

**A NEW LARGE BODY HELOHYID (ARTIODACTYLA)
FROM THE BRIDGERIAN MIDDLE EOCENE WASHAKIE FORMATION OF SOUTHERN WYOMING**

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ABSTRACT

We report on a new genus and species of helohyid, *Heliosus apophis* from the middle Eocene Washakie Formation lower Adobe Town Member of Wyoming, which is recognized as latest Bridgerian in age (upper Bridger D/ Twinbuttean Biozone), with an estimated age of 47 Ma. The holotype consists of a left dentary with P₄-M₃ and an associated humerus. Body mass equations using humeral measurements indicate a large body between 232 to 706 kg, with a smaller estimated body mass based on dental remains between 45-64.6 kg, similar to extant wild pigs. The left dentary features bunodont teeth and lacks distinct paraconid cusps on the lower molars. The holotype is larger than *Helohyus*, including the largest species *Helohyus lentus*, but about half the size of *Achaenodon* from the Uinta Formation of Utah. The holotype is comparable in size to *Parahyus vagus*, but differs in the following features: it lacks distinct paraconids on the lower molars, it has a more reduced P₄, and it has a narrower hypoconulid heel on the M₃. *Heliosus apophis* is important because it establishes an early presence of large artiodactyls in North America during the Middle Eocene.

INTRODUCTION

Pigs originated sometime during the early Eocene, during a period of great diversification within the Order Artiodactyla. Molecular studies of living pigs and peccaries (Superfamily Suoidea) show evidence for an early divergence of the group from other artiodactyls, including whales (Marcot, 2007), yet the fossil record of the group only extends back to the latest Eocene in North America and Asia (Prothero, 2009). The Superfamily Suoidea is split into two families, the peccary Family Tayassuidae (with a fossil record beginning in the latest Eocene of North America, Prothero, 2009), and the domestic pig Family Suidae (with a fossil record beginning in the late Eocene of Asia, (Ducrocq et al. 1998; Harris and Li-Ping, 2007). A third group of pig-like mammals is also known from the fossil record, the extinct Family Entelodontidae or “hell-pigs,” which came to dominance in the late Eocene and extended into the Miocene (Foss, 2007a; Vislobokova, 2008). Recent phylogenetic studies have argued that members of the Entelodontidae family may be unrelated to modern pigs and peccaries (O’Leary and Gatesy, 2008; Spaulding et al. 2009). This diverges from the traditional view that supports a monophyletic grouping that included the three families Tayassuidae, Suidae, and Entelodontidae as a monophyletic clade named Suiformes (Theodor et al. 2005; Geisler et al. 2007). In addition to these three families, there are a handful of fossil mammals that resemble pigs that pre-date the late Eocene, and have been reported from the middle Eocene (Uintan and Bridgerian North American Land Mammal Ages). These fragmentary

fossils have been loosely grouped within a family called the Helohyidae, and their relationship to Entelodontidae, Tayassuidae, and the Suidae families is not well understood (Theodor et al. 2005; Foss, 2007b).

In this paper, we describe a new genus and species of a large-bodied artiodactyl from the middle Eocene Washakie Formation in Southwestern Wyoming belonging to the family Helohyidae and examine its relationship to other contemporary Eocene artiodactyls.

GEOLOGICAL SETTING

FHPR 13976 was discovered in southwestern Wyoming within the Washakie Basin, a large topographic basin that preserves stratigraphic rock layers ranging from early Paleocene through middle Eocene time. Stratigraphically within the Washakie Basin is the middle Eocene Washakie Formation, which is separated into two members, the lower Kinney Rim and Adobe Town Members (Roehler, 1973; Turnbull, 1978). The Adobe Town Member is separated into lower and upper informal units, which bracket the Bridgerian and Uintan North American Land Mammal Ages (NALMA). (Lutetian Age; Turnbull, 2002). Stratigraphically the fossil locality is below Bed 620 of Turnbull (1978), Flynn (1986), and McCarroll et al. (1996), within the upper portion of the lower unit of the Adobe Town Member. The lower Adobe Town Member consists of mudstone and siltstone variegated beds, which are a dull grayish color, while the upper Adobe Town Member consists of mudstone and siltstone variegated beds which tend to be lighter white in

