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

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Abstract

A calvarium, mandible and partial skeleton of *Helaletes nanus* and a partial upper dentition of *Helaletes intermedius*, both from the middle Eocene (Bridgerian) of Wyoming, are described and illustrated. Previously unrecognized cursorial specializations 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 hindlimb was later reversed. Only four described specimens are presently referred to *H. intermedius*. Due to morphological differences 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*.

Key Words

*Helaletes, Hyrachyus, Paralophiodon, Rhinocerolophiodon, Indolophidae, Tapiroidea, Eocene, fossil mammal.*

Introduction

The Yale Peabody Museum (YPM) is fortunate 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 complete 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 *Lophiates* and *Deperetella*. More recently, Reshetov (1977, 1979) described in much greater detail the osteology of *Lophiates*. 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 apomorphies 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 C₁⁻M₃, alveoli or roots, or both, for right I₁⁻³ (Fig. 1A–C; when Peterson, 1919, described this specimen it included the crowns of right I₁⁻³ which have since been lost); fragments of mandible including the symphyseal region, right dentary with P₄-M₃ and roots of P₂, and left dentary fragment with P₄, M₁, M₃ and roots of M₂ (Fig. 1D–F); fragments of several cervical, a thoracic(?) and four lumbar vertebrae; anterior part of the sacrum (Fig. 21, 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 Helalites boops (= Helalites 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.

**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 tapiroïds 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 P3–4. Similarly, a large nasal incision is seen in other tapiroïds such as the Eocene-Oligocene helaletid *Colodon* (Radinsky, 1963a), in *Protapirus* and *Tapis* (Hatcher, 1896) and in *Lophiolaletes* (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 tapiroïd 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*, *Lophiolaletes* 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 C1 and P2 (P1 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*.

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*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).

![Fig. 3](image)

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.

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

**Referred Specimen**

YPM 15233, occipital region of skull preserving posterior tip of sagittal crest and right occipital condyle; right maxilla with P²–M³ (Fig. 4: crowns of all teeth damaged except for M³); and left maxilla with P²–M³ (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 M³ all are damaged to various degrees. The labial faces of left P²–M² 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 M³ is missing. The teeth of the right maxilla have suffered less damage (Fig. 4). Both the labial and lingual faces of P² are missing. The posterolabial corner, including the entire metacone, is missing from P³. The lingual face of P⁴, including the protocone-hypocone, has been sheared off. The anterolabial corner, bearing the parastyle, is missing from M¹. The anterolabial corner, bearing part of the parastyle, and the tip of the protocone are missing from M². M³ 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 decided 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 comparable in size to YPM 11082, a complete

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**Fig. 4**
Right maxilla with P²–M³ of *Helaeles intermedius*, YPM 15233. Drawing by Ruth Santer.
skull, approximately 20 cm long, referred to *Hyrachys 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 *Helalites 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 anteromonost face 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 $P^3$s, 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 metaloph runs from the anterolinguinal corner of the paracone to the anterolabial corner of the protocone. An even lower metaloph runs from the posterolinguinal corner of the paracone of $P^3$ to the postero- labial corner of the protocone such that the small hypocone lies entirely posterior to the metaloph. This condition differs from *Helalites nanus* in which the metaloph runs to the hypocone when present in $P^2-4$ (Radinsky, 1963a, p. 43).

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**Table 1**

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

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P^2$</td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td>$P^3$</td>
<td>approx. 10.0</td>
<td>11.5</td>
</tr>
<tr>
<td>$P^4$</td>
<td>10.5</td>
<td>approx. 12.9</td>
</tr>
<tr>
<td>$M^1$</td>
<td>13.6</td>
<td>14.5</td>
</tr>
<tr>
<td>$M^2$</td>
<td>16.1</td>
<td>16.7</td>
</tr>
<tr>
<td>$M^3$</td>
<td>15.6</td>
<td>16.8</td>
</tr>
</tbody>
</table>
P₄ is very similar in morphology to P³, 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 P³, only the lophs are slightly higher and better-developed in P₄. The lingual face of the right P₄ of YPM 15233 is missing, but on the left P₄ 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 P₄ of PU 10166 which bears a large and distinct hypocone.

