

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

Spencer G. Lucas, Robert J. Emry, and Scott E. Foss

(SGL) New Mexico Museum of Natural History and Science, 1801 Mountain Road N. W., Albuquerque, New Mexico 87104 U.S.A.; (RJE) Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 U.S.A.; (SEF) Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115-2861 U.S.A.

*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 Eocene-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-Orellan) 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-

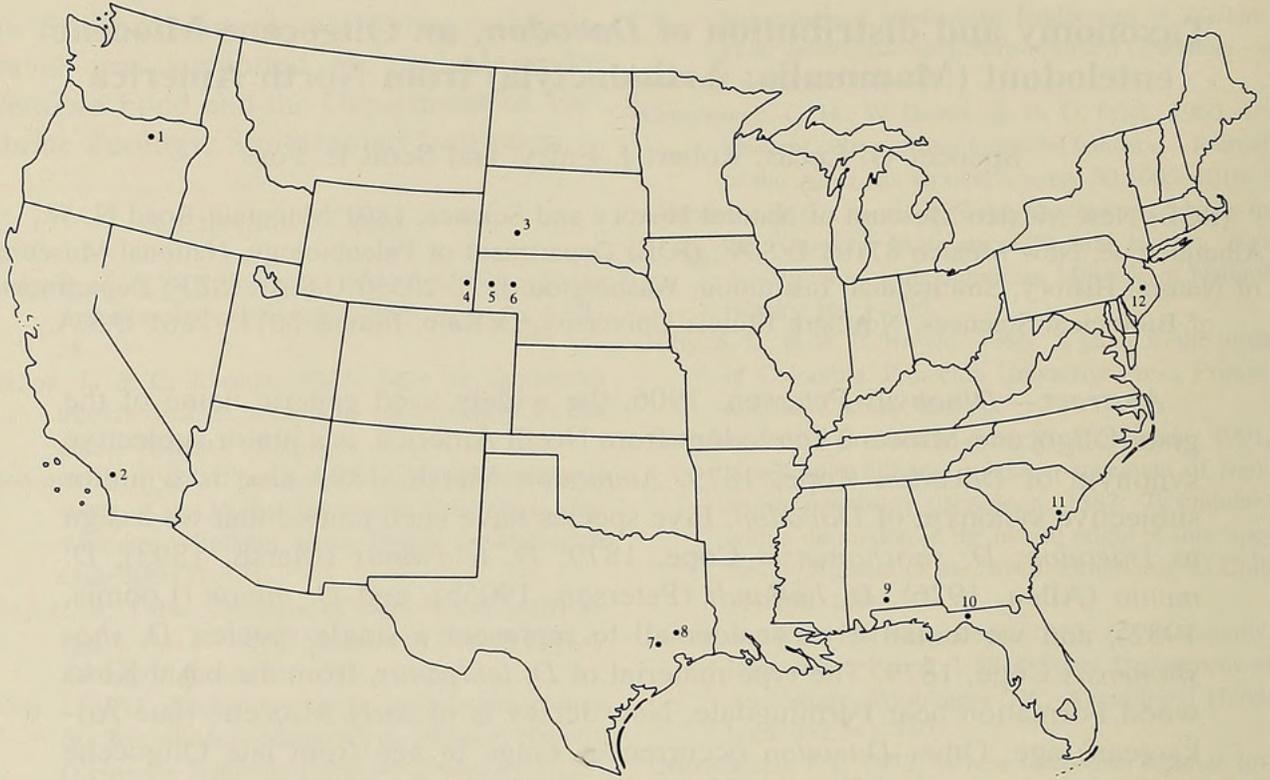


Fig. 1. Map of the United States showing distribution of fossils of the giant entelodont *Daeodon*. Localities are: 1. Unnamed unit above Haystack Valley Member, John Day Formation, Oregon. 2. Bolero Lookout local fauna, "Sespe Formation", Santa Ana Mountains, California. 3. Big Badlands, South Dakota. 4. Lusk-Hat Creek Breaks, Wyoming. 5. Pine Ridge escarpment, Nebraska. 6. Agate Springs quarry, Nebraska. 7. Washington County, Texas. 8. San Jacinto County, Texas. 9. Vicksburg Group, Conecuh River, Escambia County, Alabama. 10. Franklin Phosphate Pit, Florida. 11. Ashley River Phosphates, South Carolina. 12. Farmingdale, Monmouth County, New Jersey.