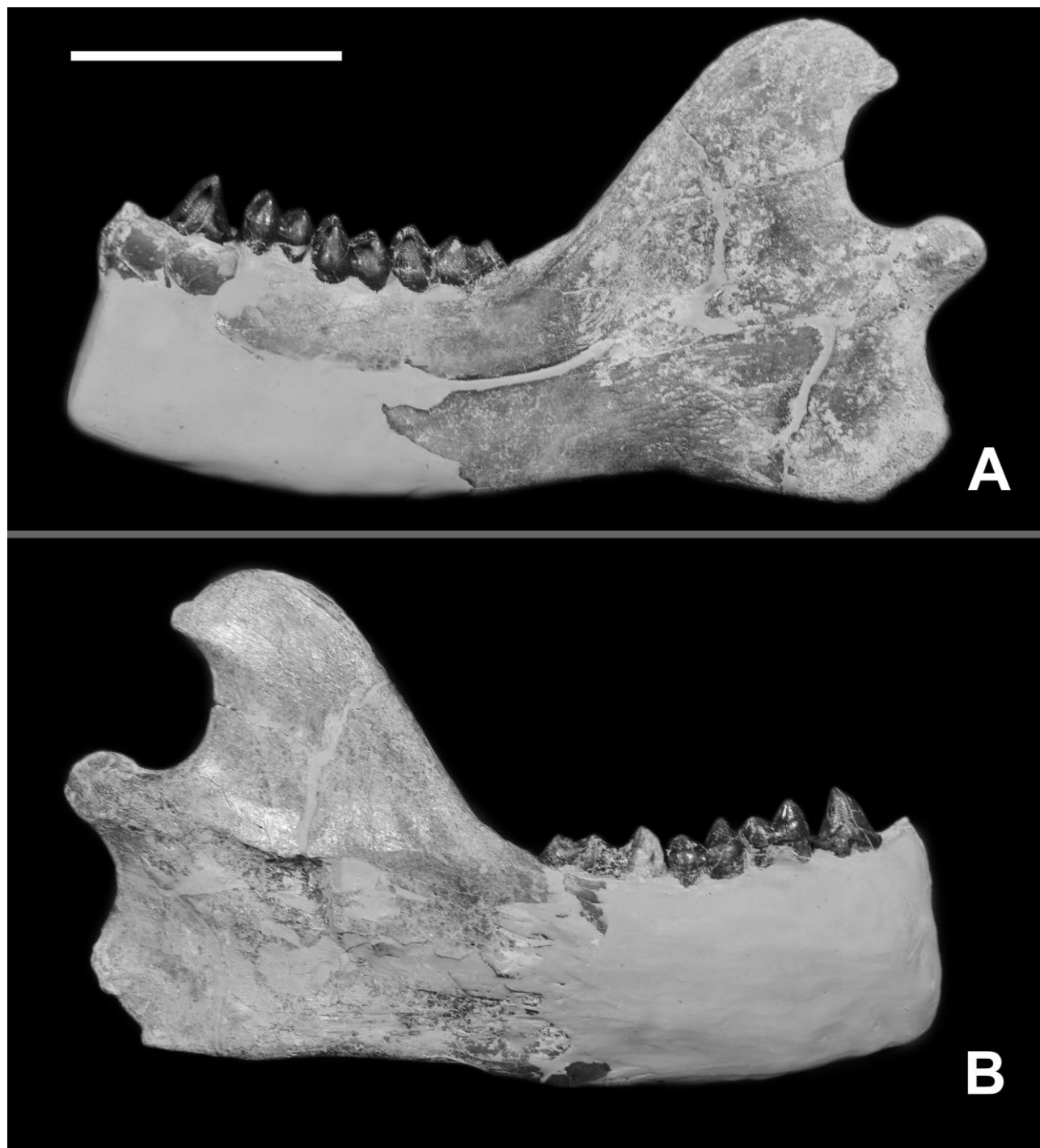


FIGURE 1. *Heliosus apophis* FHPR 13976. A, buccal view of dentary B, lingual view of dentary. Scale bar equals 5 cm.

color, although both units also contain widespread brown ribbon sandstones representing fluvial deposits inundating a near shore lake system. The lower Kinney Rim Member is interpreted as being more lacustrine, with olive green mudstones and shales, and the absence of brown sandstones

(Roehler, 1973). Both the lower portion of the Adobe Town Member and Kinney Rim Member contain numerous aquatic fossils such as fossil turtles, fish, crocodilians, and abundant gastropods that indicate a more lacustrine depositional environment. The upper section of the Adobe

