Taxonomy and distribution of *Daeodon*, an Oligocene-Miocene entelodont (Mammalia: Artiodactyla) from North America

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Abstract.—*Dinohyus* Peterson, 1906, the widely used generic name of the giant Oligocene-Miocene entelodont from North America, is a junior subjective synonym of *Daeodon* Cope, 1879. *Ammodon* Marsh, 1893 also is a junior subjective synonym of *Daeodon*. Five species have been named that we assign to *Daeodon*: *D. shoshonensis* Cope, 1879, *D. leidyanus* (Marsh, 1893), *D. mento* (Allen, 1926), *D. hollandi* (Peterson, 1905b), and *D. minor* (Loomis, 1932), and we tentatively consider all to represent a single species, *D. shoshonensis* Cope, 1879. The type material of *D. leidyanus*, from the basal Kirkwood Formation near Farmingdale, New Jersey is of early Miocene (late Arikareean) age. Other *Daeodon* occurrences range in age from late Oligocene (Arikareean) to early Miocene (Hemingfordian).

Entelodontidae is a family of Holarctic Oligocene-Miocene suiform artiodactyls. Entelodonts were always among the largest artiodactyls of their times, and the later forms became gigantic, some with skulls nearly one meter long. They appeared in North America during the late Eocene (Duchesnean) as immigrants from Asia (Brunet 1979, Emry 1981, Lucas 1992) and became relatively conspicuous members of latest Eocene-early Oligocene (Chadronian-Orellean) mammalian fossil assemblages in the western United States. They persisted through the late Oligocene into the early Miocene (Whitneyan-Hemingfordian) before becoming extinct. The giant genus, usually called *Dinohyus*, represents a later lineage of Asian entelodonts that immigrated into North America near the end of the Oligocene (Brunet 1979), and became geographically widespread in the early Miocene, though apparently never abundant.

Peterson (1905b) named *Dinohyus* for complete skeletal material from Nebraska that he later monographed (Peterson 1909). However, an entelodont from the Miocene of Oregon, *Daeodon* Cope, 1879, belongs to the same genus as *Dinohyus* and thus has priority. Furthermore, *Ammodon* Marsh, 1893, from the Miocene of New Jersey, also is a synonym of *Daeodon*. The purpose of this article is to establish the synonymy of *Daeodon, Ammodon* and *Dinohyus* and to summarize the distribution of *Daeodon*, which had a broad range in the United States (Fig. 1).

Abbreviations used.—In this article, AM refers to Amherst Museum, Amherst University, Amherst; AMNH to the American Museum of Natural History; CM to the Carnegie Museum of Natural History, Pittsburgh; LACM to the Natural History Museum of Los Angeles County; MCZ to the Museum of Comparative Zoology of Harvard University, Cambridge; UNSM to the University of Nebraska State Museum, Lincoln; SDSM to the South Dakota School of Mines, Rapid City; TMM to the Texas Memorial Museum, Austin; UCMP to the University of California Museum of Paleontol-

ogy, Berkeley; USNM to the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and YPM to the Yale Peabody Museum, New Haven.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Entelodontidae Lydekker, 1883
Genus *Daeodon* Cope, 1879


*Dinochoerus* Peterson, 1905a:212.


*Dinohyus*?—Allen, 1926, p. 450, pl. 1.

Type species.—*Daeodon shoshonensis* Cope, 1879.

Included species.—Only the type species.

Revised diagnosis.—*Daeodon* is the larg-
est entelodont (LP₄ = 45–53 mm), also distinguished from other entelodonts by the following combination of autapomorphous characters: I₁ very small (possibly absent); I₃ larger than P₂; incisorcanine diastema very short or absent; diastemata between all premolars, largest between P₁ and P₂; lower molars lacking paraconids and with triconids and talonids of subequal height; alveolar border of premxillary very short; jugal flange relatively small (compared to Archaeotherium); infraorbital foramen above posterior portion of P₃; symphysal tubercle very small or absent; large posterior tubercle (under P₃/M₁) on lower jaw; mandibular angle slopes gently posteriorly; trapezium absent; unciform completely separated from magnum by semilunar; metatarsal V absent; fibula and tibia co-ossified.

