size to YPM 11082, a complete

Fig. 4
Right maxilla with P^2–M^3 of *Helaletes*
intermedius, YPM 15233. Drawing by Ruth
Santer.
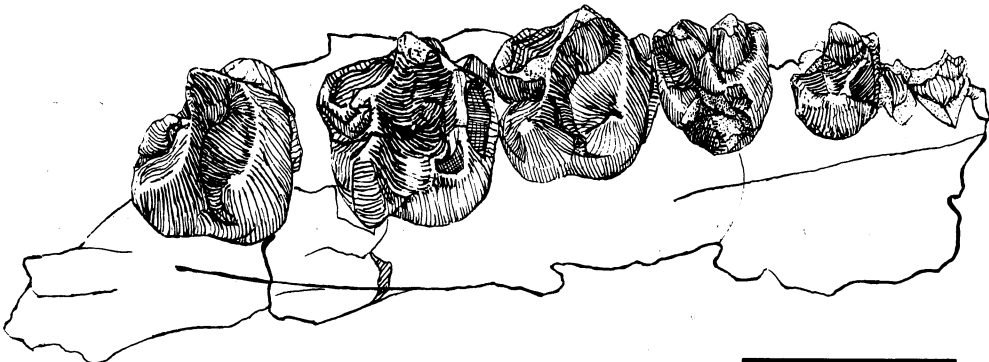
2 cm

skull, approximately 20 cm long, referred to *Hyrachyus modestus* (Leidy, 1870) by Radinsky (1967b; YPM 11082, also from the Bridger Basin, is the type specimen of *Colonoceras agrestis* Marsh, 1873 and is illustrated in Troxell, 1922). Dental measurements of YPM 15233 are given in Table 1.

A small P^1 was apparently present in YPM 15233, as it is in Princeton University (PU) 10166 [the type specimen of *Desmatotherium guyotii* Scott, 1883, but referred to *Helaletes intermedius* by Radinsky (1963a), and the only other known specimen referred to this taxon in which the upper premolars are preserved: illustrated in Radinsky, 1963a, pl. 2, fig. 4]. This is indicated by the trace of an impression for the posterior root of P^1 preserved on the broken anteromost faces of both maxillae of YPM 15233. P^{2-4} of YPM 15233 each bear a single large root lingually and two smaller roots each labially.

P^2 is small and triangular in outline. On both sides of YPM 15233 the labial face of P^2 is missing, but most likely it bore a distinct paracone and metacone as in PU 10166. The lingual half of the left P^2 is preserved in YPM 15233 and differs from the corresponding tooth in PU 10166 (*contra* Radinsky, 1963a, p. 43). In YPM 15233, P^2

bears a simple protocone whereas in PU 10166 P^2 is slightly longer labially and bears an incipient lingual groove separating off a minute hypocone (Radinsky, 1963a, pl. 2, fig. 4).

P^3 is also triangular in outline. As in many tapiroids (Butler, 1952), it is the most molariform of the premolars. Labially, P^3 bears a small parastyle and a high, conical paracone. The posterolabial part of both P^3s, which bore the metacones and metastyles, if present, are missing in YPM 15233. Lingually, P^3 bears a distinct protocone which is separated from the small, posterolingually placed, hypocone by a shallow groove. The hypocone is very slightly better developed on the left P^3 than on the right P^3 of YPM 15233. PU 10166 differs from YPM 15233 in bearing a much better developed hypocone on P^3. On P^3 a low protoloph runs from the anterolingual corner of the paracone to the anterolabial corner of the protocone. An even lower metaloph runs from the posterolingual corner of the paracone of P^3 to the posterolabial corner of the protocone such that the small hypocone lies entirely posterior to the metaloph. This condition differs from *Helaletes nanus* in which the metaloph runs to the hypocone when present in P^{2-4} (Radinsky, 1963a, p. 43).

Table 1

Dental measurements (in mm) of YPM 15233, an upper dentition of *Helaletes intermedius* (measurements from right side; left side unmeasurable).