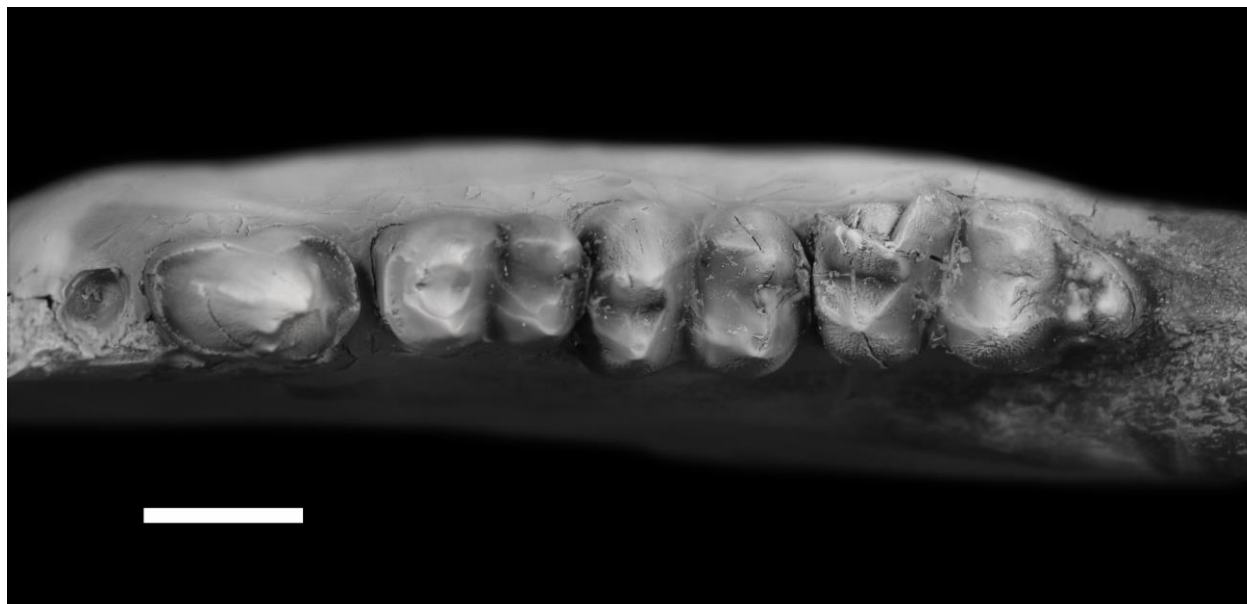


FIGURE 2. *Heliosus apophis* FHPR 13976. Occlusal view of dentition. Scale bar equals 1 cm.

Town Member is more fluvial, and these types of aquatic fossils are rarer, indicating a better drained environment over time as the basin was filled with sediment. The Washakie Basin lacks any Duchesnian NALMA fossil localities, indicating deposition in the basin ended by around 40 Ma.

Locality Information—FHPR 13976 was collected on land managed by the Bureau of Land Management (BLM) under research permit PA13-WY-205. Located along Willow Creek Rim, the locality is near the corner stake for Sections 5,4,8,9 in T15N R95W, and is near the Field Museum Locality FM 2-72 WDT, as plotted by Turnbull (1978).

Age of Locality—The exact stratigraphic location of the Bridgerian-Uintan NALMA boundary in the Washakie Formation is still under study. The currently known mammalian fauna from the lower Adobe Town member in the surrounding area indicates that the unit is late Bridgerian NALMA, with fossils of *Helalestes nanus*, *Uintatherium anceps*, and *Stylinodon mirus* known from the nearby Willow Creek area “Marsh’s Bone Pile Locality” (unpubl. data; Turnbull, 2004). Based on this fauna the locality is most likely equivalent to the Bridger D horizon in the Bridger Formation, or Twinbuttean (biochron Br3) subage of the Bridgerian NALMA (Murphey and Kelly, 2017). The new fossil was recovered from beds stratigraphically above these more established late Bridgerian fossil sites. In the same stratigraphic position as the new locality, the immediate area has so far produced the late Bridgerian brontothere *Mesatirhinus* sp. (FMNH PM 36045), *Hyopsodus* sp. and *Centetodon* sp.

which are known from the Twinbuttean (biochron Br3) subage (Gunnell et al., 2009). Interpretation of the paleomagnetic stratigraphic analysis of the formation by Flynn (1986) places the locality either near the base of Chron 20n or Chron 21n (see discussion in McCarroll et al., 1996 and Tsukui, 2016). Based on the available biostratigraphy and its comparison to the paleomagnetic stratigraphy of the Uinta Formation, the locality is more likely to be within the older Chron 21n, and hence the fossil is dated to around 47 million years old (± 0.5 Ma).

Institutional Abbreviation—FHPR, Utah Field House Museum of Natural History, Vernal, Utah

MATERIALS AND METHODS

The holotype is catalogued at the Utah Field House Natural History Museum in Vernal, Utah, as FHPR 13976. It was discovered in the field on August 20, 2017, eroding from a weathered mudstone. A large humerus associated with the jaw was discovered less than a meter away. Breakage of the anterior half of the jaw was likely pre-depositional, as few fragments were found near the exposed jaw when discovered. The specimen was prepared with B72 acrylic glue, as well as some cyanoacrylate to mend several fracture surfaces together. A clay polymer was applied to fill in cracks and gaps within the fossil, preventing breakage during casting. A silicon mold was used to make a white resin cast of the fossil for study.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Suborder Suina Gray, 1825

Family Helohyidae Marsh, 1877

Genus *Heliosus* n. gen.*Heliosus apophis* n. sp.