Distribution.—Late Oligocene-early Miocene of Oregon, California, South Dakota, Wyoming, Nebraska, Texas, Alabama, Florida, South Carolina and New Jersey (Fig. 1).

Discussion.—The holotype of D. shoshonensis, AMNH 7387 (Fig. 2), represents an individual slightly smaller than CM 1594, the holotype of Dinohyus hollaudi. AMNH 7387 is a much damaged fragment of the mandibular symphysis with the roots and/or alveoli of the incisors, canines and P₁’s. The three incisors are procumbent and increase in size from I₁ to I₃. The canines are large and circular in cross section. A small diastema separates the canine and the P₁, and a larger diastema evidently separates the P₁ and the P₂. No diastema separates the I₁ and canine. The tooth crowns are broken and absent, so it is impossible to describe crown morphology or to use wear on the teeth to estimate the relative age of the individual. Chin tubercles are absent.

Several characteristics observable on AMNH 7387, including the relative size of incisors and diastemata and the lack of chin tubercle—do diagnose one genus of giant North American entelodonts to which the name Dinohyus is usually applied. The holotype (CM 1594) of D. hollaudi, the type species of Dinohyus, displays all the features of the holotype of Daeodon shoshonensis, except that it has a very small tubercle on the chin. The size of the chin tubercle ranges from very small to absent in specimens that we assign to Daeodon, quite different from the large chin tubercle found in Archaeotherium and similar North American entelodonts (e.g., Peterson 1909). Therefore, we conclude that Dinohyus is a junior subjective synonym of Daeodon.

The holotype P₄ of Ammodon leidyanus (Fig. 3A–D) is very similar to the P₄ of the holotype of Dinohyus hollaudi (Fig. 3G). The teeth differ only in the slightly larger size (about 15%), longer talonid (due to the larger posterior cingulid) and more prominent posterior ridges on the trigonid slope on the A. leidyanus holotype (also see Peterson 1909:68). The referred M₃ of A. leidyanus differs from that tooth in the holotype of D. hollaudi only in being slightly longer (about 4%) and having a larger hypoconulid (Fig. 3E–G). We believe that these differences do not merit generic separation of the holotypes of A. leidyanus and D. hollaudi, and they do not even merit separation at the species level (see below). We thus consider Dinohyus and Ammodon to represent a single genus, which should be termed Daeodon.

Simpson (1945:144) suggested that Daeodon, Dinohyus and Ammodon represent a single genus. Brunet (1979:90) also recognized the close similarity of the type material of Ammodon to that of Dinohyus, but preferred not to synonymize the two genera because Dinohyus is based on more nearly complete type material. We prefer to synonymize all three genera.

Daeodon shoshonensis Cope, 1879

Daeodon shoshonensis Cope, 1879:77.—Peterson, 1909:64, fig. 18.
Ammodon leidyanus.—Marsh, 1893:409, pl. 9, figs. 2–3.—Peterson, 1909:67, figs. 20–21.
Fig. 3. Referred specimen and lectotype of *Ammodon leidyanus* (A–F), compared to holotype of *Dinohyus hollandi* (G). A–D, YPM 12040, right P₄, lingual (A–B) and occlusal (C–D) views. E–F, YPM 12041, left M₃, occlusal views. G, Occlusal view of left P₃-M₁ of CM 1594. Drawings from Peterson (1909). Bar scales = 20 mm.

*Dinochoerus hollandi.*—Peterson, 1905a: 212.


Not *Daeodon calcinsi.*—Peterson, 1909:64, fig. 19.


*Dinohyus (?) mento.*—Allen, 1926:450, pl. 1.