Tooth	Length	Width
P^2	8.5	
P^3	approx. 10.0	11.5
P^4	10.5	approx. 12.9
M^1	13.6	14.5
M^2	16.1	16.7
M^3	15.6	16.8

P[4] is very similar in morphology to P[3], although larger. There is a low, but distinct, parastyle. The paracone and metacone are sharp, conical, subequal in size and distinct from one another. The protoloph-metaloph configuration is as seen in P[3], only the lophs are slightly higher and better-developed in P[4]. The lingual face of the right P[4] of YPM 15233 is missing, but on the left P[4] an incipient hypocone is present just posterior to the moderate-sized protocone, but is not separated from the protocone by a distinct lingual groove. This contrasts with the P[4] of PU 10166 which bears a large and distinct hypocone.

M[1-2] are virtually identical to each other in morphology, except for size. Both are rectangular in outline and, although broken in YPM 15233, apparently bore prominent parastyles. The paracones are high, sharp, triangular in cross section, placed on the far labial edges of the teeth and separated from the metacones by shallow, but distinct, notches in the ectolophs. The metacones are slightly lower than the paracones, lingually displaced and only very slightly convex labially. M[1-2] bear distinct cingula labial of the metacones. The protocones and hypocones are sharp, conical and subequal in height. The protolophs run from the anterolingual bases of the paracones to the middle of the labial faces of the protocones and likewise the metalophs run from the anterolingual bases of the metacones to the middle of the labial faces of the hypocones. Due to the lingual displacement of the metacones, the metalophs are slightly shorter than the protolophs. Both protolophs and metalophs are sharp, high, and slightly curved, with their convex faces directed anteriorly. The posterior part of the metacone of M[2] is very slightly shorter than that of M[1]. M[1-2] bear low, poorly-developed anterior and posterior cingula.

M[3] is similar to M[1-2] but much narrower posteriorly and thus the metaloph of M[3] is relatively shorter than on M[1-2]. The parastyle is well-developed on M[3]. The anterior cingulum is low and continuous with the parastyle, but does not reach the protocone lingually as on M[1-2]. The metacone of M[3] is relatively smaller and lower than on M[1-2], further displaced lingually, more distinctly convex labially, and lacks the labial cingulum seen on M[1-2]. The protoloph and metaloph of M[3] are also more strongly curved than in M[1-2] and there is no posterior cingulum on M[3]. M[1-3] each bear two roots lingually and two roots labially.

The bases of the ascending walls of both maxillae of YPM 15233 are preserved and thin rapidly upward, but are broken off. Thus, while this may support Radinsky's (1963a, p. 51) suggestion that *Helaletes intermedius*, like *Helaletes nanus*, had a greatly enlarged nasal incision, it does not definitively demonstrate it. The infraorbital foramen is single and positioned above P[4]–M[1] and the anterior border of the orbit is above M[1]–M[2]. This also suggests that *H. intermedius* may have had a greatly enlarged nasal incision.