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

*Daeodon* Cope, 1879:77.—Loomis, 1932:361, figs. 1–2.—Simpson, 1945:144.—Gallagher et al., 1995:257, fig. 2C–D.—Lucas et al., 1996:15.

*Ammodon* Marsh, 1893:409, pl. 9, figs. 2–3 [not *Ammodon* Marsh, 1893:410, pl. 9, fig. 4].—Peterson, 1909:67, figs. 20–21 [not *Ammodon*? Marsh, 1893:410, pl. 9, fig. 4].—Peterson, 1909:67, figs. 20–21 [not *Ammodon*?, Peterson, 1909:68, fig.

22.—Troxell, 1920:252, pl. 3, figs. C–D.—Brunet, 1979:90.

*Dinochoerus* Peterson, 1905a:212.

*Dinohyus* Peterson, 1905b:719 [replacement name for *Dinochoerus* Peterson, 1905a, preoccupied by *Dinochoerus* Glögger, 1841, p. 131].—Peterson, 1906:49, pls. 16–17.—Peterson, 1909:66, figs. 29–80, pls. 45–61.—Simpson, 1930:169, fig. 16.—Wilson, 1957:641, figs. 2–4, table 1.—Parris & Green, 1969:7, figs. 1–2, table 1.—Brunet, 1979:90.—Westgate, 1992:685, figs. 1–2.—[not *Dinohyus*, Schläijker, 1935:157, pl. 21].

*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 ( $LP_4 = 45\text{--}53$  mm), also distinguished from other entelodonts by the following combination of autapomorphous characters:  $I_1$  very small (possibly absent);  $I_3$  larger than  $I_2$ ; incisorcanine diastema very short or absent; diastemata between all premolars, largest between  $P_1$  and  $P_2$ ; lower molars lacking paraconids and with trigonids and talonids of subequal height; alveolar border of premaxillary very short; jugal flange relatively small (compared to *Archaeotherium*); infraorbital foramen above posterior portion of  $P^3$ ; symphyseal tubercle very small or absent; large posterior tubercle (under  $P_4/M_1$ ) 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 hollandi*. AMNH 7387 is a much damaged fragment of the mandibular symphysis with the roots and/or alveoli of the incisors, canines and  $P_1$ 's. The three incisors are procumbent and increase in size from  $I_1$  to  $I_3$ . The canines are large and circular in cross section. A small diastema separates the canine and the  $P_1$ , and a larger diastema evidently separates the  $P_1$  and the  $P_2$ . No diastema separates the  $I_3$  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 ho-

lotype (CM 1594) of *D. hollandi*, 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  $P_4$  of *Ammodon leidymanus* (Fig. 3A–D) is very similar to the  $P_4$  of the holotype of *Dinohyus hollandi* (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. leidymanus* holotype (also see Peterson 1909:68). The referred  $M_3$  of *A. leidymanus* differs from that tooth in the holotype of *D. hollandi* 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. leidymanus* and *D. hollandi*, 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 leidymanus*.—Marsh, 1893:409, pl. 9, figs. 2–3.—Peterson, 1909:67, figs. 20–21.