*Daeodon minor* Loomis, 1932:361, figs. 2–3.

*Dinohyus* sp.—Parris & Green, 1969:7, figs. 1–2, table 1.

*Dinohyus* aff. *D. hollandi.*—Westgate, 1992:685, figs. 1–2. Holotype.—AMNH 7387, symphyseal fragment (Fig. 2). Horizon and locality of holotype.—John Day Formation, Bridge Creek, Wasco County, Oregon.

**Principal referred specimens.**—From the basal Kirkwood Formation near Farmingdale, New Jersey: holotype of *Daeodon leidyanus* (Marsh, 1893), YPM 12040, right P₄ (Fig. 3A–C); YPM 12041, left M₃ (Fig. 3E–F).

From the lower part of the Harrison Formation, Agate Spring fossil quarry, Sioux County, Nebraska: holotype of *D. hollandi* (Peterson, 1905a), CM 1594, a nearly complete skeleton (Peterson 1906, pls. 16–17; 1909, figs. 29–80, pls. 45–61).

From the lower part of the Harrison Formation, *Stenomylus* quarry near Agate, Nebraska: holotype of *Daeodon minor* (Loomis, 1932), AM 31–32, lower jaws with de-
cidouous dentition, an associated m1, associated deciduous upper teeth, and miscellaneous other associated skeletal elements.

From a Miocene? horizon in Ashley River phosphate deposits near Charleston, South Carolina: holotype of *Daeodon mento* (Allen, 1926), MCZ 17015, edentulous symphyseal region of lower jaw (Allen 1926, pl. 1).

For additional referred specimens from these and other localities see references cited in the synonymy above.

**Description.**—We redescribe here the holotype and only referred specimen of *D. leidyanus*. The holotype, AMNH 7387, a right P4, is a submolariform tooth with a prominent talonid. The enamel of the tooth crown is rugose and linedate except for the occlusal tip of the trigonid cusp. The trigonid is a single, bulbous, blunt cusp much taller than the remainder of the tooth. The talonid is a low, semicircular posterior projection of the crown that occupies almost half of the occlusal area of the tooth. A thick, rugose cingulid surrounds the labial, lingual and posterior edges of the talonid. Two cuspidate ridges extend from near the apex of the trigonid down its posterior slope onto the talonid. The talonid between these ridges is rugose and cuspidate. Measurements are in Table 1.

The referred left M3 (YPM 12041) is a rectangular tooth in occlusal view. Its enamel is rugose and linedate except for the cuspid occlusal tips. A cingulid surrounds the crown anteriorly and labially but is discontinuous lingually. The trigonid consists of a thick, blunt metaconid and a somewhat smaller and lower protoconid. A transverse lophid connects these two cuspids; it is lower than the cuspids and has a notch in the middle. A rudimentary paraconid/paracristid can be seen in a bulge between the metaconid and protoconid, above the cingulid, on the anterior face of the tooth. A deep, transverse notch separates the trigonid from the talonid. The posterior slope of the protoconid and the anterior face of the hypoconid most nearly bridge this notch. The hypoconid and entoconid are low, bulbous, blunt cuspids separated by a narrow notch in the lophid that connects them. This lophid is slightly oblique (i.e., the entoconid is slightly posterior to the hypoconid) to a transverse line through the tooth axis. Behind and slightly lingual to the hypoconid is a prominent, blunt hypoconulid. This hypoconulid is lower than the hypoconid and entoconid and forms a small posterior projection. Lingual to the hypoconulid are two, small cingulid cuspids behind the entoconid.

**Discussion.**—Hay (1902:656) correctly noted that mention of the name *Elotherium leidyanum* by Marsh (1871:10; 1874:534) did not constitute proper proposal of a new species. Indeed, Marsh’s (1871, 1874) uses of the name do not even constitute an indication as defined in Article 12 of the International Code of Zoological Nomenclature. Rhoads (1903:237) thus quite correctly declared Marsh’s (1871) *Elotherium leidyanum* a nomen nudum.