Taxonomic Status of Specimens Referred to *Helaletes intermedius*

Only four specimens have been described which may be referable to *Helaletes intermedius* as presently construed (genus last revised by Radinsky, 1963a). These specimens are: 1) PU 10095, a right M[1-3] from late Bridgerian beds, Bridger Basin, Wyoming, the holotype of *Hyrachyus intermedius* Osborn, Scott and Speir, 1878, p. 51; 2) PU 10166, a right maxilla fragment bearing P[2]–M[3] and root of P[1] and an isolated right upper canine, probably from late Bridgerian strata, either Bridger or Washakie Basin, Wyoming (see Radinsky, 1963a, p. 49), the holotype of *Desmatotherium guyotii* Scott, 1883, p. 46; 3) YPM 15233 (described above); and 4) American Museum of Natural History (AMNH) 12672, right and left dentaries with C_1, P_2–M_3 (Fig. 5) from Bridger D_1 beds, Bridger Basin, Wyoming, previously referred to *Ephyrachyus* (=*Hyrachyus fide* Radinsky, 1967b) by Wood (1934, p. 236, fig. 13) but tentatively
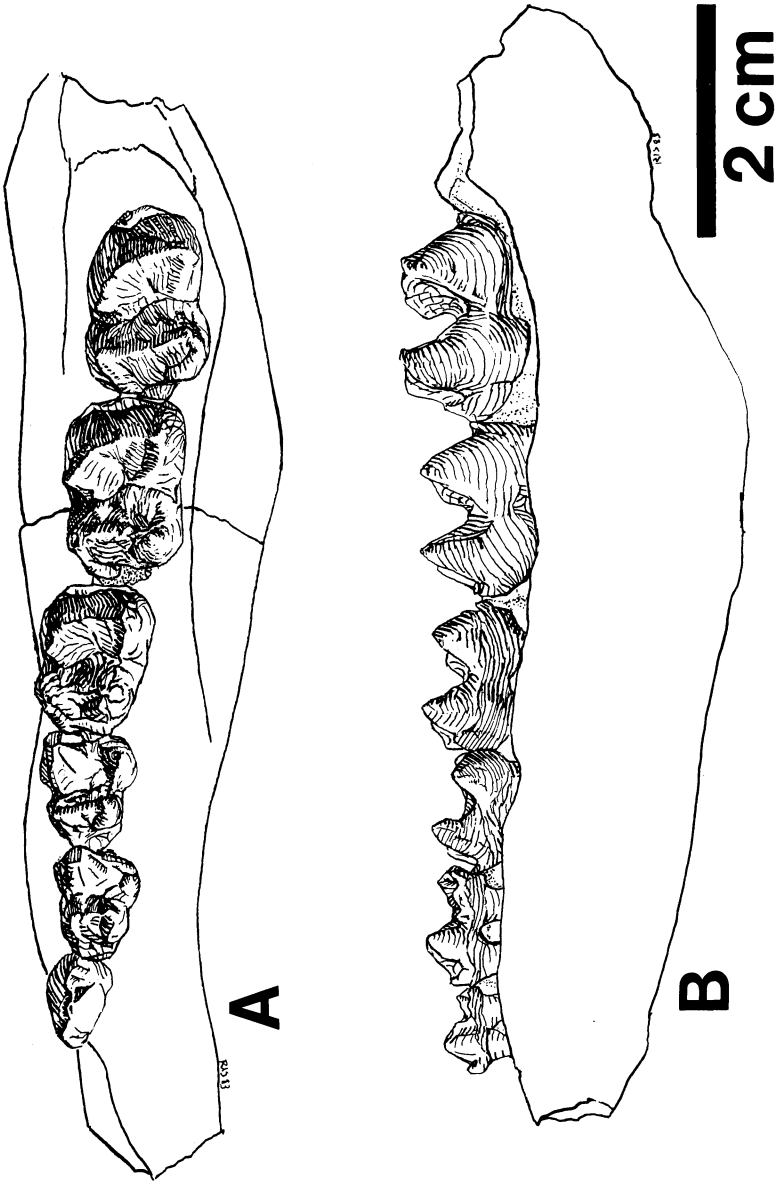
Fig. 5
Right dentary with P$_2$–M$_3$ of *Helaletes intermedius*, AMNH 12672: *A*) occlusal view of dentition; *B*) lingual view of dentition. Drawing by Ruth Santer.

referred to *Helaletes intermedius* by Radinsky (1963a, p. 44, footnote).

AMNH 12672 consists of only lower teeth and therefore is not directly comparable to the other three specimens; it will not be further considered here. PU 10095 consists of only the three upper molars which are very slightly smaller than the upper molars of PU 10166 and YPM 15233 (Radinsky, 1963a, p. 49, table 7), but otherwise are virtually identical in morphology to the molars in the latter specimens. As Radinsky (1963a) discussed, on the basis of the known morphology PU 10095 cannot be distinguished specifically from either PU 10166 or YPM 15233.

PU 10166 and YPM 15233, however, both preserve the premolars and it is not at all clear whether these specimens pertain to the same species-level taxon (i.e., either species or subspecies). As described above, the premolars of PU 10166 are much more molariform than those of YPM 15233, but it is not possible to judge intra- or interspecific variability on the basis of only two specimens. Primarily as a matter of convenience, Radinsky (1963a) referred both of these specimens, along with PU 10095, to a single species which thus took the oldest available name, *Helaletes intermedius*. If the alternative possibility is taken, to regard PU 10166 and YPM 15233 as distinct species (or possibly subspecies), then PU 10095 would not be referable to either species with certainty and the name it carries would be relegated to the status of a *nomen dubium* or *nomen vanum* (Simpson, 1945); the name *H. guyotii* would be resurrected as valid for PU 10166; and a new name would have to be coined for YPM 15233. As it is not clear that the latter case (that two species are represented by the known specimens) is closer to the "truth" than regarding the specimens as pertaining to a single taxon, I here retain Radinsky's (1963a) taxonomy and refrain from establishing a third name for YPM 15233. However, I stress that in my opinion both possibilities are at present equally plausible.

