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THE EARLY EVOLUTION OF THE NORTH AMERICAN PECCARIES (ARTIODACTYLA: TAYASSUIDAE)

DONALD R. PROTHERO
Department of Geology, Occidental College, Los Angeles, CA 90041; prothero@oxy.edu

ABSTRACT—The understanding of the systematics of the earliest peccaries in North America has long been hampered by poor and relatively scarce material, but new collections help redefine the species and genera, and add greatly to our knowledge of their anatomy and temporal range. The genera *Perchoerus* and *Thinohyus* were confused due to their poor type specimens, but comparison with topotypic specimens of White River Whitneyan *Perchoerus probus* and John Day *Thinohyus lentus* shows that the two genera can easily be distinguished. Even though there are only slight differences in the size and proportions of teeth, the skulls of *Thinohyus* are much more robust, dolichocephalic, with weaker sagittal crests than seen in *Perchoerus*. *Thinohyus* has a large posterior cingulum on M3 with a postero-internal cusp, and diastemata between the canines and first premolars, and sometimes between the first and second premolars. The earliest species of *Perchoerus* is the tiny Chadronian taxon *P. minor*, the smallest peccary yet known, which marks the immigration of peccaries from Asia in the early Chadronian (at least 36 Ma). It was previously known only from a lower jaw, but its skull and upper teeth are described based on new material. Slightly larger is the rare Orellan taxon *P. nanus*, also originally known only from a lower jaw, but here redescribed based on new skull material. Most known *Perchoerus* fossils are of the largest species, the Whitneyan taxon *P. probus*, although at no time are *Perchoerus* fossils as common as those of most other White River mammals. By the late Whitneyan, the much more robust and dolichocephalic taxon *Thinohyus* appeared in the John Day region of Oregon. Only two valid species are recognized: *T. lentus* (including *T. osmonti*, and possibly *T. pristinus*) and the disjunctly larger and more robust *T. rostratus*. The John Day taxa "*Chaenohyus decedens*," "*Thinohyus trichaenus*," and "*T. subaequans*" are here referred to *Perchoerus probus*.

INTRODUCTION

The family Tayassuidae, also known as the peccaries or javelinas, is a very successful group of suoid artiodactyls with three genera and species still living today in the New World. These species are *Dicotyles tajacu*, the collared peccary; *Tayassu pecari*, the white-lipped peccary; and *Catagonus wagneri*, the Chacoan peccary, known only from fossils until living specimens were discovered in the Gran Chaco of Paraguay in 1975. However, peccaries were much more diverse over the past 37 million years, with at least 20 genera and an unknown number of valid species represented in the fossil record of North America. Despite a relatively long-ranging history (Chadronian to Recent in North America), relatively little research on their evolution has been published in the last century. The most recent review was the dissertation of David Wright (1991) and his summary chapter (Wright, 1998), but his research focused on Miocene peccaries and did not examine the Eocene or Oligocene taxa in detail. Wright (1998:393-394) briefly discussed some of his preliminary observations of the early North American peccaries, but did not attempt a full systematic revision, or resolve the issues about the confusion over generic distinctions or the validity of the many named species. Even though peccaries are relatively rare compared to most White River or John Day mammalian fossils, there are now dozens of decent skulls and jaws in the collections which make it possible to resolve many of the confusing issues of early peccary systematics. In the early 1960s, Ruben A. Stirton and Michael O. Woodburne began such a project, but their work only saw publication as an abstract (Stirton and Woodburne, 1965). Woodburne's (1969) monograph on the Miocene peccaries *Cynorca* and *Dyseohyus* is the definitive treatment of these genera, but he did not discuss earlier taxa.

METHODS

For this study, all relevant peccary fossil material in the following collections was examined: American Museum of Natural History, New York, NY (AMNH), and the Frick Collection at the AMNH

(F:AM); Harold Cook Collection at the AMNH (HC); Field Museum of Natural History, Chicago, IL (FMNH): John Day Fossil Beds National Park (JODA); Natural History Museum of Los Angeles County (LACM); California Institute of Technology collection, now at the LACM (LACM-CIT); Condon Collection, University of Oregon (UOMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM): South Dakota School of Mines Museum, Rapid City, SD (SDSM); University of California Museum of Paleontology, Berkeley, CA (UCMP): University of Colorado Museum, Boulder, CO (UCM); University of California, Riverside (UCR, now recatalogued in the UCMP);Yale Peabody Museum, New Haven, CT (YPM), and the Princeton University collections, now housed at the YPM (YPM-PU). Photographs and measurements of the type material from the Academy of Natural Sciences of Philadelphia (ANSP) were provided by Dr. Ted Daeschler and of the JODA specimens by Ted Fremd. All specimens were measured with dial calipers, and data were plotted on Excel spread sheets.

SYSTEMATIC PALEONTOLOGY

Perchoerus Leidy, 1869

Palaeochoerus Leidy, 1856 (non Pomel, 1847)
Thinohyus Marsh, 1875 (in part)
Chaenohyus Cope, 1879
Bothrolabis Cope, 1888

Type species—*Perchoerus probus* (Leidy, 1856)

Included species—Type and *P. minor* Cook, 1922, and *P. nanus* Marsh, 1894.

Diagnosis—Smaller peccaries (M1-3 length = 30-47 mm) with well-developed sagittal crests, and relatively brachycephalic, gracile skulls with less robust occiput and zygomatic arches compared to *Thinohyus*; no diastemata between canines and first premolars; M3 relatively short antero-posteriorly compared to M3 of *Thinohyus* due to relatively small posterior cingulum and lack of a postero-internal heel.

Description—A full description was given by Scott (1940:493-501).

Distribution—Chadronian through Whitneyan, Great Plains (South Dakota, Nebraska, Colorado, eastern Wyoming), and Whitneyan-Arikareean, John Day Formation, Oregon.

Discussion—A central issue in the systematics of late Eocene to early Miocene peccaries of North America is the confusion over the distinction between the genera *Perchoerus* and *Thinohyus*. Leidy (1869) named *Perchoerus probus* on the basis of a few jaw fragments (ANSP 10588 is designated the type specimen, but Leidy also mentioned ANSP 10590 and ANSP 10591) with no associated skull material. Leidy (1856) had originally attributed this material to the European genus *Palaeochoerus* (Pomel), but in 1869 erected his new genus. These specimens came from an undetermined level in the White River Group. Marsh (1875) named *Thinohyus lentus* based on a badly broken juvenile skull (YPM 11783), which has never previously been illustrated in the scientific literature. Marsh (1875) gave the type locality of *T. lentus* as “Miocene of the John Day River, Oregon,” which cannot be refined to a more specific level in the context of the modern stratigraphy (Fremd et al., 1994).

Based on such incomplete type material, it is no surprise that later authors often confused the distinctions between the two genera, and could not decide to which genus certain species should be allocated. Matthew (1907) regarded *Thinohyus* as a junior synonym of *Perchoerus*. Cope and Matthew (1915), Pearson (1923), and Scott (1940) concurred with this opinion. However, Stirton and Woodburne (1965), McKenna and Bell (1997), Wright (1998), and Harris and Liu (2007) regarded the two genera as distinct. Wright’s (1998) diagnosis of *Thinohyus*, however, is based entirely on the poorly preserved juvenile type specimen. Most of his diagnostic characteristics distinguishing *Perchoerus* from *Thinohyus* are features of the former’s type skull that are due to its juvenile nature, or due to the crushing and poor preservation of the specimen. Comparison of the juvenile type specimen with numerous well preserved

adult topotypic skulls of *Thinohyus* from the John Day beds in the AMNH and YPM collections show that these distinctions are not valid.

For example, Wright (1998:393) defined *Thinohyus* by such features as "choanal margin opens medial to M3," in contrast to *Perchoerus*, where the choanal margin opens approximately 15 mm posterior to M3. Wright conceded that this "may be influenced by the young age of the specimen." Indeed, examination of the other adult John Day skulls referable to *Thinohyus lentus* (such as YPM 10207, 14635, 14640, and 14639) shows that none of them exhibit the condition in the type specimen, YPM 11783. The same can be said of nearly every other character in Wright's (1998) diagnosis of *Thinohyus lentus* based on the broken juvenile type specimen. For example, "articular surface of glenoid fossa approximately in plane of basioccipital" is true only of YPM 11783, while all the other John Day *Thinohyus* exhibit the condition found in *Perchoerus*, where this plane is slightly ventral to the basioccipital. Wright (1998) claimed that the "palatine wall of choanal fossa medial to maxillary foramen inflated laterally" diagnoses *Perchoerus* and not the type specimen of *Thinohyus lentus*, but nearly all the referred skulls of *T. lentus* have this condition as well. Other "diagnostic features" proved to be highly variable, such as the "upper molar paracone and protocone separated by a protoconule," which is found only in the type of *T. lentus*, but not the other specimens referable to this species, yet this feature does occur in some specimens of White River *Perchoerus probus*. Finally, the "postglenoid canal passes between the post-tympanic process of squamosal and postglenoid process of jugal, ventral and parallel to external auditory meatus" characterizes only YPM 11783. All other specimens referable to *T. lentus* have the condition found in *Perchoerus*, namely "tympanic process of squamosal dorsoventrally deep, external auditory meatus directed dorsally."

Once these invalid diagnostic features are set aside, the next step is to lay out topotypic samples of White River *Perchoerus* and John Day *Thinohyus* and see if there are distinctions that might hold up (Figs. 1, 2). Wright (1998) mentioned that *Perchoerus* has a strong sagittal crest, while *Thinohyus* does not, and indeed that seems to be valid. Much more impressive, however, is the overall proportions and robustness of the skull of *Thinohyus*. Most specimens from the John Day Formation are much larger and more robust than any White River specimen, with a wider, thicker zygomatic arch, a broader and shallower occiput, and a much longer rostrum (dolichocephaly). Related to this dolichocephaly is the fact that nearly every John Day *Thinohyus* skull has a slight diastema between the canines and the first premolars, and sometimes a small diastema between P1/p1 and P2/p2, a feature that does not occur in any of the White River *Perchoerus* skulls I have seen, which are all relatively brachycephalic.

Despite the striking differences in the overall size and proportions of the skull, the teeth of the much larger John Day skulls overlap in size those of the White River skulls (Fig. 3). Since so many specimens are isolated teeth, jaws and maxillae, this makes diagnosing specimens based on teeth alone very difficult. Nevertheless, the skull proportions and size differences appear to be very consistent (*contra* Wright, 1998). They cannot be attributed to sexual dimorphism, since there appear to be robust skulls of *T. lentus* from the John Day with both the larger male canines (e.g., UCMP 393) and those with smaller, apparently female canines (e.g., YPM-PU 10788, AMNH 7392). Likewise, there are the more brachycephalic, gracile skulls of *P. probus* from the White River Group with both male canines (e.g., YPM 11910, F:AM 73722) and female canines (e.g., YPM 10209, YPM-PU 16442, F:AM 73745). Thus, the overall skull size, robustness, lack of sagittal crest, dolichocephaly, and development of canine-first premolar diastema are features that consistently separate both male and female specimens of John Day *Thinohyus lentus* from White River *Perchoerus probus*, and are thus the basis for my assignment of other specimens to these two distinctive genera.

Perchoerus minor Cook, 1922

Figure 4-7, Table 1

Type specimen—AMNH 86222 (originally HC 458), right and left rami with right p3-m3, left p3-4, m2 and partial m3 (Fig. 4), from the "lowermost clays of the Chadron Formation, 9 miles north of Crawford, Nebraska" (early or middle Chadronian).

Referred specimens—AMNH 86221 (HC 1090), partial ramus with m3, from the type locality; USNM 206190, partial juvenile skull, isolated maxillae and ramal fragments, from the Ledge Creek

locality, Natrona County, Wyoming (Skinner and Gooris, 1966: fig. 3), 245 feet above the base (Chron C15r, about 35.5 Ma, early Chadronian, equivalent to just above Ash B at Flagstaff Rim; Prothero, 1985; Prothero and Swisher, 1992; Prothero and Emry, 1996); UNSM 372193, skull fragment, right ramus with m2-3, Munson Ranch East, 5 feet below the PWL (latest Chadronian); YPM-PU 12736, right ramus with p4-m3, White River Group, possibly Brule Formation, Cottonwood Creek, Big Badlands, SD (?Orellan); YPM-PU 13599, right and left ramal fragments, 3/4 miles southeast of Rock Springs, Corral Draw, Big Badlands, SD, Peanut Peak Member, Chadron Formation (late Chadronian); YPM 14651, left ramus with m2-3, White River Group, Big Badlands, level unknown; AMNH 12314, right and left rami with m2-3; YPM 14656, right ramus, White River Group, Big Badlands, level unknown; YPM 14648, right and left rami with m1-3, Big Badlands, White River Group, level unknown; FMNH PM20802, left m3, Crazy Johnson Member, Chadron Formation, Big Badlands, SD (middle Chadronian); FMNH PM22407, right ramus with m1-3, Ahearn Member, Chadron Formation, Big Badlands, SD (early Chadronian); FMNH PM23606, left P4-M2, right M2-3, Chadron Formation, Big Badlands, SD (Chadronian); FMNH PM39979, lower molar, Crazy Johnson Member, Chadron Formation, Big Badlands, SD (middle Chadronian); FMNH PM44572, left M3, Peanut Peak Member, Chadron Formation, Big Badlands, SD (late Chadronian); FMNH PM45051, molar fragment, Ahearn Member, Chadron Formation, Big Badlands, SD (early Chadronian).

