

## A NEW GENUS OF HESPERHYINE PECCARY (ARTIODACTYLA: TAYASSUIDAE) FROM THE LATE OLIGOCENE OF OREGON

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**Abstract**—*Thinohyus* *osmonti* was based on a nearly complete skull and jaws (UCMP 393) found in the upper John Day beds (upper Oligocene) of Oregon, and named by W.J. Sinclair in 1905. Since its discovery, it has been transferred from one primitive peccary genus to another (*Thinohyus*, *Bothrolabis*, *Perchoerus*), without a careful examination of the excellent fossils. It is not referable to *Thinohyus* from the John Day beds, since it has a much more advanced skull, with a narrow rostrum and shallow facial vacuities, not the convex conical rostrum found in *Thinohyus* and more primitive peccaries. It was assigned to that genus only because its teeth are the same size and it came from the same beds. Careful re-examination of the skull shows that it has the diagnostic plesiochoanal fossa found only in the newly recognized subfamily Hesperhyinae, as well as other derived characters of that group. It is a relatively primitive member of that group (in the same trichotomy as *Stuckyhyus siouxiensis* and *Floridachoerus olseni*) consistent with its temporal placement in the late Arikarean. It belongs in a new genus, here designated *Fremdohyus*.

### INTRODUCTION

In 1905, William J. Sinclair described a skull and jaws (UCMP 393; Fig. 1) collected in 1899 from the “*Diceratherium* beds, Middle John Day, West side of the John Day Valley, about six miles north of Clarno’s Ferry, Gilliam County, Oregon” (Sinclair, 1905, p. 138). This locality is currently UCMP locality 839, called Black Rock 3 in the UCMP catalogue, and considered to be Arikarean in age. Another specimen from this expedition (UCMP 1988) is a skull fragment with a partial palate, which was collected at UCMP locality 892, McCallister’s Ranch, “about 150 feet above the top of the Lower John Day” (also Arikarean). These are the only known specimens of *T. osmonti* so far identified. Sinclair provided a brief description and a single figure (Fig. 1), and since then the taxon has almost been forgotten. Few later authors mentioned the taxon, and it appears only briefly in the Fossilworks page (Alroy, 2016) for the Paleobiology Database (PBDB) without any comment on its validity, except to list long-invalid taxa such as “*Bothrolabis rostratus*” and “*Bothrolabis (Thinohyus) decedens*” as its sister taxa. The site does not mention that Prothero (2009) synonymized “*Bothrolabis (Thinohyus) decedens*” with *Perchoerus probus*, and that “*Bothrolabis rostratus*” is now *Thinohyus rostratus*, the largest valid species of *Thinohyus*.

In his review of the fossil Tayassuidae, Wright (1998) did not mention “*T. osmonti*” at all, and only gave a brief discussion of *Thinohyus* and *Perchoerus*. Prothero (2009) provided a complete revision of *Thinohyus* and *Perchoerus*, dealt with the invalid wastebasket genera *Bothrolabis* and *Chaenohyus*, and updated the taxonomy of the valid and invalid species in those genera. At that time, Prothero (2009) did not see much difference between *T. (B.) osmonti* and *T.*

*lentos*, because the size of the specimen was within the normal range of John Day *Thinohyus*. The differences only became apparent when Prothero (2015) revised the hesperhyine peccaries, and recognized that features found in the hesperhyines were also preserved in “*T. osmonti*”. Wright (1991, 1998) first defined these hesperhyine synapomorphies but apparently he never saw the Berkeley specimens of “*T. osmonti*”.

### METHODS

I examined all the relevant materials in the American Museum of Natural History, New York, NY (AMNH), the University of California Museum of Paleontology, Berkeley, CA (UCMP), University of Nebraska State Museum, Lincoln, NE (UNSM), and the Yale Peabody Museum, New Haven, CT (YPM). All specimens were measured by dial calipers, and data were plotted in Excel spreadsheets. Photos were edited in Photoshop by E. Prothero. Figure 2 shows the terminology of the upper and lower teeth employed in this paper. Figure 3 shows a diagram of the nasal and choanal region of a typical hesperhyine.

### SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus 1858

Order Artiodactyla Owen 1848

Family Tayassuidae Palmer 1897

Subfamily Hesperhyinae Prothero, 2015

*Fremdohyus* new genus

Figs. 1, 4-7

*Thinohyus (Bothrolabis)* Sinclair 1905 (in part)

*Thinohyus (Bothrolabis)* Merriam and Sinclair 1907

**Type and only species:** *Fremdohyus osmonti* (Sinclair, 1905)

**Diagnosis:** Small hesperhyine peccary with well-developed plesiochoanal fossa, fused pterygoids, narrow orbito-maxillary fossa, long, narrow, concave rostrum with shallow facial vacuities. Distinguished from most other hesperhyines by its small size, but larger than *Marshochoerus socialis* (formerly “*Cynorca sociale*”).

**Etymology:** In honor of Theodore Fremd, for his years of untiring work on the John Day fossil beds, especially the peccaries.

**Redescription:** Sinclair (1905) provided a brief description, but neglected most of the important features that are significant for tayassuid systematics today, so it is necessary to redescribe the taxon.

UCMP 393 (Figs. 1, 4, 6) is a remarkably well-preserved skull and associated mandible, with only a few parts missing or restored with plaster. As Sinclair (1905, p. 138) noted, in lateral view (Fig. 4A) the dorsal profile of the skull is relatively flat, especially compared to the arched profile of *Thinohyus* and many other peccaries. There is a shallow facial fossa behind the maxillary-premaxillary suture. There is also a very shallow preorbital fossa. There may be a small foramen above the P4 just below the facial fossa, but it is difficult to tell due to the breakage of the specimen.

The zygomatic arch (partially restored in plaster) has a large



FIGURE 1. Sinclair’s (1905) original illustration of UCMP 393.

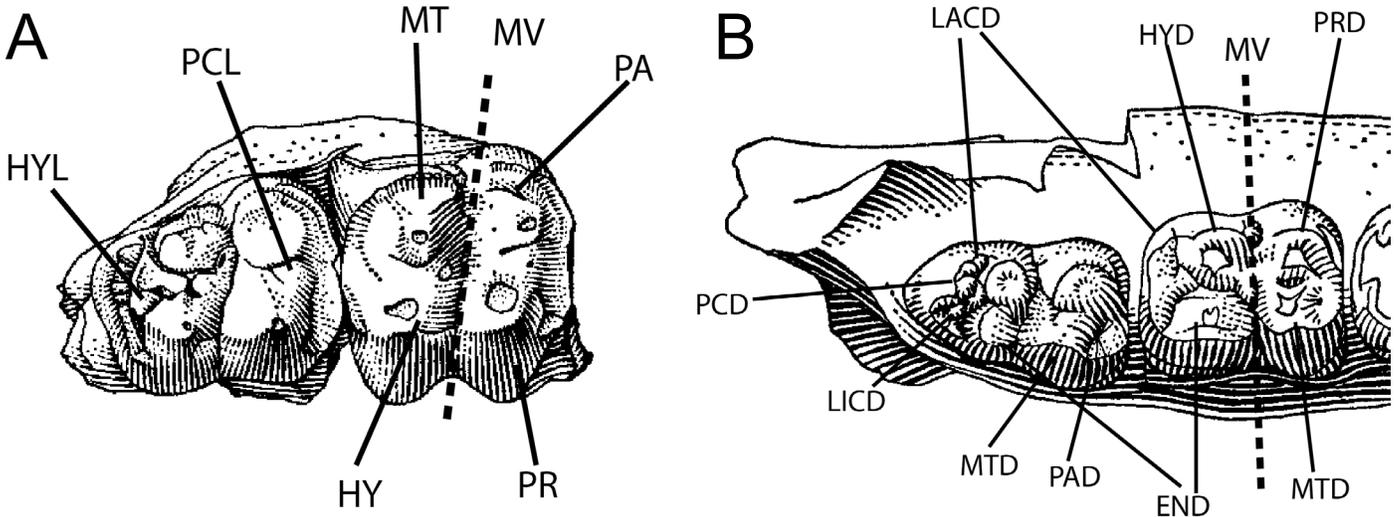


FIGURE 2. Typical peccary molars showing the dental terminology employed in this paper. **A**, holotype right M2-M3 of *Marshochoerus socialis* (after Woodburne, 1969 Fig. 1B). **Abbreviations:** HY= hypocone; HYL = hypoconule; MT = metacone; MV = median valley; PA = paracone; PCL = paraconule; PR = protocone. **B**, "*Cynorca*" *occidentale*, left m2-3, USNM 22927 (after Woodburne, 1969, Fig. 6B): END = entoconid; HYD = hypoconid; LACD = labial cingulid; LICD = lingual cingulid; MTD = metaconid; MV = median valley; PAD = paraconid; PCD = postcingulid; PRD = protoconid.