There are five named species based on specimens of *Daeodon*: the type species *D. shoshonensis* (Cope 1878), *D. leidyanus* (Marsh 1893), *D. hollandi* (Peterson 1905) *D. mento* (Allen 1926), and *D. minor* (Loomis 1932). Each species is known from one or a few specimens. Except for the ho-

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<td>44.1</td>
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¹ From Sinclair (1905); measurements only to the nearest millimeter.
² From Wilson (1957).
loctype of *D. hollandi*, a complete skull and jaws, there is little morphological overlap among the holotypes of *Daeodon* species. Therefore, we find it difficult to evaluate the validity of these taxa and offer the tentative, conservative conclusion that they represent a single species. Measurements (Tables 1–2) and the relatively narrow range of meristic variation in the specimens that we assign to *Daeodon* support this conclusion.

The holotype of the type species of *Dinohyus*, *D. hollandi*, displays all the features of the holotype of *Daeodon shoshonensis*, except that it has a very small tubercle on the chin. Size of the chin tubercle ranges from very small to absent in specimens that we assign to *Daeodon*, quite different from the large chin tubercle found in adult *Archaeotherium* and similar North American entelodonts (Lucas et al. 1997). Therefore, we conclude that *Dinohyus* is a synonym of *Daeodon* (Lucas et al. 1996, 1997).

The holotype P1 of *Anmodon leidyanus* Marsh, 1893 is very similar to the P1 of the holotype of *Dinohyus hollandi* (compare illustrations in Marsh (1893) and Peterson (1909)). The teeth differ only in the slightly larger size (about 15%), longer talonid (due to the larger posterior cingulid) and more prominent posterior ridges on the trigonid slope on the *A. leidyanus* holotype (also see Peterson 1909:68). The referred M1 of *A. leidyanus* differs from that tooth in the holotype of *D. hollandi* only in being slightly longer (about 4%) and having a larger hypocoonulid. We believe that these differences do not merit species-level separation of the holotypes of *A. leidyanus* and *D. hollandi*.

*Daeodon mento* (Allen 1926) is based on an edentulous mandibular symphysis slightly larger than the holotype of *D. shoshonensis*. The two specimens are otherwise essentially identical, so we consider *D. mento* to be a junior subjective synonym of *D. shoshonensis*.

*Daeodon minor* (Loomis 1932) is based on the remains of a very young individual, consisting of lower jaws with deciduous premolars, an m1 thought to be associated, associated upper deciduous teeth and various postcranial elements. Loomis (1932:361) listed the postcranial elements, but did not describe them because they were so young that the epiphyses were lacking. Loomis (1932:362) noted that the specimen is from the same area and same strata that produced the type and referred material of *D. hollandi*; however, because of its small size, complete lack of the anterior tuberosity on the lower jaw, and small size of the posterior tuberosity, Loomis gave the specimen a new species name and referred it to the genus *Daeodon*. Surely this is a juvenile individual of the same taxon previously called *Dinohyus hollandi*, considered here to be a synonym of *Daeodon shoshonensis*.

*Dinohyus minimus* Schlaijker, 1935, is based on the symphyseal region of a juvenile lower jaw (MCZ 2894) from the lower Harrison Formation of Wyoming (Schlaijker 1935:157–159, pl. 21). Note its similarity to *Archaeotherium trippensis* from the Turtle Butte Formation of South Dakota (Skinner et al. 1968:419–425, figs. 14–15). The holotypes of "*Dinohyus* minimus and *Archaeotherium trippensis* both have small chin tubercles, but are juveniles, and in other diagnostic features resemble *Archaeothe-

**Table 2.—Measurements (in mm) of upper cheek teeth of selected specimens of *Daeodon*.

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1 From Parris & Green (1969); measurements only to the nearest millimeter.
Fig. 4. Astragali of Daeodon. A–C, CM 1548, left astragalus, anterior (A), posterior (B) and lateral (C) views. D–F, CM 2493, left astragalus, anterior (D), posterior (E) and lateral (F) views. Bar scale is 20 mm long.

ria, not Daeodon. A small chin tubercle thus is a feature of juvenile, but not of adult, Archaeotherium. The three permanent incisors of MCZ 2894 are approximately the same size. Thus we believe that the species should be transferred to Archaeotherium.