Diagnosis—Smallest species of *Perchoerus* (m1-3 length = 34-42 mm); m3 with very simple non-expanded talonid (no“basin”); upper and lower molar cusps generally simpler in ornamentation and construction than in other species of *Perchoerus*; jaw shallower in lateral view and more slender than in other species of *Perchoerus*.

Description—Cook’s (1922) description of *P. minor* was very brief, and the type specimen is a highly worn pair of rami, so it was not very useful in recognizing other specimens referable to the species. Many of the features that Cook described, such as “extreme crowding of the lower incisors,” are largely due to the taphonomic distortion and poor preservation of the type specimen, and do not appear in any other referred specimens. About the only criterion for diagnosing the species that can be used based on Cook’s type specimen is its extremely small size. Indeed, it is the smallest peccary specimen yet found in North America (Fig. 4). However, since Cook’s (1922) paper, a number of very small lower jaw fragments from the Chadronian (see Referred Specimens above) have been found, all of which are very close in size to Cook’s type. There are some fragmentary upper dentitions that are also tiny compared to normal *Perchoerus*, and thus are referred to this species. In addition, a partial juvenile skull (USNM 206190) from the early Chadronian Ledge Creek locality (Skinner and Gooris, 1966; Prothero, 1985) shows some of the non-dental features of this species. The skull is associated with detached fragmentary maxillae containing left and right dP2-4, M1 erupted, and M2 beginning to erupt (Fig. 5). The dimensions of the M1 are consistent with other specimens referred to *P. minor*, and in the right size range to match the lower jaws referred to that species, as well as the type.

Based on the referred specimens listed above (especially USNM 372193; Fig. 6), the description of the lower jaw given by Cook (1922) is modified as follows: p2 simple; single, blade-like tooth with slightly recurved point; no accessory ridges as seen in *P. probus*, nor any labial or lingual cingula; p3 like p2 with slight development of talonid, sometimes showing a basin; distinct posterior conulid connecting main cuspid to posterior ridge; p4 much like p3, except with doubled main cuspid; anterior ridge descends from labial main cuspid to anterior conulid; anterior conulid more strongly developed than in p3; posterior conulid variable, from poorly developed in some specimens (YPM 14656) to doubled in others (YPM 11784); lingual cingulum absent or poorly developed.

The m1 is composed of two distinct, oval-shaped parts of equal size, the trigonid and talonid. Lines drawn through the metaconid-protoconid tips and from the entoconid to the hypoconid passes anterolabially, and both lines are parallel to each other. An arcuate ridge that is concave dorsally and anteriorly connects the posterior protoconid to the metaconid. The main transverse valley between the trigonid and talonid is interrupted by a ridge that connects the protoconid to the hypoconid. The main transverse valley forms the anterior border of an elongate conulid that extends lingually from the ridge between the protoconid and hypoconid. The base of the hypoconid extends lingually to the base of the entoconid. The hypoconulid is posterolingual to the hypoconid and merges with the posterior cingulum,

which extends around the postero-labial corner of the tooth, but does not pass on to the labial surface. The protoconid and metaconid are separated by a longitudinal groove that terminates anteriorly at the protoconulid and posteriorly at the metalophid. The m2 is similar to the m1, but larger. The trigonid in unworn specimens is noticeably higher than the talonid, with a broad bulbous protoconid and a merged metaconid-protoconid; both cusps tend to form circular 'lakes' as their tips wear away. The hypoconid on the talonid is lower than the cusps of the entoconid-hypoconulid, which when worn form arcuate 'lakes' in the enamel, rather than circular or round 'lakes.' With even greater wear, the cusps disappear entirely leaving only two ovoid 'lakes' in the enamel where the trigonid and talonid used to be.

The m3 is the most diagnostic tooth. It is not only the smallest m3 of all *Perchoerus* species, but the hypoconulid is shorter and not basined as in *P. probus*, making it much less elongate than that of *P. probus*. The labial part of the trigonid forms one distinct blunt cusp, with two distinct labial wear facets on the protoconid. The arcuate cusp between the posterior walls of the protoconid and metaconid is particularly prominent in less worn specimens. The labial part of the trigonid consists of one large cusp (mostly paraconid), with a small posterior metaconid on its posterior edge. The talonid is much lower than the trigonid, with a distinct bulbous entoconid and hypoconid that wear to form transverse lophs. A distinct crest in the valley between the trigonid and talonid connects the anterior bases of the hypoconid and entoconid. The m3 hypoconulid is shaped like a broad semicircle in crown view, with a large labially-inclined wear facet on the lingual part of the hypoconulid, and a much lower lingually-inclined facet on the internal labial part of the cusp. There is no large elevated hypoconulid cusp with an internal basin, as seen in *P. probus*.

The mandibular foramen is 53.4 mm posterior to the anterior end of m1, and essentially level with the tooth row. An additional pair of small mental foramina is present on the type specimen anterior to the mandibular foramen, and below the anterior end of p4 and the posterior root of p2, but most specimens are not complete enough to show both foramina. The entire ramus is much more slender and shallower than comparable rami of *P. probus*. The jaw is only 19-24 mm deep at the level of the mental foramina, and about 19-22 mm wide at the level of the symphysis. The rear of the symphysis occurs at the level of anterior p3 in most specimens.

The skull and upper dentition of *P. minor* were unknown at the time of Cook's (1922) or Scott's (1940) descriptions of the species, but they are now known from several partial specimens. These include the partial skull of a juvenile individual (USNM 206190: Fig. 5), as well as isolated maxillary fragments (UCR specimens, now UCMP 310030, 310031). USNM 206190 has a well-preserved braincase and frontals, and broken and detached maxillae that preserve the M1 (erupted) and M2 (in the crypt) on the left side and M1 erupted on the right side. Both sides preserve dP2-4 and the right side also preserves the base of the canine. The dP4 is a simple bladelike tooth with a slightly recurved tip and a faint lingual cingulum that encloses a basin on the posterior edge. The dP3 is basically a triangular tooth, but it is so highly worn in USNM 206190 that there is not much cusp or crest morphology remaining. It has a high bladelike paracone and slightly lower metacone, a faint paraconule, and a broad shelf-like area in the hypocone position, but no protocone. There are no cingula on the dP3. The dP4 is more quadrate in shape, with well-developed paracone and metacone forming a faint ectoloph crest. The protocone and hypocone areas are highly worn, forming elongate lobes that more closely resemble the protoloph and metaloph of a *Mesohippus* or primitive rhino tooth rather than the tooth of an artiodactyl.

M1 is virtually unworn in USNM 206190. The large, slightly bladelike paracone is the highest cusp on the crown, followed by a lower, but even more bladelike metacone. A well-developed labial cingulum connects these two cusps. The protocone is slightly lower and oriented posterolabially to the paracone. A large triangular paraconule sits between the paracone and protocone, joined to the anterior cingulum by a distinct crest originating at the anterior base of the paracone. In the posterior labial part of the tooth is a prominent metaconule, and labial to this, a short cusp emerging from the posterolabial lingual cingulum that represents the true hypocone. As in most artiodactyls, the cusp in the hypocone position is not a true hypocone, but a labially shifted metaconule. In USNM 206190, there are two additional cusps that sit anterolingual and posterolingual to the metaconule and enclose a valley between the metaconule and the metacone. The posterolingual cingulum is very pronounced, and curves continuously into the prominent posterior cingulum.

The erupting M2 on the left maxilla of USNM 206190 is completely unworn, since it was still in its crypt, although the anterolingual corner has been broken off. The preserved parts of the tooth consist of a very large robust paracone (the highest cusp on the tooth) followed by a low metacone that is capped by an oval-shaped crest on the tip. The large protocone is equidistant from the paracone and metacone, making the tooth seem almost triangular in crown view. Between the metacone and the protocone is a large robust metaconule, which bears two tiny accessory cusps anterolingually and posterolingually, enclosing the valley between the protocone and metaconule. The posterior of these cusps sits on the posterolingual cingulum, and may actually be the true hypocone.

The skull fragment of USNM 206190 clearly belonged to a juvenile individual based on its unfused sutures, associated maxillae retaining dP2-4, and an unerupted M2. Nonetheless, it is dramatically smaller than any skull of *P. nanus* and especially *P. probus* (Fig. 7), and this difference is not due to its juvenile nature. In dorsal view, the skull is broken at the nasal-frontal suture. The frontals are broad and flat, with broad triangular supraorbital processes on each side. Several large supraorbital foramina are symmetrically placed along the midline on the anterior half of the frontals along with foramina just above the orbital region. The parietals are domed and bulbous to cover the braincase, with strong parasagittal crests that converge in a "Y"-shaped pattern to form a prominent sagittal crest. This crest, in turn, meets strong lambdoid crests to form a very high, arched nuchal crest.

As seen in Figure 5, the anterior part of the skull is completely broken off. Although both orbits are present, neither is well preserved, and the foramina discussed by Pearson (1923) are not visible. Both auditory bullae are very large and well ossified, and the well-preserved glenoid facets jut out immediately lateral to the base of the bullae. They are level with the base of the bullae, but the skull is too broken to determine their relative height with respect to the tooth row or other skull landmarks. The distal ends of both glenoids are broken off, and there is no preservation of any of the rest of the zygomatic arch. The preservation of USNM 206190 is too poor to determine the state of most of the basicranial foramina. The occipital condyles are robust and widely flaring, with a large notch between them that merges with the foramen magnum.

In occipital view, USNM 206190 has a broad arcuate nuchal-lambdoid crest that rises very prominently in the dorsal direction, as in other species of *Perchoerus* (Fig. 7D). This nuchal crest is also constricted in the lateral direction just below its apex, making it appear even more prominent than in other mammals. There is a deep occipital fossa ("hollowed out area" of Pearson, 1923:67) in the dorsal part of the occiput just inside of the nuchal-lambdoid crests. There are rough "crests" in the area where the exoccipitals, supraoccipital, and basioccipital meet, although these may be due to the unfused sutures in this juvenile individual.

In lateral view, the high triangular and posteriorly protruding angle of the occiput is very apparent (Figs. 5, 7). So too are the prominent supraorbital processes and the bulging rounded braincase surmounted by the well-defined parasagittal and sagittal crests. Some of these features may be due to the juvenile nature of the specimen, but they are similar to the condition found in the adult specimens of *Perchoerus* described by Pearson (1923) and Scott (1940).

Discussion—Even though there are only fragmentary skulls and upper teeth known for this taxon in addition to the type lower jaw, it is clear that *Perchoerus minor* is a valid taxon applicable to the tiny peccary specimens found in various Chadronian deposits. This difference in size is not very striking in the teeth (Fig. 3), but it is quite apparent in the comparisons of overall size of the skull and jaws (Figs. 2, 7).

The oldest stratigraphically well-documented specimens of *P. minor* come from the Chadronian of Ledge Creek, Wyoming (Skinner and Gooris, 1966; Prothero, 1985; Prothero and Emry, 2004), which is now considered middle Chadronian (early Chron C15r, 35.5 Ma, *Leptomeryx mammifer* Zone of Prothero and Emry, 2004). There are also some specimens from the early Chadronian of northwestern Nebraska, but Cook's original locality data is not precise enough to tell from what level in the Chadron Formation they came. Some specimens also come from the early Chadronian Ahearn Member of the Chadron Formation in the Big Badlands of South Dakota. The oldest well-dated specimen (from Ledge Creek) is 35.5 Ma in age, although the Ahearn specimens probably are 36-37 Ma in age (Prothero and Emry, 2004:fig. 5.2). Thus, the immigration of the Tayassuidae into North America from Asia can be

pinned down to 35.5-36 Ma, but there is no evidence yet of any peccaries in the earliest Chadronian (36.5-37 Ma) *Bathygenys* Zone of Prothero and Emry (2004).

Now that these extremely small, early, and primitive *Perchoerus* specimens are better known, it would be valuable to compare them to their presumed sister taxa among the Asian Palaeochoeridae, and evaluate whether the Eurasian groups can really be assigned to the Tayassuidae as some have argued (see discussion in Wright, 1998, and Harris and Liu, 2007). Such a comparison, however, is beyond the scope of this paper.

Table 1. Dimensions and statistics of *Perchoerus minor* (in mm).

Measurement	N	Mean	Standard Deviation
Skull length, premaxilla to occiput	0	--	--
Skull length, canine to occiput	0	--	--
Occipital height	1	43	--
Skull width, posterior zygoma	1	50	--
Length, I1-M3	0	--	--
Width of palate at P2	0	--	--
Width of palate at M1	0	--	--
Length, canine to P3	0	--	--
Length, canine to M1	0	--	--
Length, M1-3	0	--	--
Length M1	3	9.9	1.1
Width M1	3	11.2	1.5
Length M2	1	11.7	--
Width M2	2	13.7	1.1
Length M3	1	11.3	--
Width M3	1	12.5	--
Length P1-M3	0	--	--
Upper canine length	0	--	--
Upper canine width	0	--	--
Length m1	2	11.2	0.3
Width m1	2	8.0	0.1
Length m2	4	12.1	0.9
Width m2	4	9.1	0.2
Length m3	5	15.6	1.0
Width m3	5	8.5	0.9
Length m1-3	1	3.8	--
Length p1-m3	1	65	--
Length canine-m1	0	--	--
Lower canine length	0	--	--
Lower canine width	0	--	--

Perchoerus nanus (Marsh, 1894)
Figs. 7-10, Table 2

Thinohyus nanus Marsh, 1894
Perchoerus nanus Hay, 1902
Perchoerus nanus Scott, 1940

Type specimen—YPM 11784, left ramus with p3-4, m1-3 (Fig. 8), from "Miocene of South Dakota, exact horizon not known." According to Scott (1940:503), Marsh referred to the White River Group as Miocene, so it is from an unknown level in the White River Group.