M₁⁻²- 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 ectlolophs. The metacones are slightly lower than the paracones, lingually displaced and only very slightly convex labially. M₁⁻² 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 metacones 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 metacones 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 M² is very slightly shorter than that of M¹. M₁⁻² bear low, poorly-developed anterior and posterior cingula.

M³ is similar to M₁⁻² but much narrower posteriorly and thus the metaloph of M³ is relatively shorter than on M₁⁻². The para- style is well-developed on M³. The anterior cingulum is low and continuous with the parastyle, but does not reach the protocone lingually as on M¹⁻². The metacone of M³ is relatively smaller and lower than on M¹⁻², further displaced lingually, more distinctly convex labially, and lacks the labial cingulum seen on M¹⁻². The protoloph and metaloph of M³ are also more strongly curved than in M¹⁻² and there is no posterior cingulum on M³. M¹⁻³ 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 P⁴-M¹ and the anterior border of the orbit is above M¹-M². 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 M¹⁻³ 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 P²-M³ and root of P¹ 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 guyottii* Scott, 1883, p. 46; 3) YPM 15233 (described above); and 4) American Museum of Natural History (AMNH) 12672, right and left dentaries with C₁, P₂-M₃ (Fig. 5) from Bridger D₁ beds, Bridger Basin, Wyoming, previously referred to *Ephyrachyus* (= *Hyrachyus fide* Radinsky, 1967b) by Wood (1934, p. 236, fig. 13) but tentatively
Right dentary with P2-M3 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 P3-4 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 M3 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 (*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) - *Helaeletes* (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 *Helaeletes, 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 P2–4, and P2–4 with metaloph bypassing the hypocone (autapomorphies of this line). Likewise, *Selenaletes* possesses the autapomorphies of extremely small size and a greatly reduced M3 (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 *Helaeletes, 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 *Helaeletes intermedius* the metaloph bypasses the hypocone on P3–4 as in *Dilophodon*. Thus, by Radinsky’s (1963a) criterion this species, but not *Helaeletes 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 *Helaeletes 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 specialization 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 important morphological differences seen between 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 tapiroids and tapiroids is in need of further 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 ambiguous (for other examples, see especially Radinsky 1963a, 1965b).

**Acknowledgments**

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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).