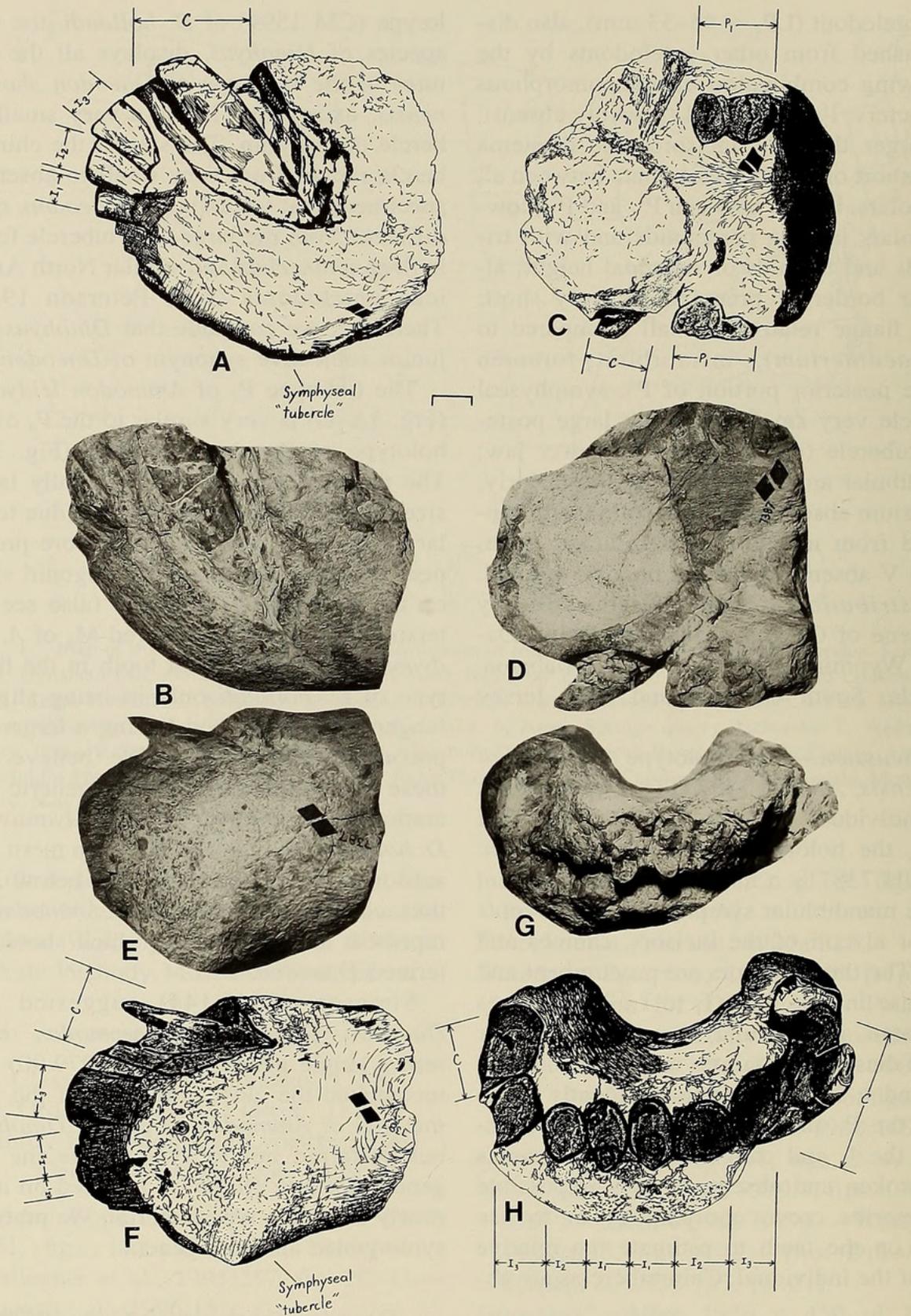


Fig. 2. Holotype of *Daeodon shoshonensis*, AMNH 7387, symphyseal fragment with roots, alveoli or partial crowns of left and right  $I_{1-3}$ , C and  $P_1$ . A-B, Labial views. C-D, Occlusal views. E-F, Ventral views. G-H, Anterior views. Bar scale = 20 mm.