Referred specimens—LACM (CIT) 79/90, partial skull with left P3-M3, right P2-M3, and jaws with left p4-m3 and right p3-m3, from the lowermost "Oreodon beds" near the contact with the Chadron Formation, one mile west of the railway tracks, halfway between Horn and Orella, Nebraska, early

Orellan; AMNH 1200, lower jaw, *Metamynodon* channels, Big Badlands, Cheyenne River, SD (level unknown); YPM 14648, left m1-3, left m2 of another individual, Big Badlands, South Dakota (level unknown); YPM 14656, part of right ramus with p4-m3, Washington County, SD (level unknown); YPM 14654, right and left rami with p4-m3, Washington County, SD (level unknown); UCMP 36334, right and left maxillae with P4-M2, Chimney Canyon, Logan County, Colorado; YPM 10209, skull, from the White River Group, Sturgis, SD (level unknown); YPM-PU 10510, partial skull with P4-M3, "Oreodon beds," Big Badlands, SD, Orellan; YPM-PU 10511, left ramus with p4-m3, "Oreodon beds," Big Badlands, SD, Orellan; YPM-PU 12736, left and right rami, Cottonwood Pass, Big Badlands, SD, Orellan; F:AM 73731, skull and jaws, Big Badlands, SD, Orellan; YPM 1656, lower jaw, Big Badlands, SD, ?Orellan; FMNH P12152, skull and jaws, Big Badlands, SD, Orellan; FMNH PM23608, right M1-2 in maxilla fragment, Lower Nodular Zone, Big Badlands, SD, Orellan; FMNH PM41815, right M3, Lower Nodular Zone, Big Badlands, SD, Orellan; FMNH PM46421, right m2-3, Lower Nodular Zone, Big Badlands, SD, Orellan; FMNH PM46429, left jaw fragment, Lower Nodular Zone, Big Badlands, SD, Orellan; FMNH PM49164, right M3, Lower Nodular Zone, Big Badlands, SD, Orellan.

Diagnosis—medium-size species of *Perchoerus* (m1-3 length = 38-44 mm); distinguished from *P. minor* by its larger size, slightly larger teeth, and more elongate and complex hypoconulid on m3; distinguished from *P. probus* by its much smaller size, slightly smaller cheek teeth, trapezoid-shaped upper molars, much smaller M3 with a reduced metacone and posterior cingulum, and shorter m3 hypoconulid with more complex cusp patterns.

Description—Marsh's (1894:271) description of the type lower jaw (Fig. 8A) of *P. nanus* (YPM 11784) was very brief and uninformative, emphasizing only the size difference between this specimen and the much larger Whitneyan *P. probus*. Marsh (1894) did not illustrate YPM 11784, so Figure 8A is the first image of this material to appear in print. In addition to the type lower jaw, Scott (1940) and Pearson (1923) briefly described a partial upper skull, YPM-PU 10510, and another ramus, YPM-PU 10511 (Fig. 8B-C), which they referred to this species. Pearson (1923) noted that it was the "smallest *Perchoerus* that I have seen."

Since these publications, a number of additional small Orellan specimens of *Perchoerus* have turned up in collections that can be referred to *P. nanus* (see Referred Specimens above). The most important of these is a beautiful, nearly complete, skull with relatively unworn dentition, LACM (CIT) 79/90, with associated jaws that closely match the type of *P. nanus* in size (Figs. 7, 9, 10). This, along with the partial skull (YPM-PU 10510), provides the basis for greater understanding of the skull and upper dentition morphology of this species.

The skull of LACM (CIT) 79/90 (Fig. 9) is nearly complete except for the broken anterior end of the rostrum, and some breakage around the zygomatic arch and basicranium. Portions of the palate and maxillae have been restored in plaster, and there are numerous fractures throughout the skull that make it hard to determine the position of sutures or recognize foramina. In dorsal view, the skull has a very strong, elevated sagittal crest that runs from the nasal-frontal suture back to the elevated nuchal-lambdoid crest (Fig. 9A). The sagittal crest is relatively longer than in *P. probus* or *P. minor*, with much weaker development of the parasagittal crests that merge into the anterior end of the sagittal crest, as seen in other taxa. As in other specimens of *Perchoerus*, the supraorbital processes are triangular in dorsal view, and protrude out over the orbit. However, they are not as large, robust, or protruding as in *P. probus*, but more like the condition in *P. minor*. As in *P. minor*, the sagittal crest of LACM (CIT) 79/90 descends sharply and is demarcated by a distinct groove from the relatively small, bulbous braincase. This contrasts with the condition in *P. probus*, where the distinction between the braincase and sagittal crest is much less clear. There are several small supraorbital grooves and foramina in the frontals just above the orbit. The nasals and maxillaries of LACM (CIT) 79/90 are too damaged to reliably describe.

In occipital view (Fig. 7D), LACM (CIT) 79/90 bears the high nuchal-lambdoid crest characteristic of all *Perchoerus*, with a narrow constriction just below the apex of the nuchal crest and a deep occipital fossa beneath and inside the nuchal-lambdoid crests. Unlike the condition in *P. minor*, there is a simple suture where the exoccipitals and supraoccipital meet above the foramen magnum, with no additional crests or rugosities. There are two knob-like swellings where the exoccipitals meet above the foramen magnum.

In right lateral view (Fig. 9B), LACM (CIT) 79/90 has a large foramen between the lacrimal and the frontal and nasal (although this may be due to breakage, since it is not present in other skulls of *Perchoerus*). There is a small lacrimal process in the front of the orbit and a small lacrimal foramen within the anterior edge of the orbit. The lacrimal is dorsoventrally wider than it is long anteroposteriorly. The dorsal and ventral borders are parallel to one another, as in other *Perchoerus*. There is a distinct infraorbital foramen about 8 mm above the posterior root of P3. The posterior lip of this foramen is directed posterodorsally. The infraorbital foramen is in about the same position anteroposteriorly with respect to the tooth row as in other *Perchoerus*, but is situated much more ventrally and closer to the base of the teeth compared to *P. probus*. Only the jugal portion of the zygomatic arch is preserved, and the anterior part is also missing. The postorbital process of the jugal is not preserved. The lateral surface is parallel to the midline of the skull, and the anterior part slopes abruptly anteromedially to the surface of the maxillary. The arch has been warped downward posteriorly due to post-mortem distortion.

In palatal view (Fig. 9C), the right auditory bulla of LACM (CIT) 79/90 is broken and damaged, but the left shows the expanded bulla lacking cancellous bone inside, as seen in most other *Perchoerus*. The occipital condyles are large and robust, unlike the small thin rings found in *P. minor* and more like the condition in *P. probus*. The tympanohyal pit is impressed into the posterolateral corner of the bulla, as in other *Perchoerus*, but not as deeply. The base of the paroccipital process is present, but the tip is broken off. The glenoid fossa is higher than the plane of the cheek teeth and incisors, and posterior to the postorbital processes of the frontal. The glenoid fossa is broken laterally so that the condition of the preglenoid fossa cannot be determined. Most of the basicranial foramina (foramen rotundum, optic foramen, anterior lacerate foramen, hypoglossal foramen, condyloid foramen) are too broken to be seen in LACM (CIT) 79/90. However, the stylomastoid foramen can be seen immediately posterolateral to the tympanohyal pit, as in other *Perchoerus*. The post-glenoid process is 6 mm ventral to, and underhangs anteriorly the surface of the glenoid fossa. There is a ridge directed anteromedially from the post-glenoid process, not medially as in *P. probus*. The posterodorsal ridge that ascends from the tip of the postglenoid process would have probably reached the auditory process of the squamosal as in other *Perchoerus*, but it is broken and missing in LACM (CIT) 79/90. Thus, the dorsal extremity of the post-glenoid canal is missing as well. The ventral exit opens 4 mm medial and slightly anterior to the tip of the post-glenoid process, on the anteromedially-directed ridge between the post-glenoid process and the bullae. In most *P. probus*, this ridge is directed posteromedially, rather than anteromedially.

In the upper dentition (Fig. 9C), the front end of LACM (CIT) 79/90 is broken anterior to the base of the canines, so no incisors or their alveoli are present. The roots of the canines are preserved in their alveoli, but the canines themselves are too broken to even estimate their cross-sectional dimensions. The alveolus for P1 is preserved, but no tooth is present. P2 is a simple bladelike tooth with a strongly convex labial side and a distinct ridge on the lingual side running from tip to base. There is a small posterior cingulum, but no lingual or labial cingula. P3 is an anteroposteriorly elongate tooth that has a large triangular paracone with a faint labial cingulum. The anterior and posterior cingula on the paracone connect to a robust labial cingulum bearing a small posteromedial cusp in the protocone position. The tip of the paracone shows some wear, forming a small fossette or ‘lake,’ and there are indications that the cusp is slightly twinned from the wear pattern. P4, on the other hand, is short anteroposteriorly and wider labio-lingually than P3. There is a well-developed twinned cusp that probably represents a fused paracone-metacone, with two distinct wear fossettes at their tips. The protocone is much larger than in P3, and triangular in shape, and rises almost to the height of the paracone-metacone. There is a faint labial cingulum along the base of the paracone-metacone that merges with a strong posterior cingulum, which in turn wraps around to the labial base of the protocone. A ridge projects posteriorly from the apex of the protocone and connects with the posterior cingulum, forming two distinct basins: one between the paracone-metacone and the protocone, and one posterolingual to the protocone, enclosed by the posterior cingulum.

M1 is roughly trapezoidal in crown view, with a prominent paracone and a significantly smaller metacone. The paracone protrudes anterolabially from the crown of the tooth giving it the trapezoidal outline, rather than a simple rectangular outline as in most molars. The protocone and metaconule in LACM (CIT) 79/90 are highly worn, producing broad lake-like protolophs and metalophs that resemble

the condition in perissodactyls like *Mesohippus* and some rhinos. There is a well-developed labial cingulum on the metacone, but not on the paracone. There are no lingual, anterior, or posterior cingula. M2 is even more trapezoidal in crown view than M1, with a very large paracone protruding from the anterolabial corner of the tooth. The metacone is significantly smaller and in line with the long axis of the tooth; it bears distinct wear facets anteriorly and posteriorly. Although somewhat worn, there is a large protocone, with a distinct paraconule between it and the paracone, and a very large anterior cingulum. There is a large cusp in the hypocone position that is probably a metaconule, and an additional cusp between it and the metacone. Both of these cusps merge with a prominent posterior cingulum that wraps around to form a distinct labial cingulum.

M3 is much smaller than M2, and much smaller in relative proportions than the M3 of *P. probus* (it is unknown in *P. minor*). It also shows the peculiar trapezoidal shape, with the ectoloph oriented anterolabially, rather than parallel to the long axis of the tooth or the skull. The paracone stands alone on the anterolabial corner of the tooth. Lingual to it are a large paraconule and an even larger protocone, bordered by a strong anterior cingulum. The small metacone lies posteromedial to the paracone, and labial to it is another small cusp and a metaconule in the hypocone position. The lingual cingulum forms a bumpy cuspule-bearing ridge which merges with the metaconule, and then wraps around to form a large posterior cingulum with numerous small cuspules.

The mandible of LACM (CIT) 79/90 is badly broken (Fig. 10), but some of the cheek teeth are well preserved. In size and morphology, they compare closely with YPM 11784, the type of *P. nanus* (Fig. 3), such that it is reasonable to refer the associated skull with this taxon as well. There are a few incisor alveoli preserved in LACM (CIT) 79/90, but the symphysis is too badly broken for further description. There are broken roots for large lower canines, but the crowns are not preserved. The premolars and their alveoli are missing in a badly broken region if the mandible, so the only well-preserved teeth are p4-m3. The p4 is broken as well, but has a high crest that culminates in a high protoconid, and an anterior crest that wraps lingually and posteriorly from this cusp and presumably connects to the paraconid (which is now broken completely away). The hypoconid is much lower, and connected to the protoconid with a continuous ridge. A large conical metaconid sits in the center of the crown of the tooth, isolated from the paraconid-protoconid-hypoconid ridge by a deep valley.