Another problem concerning the taxonomy of specimens presently referred to *H. intermedius* is whether they should really be referred to *Helaletes*. As I pointed out in the description of YPM 15233, the metaloph configuration on P^{3-4} in *H. intermedius* differs from that in *Helaletes nanus*. In *H. intermedius* the hypocone lies posterior to the metaloph whereas in *H. nanus* the hypocone is incorporated into the metaloph. Also, the M_3 of AMNH 12672 (referred to *H. intermedius*) bears a much smaller hypoconulid than in *H. nanus*. If *H. intermedius* becomes better known, through the discovery of more specimens, it may prove to be generically distinct. If so, then Scott's (1883) genus, *Desmatotherium*, would be resurrected.

Tapir Evolution from *Heptodon* to *Protapirus*

The family Tapiridae includes the extant genus *Tapirus* and a number of extinct genera (Table 2). Morphologically the most primitive, and also earliest known, tapirid is *Protapirus* of the Oligocene of Europe and North America. *Protapirus* is generally very similar in morphology to extant *Tapirus* (Radinsky, 1965a). *Protapirus* bears modifications of the skull for a well-developed proboscis, as in *Tapirus*, and differs from the latter genus primarily in having less molariform premolars (Hatcher, 1896). The "origin" or "ancestry" of *Protapirus* and the Tapiridae has been a subject of continued debate among students of early tapiroids (see historical resume in Radinsky, 1963a, pp. 94–5). I believe that this may, in part, be a shortcoming of methodology and epistemology for, as has been argued elsewhere (Engelmann and Wiley, 1977; Schoch, 1982a, 1983), in a strict sense ancestor-descendant relationships may be unrecognizable. However, it can be heuristic to postulate evolutionary scenarios which may involve hypothetical ancestor-descendant relationships.

In the last thorough discussion of the subject, Radinsky (1963a) concluded that species referable to the following genera may have formed a graded lineage leading from *Heptodon* sp. to *Protapirus* sp.: *Heptodon* (early Eocene) - *Helaletes* (middle Eocene) - ? *Colodon* (late Eocene to early Oligocene) - *Protapirus* (early Oligocene to early Miocene). Radinsky (1963a) arrived at this sequence by considering known early Tertiary tapiroids and noting that all members of all tapiroid families (Table 2) other than the Helaletidae bear presumed apomorphic character-states which would exclude them from the ancestry of the Tapiridae (or because they occur in the wrong place and time interval to be ancestral to the true tapirs). Among the Helaletidae, *Heptodon* is generally primitive (plesiomorphic) relative to *Helaletes, Dilophodon, Selenaletes, Hyrachyus* and *Colodon*. Radinsky (1963a) excluded the *Dilophodon* line from the ancestry of the Tapiridae because it shows a tendency (not seen in the earlier, Bridgerian, *D. minusculus* but well developed in the later, Uintan, *D. leotanus*) toward small size, shortened P_{2-4}, and P^{2-4} with metaloph bypassing the hypocone (autapomorphies of this line). Likewise, *Selenaletes* possesses the autapomorphies of extremely small size and a greatly reduced M_3 (Radinsky, 1966b), thus barring it from the ancestry of the Tapiridae. After completing his monograph on the Isectolophidae and Helaletidae (Radinsky, 1963a), Radinsky (1965b, 1966a, 1967b) transferred *Hyrachyus* (and the closely related genus *Chasmotherium*) from the Rhinocerotoidea to the Helaletidae, Tapiroidea, even though *Hyrachyus* shares a number of apomorphies with rhinocerotoids (Savage, Russell and Louis, 1966, p. 15) which exclude it from the ancestry of the Tapiridae (*Chasmotherium* is not only easily confused with *Hyrachyus*, but is also an extremely autapomorphic genus [see Radinsky, 1967b, and Savage, Russell and Louis, 1966] and thus is also excluded from the ancestry of the Tapiridae). *Hyrachyus*

has recently been reassigned to the Rhinocerotoidea (Schoch, 1982b).