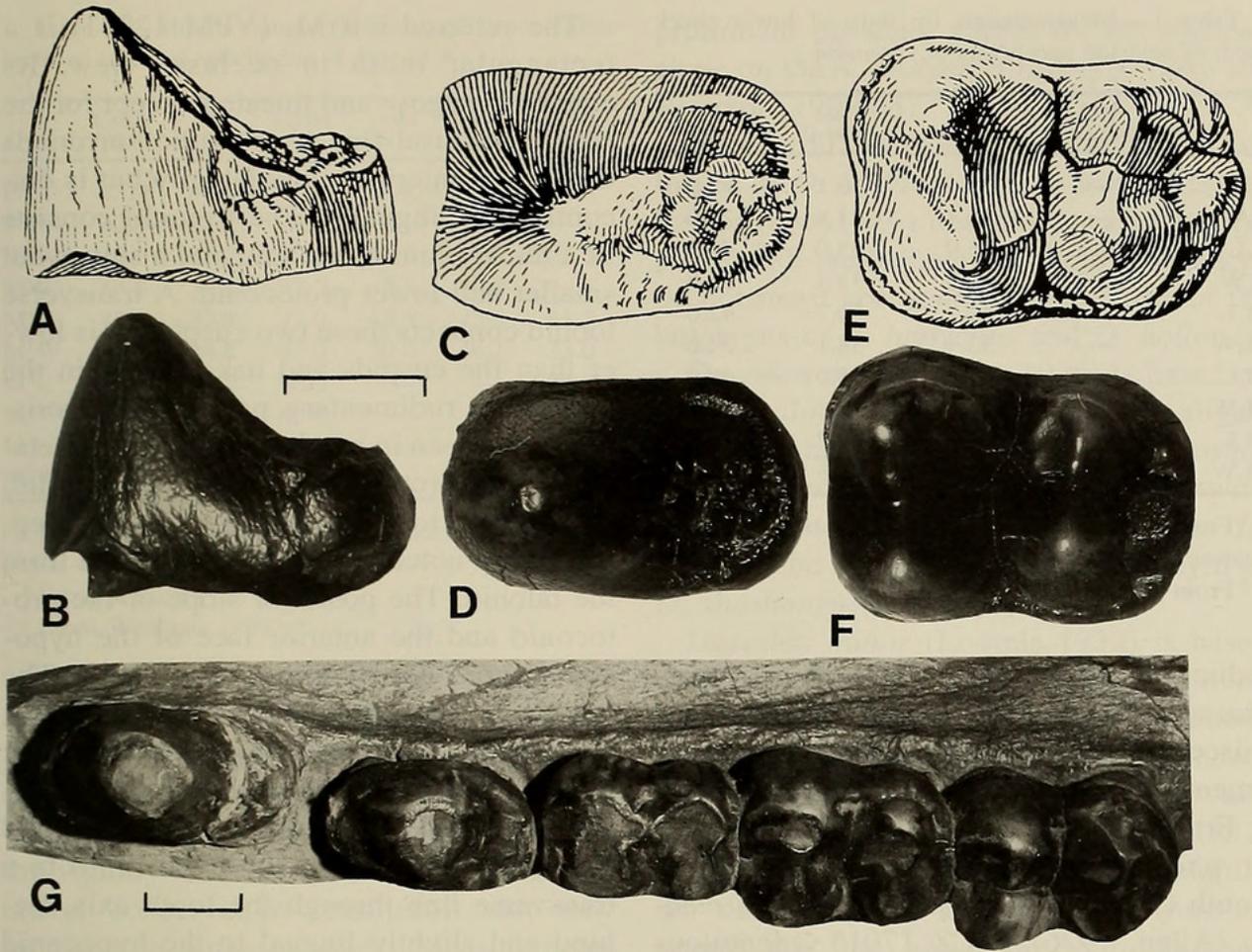


Fig. 3. Referred specimen and lectotype of *Ammodon leidymanus* (A-F), compared to holotype of *Dinohyus hollandi* (G). A-D, YPM 12040, right P<sub>4</sub>, lingual (A-B) and occlusal (C-D) views. E-F, YPM 12041, left M<sub>3</sub>, occlusal views. G, Occlusal view of left P<sub>3</sub>-M<sub>3</sub> of CM 1594. Drawings from Peterson (1909). Bar scales = 20 mm.