The m1 of LACM (CIT) 79/90 is very worn, such that the trigonid and talonid are reduced to oval-shaped knobs with deep fossettes (as is typical of the m1 of most older peccary skulls). There is a vestige of the separation between the paraconid and protoconid and between the metaconid and hypoconid, so that the wear fossettes for each cusp forms a separate distinct oval. No cingula are visible, although the tooth may be too worn to determine whether or not they existed. The m2 is slightly less worn than the m1, and has a slightly larger more rounded talonid compared to its constricted trigonid. The paraconid is the highest cusp on the tooth, with a circular apical wear facet, whereas the much lower protoconid has a long oval-shaped wear facet. Both teeth have a very large posterior-facing wear surface formed by transverse occlusion of the upper cusps in the valley between the trigonid and talonid. No cingula are visible on m2. The m3 is the least worn molar, but its degree of wear still indicates that LACM (CIT) 79/90 was a relatively old individual. The paraconid and protoconid are large conical cusps, with the protoconid slightly more oval in occlusal view, and the paraconid completely circular. The protoconid has a small teardrop-shaped wear fossette on its posterior slope. The metaconid is slightly lower than the paraconid, with large flat wear facets on the anterolateral and posterolateral surfaces. It is not lined up with the hypoconid precisely parallel to the paraconid-protoconid axis and perpendicular to the long axis of the tooth, but instead is displaced slightly posteriorly toward the hypoconulid. The hypoconid is a low triangular-shaped cusp, with a small ridge on the lingual side that does not quite connect to the metaconid. A distinct ridge runs along the anterior edge of the talonid, connecting the metaconid and hypoconid, and separating the talonid from the trigonid; this ridge is covered by a series of small tubercles. The hypoconulid of the m3 on LACM (CIT) 79/90 is large and blunt and composed of a series of small cusps that wrap around the entire crest of the hypoconulid. The hypoconulid encloses a small pocket or valley in its interior. Compared to the m3 of *P. probus*, however, the hypoconulid of LACM (CIT) 79/90 is not nearly as long, so the entire m3 is not as elongate in *P. nanus* as it is in *P. probus*. However, the m3 hypoconulid of LACM (CIT) 79/90 is significantly longer than that of USM

372193 (referred to *P. minor*) or the type of *P. minor*, so it is intermediate in size and proportions between *P. minor* and *P. probus*.

Discussion—Comparison of LACM (CIT) 79/90 to other referred specimens of *P. nanus*, such as YPM-PU 10510, shows that they are nearly identical in size and in most details of the upper dentition. Both have clearly twinned cusps of the paracone-metacone on P4, a feature not seen as strongly developed on most specimens of *P. probus* (as originally noted by Scott, 1940:602). The upper molars of YPM-PU 10510 are not quite as trapezoidal in shape as those of LACM (CIT) 79/90, but this appears to be a minor individual difference. However, they do show a more trapezoidal shape than do the molars of *P. probus*. Both YPM-PU 10510 and LACM (CIT) 79/90 have a highly reduced M3, with a reduced metacone, compared to nearly all specimens of *P. probus*, which have a large M3 with a considerable area of cusps and crests on the posterior end.

Table 2. Dimensions and statistics of *Perchoerus nanus* (in mm).

Measurement	N	Mean	Standard Deviation
Skull length, premaxilla to occiput	0	--	--
Skull length, canine to occiput	1	113.0	--
Occipital height	1	57.0	--
Skull width, posterior zygoma	1	65.5	--
Length, I1-M3	1	65.6	--
Width of palate at P2	1	17.8	--
Width of palate at M1	1	20.0	--
Length, canine to P3	1	12.2	--
Length, canine to M1	1	28.0	--
Length, M1-3	4	35.8	4.4
Length M1	5	11.0	0.8
Width M1	5	11.3	2.3
Length M2	5	12.2	0.8
Width M2	5	11.4	2.3
Length M3	5	14.0	2.6
Width M3	5	11.8	2.6
Length P1-M3	1	58.0	--
Upper canine length	0	--	--
Upper canine width	0	--	--
Length m1	12	11.8	0.5
Width m1	12	8.9	3.0
Length m2	12	12.7	0.8
Width m2	12	10.2	3.0
Length m3	12	16.1	2.0
Width m3	12	9.4	2.7
Length m1-3	12	39.6	2.5
Length p1-m3	0	--	--
Length canine-m1	0	--	--
Lower canine length	0	--	--
Lower canine width	0	--	--

Perchoerus probus (Leidy, 1856)

Figs. 11-14, Table 3

Palaeochoerus probus Leidy, 1856
Perchoerus probus Leidy, 1869
Chaenohyus decedens Cope, 1879, 1888
Palaeochoerus subequans Cope, 1879
Hyotherium americanum Scott and Osborn, 1887
Bothrolabis subaequans Cope, 1888

Bothrolabis trichaenus Cope, 1888
Thinohyus robustus Marsh, 1894
Thinohyus decedens Sinclair, 1905
Thinohyus subaequans Peterson, 1905
Perchoerus trichaenus Cope and Matthew, 1915
Perchoerus subaequans Cope and Matthew, 1915
Perchoerus decedens Pearson, 1923
Perchoerus probus Scott, 1940

Type specimen—ANSP 10588, isolated jaw fragments (Fig. 11), from an unknown level in the White River Group.

Referred specimens—From the Whitneyan, White River Group, South Dakota and Nebraska: SDSM 2838, skull and jaws; AMNH 1282, adult skull; AMNH 585, juvenile skull; AMNH 695, juvenile skull; AMNH 9794, skull and jaws; AMNH 9813, skull and jaws; AMNH 9812, jaws; F:AM 73742, skull; FA:M 73722, skull; F:AM 73726, skull; F:AM 73762; skull; F:AM 73758, jaws; F:AM 73752, skull; F:AM 73725, skull; F:AM 73730, skull; F:AM 73721, skull and jaws; F:AM 73713, jaws; F:AM 73709, skull; F:AM 73745, jaws; F:AM 73744, skull; F:AM 73729, skull; YPM-PU 11131, skull; YPM-PU 11115, skull; YPM-PU 11021, skull; YPM-PU 10679, jaws; YPM-PU 12579, skull; YPM-PU 16442, skull; YPM 11990, skull; YPM 19048, partial lower jaw with p4-m2; YPM-PU 10146, skull and lower jaw, holotype of "*Hyotherium americanum*"; RAM 1683, skull. From the early Arikareean, John Day Formation, Oregon: UOMNH F 669, holotype of "*Chaenohyus decedens*"; UOMNH F 680, holotype of "*Palaeochoerus subaequans*"; AMNH 7390, holotype of "*Bothrolabis trichaenus*"; additional specimens in the JODA collections.

Diagnosis—Largest species of *Perchoerus* (m1-3 length = 44-49 mm); distinguished from *P. minor* by its larger size; distinguished from *P. nanus* by its much larger size, slightly larger cheek teeth, much larger M3 with a enlarged metacone and posterior cingulum, and longer m3 hypoconulid with more complex cusp patterns; distinguished from *Thinohyus* by its relatively brachycephalic, less robust skull, lacking diastemata.

Description—Nearly all well preserved material of *Perchoerus probus* was described in detail by Scott (1940:493-506) and Pearson (1923), and because few well preserved specimens have been found since then, no further description is necessary.

Discussion—Although the type specimen of *P. probus* (Fig. 11) is less than adequate, several additional specimens described by Leidy (1869) leave no question about the validity of the name. *Perchoerus probus* is the most common of all *Perchoerus* species, and most specimens come from the Whitneyan of the White River Group of South Dakota or Nebraska. A few specimens called "*Chaenohyus*" and *Thinohyus* from the John Day are also referable to this taxon (see below). In most cases, *P. probus* can be easily recognized by its relatively large but brachycephalic skull with no diastemata, and by the fact that it lacks the expanded robust skull dimensions of *Thinohyus*.

Now that there are relatively larger samples showing variability and clear criteria for recognizing this taxon, many of the other named tayassuid taxa from the White River and John Day groups are now assignable to *P. probus*. For example, Scott and Osborn (1887:155) briefly mentioned (but did not describe) a badly worn and broken skull from an unknown level in the White River Group as "*Hyotherium americanum*" (YPM-PU 10146). The type specimen is a partial skull missing the rostrum and anterior dentition, and retaining only a few worn molars on each side, plus part of the zygomatic arches and the braincase. Their descriptions and comparisons with other named taxa were inadequate. Based on the size of the teeth and skull, and on the limited diagnostic features due to the poor quality of the specimen, it seems clear that "*Hyotherium americanum*" is a junior synonym of *Perchoerus probus*.

Cope (1879:373) named the genus and species *Chaenohyus decedens* on the basis of a partial skull (UOMNH F669) from the Condon Collection (Fig. 12). It was collected from an unknown level "in the region of the John Day River." The type specimen consists of the anterior part of a skull preserving only highly worn P4-M3. The upper canine is missing, but a large alveolus suggests that it is from a robust male individual. Cope (1879, 1888) diagnosed *Chaenohyus* mainly on the presence of three upper

premolars and a diastema between P1 and P2. However, the type specimen is broken in the area of the premolars and diastema, and none of the premolars are preserved, such that only the P3 and P4 alveoli are clearly present (Fig. 12). There is a broken peg-like root of a tooth immediately behind the upper canine that probably represents P1, although it is too fragmentary to determine more. Thus, there is no clear evidence of any diastema between P1 and P2, nor of a count of three premolars, since the broken area on the specimen probably once contained P2, not a diastema. If so, then the specimen had P1-4 like most peccaries, and no diastema, and cannot be distinguished from *Perchoerus* on these features. Merriam (in Sinclair, 1905, p. 135) made similar observations and also concluded that *Chaenohyus* was invalid.

The rest of Cope's (1879, 1888) 'diagnostic characters' are highly variable, or now found in other peccaries besides *Chaenohyus*. Cope wrote that M1-3 were slightly more convex externally, but this is within the range of variation of most *Perchoerus*. He also thought the M1 was much smaller than M3 relative to other peccaries, but again this is within the range of variation of normal *Perchoerus*. Likewise, the presence of external tubercles and a labial cingulum on M1-3 are also found on *Perchoerus*. About the only feature mentioned by Cope is the relatively high-domed forehead and brachycephalic rostrum relative to other John Day *Thinohyus*, but this condition is found in a number of specimens of *Perchoerus probus (*e.g., SDSM 2838). Sinclair (1905) was more impressed by the brachycephaly of *Thinohyus decedens*, and referred additional specimens (UCMP 556, a skull; UCMP, associated mandible) to the taxon. However, he did not compare *Thinohyus decedens* to White River *Perchoerus probus*, but only to other John Day taxa. Thus, the type specimen of *Chaenohyus decedens* cannot be distinguished from the known range of variation of *Perchoerus probus*, and I regard Cope's taxon as a junior synonym.

A number of authors have wrestled with the affinities of *Chaenohyus*, or referred additional specimens that do not match the type of this taxon. Pearson (1923) recognized that it was referable to *Perchoerus*, but kept the species name as *Perchoerus decedens* without fully justifying how it could be distinguished from *P. probus*. Sinclair (1905) and Peterson (1905), on the other hand, referred it to *Thinohyus decedens*, even though it bears little resemblance to typical John Day *Thinohyus*; this assignment was followed by Albright (1999). A number of specimens in the Frick Collection were labeled "*Chaenohyus,*" although close inspection shows that they do not resemble the type specimen, and are simply White River *P. probus*. Wright (1998) considered *Chaenohyus decedens* to be *nomen dubium*, but the type specimen is complete enough that its assignment to *P. probus* is clear. Thus, it is now clear not only from the original Condon specimens, but also from recently collected material (e.g., several specimens from the JODA collections) that *Perchoerus* and *Thinohyus* co-existed in the Arikareean of Oregon.

In the same paper where he named *Chaenohyus decedens*, Cope (1879:374) erected the taxon "*Palaeochoerus subaequans*." In his 1888 paper, he transferred it to *Bothrolabis subaequans*. His type specimen (UOMNH P690) is a nearly complete skull and lower jaw (Fig. 13) from an unknown level in the John Day beds, also from the Condon Collection. It has relatively small canines, suggesting a female individual. Cope (1879, 1888) diagnosed "*Bothrolabis subequans*" based on its short muzzle, a rudimentary secondary lingual cusp on P1, and a number of other subtle features that are typical of *Perchoerus probus*, but he made no comparisons to the White River taxon. A close examination of the specimen (Fig. 13) shows that it falls within the known range of variation of *P. probus*. The skull is relatively brachycephalic, with no true diastemata between the premolars or canines. In dental and skull dimensions, it is completely within the range of *P. probus* as well. All other characters listed by Cope (1888, p. 66) are primitive features of *Perchoerus*, and not typical of *Thinohyus*, so they further support the synonymy of this taxon with *P. probus*. Later authors have had trouble deciding what to do with this taxon. Peterson (1905) reassigned it to *Thinohyus subaequans*, but did not justify how this assignment was made, other than its John Day provenance. Cope and Matthew (1915) assigned it to *Perchoerus subaequans*, but made no comparisons with *P. probus* or justify the distinctions between the two taxa. Wright (1998) considered it to be a *nomen dubium*, although the specimen is relatively complete and easily compared with other well-preserved taxa.