Radinsky (1963a) noted that *Helaletes, Colodon* and *Protapirus* all share the derived condition of an enlarged nasal incision (skull not known for *Dilophodon* or *Selenaletes*), perhaps indicating a close relationship between these genera. As described above, in *Helaletes intermedius* the metaloph bypasses the hypocone on P^{3-4} as in *Dilophodon*. Thus, by Radinsky's (1963a) criterion this species, but not *Helaletes nanus,* can also be excluded from the ancestry of the Tapiridae. As Radinsky (1963a) noted, *Colodon occidentalis* had lost the fifth metacarpal, which is present in *Protapirus,* and thus also is excluded from the ancestry of the Tapiridae. On the basis of the extreme similarity seen between the dentition of the poorly known ? *Colodon hancocki* and *Protapirus* sp., Radinsky (1963a) suggested that the former species gave rise to the Tapiridae.

In describing the skeleton of *Heptodon posticus,* Radinsky (1965a) explicitly assumed that *Heptodon* was probably ancestral to modern tapirs, perhaps through the intermediate form *Helaletes nanus* (cf. Radinsky, 1963a, p. 74, fig. 14). In his concluding remarks on the evolution of the tapiroid skeleton, Radinsky (1965a, pp. 101–2) suggested that "at some point in evolution from *Heptodon* to *Tapirus,* there was a trend toward increasing cursorial specialization." This is indicated by features in *Tapirus* such as loss of the clavicles, reduction of the acromions of the scapulae and fusion of the radii and ulnae. However, since modern tapirs are relatively heavy and stout, at some later point in time this trend was reversed. Radinsky (1965a, p. 102) further noted that

it is significant that the cursorial modifications [of *Tapirus*] mentioned above are confined to the fore limb; the same is true in other tapiroid lineages descended from *Heptodon.* This fact suggests that the hind limb of *Heptodon* was more specialized than the fore limb and had in fact ap-

proached its biomechanical limit of speciali-
zation for running (except for lengthening
of distal limb segments in some tapiroid
lineages). Thus, further modifications for
running would be more likely to appear in
the less specialized front limb.

As I have described above, all of the im-
portant morphological differences seen be-
tween the postcranial skeletons of
Heptodon and *Helaletes* are modifications
of the hindlimb, and these modifications
are toward a more cursorial condition in
Helaletes. These observations contradict
the conclusions of Radinsky (1963a,
1965a). At least one presumed descendant
lineage of *Heptodon* further modified the
hindlimb for cursoriality. Either *Helaletes* is
not on the direct line to *Tapirus*, or *Tapirus*
has so completely reversed the initial trend
toward a cursorial condition of the hindlimb
that the modifications seen in *Helaletes
nanus* have been completely eradicated.

Concluding Remarks

As I hope is evident from the above
discussion, the subject of the phylogeny of
the tapirids and tapiroids is in need of fur-
ther study. As presently constituted, most
families of tapiroids appear to represent
either grade-levels, or geographical
clusters, or both (Table 2). Furthermore, it is
not even always clear what is and what is
not a tapiroid, as exemplified by the case of
Hyrachyus (Schoch, 1982b). Further, the
genus- and species-level taxonomy of
many tapiroids, for example *Helaletes
intermedius* discussed above, is ambigu-
ous (for other examples, see especially
Radinsky 1963a, 1965b).

Table 2

List of genera either currently, or previously, referred to the Tapiroidea. References cited only in this table may be found by consulting Savage and Russell (1983), Simpson (1945) and the irregular series *Bibliography of Fossil Vertebrates* (cited in Savage and Russell, 1983).