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

*Dinohyus hollandi*.—Peterson, 1905b: 719.—Peterson, 1906:49, pls. 16–17.—Peterson, 1909:66, figs. 29–80, pls. 45–61.—Wilson, 1957:641, figs. 2–4, table 1.—Brunet, 1979:90.

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

*Ammodon leidymanus*.—Troxell, 1920:252, pl. 3, figs. C–D.—Brunet, 1979:90.

*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 leidymanus* (Marsh, 1893), YPM 12040, right P<sub>4</sub> (Fig. 3A–C); YPM 12041, left M<sub>3</sub> (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-

Table 1.—Measurements (in mm) of lower cheek teeth of selected specimens of *Daeodon*.

	YPM 12040/12041	CM 1594	TMM 40224-1 <sup>2</sup>	NM <sup>2</sup>
P <sub>3</sub> L	—	53.6	60.1	55.0
P <sub>3</sub> W	—	30.1	31.8	29.0
P <sub>4</sub> L	52.3	46.9	55.0	46.0
P <sub>4</sub> W	33.2	29.3	32.5	28.0
M <sub>1</sub> L	—	42.7	50.7	42.0
M <sub>1</sub> W	—	33.4	38.1	34.0
M <sub>2</sub> L	—	47.3	55.0	49.0
M <sub>2</sub> W	—	39.0	44.1	40.0
M <sub>3</sub> L	52.4	50.0	55.2	55.0
M <sub>3</sub> W	39.5	38.9	44.8	40.0

<sup>1</sup> From Sinclair (1905); measurements only to the nearest millimeter.

<sup>2</sup> From Wilson (1957).

ciduous 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. leidymanus*. The holotype, AMNH 7387, a right P<sub>4</sub>, is a submolariform tooth with a prominent talonid. The enamel of the tooth crown is rugose and lineated except for the occlusal tip of the trigonid cuspid. The trigonid is a single, bulbous, blunt cuspid 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 M<sub>3</sub> (YPM 12041) is a rectangular tooth in occlusal view. Its enamel is rugose and lineated 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 leidymanum* 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 leidymanum* a nomen nudum.

There are five named species based on specimens of *Daeodon*: the type species *D. shoshonensis* (Cope 1878), *D. leidymanus* (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-

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

	LACM 140397	CM 1594	SDSM 675 <sup>1</sup>	TMM 40223-1 <sup>2</sup>	USNM 25809 <sup>3</sup>	UCMP 953
P <sup>3</sup> L	43.9	43.5	48.0	—	—	37.5
P <sup>3</sup> W	32.8	33.2	27.0	—	—	—
P <sup>4</sup> L	39.6	37.2	34.0	41.0	38.2	25.5
P <sup>4</sup> W	44.6	38.6	37.0	45.5	39.9	—
M <sup>1</sup> L	47.6	42.9	42.0	45.8	45.5	31.5
M <sup>1</sup> W	49.7	44.8	45.0	50.0	46.1	33.0
M <sup>2</sup> L	48.4	45.2	46.0	—	—	33.0
M <sup>2</sup> W	56.4	47.3	49.0	—	—	33.5
M <sup>3</sup> L	45.5	42.7	—	—	—	31.0
M <sup>3</sup> W	51.2	46.5	—	—	—	28.0

<sup>1</sup> From Parris & Green (1969); measurements only to the nearest millimeter.

<sup>2</sup> From Wilson (1957).