In his 1879 paper, Cope (1879:373) named *Thinohyus trichaenus*, which he transferred to *Bothrolabis trichaenus* in 1888. It was based on AMNH 7390, a partial maxilla and ramus (Fig. 14) from the John Day beds, with relatively large canines suggesting that it was a male individual. Cope (1888:66)

diagnosed it on the basis of supposedly smaller molars, single-rooted p4, and upper M3 with two rows of tubercles and a lingual tubercle at the end of the anterior valley. Closer examination of the specimen shows that the M3 is within the normal range of variation of *P. probus*, and the fact that it lacks any diastemata between the canines or premolars suggests that it has the primitive brachycephalic proportions of *Perchoerus*. Its tooth size also falls entirely within the broad range of variation of *P. probus* and *T. lentus*. The supposed distinctiveness of the M3 breaks down when comparing it to the wide range of variation of cusps and valleys in the M3s of most other *Perchoerus* and *Thinohyus*. Therefore, there are no diagnostic features in Cope's definition that justify the taxon. Pearson (1923:90) noted many of the same problems with diagnosing the taxon, but nonetheless retained *Perchoerus trichaenus*, as did Cope and Matthew (1915).

Table 3. Dimensions and statistics of *Perchoerus probus* (in mm).

Measurement	N	Mean	Standard Deviation
Skull length, premaxilla to occiput	5	192.4	18.7
Skull length, canine to occiput	5	121.2	9.5
Occipital height	5	65.8	6.4
Skull width, posterior zygoma	6	105.3	7.5
Length, I1-M3	8	116.9	12.5
Width of palate at P2	9	27.1	5.4
Width of palate at M1	9	26.5	4.8
Length, canine to P3	8	21.3	2.1
Length, canine to M1	9	40.3	3.8
Length, M1-3	18	43.3	3.3
Length M1	21	13.1	1.1
Width M1	20	13.0	1.8
Length M2	20	14.4	1.4
Width M2	18	14.6	1.5
Length M3	19	16.9	2.1
Width M3	18	14.3	1.4
Length P1-M3	9	84.6	9.7
Upper canine length	8	15.4	5.2
Upper canine width	7	8.1	1.9
Length m1	16	13.3	1.4
Width m1	15	9.4	1.4
Length m2	16	15.0	1.7
Width m2	15	11.2	1.4
Length m3	15	22.3	3.4
Width m3	14	11.4	1.8
Length m1-3	15	52.1	8.0
Length p1-m3	4	88.3	9.9
Length canine-m1	1	54.5	--
Lower canine length	3	9.8	2.0
Lower canine width	3	9.8	2.7

Thinohyus Marsh, 1875

Perchoerus Leidy, 1869 (in part)
Dicotyles Leidy, 1873 (non Cuvier, 1817)
Chaenohyus Cope, 1879 (in part)
Bothrolabis Cope, 1888 (in part)

Type species—*Thinohyus lentus* Marsh, 1875
Included species—*Thinohyus rostratus* (Cope, 1888)

Diagnosis—Larger peccaries (M1-3 length = 44-58 mm) with weak sagittal crests and relatively dolichocephalic skulls with robust occiput and zygomatic arches relative to *Perchoerus*; small to large diastemata between the canines and first premolars, and sometimes between P1/p1 and P2/p2; M3 with relatively large posterior cingulum and well developed postero-internal heel, resulting in more elongate tooth than M3 of *Perchoerus*.

Description—Most of the material was described by Marsh (1875), Cope (1888), and Sinclair (1905).

Distribution—Whitneyan-Arikareean, John Day Formation, Oregon.

Discussion—As detailed above, it seems clear that Marsh's taxon *Thinohyus* can be applied to the larger, more robust, more dolichocephalic specimens from the John Day Formation, since there is now a large topotypic sample that shows this morphology and its distinction from White River *Perchoerus*. Marsh's (1875) original description of the genus included the type species, *T. lentus*, plus YPM 11785, the type of "*Thinohyus socialis*." The latter specimen appears to be from the Barstovian Mascall Formation of Oregon, not the John Day Formation, and is reassigned to *Cynorca sociale* (Woodburne, 1969; Wright, 1998). Unfortunately, Marsh's type specimen of *T. lentus*, YPM 11783, is a badly broken juvenile skull with no rostrum preserved (Fig. 15); thus many of the diagnostic features here used to recognize *Thinohyus* cannot be determined. However, it does preserve the distinctive M3 (just barely erupted in the juvenile type specimen), thereby justifying the retention of Marsh's *Thinohyus lentus* for the larger John Day peccaries with the features outlined above.

Cope (1888) proposed the name *Bothrolabis* to include nearly all the John Day peccaries except *Chaenohyus*, refusing to even mention Marsh's (1875) taxon *Thinohyus* (although he did use that taxon in his 1879 paper). Included within *Bothrolabis* were "*B. trichaenus*" and "*B. subaequans*" (both here reassigned to *Perchoerus probus*), as well as "*B. pristinus*" and "*B. rostratus*." Sinclair (1905) pointed out that Cope's (1888:63) primary criterion for distinguishing "*Bothrolabis*" from "*Chaenohyus*" was that the former taxon retained the primitive upper premolar count of four (P1-P4), while the latter supposedly had only three upper premolars. As discussed above, this was due to the breakage of the type specimen of "*Chaenohyus decedens*," so there are no criteria for recognizing "*Bothrolabis*" other than primitive characters. The other characters used by Cope (1888), such as the oval versus triangular cross-section of the canines, or the deep fossa in the rostrum for the lower canine, have proven to be highly variable in these peccaries now that larger samples are available. Cope (1888) did not compare "*Bothrolabis*" to Marsh's (1875) *Thinohyus*, nor to White River *Perchoerus*. Most of the characteristics he used to recognize "*Bothrolabis*" are invalid since they appear in previously named taxa. Sinclair (1905) synonymized "*Bothrolabis*" with *Thinohyus*, but Cope and Matthew (1915) synonymized "*Bothrolabis*" with *Perchoerus*, as did Pearson (1923), and this synonymy has been followed ever since. Because there was much confusion as to whether *Thinohyus* could be distinguished, this decision is understandable. However, if *Thinohyus* is valid, as argued in this paper, and also by Stirton and Woodburne (1965), McKenna and Bell (1997), Wright (1998), and Harris and Liu (2007), then most of specimens once assigned to *Bothrolabis* must now be reassigned to *Thinohyus*, not *Perchoerus*.

Thinohyus lentus Marsh, 1875
Figures 15-18, Table 4

Dicotyles pristinus Leidy, 1873
Thinohyus lentus Sinclair, 1905
Thinohyus pristinus Sinclair, 1905
Thinohyus osmonti Sinclair, 1905
Perchoerus lentus Cope and Matthew, 1915
Perchoerus lentus Pearson, 1923
Perchoerus lentus Fremd et al., 1994
Thinohyus lentus Wright, 1998

Type specimen—YPM11783, broken juvenile skull with M3 erupting, rostrum missing, from an unknown level in the John Day Formation (Fig. 15).

Referred specimens—John Day Formation, level unknown: AMNH 7392, holotype of "*T. pristinus*"; AMNH 7894, skull, referred to "*T. pristinus*"; AMNH 7396, juvenile skull; UCMP 393, skull and jaws, holotype of "*T. osmonti*"; UCMP 1988, partial skull, referred to "*T. osmonti*"; YPM 10207, skull; YPM 14635, skull; YPM 14640, skull; YPM 14639, skull; additional material in the JODA collections.

Diagnosis—Smaller (M1-3 length = 44-51 mm), less robust, and less dolichocephalic species of *Thinohyus*, lacking the diastemata between P1/p1 and P2/p2.

Description—Fully described by Sinclair (1905).

Discussion—The majority of the John Day *Thinohyus* specimens in the collections can reasonably be referred to *T. lentus*. Most are known only from isolated teeth and jaws, although some skulls are quite well preserved. However, two other taxa require further discussion.

Thinohyus (*Bothrolabis*) *osmonti* (Fig. 16) was proposed as a new species by Sinclair (1905:138), and it was based on UCMP 393, a very well preserved skull with mandible. Sinclair also referred another skull fragment (UCMP 1988) to this taxon. In its overall size and dental dimensions, "*T. osmonti*" falls completely within the typical range of *T. lentus* as defined here (Fig. 17, 18). It has a well-developed diastema between P1/p1 and P2/p2, as well as a diastema between P1/p1 and the canines. The canines in the type specimen are large and robust, indicating a male individual, which likely explains the well-developed sagittal crest. Although the M3 has a large posterior cingulum, the posterointernal cusp on that cingulum is not as well developed as in most *Thinohyus*. Nevertheless, in nearly every other feature, it is a good match for the large sample of *Thinohyus lentus* now found in the collections of the UCMP, JODA, AMNH, and YPM.

Thinohyus rostratus
Fig. 19, Table 4

Bothrolabis rostratus (Cope, 1888)
Thinohyus rostratus Sinclair, 1905
Perchoerus rostratus Cope and Matthew, 1915
Perchoerus rostratus Pearson, 1923

Type specimen—AMNH 7395, a complete skull from an unknown level in the John Day Formation.

Referred specimens—YPM-PU 10788, skull and mandible, from the John Day Formation.

Diagnosis—Largest species of *Thinohyus* (M1-3 length greater than 52 mm), with the most robust skull, occiput, and zygomatic arches, and the most extreme dolichocephaly; well developed diastemata between P1 and P2, as well as between canine and P1.

Description—Previously described by Cope (1888), Sinclair (1905), and Pearson (1923).

Discussion—As most authors have noted, AMNH 7395 stands out among all the John Day peccaries in its unusually large size and robustness (Fig. 19). This cannot be attributed to sexual dimorphism, because AMNH 7395 is notably larger and more robust than presumed male skulls such as AMNH 7394 (referred to "*T. pristinus*") and UCMP 393 (type of "*T. osmonti*"). On almost every skull measurement (Figs. 17, 18), it stands out as disjunctly larger and more robust. Even more surprising, it is the only John Day tayassuid specimen that falls outside the normal range of variation of dental dimensions of *T. lentus* and *P. probus* (Fig. 17). Although I am philosophically opposed to retaining most of the oversplit taxa within this group, the unusual size and especially the unusually large teeth of this specimen (particularly given the normally conservative dental features of this group) argue for its species-level distinction. In support of this, the coefficients of variation of dental dimensions for most of the *T. lentus* material from the John Day Formation are only in the range of 3-6, typical for a single species. Adding AMNH 7395 to the sample increases the CV to 8-10, too high for a single species (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974). The same is true of the skull dimensions. Thus, based on the present sample, I retain *Thinohyus rostratus* as a separate species until additional material falsifies this conclusion.

Table 4. Dimensions and statistics of *Thinohyus lentus* and *T. rostratus* (in mm).

Measurement	N	Mean	Standard Deviation	*T. rostratus*
Skull length, premaxilla to occiput	6	227.4	23.4	255.0
Occipital height	4	78.0	4.7	78.0
Skull width, posterior zygoma	5	107.0	13.8	131.0
Length, I1-M3	5	143.0	3.0	152.0
Width of palate at P2	7	28.8	2.7	28.5
Width of palate at M1	8	27.2	3.4	29.0
Length, canine to P3	6	28.0	3.6	29.0
Length, canine to M1	6	48.2	7.2	37.0
Length, M1-3	12	44.7	2.2	55.5
Length M1	12	13.0	0.7	13.0
Width M1	12	12.3	0.8	--
Length M2	12	15.1	0.9	14.0
Width M2	9	13.3	1.4	--
Length M3	11	17.2	1.5	16.0
Width M3	11	13.4	1.8	12.0
Length P1-M3	4	86.4	4.1	--
Upper canine length	5	27.2	5.0	--
Upper canine width	5	8.5	0.9	--
Length m1	5	13.3	0.9	--
Width m1	5	8.7	0.5	--
Length m2	4	15.0	0.7	--
Width m2	4	10.2	0.9	--
Length m3	5	21.6	2.1	--
Width m3	5	11.1	1.3	--
Length m1-3	5	49.9	4.1	--
Length p1-m3	3	9.9	3.7	--
Length canine-m1	2	55.4	0.1	--
Lower canine length	3	27.8	8.4	--
Lower canine width	3	9.9	1.4	--

A NOTE ON *PERCHOERUS "GRACILIS"*

Specimen labels attached to YPM-PU 10510 and 10511 indicate that they represent the 'type' specimen of *Perchoerus* "*gracilis*." However, I have found no description or formal establishment of this species in the literature, except for a brief mention of the name in a caption in Scott (1940:739, caption for Plate LII), where the name appears twice. However, in his main text Scott (1940:501) never mentions the species, and notes only three valid species of *Perchoerus*: *P. minor* Cook from the Chadronian, *P. nanus* Marsh from the Lower Brule, and *P. probus* Leidy from the lower and upper Brule. Perhaps *P.* "*gracilis*" was a manuscript name that Scott (1940) chose not to use in the final version of the paper, but persisted in the captions to Plate LII. There appears to be no instance of any other author using the name, although it is still found on the original Princeton labels, with no modifications since those fossils were acquired by YPM. As noted above, these specimens are now referred to *P. nanus*.

Dicotyles pristinus was proposed by Leidy (1873) based on AMNH 7392, a fragmentary jaw bearing the left p3-m3 (Fig. 20). The taxon was reassigned to *Bothrolabis pristinus* by Cope (1888), then to *Thinohyus pristinus* by Sinclair (1905), and finally to *Perchoerus pristinus* by Cope and Matthew (1915) and Pearson (1923). Although the type is AMNH 7392 (see Cope and Matthew, 1915, Plate CXI, number 2), Cope (1888) and Pearson (1923) also referred AMNH 7394, a nearly complete skull (Fig. 19, center specimen), to Leidy's taxon, and most subsequent discussion has focused on this specimen, which may or may not be a good match for Leidy's type. Most of the diagnostic features of the taxon "*pristinus*" mentioned by Cope (1988), Sinclair (1905), and Pearson (1923) are based on AMNH 7394, and not on the type specimen.