Elotherium calcinsi Sinclair, 1905 is based on a skull and partial postcranial skeleton (UCMP 953) from the John Day Formation of Oregon. The specimen is of an old individual, and although the chin tubercle is small, the associated tibia and fibula are unfused (Sinclair 1905:132–134, pl. 15). Thus we tentatively exclude it from Daeodon.

Peterson (1909:69, fig. 22) referred CM 1548, an incomplete left astragalus (Fig.
4A–C), to *Ammodon?*, even though it lacks any dental association. He noted that this astragalus is slightly larger, has a more convex sustentacular facet and a more anteriorly projecting distal trochlea than astragali of "*Dinohyus* hollandi" from the Agate Springs quarry (Fig. 4). These features strike us as minor postcranial differences of uncertain taxonomic significance, and we doubt that such minor features can be used to distinguish *Daeodon, Dinohyus* and *Ammodon* from each other.

**Distribution**

The type specimen of *Daeodon leidyanus* is part of the Farmingdale local fauna, a small assemblage of land mammals from the basal Kirkwood Formation in coastal New Jersey (Tedford & Hunter 1984, Gallagher et al. 1995). Based on sequence stratigraphy and marine micropaleontological biostratigraphy, Benson (1993) concluded that the lower Kirkwood Formation is slightly older than the "Shiloh marl." The "Shiloh marl" produced the single land mammal *Tapiravis validus* described by Marsh (1871) and is older than the Pollack Farm site in Delaware, which is approximately 18 Ma and can be confidently assigned to the early Hemingfordian based on its land-mammal fauna (Emry & Eshelman 1998). Sugarman et al. (1993) reported strontium-isotope age estimates of 20.0–20.3 Ma for the "Shiloh marl."

Besides *Daeodon leidyanus*, the Farmingdale local fauna includes the horse *Anchitherium* sp., the rhinos *Diceratherium matutinum* and *Menoceras* cf. *M. cooki*, the peccary *Hesperhyus antiquus*, and the protoceratid *Prosynthetoceras* (Tedford & Hunter 1984). Although Tedford & Hunter (1984) assigned the Farmingdale local fauna an early Hemingfordian age, it is more likely to be late Arikareean because: *Diceratherium* has its last record in the late Arikareean; and Sugarman et al. (1993) gave strontium-isotope age estimates for the lower Kirkwood of 19.2–22.6 ± 0.5 Ma, which are late Arikareean ages (Tedford et al. 1987). Gallagher et al. (1995) suggested that the Farmingdale local fauna was a mixed assemblage of reworked Arikareean and Hemingfordian fossils; such an interpretation seems unnecessary and unparsimonious, when none of the faunal evidence is inconsistent with a late Arikareean age.

In the United States, *Daeodon* first occurs during the early Arikareean (late Oligocene) and last occurs during the early Hemingfordian (early Miocene) (Tedford et al. 1987). This gives the genus a duration of about 11 million years, from 18 to 29 Ma. The oldest well-dated records of *Daeodon* are in the early Arikareean of South Dakota, Wyoming and Nebraska, though its occurrence in Alabama may be equally old (Westgate 1982). The youngest well-dated records are in the Hemingfordian of Oregon, California and Texas. The ages of *Daeodon* occurrences in South Carolina and Florida are weakly constrained.

*Daeodon* clearly had a broad distribution across the United States by the late Arikareean. This distribution is consistent with immigration of the genus from Asia via Beringia during the early Arikareean.

**Acknowledgments**

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