(Figures 1-4)

Diagnosis—Large helohyid mammal, with bulbous teeth; lacks distinct paraconid cusps on the lower molars, molars feature four rounded cusps; considerably larger than *Helohyus*, including the largest species *Helohyus lentus*; about half the size of *Achaenodon* (Figure 5). Slightly smaller than *Parahyus vagus*, but differs in lacking distinct paraconids on the molars, exhibiting a more reduced P₄ which is similar in size to the M₁, and having narrow rather than wide hypoconulid heel on the M₃ (Figure 1, 5). The ratio between the length of P₄ and M₁ in *Parahyus vagus* is much greater than in *Heliosus apophis* (Table 1). Lacks the molariform P₄ and wrinkled enamel of *Perchoerus minor*. Comparable in size to *Brachyhyops wyomingensis*, but differs in lacking the preprotocristid shelf on the molars, lacking a distinct paraconid, and having a narrow hypoconulid heel on the M₃ (Figure 1, 5). Differs from *Heptacodon* and other Anthracotheres and most other middle to late Eocene artiodactyls in lacking high crested preprotocristid, postcristid, prehypocristid, and posthypocristid.

Holotype—FHPR 13976, left dentary with P₄-M₃ and associated humerus discovered by Lea Ann Jolley on August 20, 2017, under field numbers 2017-Twab-08 and 2017-Twab-09. Collected from the Washakie Formation, lower Adobe Town Member, southwestern Wyoming, Sweetwater County.

Etymology—*helio*, Greek, sun, in reference to the holotype discovered just before the August 21, 2017, solar total eclipse in Wyoming; and *sus*, Latin, pig, or swine. *apophis*, Gr., in reference to the ancient Egyptian serpent god that devoured the sun.

Description—The fossil consists of a partial left dentary containing the P₄-M₃ including the coronoid process, condyloid, and angular process, and a complete associated humerus.

Dentary—The known left dentary is fragmentary and missing pieces of the ventral surface below the first and second molars, with the anterior portion not preserved. The P₄-M₃ of the left tooth row are, however, well preserved including the entire posterior dentary, including the coronoid process, condyloid, and angular process. The coronoid fossa is much wider and lower than modern peccary and pigs, with a broad attachment for the posterior deep masseter muscle. In modern peccaries, the coronoid fossa is smaller, likely as a consequence of the canine-locking mechanism, and orientation of the posterior deep

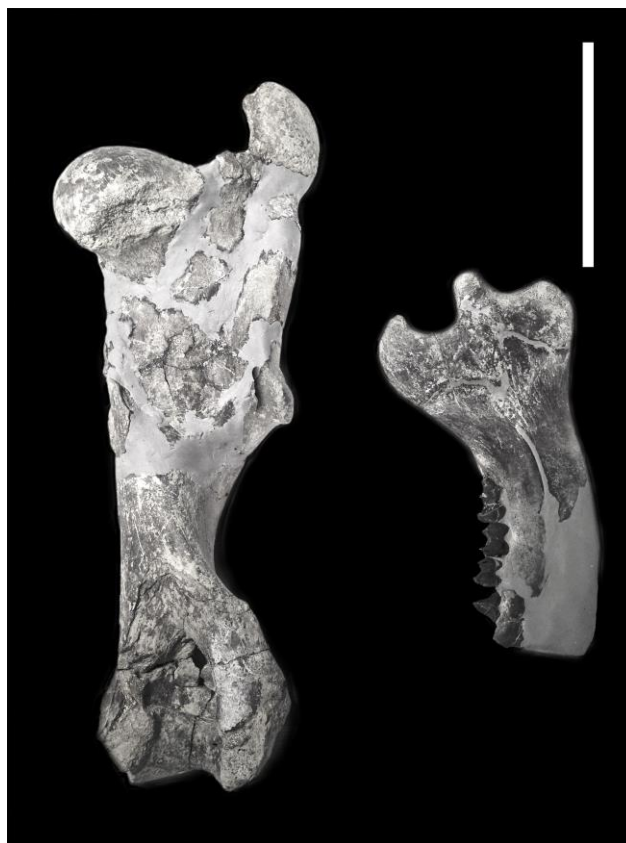


FIGURE 3. *Heliosus apophis* FHPR 13976. Posterior view of right humerus in comparison to lower left jaw. Scale bar equals 10 cm.

masseter muscle to the zygomatic arch. The angular process is broad for the attachment of a large superficial masseter, and does not project ventrally as in entelodonts (such as in *Cypretherium*). The condyloid is positioned at the level of the tooth row, similar to *Achaenodon robustus*. The depth of the dentary, however, is shallower than in *Achaenodon robustus*, and similar to early Eocene artiodactyls.