Close inspection of AMNH 7392 shows that it has very little in the way of diagnostic features, and its size range is entirely within the variation of *T. lentus*. It may indeed be a good match for AMNH 7934, but that cannot be established based on the present material. Thus, the name "*pristinus*" is probably a *nomen dubium*, or possibly a synonym of *T. lentus*. At present, I will follow the former solution, since formal synonymy with *T. lentus* would make the inadequate holotype of "*pristinus*" the senior name for the species.

CONCLUSIONS

Despite the long confusion over their systematics, there are at least three distinct species of the White River peccary *Perchoerus*: the very primitive, tiny Chadronian *Perchoerus minor* Cook, 1922; the slightly larger early Orellan *P. nanus* Marsh, 1894; and the much larger and more robust Whitneyan *P. probus* (Leidy, 1869). This difference in size and robustness is striking in the skull dimensions, but only slightly apparent in the size of the teeth. *Perchoerus* can be distinguished from John Day specimens of *Thinohyus lentus* in the former's much smaller and less robust skull dimensions (but not in the cheek teeth), in the brachycephalic skull morphology, and in lacking the distinctive posterior cingulum on M3 and the canine-first premolar diastema of *T. lentus*.

Although a great number of names have been applied to John Day peccaries, I recognize only three taxa as valid: Marsh's (1875) *Thinohyus lentus* (senior synonym of *T. osmonti*), the unusually large, robust and larger-toothed *T. rostratus*, plus a number of taxa referable to *Perchoerus probus*, including "*Chaenohyus decedens*," "*Hyotherium americanum*," and "*Bothrolabis trichaenus*." These latter specimens confirm that *P. probus* occurred not only in the Northern Great Plains, but also in the John Day region of the Pacific Northwest during the Whitneyan and Arikareean.

As noted by Lucas (1992), the appearance of peccaries could be used as one of the indicator taxa distinguishing the Duchesnean from the Chadronian North American Land Mammal ages. The earliest well-dated specimens of *P. minor* are from the early Chadronian *Leptomeryx yoderi* Zone (35.5-36.5 Ma), but no peccaries have yet been reported from the earliest Chadronian *Bathygenys* Zone (36.5-37.0 Ma) of Prothero and Emry (2004). Thus, the immigration of the Tayassuidae does not mark the very beginning of the Chadronian (as now defined), but the beginning of the early Chadronian *Leptomeryx yoderi* Zone.

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FIGURES

Figure 1. Comparison of typical skulls of *Thinohyus lentus* (YPM 10207, larger specimen) and *Perchoerus probus* (YPM 11990, smaller specimen) showing differences in the overall skull size and proportions, and the development of the longer rostrum (dolichocephaly) and canine-first premolar diastema of *Thinohyus*. Although the skulls are markedly different in these features, the teeth are nearly identical in size (see palatal view). **A**, dorsal view; **B**, lateral view; **C**, palatal view; scale bar in cm.

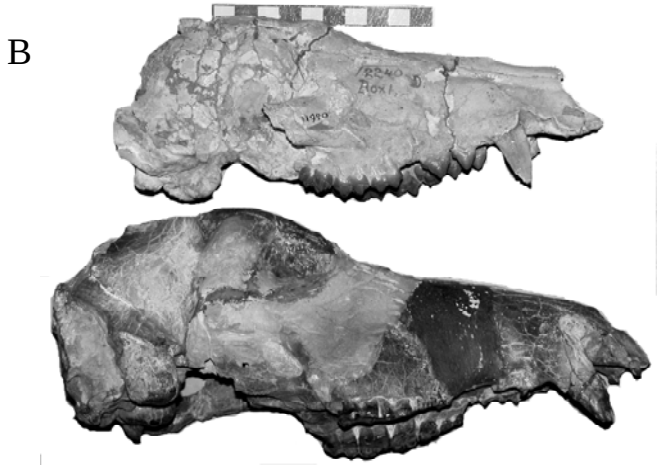


Figure 2. **A**, Plot of maximum skull width versus skull height for specimens of *P. minor* (gray square), *P. nanus* (solid triangle), *P. probus* (solid diamonds), and *Thinohyus lentus* (open circles); **B**, Plot of maximum skull width versus tooth row length from canine to M3, a proxy for diastema length. Note that specimens of *T. lentus* (open triangles) are much longer (even for the same overall skull size, as indicated by skull width) due to their canine-first premolar diastemata than specimens of *P. probus* (solid diamonds). *P. nanus* (gray square) is significantly smaller still.

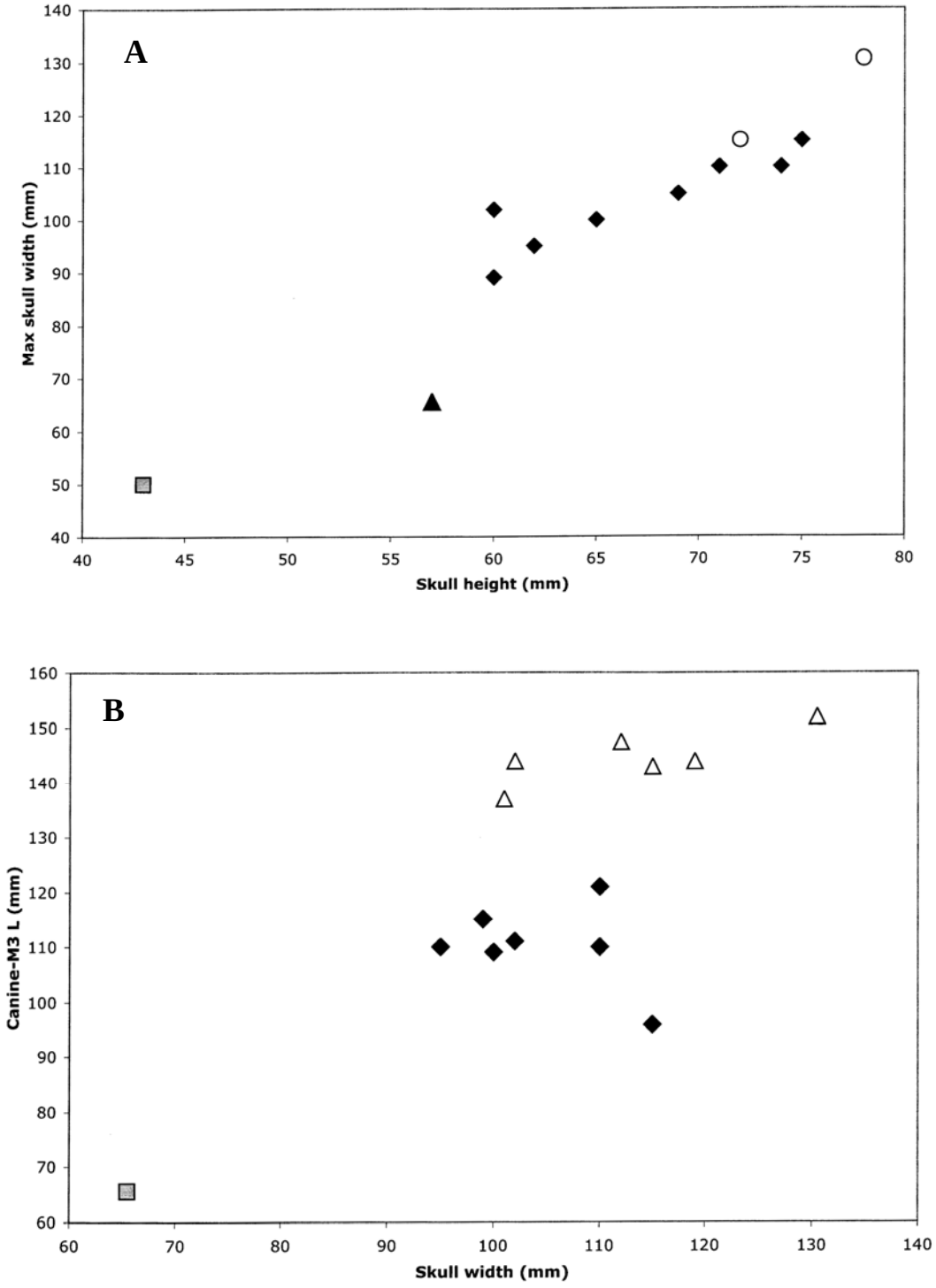
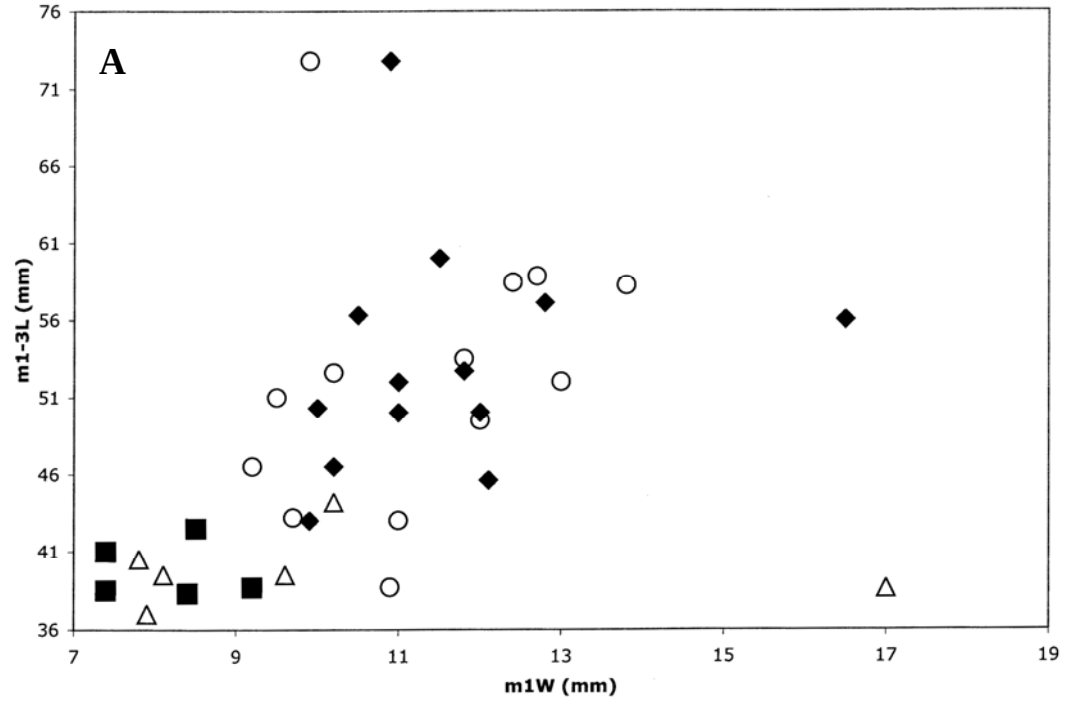


Figure 3. **A**, Plot of m1 width versus m1-3 length for specimens of Eocene-Oligocene peccaries. There is almost no separation in dental dimensions between *P. minor* (solid squares) and *P. nanus* (open triangles), and considerable overlap in the tooth size of *P. probus* (solid diamonds) and *T. lentus* (open circles); **B**, Plot of m3 length versus m3 width showing similar overlap in tooth size between *P. minor* (gray squares), *P. nanus* (open triangles), and the separate size cluster for *P. probus* (solid diamonds).



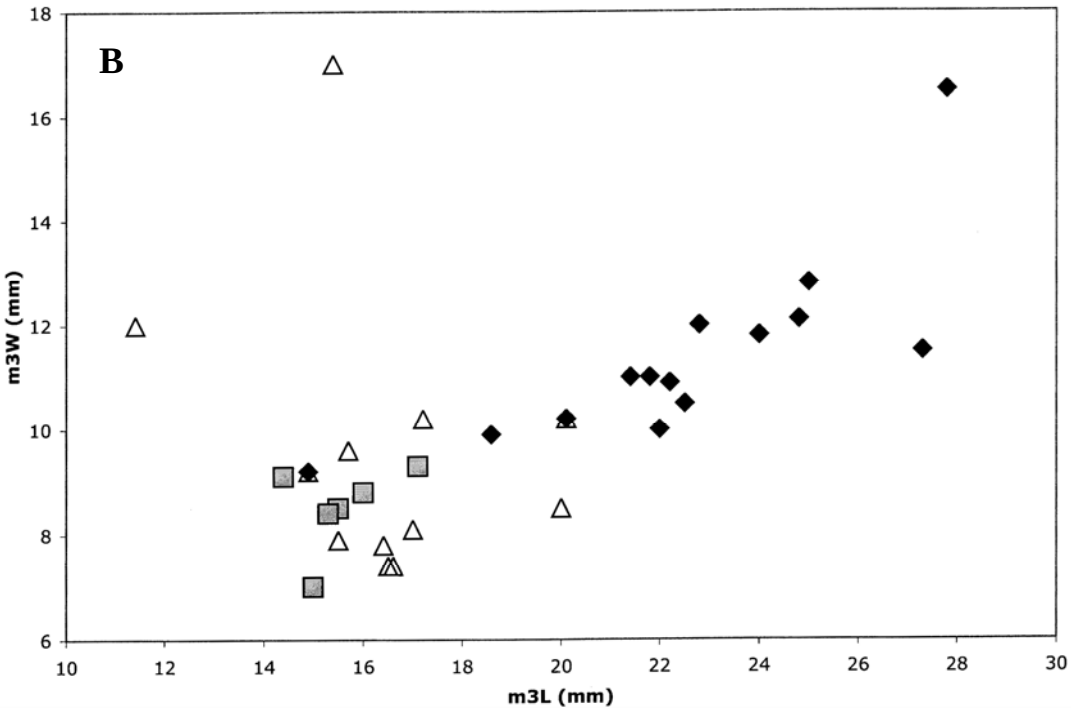


Figure 4. Type specimen of *Perchoerus minor* Cook, AMNH 86222. **A**, lateral view of left ramus; **B**, lateral view of right ramus; **C**, occlusal view. Scale bar in cm. (Photo courtesy M. Mihlbachler).