Ceratomorpha Wood, 1937[1]

Tapiroidea Burnett, 1830 (Gill, 1872)

Isectolophidae Peterson, 1919
Homogalax Hay, 1899: Early Eocene, N. Amer. & Asia.
Isectolophus Scott and Osborn, 1887
(=*Parisectolophus* Peterson, 1919
=*Schizolophodon* Peterson, 1919): Middle Eocene, N. Amer. & Asia.
Sastrilophus Sahni and Khare, 1971: Middle Eocene, Asia.
Paralophiodon Dedieu, 1977
(=*Rhinocerolophiodon* K.-H. Fischer, 1977)[2]: Middle–?late Eocene, Europe.

Helaletidae Osborn, 1892 in Osborn and Wortman, 1892
Heptodon Cope, 1882: Early Eocene, N. Amer. & Asia.
Helaletes Marsh, 1872
(=*Desmastotherium* Scott, 1883=*Chasmotheroides* Wood, 1934): Middle Eocene, N. Amer.; ?Early–late Eocene, Asia.
Dilophodon Scott, 1883 (=*Heteraletes* Peterson, 1919): Middle Eocene, N. Amer.
Selenaletes Radinsky, 1966: Early Eocene, N. Amer.
Colodon Marsh, 1890 (=?"*Mesotapirus*" Scott and Osborn, 1910=*Paracolodon* Matthew and Granger, 1925): Middle Eocene–late Olig. or early Miocene, Asia; late Eocene–late Olig., N. Amer.
Veragromovia Gabunia, 1961
(=? *Helaletes*):Middle or ?late Eocene, Asia.

Lophialetidae Matthew and Granger, 1925
Lophialetes Matthew and Granger, 1925: Middle–late Eocene, Asia.
Schlosseria Matthew and Granger, 1926: Middle–late Eocene, Asia.
Simplaletes Qi, 1980: Late Eocene, Asia.
Breviodon Radinsky, 1965: ?Middle–late Eocene, Asia.
Parabreviodon Reshetov, 1975: Late Eocene, Asia.
Eoletes Biryukov, 1974: Middle Eocene, Asia.
Kalakotia Rao, 1972: Middle Eocene, Asia.
Aulaxolophus Rao, 1972: Middle Eocene, Asia.

Deperetellidae Radinsky, 1965
Teleolophus Matthew and Granger, 1925: ?Middle–late Eocene, ?early Olig.: Asia.
Deperetella Matthew and Granger, 1925
(=*Cristidentinus* Zdansky, 1930, = *Diplolophodon* Zdansky, 1930): Middle–late Eocene, Asia.
Haagella Heissig, 1978: Middle Olig., Europe.

Lophiodontidae Gill, 1872
Lophiodon Cuvier, 1822
(=? *Hypsolophiodon* Kretzoi, 1940
=? *Leptolophiodon* Peterson, 1919):
Early–late Eocene, Europe.
Lophiodochoerus Lemoine, 1880: Early Eocene, Europe.

Tapiridae Burnett, 1830
Protapirus Filhol, 1877 (= *Tanyops* Marsh, 1894): Early and late Olig., Europe; late Olig., N. Amer.
Miotapirus Schlaikjer, 1937: Early Miocene, N. Amer.

Palaeotapirus Filhol, 1888 (=*Paratapirus* Depéret, 1902): Early-?middle Miocene, Europe; Early–middle Miocene, Asia.
Tapiravus Marsh, 1877: ?Middle-?late Miocene, N. Amer.
Megatapirus Matthew and Granger, 1923: Pleist., Asia.
Tapiriscus Kretzoi, 1951: Late Miocene or early Pliocene, Europe.
"*Selenolophodon*" - see Savage and Russell, 1983, p. 245: Middle Miocene, Asia. (This may be a gomphotheriid proboscidean; see Zhang et al., 1978, Acad. Sin., Inst. Vertebr. Paleontol. Palaeoanthrop., Mem. 14:1–64.)
Tapirus Brünnich, 1771 (non *Tapirus* Brisson, 1762: see Hershkovitz, 1954, Proc. U.S. Natl. Mus. 103:465–486: =*Pinchacus* =*[Cinchacus]* Gray, 1873 = *Tapirella* Palmer, 1903 =*Elasmognathus* Gill, 1865, *nec* Fieber, 1844 =*Acrocodia* Goldman, 1913 = *Tapirus* Scapoli, 1777 = *Tapirus* Merriam, 1895 = *Tapir* Blumenbach, 1779 = *Tapir* Zimmerman, 1780 = *Tapir* Gmelin, 1788 =*Syspotamus* Billberg, 1827 =*Rhinochoerus* Wagler, 1830 = *Tapyra* Liais, 1872): ?Early Miocene–Pleist., Europe; ?Middle Miocene–Pleist., N. Amer.; Late Miocene–Recent, Asia; ?Pliocene–Recent, S. Amer.