The P₄ is double rooted, with a single large prominent cusp. Anteriorly a single convex ridge descends the cusp, while posteriorly a concave ridge splits mid-way on the cusp into two descending ridges along its surface. Cingulum shelves are present both anteriorly and posteriorly on the P₄, with the anterior cingulum significantly lower on the tooth than the posterior cingulum. The posterior cingulum is slightly broader, with the lingual side better developed. The enamel shows some wrinkling on its surface.

The M₁ is double rooted, with four prominent bulbous cusps (metaconid, protoconid, hypoconid, and entoconid). There is no indication of a paraconid, with only a slight paracristid. The molars lack any distinct cingulum. The metaconid is much higher than the protoconid. The cristid obliqua is weak, with a slight wear facet. The talonid is composed of two cusps, the hypoconid, and the taller

Table 1. Dental Measurements of Relevant Middle Eocene Artiodactyla in mm

Genus	species	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
<i>Helohyus</i>	<i>plicodon</i> Specimen AMNH 12148 Measured by Sinclair, 1914	-	-	6	4	7.5	4.5	7	3.5
<i>Helohyus</i>	<i>plicodon</i> Specimen AMNH 12149 Measured by Sinclair, 1914	4	2	6	4	7	4	-	-
<i>Helohyus</i>	<i>milleri</i> Specimen AMNH 12151 Measured by Sinclair, 1914	9.5	5	10	7.5	11	8.5	-	-
<i>Helohyus</i>	<i>validus</i> Specimen AMNH 12694 Measured by Sinclair, 1914	-	-	-	-	-	-	12	6
<i>Helohyus</i>	<i>lentus</i> Specimen AMNH 12150 Measured by Sinclair, 1914	-	-	-	-	-	-	19	9
<i>Parahyus</i>	<i>vagus</i> Specimen YPM 10972 Measured by Gazin, 1955	26	12.8	19.3	13	21.1	14.8	34.8	17
<i>Achaenodon</i>	<i>insolens</i> Specimen AMNH 5143 Measured by Gazin, 1955	-	-	-	-	26.7	22.5	40	-
<i>Achaenodon</i>	<i>robustus</i> Specimen PU 10033 Measured by Gazin, 1955	30	17.5	22.5	17.5	24.2	19.5	36.8	23
<i>Heliosus</i>	<i>apophis</i> Specimen FHPR 13976 Measured in this paper	14.04	8.8	13.2	9.12	15.53	11.96	23.3	12.38
<i>Lophiohyus/Helohyus</i>	<i>alticeps/milleri</i> Specimen AMNH 1518 Measured by Sinclair, 1914 (Coombs and Coombs, 1977, notes that this specimen was lost)	4	2	6.5	4	7.5	4	10	5
<i>Perchoerus</i>	<i>minor</i> Specimen Measured by Prothero, 2009	-	-	11.2	8	12.1	9.1	15.6	8.5
<i>Brachyhyops</i>	<i>wyomingensis</i> Specimen FMNH PM 150 Measured by Tsubamoto et al. 2011	14.09	9.16	15.45	10.82	16.57	13.26	-	-
<i>Brachyhyops</i>	<i>trofimovi</i> Specimen MPC-M 30/67 Measured by Tsubamoto et al. 2011	15.5	12.5	16.1	12	18.9	13.8	19.3	12.5

entoconid. The hypoconulid is absent. The M₁ trigonid and talonid halves of the tooth are nearly symmetrical, giving the tooth a square shape.

The M₂ is similar in shape to the M₁, but is 54% larger. There is a tiny tubercle on the metacristid crest that might represent a tiny remnant of the paraconid, but the tooth lacks any distinct paraconid anterior to the metaconid. The protocristid and postcristid are better developed than on the M₁. The postcristid runs between the hypoconid and entoconid, with no indication of a hypoconulid. The posterior edge of the tooth has a slight shelf, which is

similar to *Perchoerus*, as well as the early entelodont *Proentelodon*.