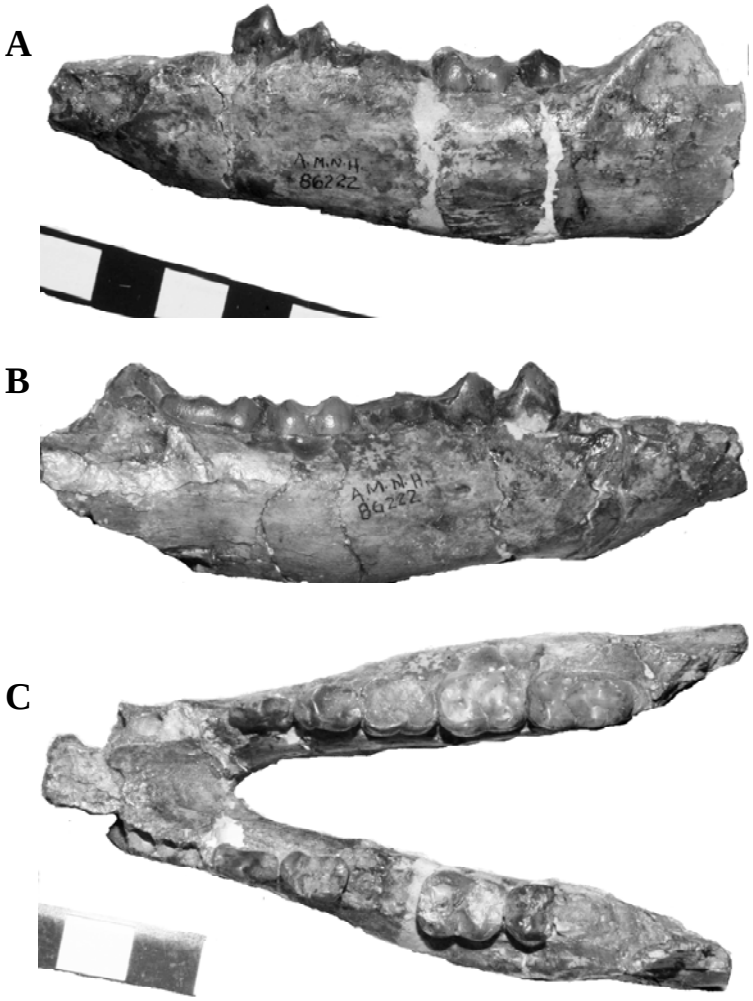


Figure 5. USNM 206190, partial skull of *P. minor* from the Ledge Creek locality, with detached maxillae. **A**, dorsal view; **B**, lateral view. Scale bar in cm.

Figure 5 (continued). USNM 206190, partial skull of *P. minor* from the Ledge Creek locality, with detached maxillae. **C**, ventral view (same scale as A and B); **D**, maxillae in crown view (see scale bar).

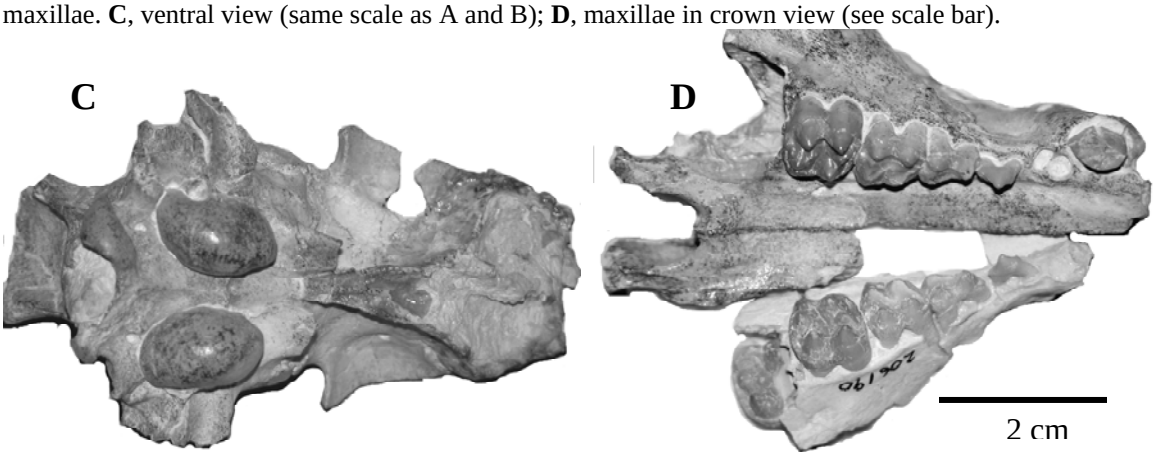


Figure 6. USNM 372193, partial ramus of *P. minor*, in lateral and occlusal views. Scale bar in cm.

Figure 7. Comparison of the skulls of *P. minor* (left, smallest specimen, USNM 206190) with *P. nanus* (middle specimen, LACM 79/90) and *P. probus* (largest specimen, LACM 17485), showing the dramatic differences in size and robustness. **A**, dorsal view. Scale bar in cm.

Figure 7 (continued). Comparison of the skulls of *P. minor* (smallest specimen, USNM 206190) with *P. nanus* (middle specimen, LACM 79/90) and *P. probus* (largest specimen, LACM 17485), showing the dramatic differences in size and robustness. **B**, lateral view; **C**, Palatal view; **D**, Occipital view. Scale bar in cm.

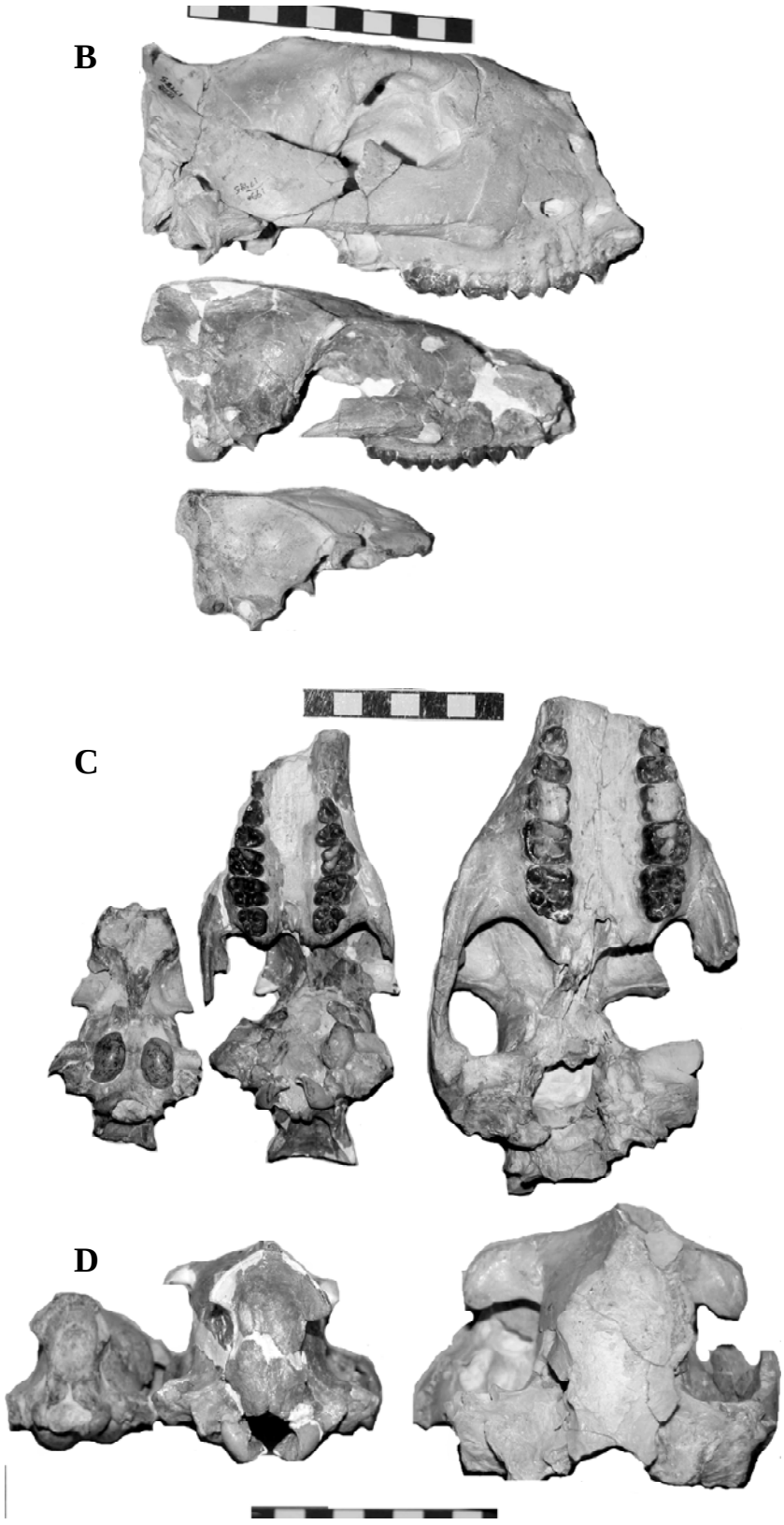


Figure 8. **A**, type specimen of *P. nanus*, YPM 11784; **B-C**, lateral and crown views of referred specimen of *P. nanus*, YPM-PU 10511, contrasted with a referred specimen of *P. probus*, YPM 10679. Black and white cm scale bar for B and C.

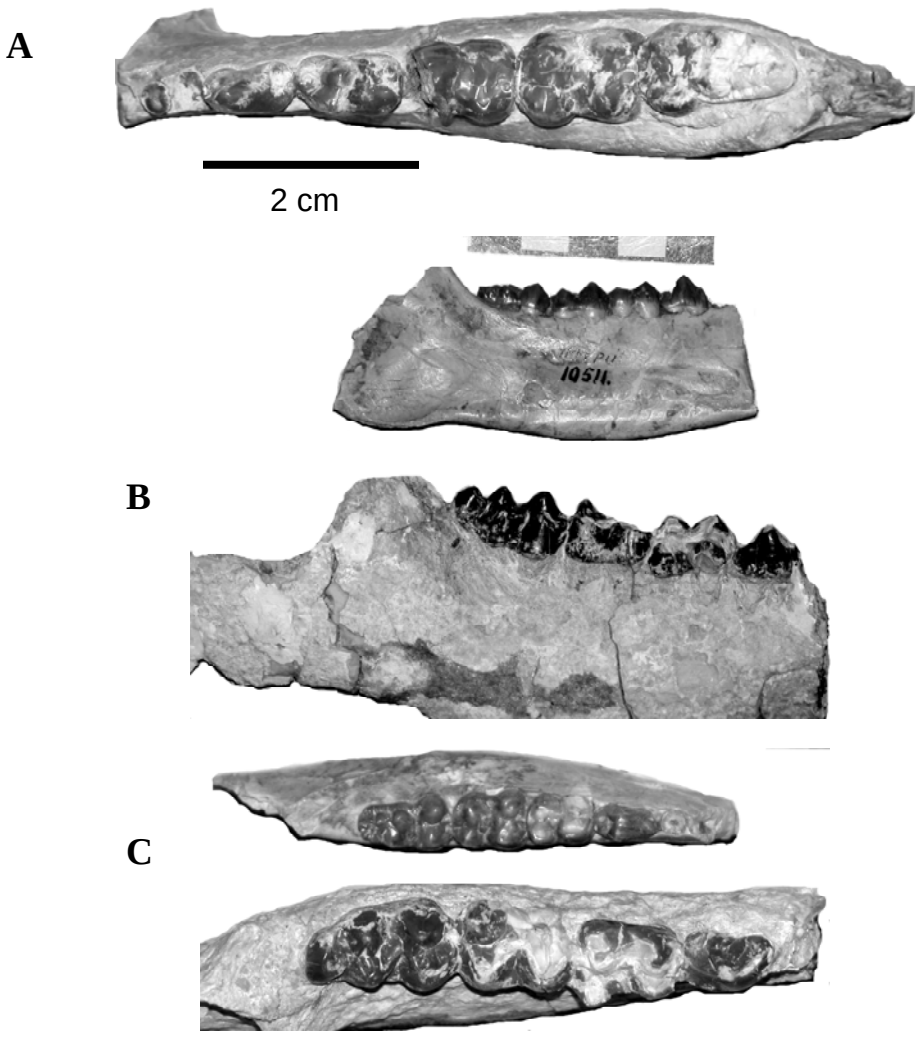


Figure 9. Referred skull of *P. nanus* [LACM (CIT) 79/90] in **A**, dorsal view. Scale bar in cm.