<sup>3</sup> From Westgate (1992).

lotype 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 P<sub>4</sub> of *Ammodon leidymanus* Marsh, 1893 is very similar to the P<sub>4</sub> 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. *leidymanus* holotype (also see Peterson 1909:68). The referred M<sub>3</sub> of A. *leidymanus* differs from that tooth in the holotype of *D. hollandi* only in being slightly longer (about 4%) and having a larger hypoconulid. We believe that these differences do not merit species-level separation of the holotypes of A. *leidymanus* 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* Schläijker, 1935, is based on the symphyseal region of a juvenile lower jaw (MCZ 2894) from the lower Harrison Formation of Wyoming (Schläijker 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-*

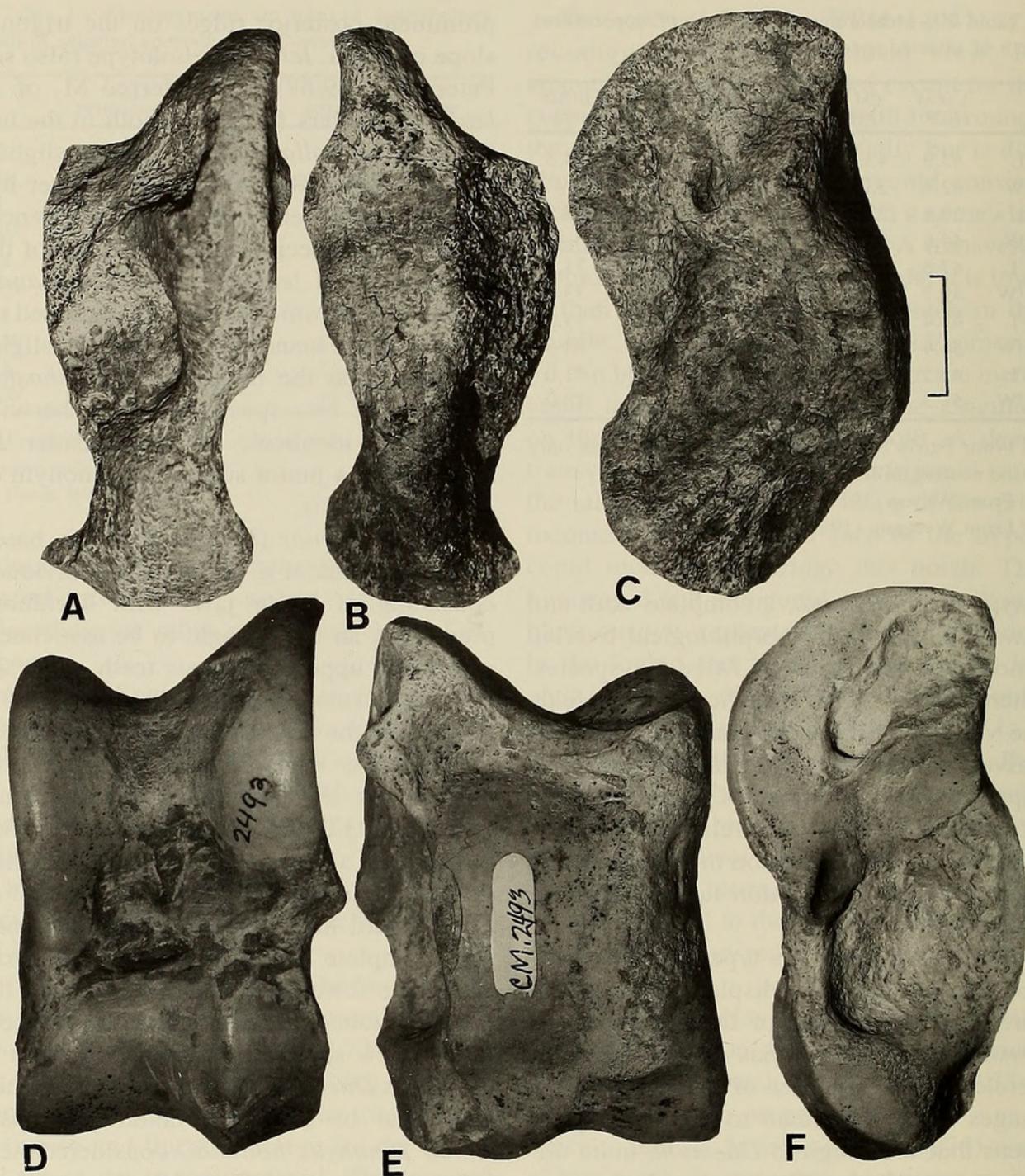


Fig. 4. Astragali of *Daeodon*. A–C, CM 1548, left astragalus, anterior (A), posterior (B) and lateral (C) views. D–F, CM 2493, left astragalus, anterior (D), posterior (E) and lateral (F) views. Bar scale is 20 mm long.