Rhinocerotoidea Gill, 1872

Hyrachyidae Wood, 1927
Hyrachyus Leidy, 1871 (=? *Panodon* Schertz, 1938 MS, see K.–H. Fischer, 1964)[3]: ?Late Paleocene of the Canadian Arctic (L. J. Hickey, R. M. West, M. R. Dawson and D. Choi, 1983, G.S.A. Abstr. Prog. 15: 219, 249, and Science 221:1153-1156), Early–middle Eocene of N. Amer. & Europe, middle to late Eocene of Asia, ?late Olig. of N. Amer. (see footnote 3).
Chasmotherium Rütimeyer, 1862: Middle Eocene, Europe & Asia; ?Middle Olig. of Europe (see Russell and Savage, 1983, p. 171).

Hyracodontidae Cope, 1879
Rhodopagus Radinsky, 1965: Early–late Eocene, Asia.
Pataecops Radinsky, 1966 (=*Pataecus* Radinsky, 1965): Middle–late Eocene, Asia.
Ergilia Gromova, 1952 (junior synonym of *Ardynia* Matthew and Granger, 1925): Early–late Olig., Asia.

Ancylopoda Cope, 1889

Eomoropidae Matthew, 1929
Lunania Chow, 1957: Late Eocene, Asia.
Paleomoropus Radinsky, 1964: Early Eocene, N. Amer.
Lophiaspis Depéret, 1910: Early–middle Eocene, Europe.

Ceratomorpha Wood, 1937, incertae sedis

Family uncertain
Atalonodon Dal Piaz, 1929: Middle Eocene, Europe.

?Hippomorpha Wood, 1937, incertae sedis

Indolophidae, new (sole included genus, *Indolophus:* see Radinsky, 1965b, for description and diagnosis of this unusual taxon).
Indolophus Pilgrim, 1925: Late Eocene, Asia.

Artiodactyla Owen, 1848

?Anoplotheriidae Bonaparte, 1850
Tapirulus Gervais, 1850: Middle Eocene–early Olig., Europe.

Notes to Table 2.

[1]It has been suggested (Schoch, 1983, G.S.A. Abstr. Prog. 15:144) that the Ceratomorpha and Ancylopoda may be sister-groups, in which case they can be regarded as infraorders of the suborder Moropomorpha, new.

[2]Pierre Dedieu (13 Juin 1977a, C. R. Acad. Sc., Paris 284 (22), série D: 2219–22; see also Dedieu, 1977b, Bull. Soc. Hist. Nat. Toulouse 113: 32–39) proposed the genus *Paralophiodon,* subfamily Paralophiodontinae (new in Dedieu, 1977a), family Isectolophidae Peterson, 1919 (="Rhinolophiodon" and "Rhinolophiodontinae" of Dedieu, 1976, Thèse 3e Cycle de Poitiers, 179 pp.), based on the type species *Paralophiodon buchsowillanus* (Desmarest, 1822) and including *P. isselensis* (J. B. Fischer, 1829), *P. leptorhynchus* (Filhol, 1888) and *P. compactus* (Astre, 1960). Independently Karl-Heinz Fischer (July 1977, Z. Geol. Wiss., Berlin 5 (7): 909–19) proposed the genus *Rhinocerolophiodon,* family Lophiodontidae Gill, 1872, based on the type and only species *Rhinocerolophiodon buxovillanum* (Cuvier, 1812). *Palaeotherium buxovillanum* Cuvier, 1812 and *Lophiodon buchsowillanum* Desmarest, 1822 are synonyms as both are based on the same type specimen (K.-H. Fischer, 1964, 1977); thus *Paralophiodon* and *Rhinocerolophiodon* are based on the same species and are synonyms.