Figure 9 (continued). Referred skull of *P. nanus* [LACM (CIT) 79/90] in **B**, lateral, and **C**, palatal views. Scale bar in cm.

Figure 10. LACM (CIT) 79/90, referred mandible of *P. nanus* in lateral and occlusal views. Scale bar in cm.

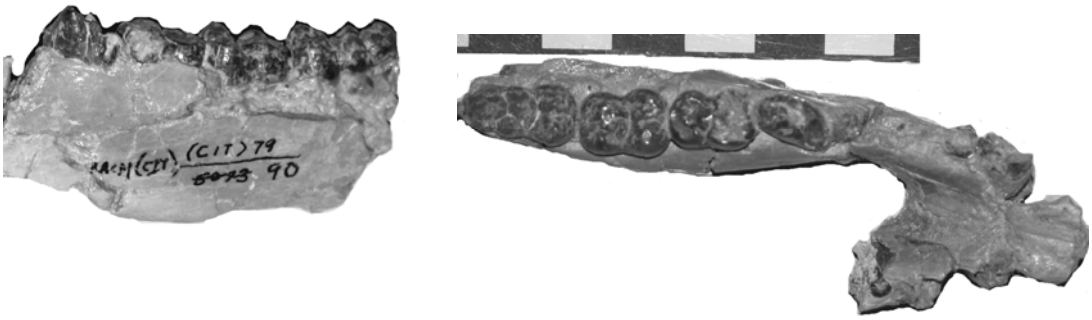


Figure 11. Holotype specimen of *Perchoerus probus,* ANSP 10588. (Stereo photo courtesy T. Daeschler).

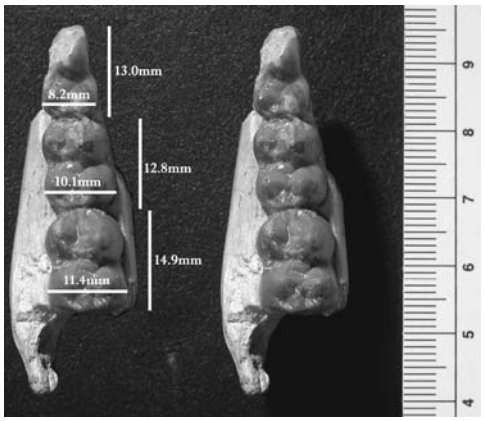


Figure 12. Type specimen of "*Chaenohyus decedens*" (UOMNH F669) (After Cope and Matthew, 1915, plates CX and CXI).

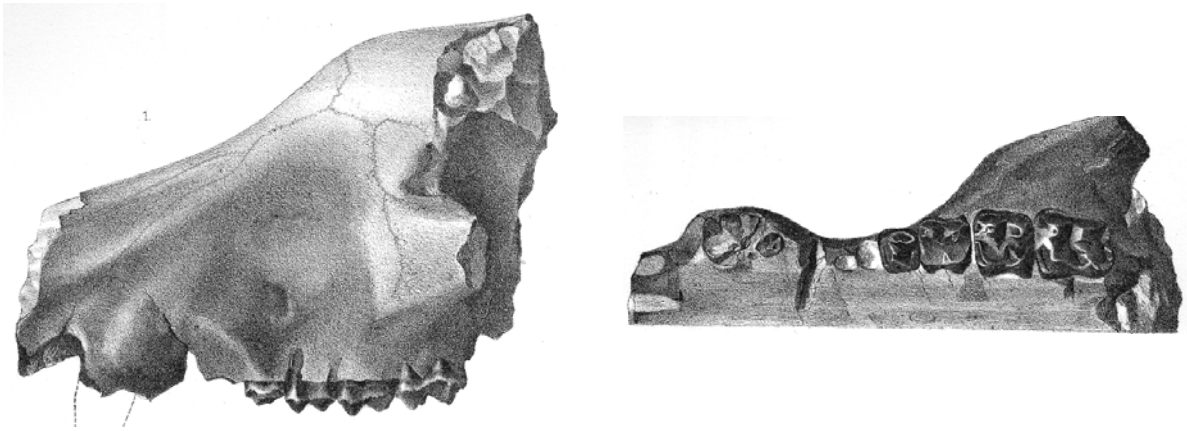


Figure 13. Type specimen of "*Palaeochoerus subaequans* (UOMNH F690) in lateral view, dorsal, and occlusal views (after Cope and Matthew, 1915, plate CX, fig. 1).

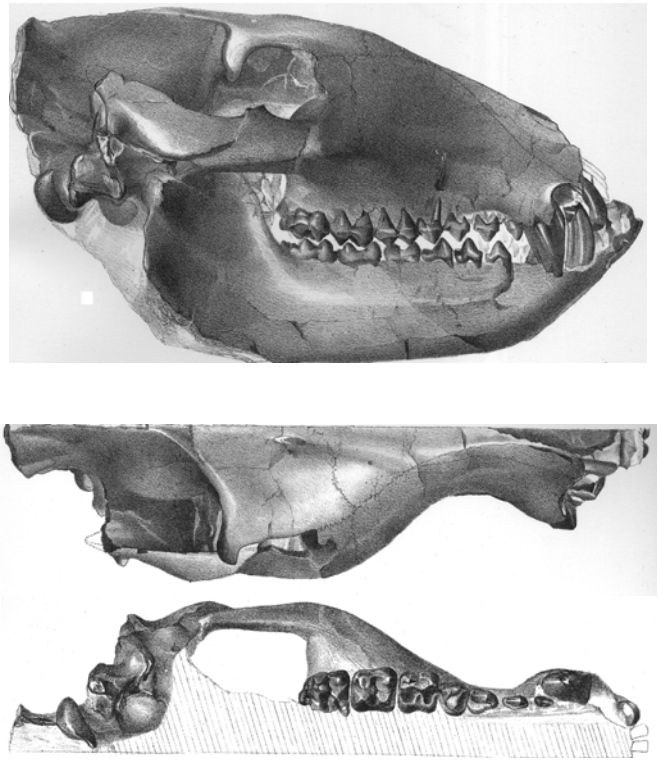


Figure 14. Type specimen of "*Thinohyus trichaenus*" (AMNH 7390). (after Cope and Matthew, 1915, plate CX).

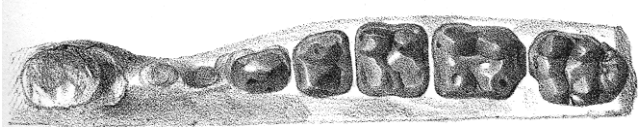


Figure 15. Type specimen of *Thinohyus lentus* (YPM 11783), palatal, dorsal, and lateral views. Scale bar in cm.

Figure 16. Type specimen of "*Thinohyus osmonti*" (UCMP 393) in **A**, lateral, and **B**, palatal, views. Scale bar in cm.

Figure 16 (continued). Type specimen of "*Thinohyus osmonti*" (UCMP 393) in **C**, dorsal view, and **D**, lateral view of mandible. Scale bar in cm.

Figure 17. Plot of M1-3 length vs. M3L of *Thinohyus*. Solid circles = referred specimens of *T. lentus*; open circle = *T. "osmonti"* holotype; x = "*C. decedens*"; open triangle = "*T. trichaenus*" holotype; open diamond = "*T. pristinus*" referred skull; solid square = *T. rostratus* holotype.

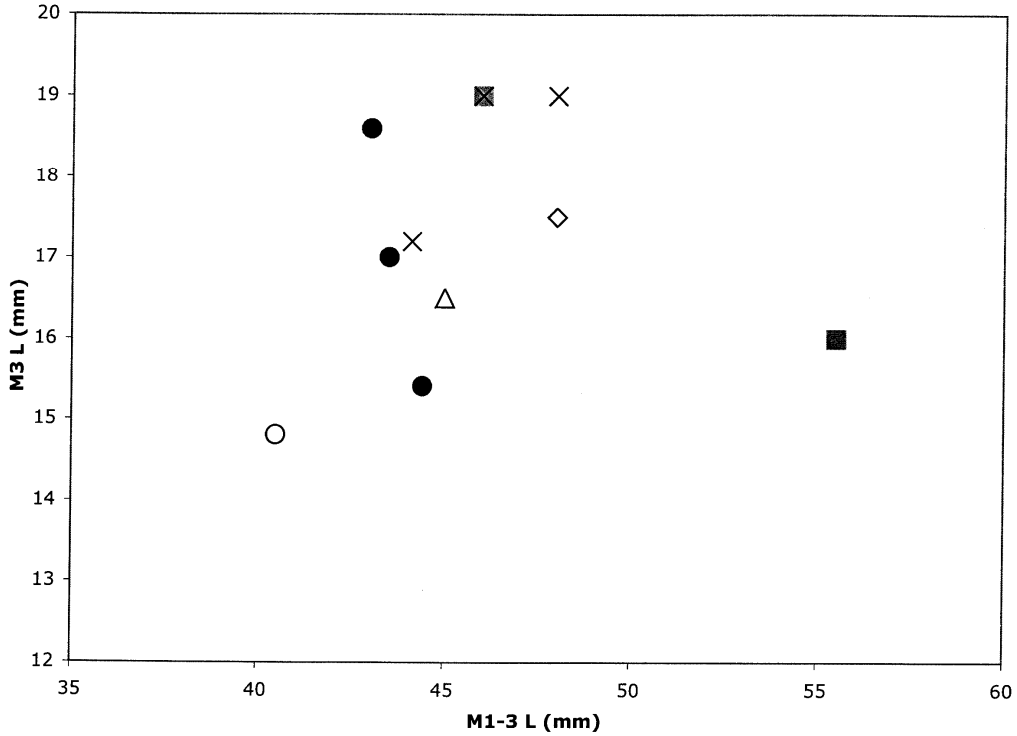


Figure 18. Plot of total skull length vs. width of palate at P2 of specimens of *P. probus* and various taxa referred to *Thinohyus*. Solid circles = referred skulls of *T. lentus*; open diamonds = referred skulls of *P. probus*; x = "*C. decedens*"; x with vertical slash = "*T. osmonti*" holotype; solid square = referred skull of "*T. pristinus*"; open diamond = *T. rostratus*.

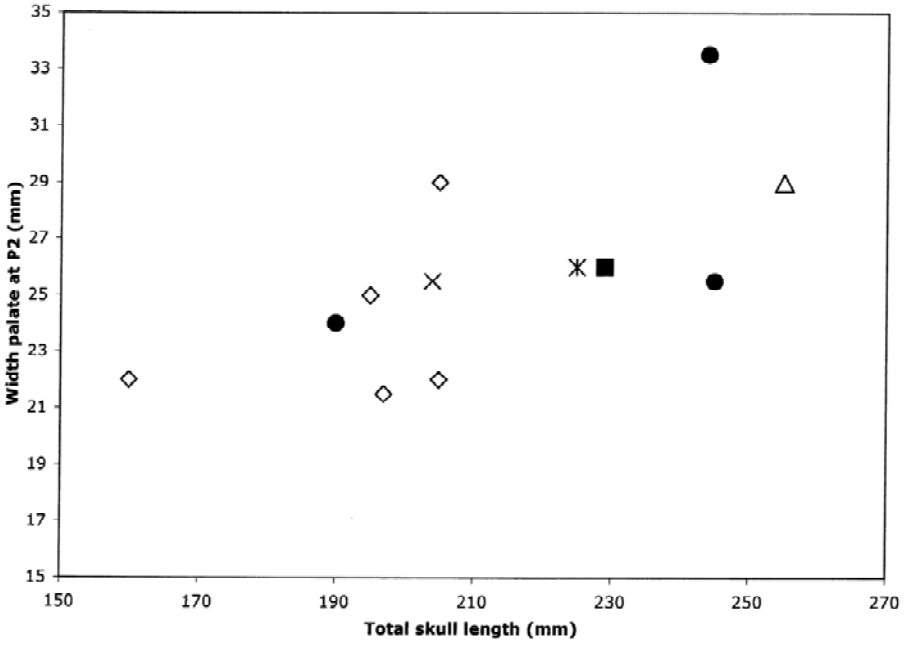


Figure 19. Holotype specimen of *T. rostratus* (AMNH 7395, largest specimen) compared to *T. lentus* (referred skull of "*T. pristinus*", AMNH 7394, medium-sized specimen) and *P. probus* (F:AM 73725, smallest specimen). Dorsal views.

Figure 19 (continued). Holotype specimen of *T. rostratus* (AMNH 7395, largest specimen) compared to *T. lentus* (referred skull of "*T. pristinus*", AMNH 7394, medium-sized specimen) and *P. probus* (F:AM 73725, smallest specimen). Ventral views.

Figure 20. Type specimen of "*Dicotyles pristinus*" Leidy, 1873 (AMNH 7392). (After Cope and Matthew, 1915, plate CXI, fig. 2).