*rium*, 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 calkinsi* 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 leidyani* 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 *Tapiravus 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 leidyani*, 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  $19.2\text{--}22.6 \pm 0.5$  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

The National Geographic Society (Grant 5412-95) and the Charles D. Walcott Fund of the Smithsonian Institution supported this research. R. Tedford and D. Whistler provided valuable information. Curators and collection managers at the AMNH, CM, MCZ and YPM generously facilitated study of their collections.

### Literature Cited

- Allen, G. M. 1926. Fossil mammals from South Carolina.—Bulletin of the Museum of Comparative Zoology 67:447–467.
- Benson, R. N. 1993. Radiolarian and diatom biostratigraphic correlation of a diverse land and marine vertebrate fossil assemblage from lower Miocene shell beds, Delaware.—Geological Society of America, Abstracts with Programs 25(6): A114.

- Brunet, M. 1979. Les grands mammifères chefs de file de l'immigration Oligocène et le problème de la limite Éocène-Oligocène en Europe. Éditions de la Fondation Singer-Polignac, Paris, 281 pp.
- Cope, E. D. 1879. On some characters of the Miocene fauna of Oregon.—Proceedings of the American Philosophical Society 18:63–78.
- Emry, R. J. 1981. Additions to the mammalian fauna of the type Duchesnean, with comments on the status of the Duchesnean "age."—Journal of Paleontology 55:563–570.
- , & R. Eshelman. 1998. The early Hemingfordian (early Miocene) Pollack Farm local fauna: first Tertiary land mammals described from Delaware. In R. N. Benson, ed., Geology and Paleontology of the Lower Miocene Pollack Farm fossil site, Delaware. Delaware Geological Survey Special Publication 24. (in press).
- Gallagher, W. B., E. J. Gilmore, D. C. Parris, & B. S. Grandstaff. 1995. Miocene mammals from the Kirkwood Formation of Monmouth County, N.J. Pp. 254–268 in J. E. B. Baker, ed., Contributions to the paleontology of New Jersey. Geological Association of New Jersey 12.
- Glöger, C. W. L. 1841. Gemeinnütziges Hand- und Hilfsbuch der Naturgeschichte I, Breslau, 495 pp.
- Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America.—U.S. Geological Survey Bulletin 179:868.
- Linnaeus. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentius Salvius, Stockholm 1: 1–824.
- Loomis, F. B. 1932. Two new Miocene entelodonts.—Journal of Mammalogy 13:358–362.
- Lucas, S. G. 1992. Redefinition of the Duchesnean land mammal "age," late Eocene of western North America. Pp. 88–105 in D. R. Prothero & W. A. Berggren, eds., Eocene-Oligocene climatic and biotic evolution. Princeton University Press, 568 pp.
- , S. E. Foss, & R. J. Emry. 1996. Giant Oligo-Miocene entelodonts from the United States.—Geological Society of America, Abstracts with Programs 28(4):15.
- , D. P. Whistler, & H. M. Wagner. 1997. Giant entelodont (Mammalia, Artiodactyls) from the early Miocene of southern California.—Natural History Museum of Los Angeles County, Contributions in Science 466:9.
- Lydekker, R. 1883. Siwalik selenodont Suinae.—Palaeontologica Indica (10)2:1–146.
- Marsh, O. C. 1871. [Untitled].—Proceedings of the Academy of Natural Sciences of Philadelphia 1871:10.
- . 1874. Notice of new Tertiary mammals III.—American Journal of Science (3)7:531–534.
- . 1893. Description of Miocene Mammalia.—American Journal of Science 146:407–412.
- Owen, R. 1848. Description of the teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of the pachyderms by the number of their toes.—Quarterly Journal of the Geological Society of London 4: 103–141.
- Parris, D. C., & N. Green. 1969. *Dinohyus* (Mammalia: Entelodontidae) in the Sharps Formation, South Dakota.—Journal of Paleontology 43: 1277–1279.
- Peterson, O. A. 1905a. Preliminary note on a gigantic mammal from the Loup Fork Beds of Nebraska.—Science 22:211–212.
- . 1905b. A correction of the generic name (*Dinochoerus*) given to certain fossil remains from the Loup Fork Miocene of Nebraska.—Science 22:719.
- . 1906. The Miocene beds of western Nebraska and eastern Wyoming and their vertebrate faunas.—Annals of the Carnegie Museum 4: 21–72.
- . 1909. A revision of the Entelodontidae.—Memoirs of the Carnegie Museum 4:41–158.
- Rhoads, S. N. 1903. The mammals of Pennsylvania and New Jersey. Privately published, Philadelphia.
- Schlaikjer, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming, IV. New vertebrates and stratigraphy of the Oligocene and early Miocene.—Museum of Comparative Zoology Bulletin 76: 97–189.
- Simpson, G. G. 1930. Tertiary land mammals of Florida.—Bulletin of the American Museum of Natural History 59:149–211.
- . 1945. The principles of classification and a classification of mammals.—Bulletin of the American Museum of Natural History 85:1–350.
- Sinclair, W. J. 1905. New or imperfectly known rodents and ungulates from the John Day series.—Bulletin Department of Geology University of California 4:125–143.
- Skinner, M. E., S. M. Skinner, & R. J. Gooris. 1968. Cenozoic rocks and faunas of Turtle Butte, south-central South Dakota.—Bulletin of the American Museum of Natural History 138: 379–436.
- Sugarman, P. J., K. G. Miller, J. P. Owens, & M. D. Feigenson. 1993. Strontium-isotope and se-