<table>
<thead>
<tr>
<th>Order</th>
<th>Author and Year</th>
<th>Age</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratomorpha</td>
<td>Wood, 1937</td>
<td></td>
<td></td>
</tr>
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<td>Tapiroidea</td>
<td>Burnett, 1830 (Gill, 1872)</td>
<td></td>
<td></td>
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<td>Peterson, 1919</td>
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<td></td>
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<td>Hay, 1899</td>
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<td></td>
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<td>(=Pariselctolophus)</td>
<td>Peterson, 1919</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(=Schiz lophodon)</td>
<td>Peterson, 1919</td>
<td>Middle Eocene, North America &amp; Asia.</td>
<td></td>
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<td>Isctolophid</td>
<td>Sahni and Khare, 1971</td>
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<td></td>
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<td>(=Meditubulodon)</td>
<td>Dedieu, 1977</td>
<td>Middle—late Eocene, Europe.</td>
<td></td>
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<td>Helaletidae</td>
<td>Osborn, 1892 in Osborn and Wortman, 1892</td>
<td></td>
<td></td>
</tr>
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<td>Heptodon</td>
<td>Cope, 1882</td>
<td>Early Eocene, North America &amp; Asia.</td>
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<td>Helaletes</td>
<td>Marsh, 1872</td>
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<td>(=Desmastotherium)</td>
<td>Scott, 1883</td>
<td>Middle Eocene, North America.</td>
<td></td>
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<tr>
<td>(=Chasmosotherium)</td>
<td>Wood, 1934</td>
<td>Late Eocene, North America.</td>
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<td>(=Helaletes)</td>
<td>Scott, 1883</td>
<td>(= Heteraletes)</td>
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<td>(=Heteraletes)</td>
<td>Peterson, 1919</td>
<td>Middle Eocene, North America.</td>
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<td>Colodon</td>
<td>Marsh, 1890</td>
<td>(=Mesotapirus) Scott and Osborn, 1910</td>
<td>Middle Eocene—late Olig. or early Miocene, Asia; late Eocene—late Olig., North America.</td>
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<td>Gabunia, 1961</td>
<td>(=Helaletes)</td>
<td>Middle or ?late Eocene, Asia.</td>
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<td>Matthew and Granger, 1925</td>
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<td>Schroesseria</td>
<td>Matthew and Granger, 1926</td>
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<td>Rao, 1972</td>
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<td>Deperetellidae</td>
<td>Radinsky, 1965</td>
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<td>Teleolophus</td>
<td>Matthew and Granger, 1925</td>
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<td></td>
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<td>(=Cristidentinus)</td>
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<td>(=Diplolophodon)</td>
<td>Zdansky, 1930</td>
<td>Middle Eocene, Asia.</td>
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<td>Heissig, 1978</td>
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<td>Gill, 1872</td>
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<td>Lophiodon</td>
<td>Cuvier, 1822</td>
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<td>Peterson, 1919</td>
<td>Early—late Eocene, Europe.</td>
<td></td>
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<td>Lemoine, 1880</td>
<td>Early Eocene, Europe.</td>
<td></td>
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<td>Tapiridae</td>
<td>Burnett, 1830</td>
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<tr>
<td>Protapirus</td>
<td>Filhol, 1877 (= Tanyops Marsh, 1894)</td>
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<td>(=?Leptolophiodon)</td>
<td>Peterson, 1919</td>
<td>Early and late Olig., Europe; late Olig., North America.</td>
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<tr>
<td>Miotapirus</td>
<td>Schlaikjer, 1937</td>
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</table>
Unusual Specimens of Helalates


Tapiroscus 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. Palaeontol. Palaeoanthrop., Mem. 14:1-64.)


Hyracodontidae Cope, 1879


Ancylopoda Cope, 1889

Eomoropidae Matthew, 1929


Ceratomorphus 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

Tapirus 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 buchowillanus* (Desmarest, 1822) and including *P. isseleensis* (J. B. Fischer, 1829), *P. leporoshynchus* (Filhol, 1888) and *P. compactus* (Astre, 1960). Independently Karl-Heinz Fischer (July 1977, Z. Geol. Wiss., Berlin 5 (7): 909–19) proposed the genus *Paralophiodon*, family Lophiodontidae Gill, 1872, based on the type and only species *Rhinocerolophiodon buxovillanum* (Cuvier, 1812) and *Palaeotherium buxovillanum* Cuvier, 1812 and *Lophiodon buchowillanum* Desmarest, 1822 are synonyms as both are based on the same type species (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 (M2–3 length = 64.4 mm) with distinct hypocones on P3–4 (i.e., the premolars are submolariform) and *Colonoceras agrestis*, a small form (M1–3 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 M1–3 from about 45 to 50 mm" whereas *H. eximius* has a "mean length of M1–3, 64 mm." Thus, even if Wood's (1934) classification of *Hyrachyus* 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

*Hyrachyus* is best known from the Bridgerian of western North America. Hickey et al. (1983, Science 221:1153–6) have reported an anomalously 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 P1–M3 and left P3–M3 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 anomalously young occurrence of *Hyrachyus*. 
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Burnett, G. T. 1830. Illustrations of the Quadrupeda, or quadrupeds, being the arrangement of the true four-footed beasts, indicated in outline. Q. J. Sci. Lit. Arts 26:336–53.


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