[3]The genus *Hyrachyus* is in need of a thorough revision. Whereas Wood's (1934) revision was probably "oversplit," Radinsky's (1967b) revision was probably "overlumped." In his classic revision, Wood (1934) recognized the Hyrachyidae as a wholly North American family composed of four genera and twelve species. Radinsky (1967b) restudied the group and reduced it to a subfamily composed of only one genus and two species of North American forms and to the group added a European species.

However, my studies based on Bridgerian (middle Eocene) specimens of *Hyrachyus* from North America indicate that there is a range of diversity in both size and non-metric morphological characters which indicates the presence of more than two species of *Hyrachyus*. As Radinsky (1967b, p. 15) himself stated, "locality data ... are not sufficient justification for taxonomic separation." Yet, Radinsky (1967b) relied heavily on locality data (namely stratigraphic position) in order to identify some specimens of *Hyrachyus* at the species-level even if this is not reflected in his formal diagnoses. Thus, for example, Radinsky (1967b) synonymized both *Metahyrachyus bicornutus,* an extremely large form (M^{2-3} length = 64.4 mm) with distinct hypocones on P^{3-4} (i.e., the premolars are submolariform) and *Colonoceras agrestis,* a small form (M^{1-3} length = 45.0 mm) with simple, non-molariform premolars with *Hyrachyus modestus* because presumably the holotypes of these specimens came from approximately the same stratigraphic level within the Bridger Basin (Bridger B). However, according to Radinsky (1967b, p. 22) the two North American species of *Hyrachyus* which he recognized were distinguished from one another on the basis of size differences only (both are supposed to have non-molariform premolars). *H. modestus* has a "mean length of M^{1-3} from about 45 to 50 mm" whereas *H. eximius* has a "mean length of M^{1-3}, 64 mm." Thus, even if Wood's (1934) classification of *Hyrachuys* may have been oversplit, it recognized valid metric and morphological distinctions not recognized by Radinsky (1967b). Even given that one does not agree with Wood (1934, p. 205) that any specimen that "possesses a degree of individuality that necessitates discussion" also needs a name, the opposite "lumper's" extreme of Radinsky (1967b) need not be taken.

Recently a number of additional species of *Hyrachyus* have been named from Asia (Rao and Obergfell, 1973, Oil Nat. Gas

Comm., Dir. Geol., Dehra Dun, India, Spec.
Pap. 3: 1–9; Chow and Qi, 1982, Vert.
PalAsiatica 20: 302–13; Huang and Qi,
1982, Vert. PalAsiatica 20: 315–26). I here
note that Chow and Qi (1982) based their
new species *Hyrachyus metalophus*
(=*Hyrachyus xintaiensis* of caption to
their plate 2) on several syntypes which
may pertain to more than one individual. I
here designate Institute of Vertebrate
Paleontology and Paleoanthropology (IVPP)
V6393–1, a dentary with P_2–M_2, the
lectotype of *Hyrachyus metalophus*
(illustrated in Chow and Qi, 1982, plate 2,
fig. 4).

Hyrachyus is best known from the
Bridgerian of western North America.
Hickey et al. (1983, Science 221:1153–6)
have reported an anomously old,
Clarkforkian (latest Paleocene-earliest
Eocene), occurrence of *Hyrachyus* from
the Eureka Sound Formation, Canadian
high Arctic. This Clarkforkian date for
Hyrachyus is based primarily on
paleomagnetic correlations, however,
which may prove to be questionable.
Moreover, the specimens on which the
report is based have yet to be described. I
have come across a crushed skull with the
root of the right canine, right P^1–M^3 and left
P^3–M^3 in the Yale Peabody Museum
collections (YPM 12072) which appears to
pertain to *Hyrachyus* cf. *H. modestus*.
Hyrachyus modestus is a typical
Bridgerian species; however, YPM 12702 is
recorded as having been collected by
Henry F. Wells during the summer of 1894
from the *Protoceras* beds (i.e., Whitneyan
= late Oligocene) of South Dakota
(supposedly Wells collected YPM 12702
from the same strata which yielded the
holotype of *Tanyops undans* = *Protapirus
obliquidens*: see Schoch, 1983, Postilla
190, 7 p.). If substantiated, YPM 12702 may
prove to be an anomously young
occurrence of *Hyrachyus*.

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