The M₃ is the largest molar, with a high metaconid (broken on lingual side), and a slightly lower protoconid. A small paracristid connects the two cusps anteriorly, while the sharper angled protocristid connects the two cusps posteriorly. The entoconid and hypoconid are nearly equal in height, and are both bulbous and elevated. Unlike the other molars, the hypoconulid is pronounced, with a narrow extension from the molar posteriorly. Several accessory cusps are found on either side of the hypoconulid of the M₃. These small accessory cusps are similar to those observed

in *Helohyus lentus*, the largest species of *Helohyus* which is only known from an isolated M_3 from the Bridger Formation. *Parahyus vagus* has a broader hypoconulid shelf, while *Achaenodon* is similar with a narrower hypoconulid heel, but both taxa lack the accessory cusps on either side of the hypoconulid. Modern peccaries often have accessory cusps along with the hypoconulid on the M_3 ; this is taken to extremes in several members of the Suoidea which feature bizarre duplication of cusps along the M_3 posterior heel (such as in *Kopochoerus*). Most entelodonts, on the other hand, have reduced or lost the hypoconulid on the M_3 , such as in late Eocene *Archaeotherium*. In the early entelodont *Brachyhops* the hypoconulid is a small knob on the posterior margin of the M_3 , and only in the most primitive entelodont (*Proentelodon*) is there a well-developed hypoconulid. The teeth show minute crenulations along the lingual and buccal surfaces of the teeth, and lack any of the deep furrowing between cusps, which is characteristic of modern members of the Suoidea Superfamily.

Dental Measurements (mm)— $P_4L=14.04$, $W=8.80$; $M_1L=13.20$ $M_{1tri}=8.94$ $M_{1tal}=9.12$; $M_2L=15.53$ $M_{2tri}=11.96$, $M_{2tal}=11.78$; $M_3L=23.30$, $M_{3tri}=12.38$ (est.), $M_{3tal}=11.44$. Depth of dentary below $M_2 = 38.48$.

Humerus—The preserved right humerus bears a striking resemblance to a modern cow (*Bos taurus*) both in size and morphology. The major (lateral) tuberosity extends well above the proximal head of the humerus, indicating a lack of circumduction of the shoulder joint, typical of large ungulate mammals. The deltoid tuberosity is well developed along the shaft on the lateral side of the bone, slightly more proximal than midway down the shaft. The olecranon fossa is deep, with a broad trochlea and capitulum, which are not deeply grooved. The overall robust humerus likely supported a large animal, providing mainly motion in the sagittal plane, typical of cursorial large bodied mammals such as cattle.

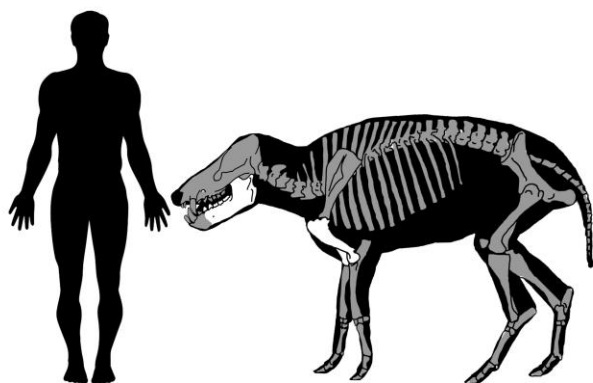


FIGURE 4. Body mass comparison of *Heliosus apophis* to a modern human.

Humeral Measurements—Greatest length (proximal-distal) = 31 cm; least circumference of shaft = 17 cm; greatest width of proximal end = 120.05 mm; least width of proximal end = 60.57 mm; greatest width of distal end = 81.91 mm; least width of distal end = 61.08 mm.

Body Mass Estimate—Few fossils have been found from the middle Eocene that compare to this specimen in terms of its body mass. Previous early to middle Eocene artiodactyls were slender small deer-like creatures, such as *Diacodexis* and *Antiacodon*, which were no bigger than a jackrabbit. FHPR 13976 is considerably larger. Utilizing the body mass equations developed by Christiansen (1999: table 2) for the preserved associated fossil humerus (length = 31 cm, least circumference = 17 cm), the new helohiid fossil in life was between 232 to 276 kg based on humeral length, and 684 kg to 706 kg based on humeral least circumference. Using the body mass equations developed by Scott (1983) for artiodactyls yielded a body mass range from 260 to 651 kg based on humeral measurements. These estimates are larger than living pigs and peccaries which typically range from 22 to 215 kg (Janis, 1990), although there are numerous reports of domestic and wild pigs (*Sus*) reaching sizes over 700 kg. Using Legendre's (1986) equation for determining body mass from the area of the lower first molar yielded a body mass of 47 kg. Using Damuth's (1990) equations for determining body mass for nonselenodont ungulates from the total length of the molar row yielded a body mass of 64.6 kg, and using the premolar and first and second molars yielded 45 kg. Helohiids might have relatively smaller dental lengths and widths compared to body mass than other ungulates. With this wide range of body size estimates, *Heliosus* likely had a body mass similar to modern pigs.

Comparison to contemporary early to middle Eocene small bunodont artiodactyls like *Antiacodon*, *Bunophorus*, *Microsus*, and *Helohyus* demonstrates a considerable size-gap with the larger *Heliosus apophis* during the Bridgerian NALMA in North America. Using first molar area of contemporary Bridgerian artiodactyl species *Helohyus plicodon* yielded an estimated body mass of 3.8 kg while *Antiacodon pygmaeus* had an estimated body mass of 1.1 kg using the equation of Legendre (1986). See table 1 for comparison of dental measures.