- quence stratigraphy of the Miocene Kirkwood Formation, southern New Jersey.—Geological Society of America Bulletin 105:423–436.
- Tedford, R. H., & M. E. Hunter. 1984. Miocene marine-nonmarine correlations, Atlantic and Gulf Coastal Plains, North America.—Palaeogeography, Palaeoclimatology, Palaeoecology 47: 129–151.
- , M. F. Skinner, R. W. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. Macdonald, & S. D. Webb. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian interval (late Oligocene through earliest Pliocene deposits) in North America. Pp. 153–210 in M. O. Woodburne, ed., Cenozoic mammals of North America, Geochronology and Biostratigraphy, University of California Press, Berkeley, 336 pp.
- Troxell, E. L. 1920. Entelodonts in the Marsh collection.—American Journal of Science (4)50:243–255, 361–386, 431–445.
- Westgate, J. W. 1992. *Dinohyus* aff. *D. hollandi* (Mammalia, Entelodontidae) in Alabama.—Journal of Paleontology 66:685–687.
- Wilson, J. A. 1956. Miocene formations and vertebrate biostratigraphic units, Texas Coastal Plain.—American Association of Petroleum Geologists Bulletin 40:2233–2246.
- . 1957. Early Miocene entelodonts, Texas coastal plain.—American Journal of Science 255:641–649.



Lucas, Spencer G., Emry, Robert J., and Foss, Scott E. 1998. "Taxonomy and distribution of *Daeodon*, an Oligocene-Miocene entelodont (Mammalia: Artiodactyla) from North America." *Proceedings of the Biological Society of Washington* 111, 425–435.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/109906>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/48793>

**Holding Institution**

Smithsonian Libraries and Archives

**Sponsored by**

Biodiversity Heritage Library

**Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Biological Society of Washington

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.