The new specimen compares more closely in size with younger Uintan genera like *Parahyus* and *Achaenodon*, both of which reached the size of large modern pigs (between 200 and 285 kg; Foss, 2001; Townsend, 2004) and are known from slightly younger rock units in the Uintan NALMA.

DISCUSSION AND CONCLUSIONS

The phylogeny of artiodactyls is highly debated among researchers. One paradigm has argued for the earliest

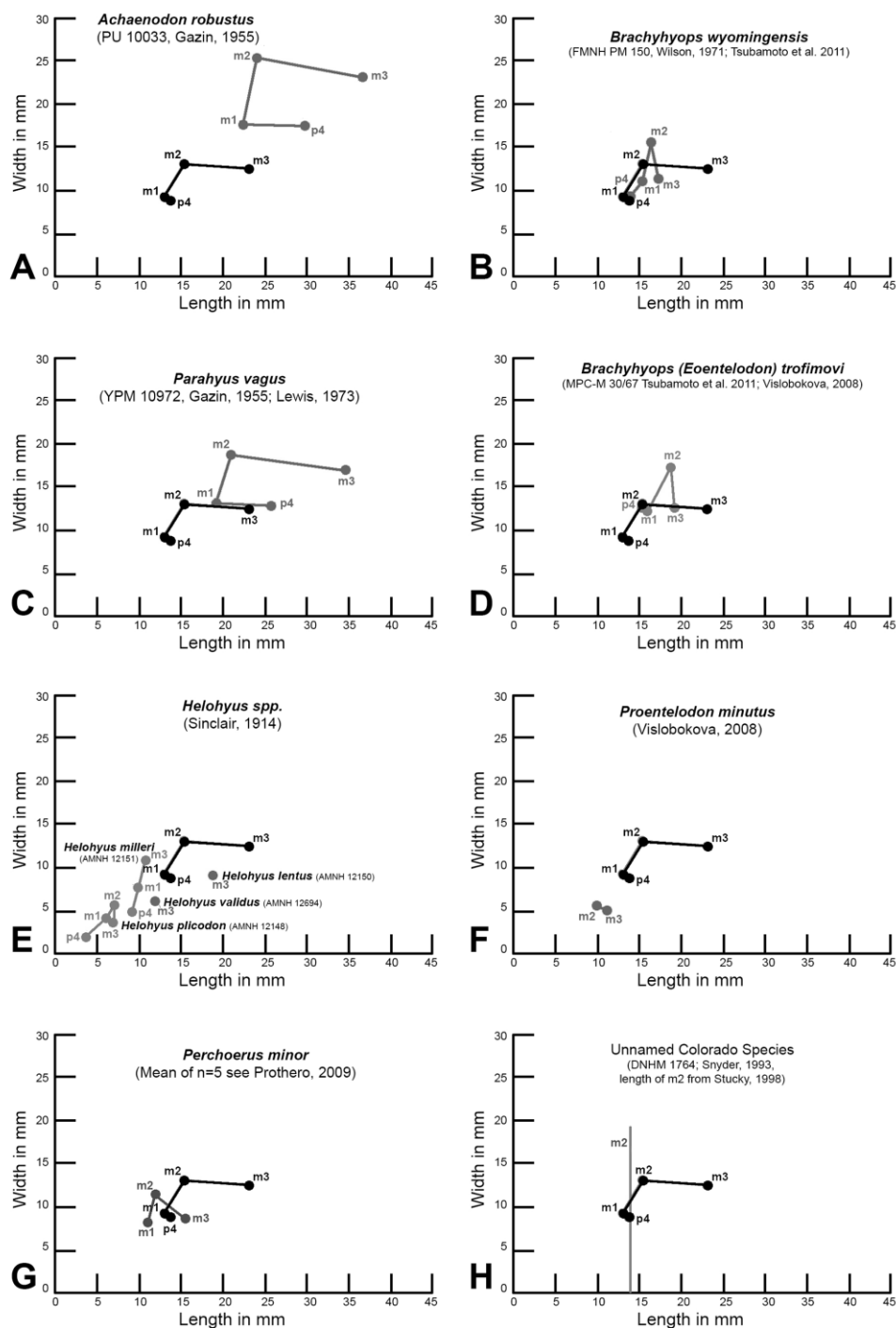


FIGURE 5. Dental length and width of P₄ through M₃ of *Heliosus apophis* (in black), compared to other fossil specimens of early pig-like mammals (in gray). A, *Heliosus apophis* is smaller than *Achaenodon robustus*, with a P₄ that is subequal in size with the M₁. B, Although nearly the same size as *Brachyhyops wyomingensis*, *Heliosus apophis* lacks the reduced M₂ hypoconulid that characterizes early entelodontids, and exhibits a much longer M₃. C, *Heliosus apophis* is smaller and lacks the longer P₄ relative to the M₁ found in *Parahyops vagus*. D, Although nearly the same size as the Asian *Brachyhyops (Eoentelodon) trofimovi*, *Heliosus apophis* lacks the reduced M₃ that characterizes early Entelodontids. E, *Heliosus apophis* is larger than known species of *Helohyus*. F, *Heliosus apophis* is larger than the Asian *Proentelodon minutus*, which closely resembles *Helohyus* from North America. G, *Heliosus apophis* is larger than *Perchoerus minor*, with a longer M₃. H, A unnamed helohyid specimen from the Uintan of Northwestern Colorado is reported in the literature, which may compare with this specimen, given its similar M₂ length. Further study is needed.

divergence of pigs and peccaries from all other artiodactyls, while another line of thought suggests that camels and llamas (Suborder Tylopoda) were the earliest artiodactyls to diverge. The anatomy of the teeth supports an early divergence of pigs and peccaries from other artiodactyls, as pigs and peccaries (Superfamily Suoidea) have bulbous teeth which are often highly crenulated and used in crushing hard food, which facilitates a more omnivorous diet. Furthermore, pigs and peccaries have a simplified gut, while most other artiodactyls, including the Suborder Tylopoda, exhibit a more complex gut and teeth which facilitate chewing or grinding of tough vegetation such as grasses. The premolar and molar anatomy of these other artiodactyls exhibit crescent shaped crests that are worn down with use, and are referred to as a selenodont condition. The selenodont condition is found within Tylopoda, as well as other more derived artiodactyls, like the Ruminantia. The fossil record of artiodactyls exhibiting these two dental conditions extends back to the middle Eocene. Prior to this, in the early Eocene, the teeth of artiodactyls closely resembled the primitive tribosphenic molars found in early Paleocene condylarths (such as Arctocyonidae) and lack any of these dental specializations. Examples of this primitive style of dentition are found in the early Eocene *Diacodexis* and middle Eocene *Antiacodon*. The early to middle Eocene was a critical time in the evolution of artiodactyls, as their dental morphology diverged toward these two different dietary specializations that are found in living artiodactyls today. *Heliosus apophis* demonstrates an early origin for the bulbous pig-like dentition, extending this split within artiodactyls deeper back in time.

The Helohyidae family includes several taxa known from the Middle Eocene of North America, including the Bridgerian genus *Helohyus* as well as the Uintan genus *Achaenodon*. The older *Helohyus*, however, differs greatly in terms of size and anatomy when compared to the younger and much larger genus *Achaenodon*. Gazin (1955) postulated a linear ancestor-descendant relationship between small rabbit-like *Helohyus* and large hippo-like *Achaenodon*, and supported a close relationship. Others, like Zittel (1893), Matthew (1899) and Colbert (1938), viewed *Achaenodon* as the earliest member of the Entelodontidae family, and *Helohyus* as a member of the more primitive Dichobunidae family. However, more recent reviews of the Helohyidae family by Stucky (1998) and Foss (2007b) have upheld Gazin's (1955) view of a close the relationship between *Helohyus* and *Achaenodon*. As Foss (2007b) points out, *Achaenodon* lacks many of the characteristics of later members of the Entelodontidae, despite its similar larger body mass.

FHPR 13973 provides some insight into the relationship of these two taxa, in particular because it is found within the latest Bridgerian strata, and is a useful

morphological link between the earlier *Helohyus* and later *Achaenodon*. In terms of size and morphology the new fossil is intermediate between the two and closely related to the intermediate sized *Parahyus vagus*.

Heliosus represents a large North American artiodactyl living in the Middle Eocene (Bridgerian NALMA) and indicates a rapid increase in body mass. The discovery of *Heliosus* also suggests that the paucity of Helohyidae fossils does not indicate a lack of morphologic and taxonomic diversity, but rather our current fairly incomplete record of their occurrence.

ACKNOWLEDGEMENTS

We are proud to contribute this article in dedication to the memory of James G. Honey, who aided the senior author in his pursuit of the study of fossil mammals in the American West and was ever enthusiastic to share his knowledge and love for paleontology. His enthusiasm for fossil mammals was contagious, love of fieldwork magical, and he was there in the field to help inflate or repair a tire or two. He is missed. We are also indebted to Steve Sroka at the Utah Field House Museum of Natural History which served as our repository for this fossil, and Brent Breithaupt at the Wyoming Bureau of Land Management.

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