ventrolateral process on the jugal portion of the arch. The maxillary is very rugose anterior to the base of the jugal arch. A large, triangular-shaped postorbital process curves down from the top and posterior of the orbit, and a similar ventral, triangular-shaped postorbital process rises up from the zygomatic arch behind the orbit. The lacrimal region of the skull is badly broken, so it is difficult to assess any foramina in the orbit or lacrimal region. The braincase is relatively narrow, and there is a robust sagittal crest rising from the top of the braincase, forming a convex arch in lateral view (Fig. 4A). The posterior portion of the zygomatic arch is robust, with a large process that rises anterodorsally from the back end of the zygoma.

In dorsal view (Fig. 4B), the narrow rostrum is apparent, with the shallow facial vacuities on each side. There are large canine buttresses on each side, correlated with the large canines in UCMP 393. These usually indicate male individuals in peccaries. As Sinclair (1905, p. 139) noted, there is a large convex swelling on either side of the median line between the orbits on the frontal bone, which encloses a deep trough that extends anteriorly to the supraorbital foramina. The supraorbital processes are large and rugose, extending lateral to the orbit. The frontal region is slightly concave and forms a diamond-shaped area between the supraorbital ridges, and the parasagittal ridges, which then merge into a sharp sagittal crest.

In posterior view (Fig. 4C), the large parasagittal ridges on the frontal and parietal above the braincase merge into the prominent sagittal crest. The sagittal crest then splits into a large, curved lambdoid crest, arching above the occiput. The large, rugose postorbital processes are also striking in posterior view. Much of the posterior part of the occiput and zygomatic arch is broken and distorted, but its heavy,

rugose nature is still apparent.

In ventral view, the skull of UCMP 393 (Fig. 4D) shows some breakage and distortion, but most features (other than sutures) are well preserved. The rostral part of the skull is long and narrow, with an arched palate. The rostrum narrows posterior to the canine buttresses. Some of the palatine and premaxillary sutures are still visible, although most are obscured by breakage. The distinctive plesiochoanal fossa (shown in closer detail as "PCF" in Fig. 4E) is well developed, with a medial ridge surrounded by shallow curved vacuities around it. Some of the neochoanal fossa ("NCF" in Fig. 4E) is also preserved, although its posterior part is broken. Most of the pterygoid ridge is broken, but a portion of the fused pterygoids can still be seen. There is also a narrow orbito-maxillary fossa ("OMF" in Fig. 4E) lateral to the plesiochoanal fossa and immediately posterior to the tooth row (Fig. 4E). The rugose areas of the ventral border of the narrow zygomatic arches are also conspicuous in ventral view (Fig. 4D). Large glenoid fossae and robust postglenoid processes are also visible. Large bony auditory bullae are preserved, but most of the braincase and ear region is too badly broken for interpretation. The basioccipital region is also badly broken up, although the occipital condyles are well preserved. The ventral view (Fig. 4D) also shows how much the sagittal and lambdoid crests overhang the posterior part of the occiput.

The upper incisors (Figs. 4A-B) are partially broken, but as Sinclair (1905, p. 139) noted, the I1 has a broader crown than I2 or I3. I2 is completely broken, but its cross-section shows that it was a relatively small tooth. I3 is long and laterally compressed, with a fairly long pointed crown (Fig. 4A). There is a long diastema between I3 and the upper canines. The upper canines are very large (Table 1), probably indicating that UCMP 393 represents a male individual.

The upper canines are oval in cross-section near the base, but become triangular in cross-section near the crown, due to the flat posterior facet for occlusion with the lower canines. P1 (or probably a retained dP1) is a short, simple conical tooth with two roots, separated from the upper canine and P2 by short diastemata. These diastemata are a derived character in more advanced peccaries, and not found in *Thinohyus*, *Perchoerus*, or more primitive taxa, in which the posterior border of the canine partially overlaps the P1 (or dP1). P2 (Fig. 4A, D) is a larger, two-rooted blunt blade-like tooth, with no diastema between it and the P3. It has a faint lingual cingulum on the posterior part of the tooth. P3 (Fig. 4D) has an oval-shaped crown, with a broad, rounded anterior cusp (worn into having different fossettes on each side), and a prominent transverse posterior crest, largely formed by wear.

The crowns of P4-M3 of UCMP 393 (Fig. 4E) are deeply worn and almost featureless, but a slightly less worn dentition is seen in UCMP 1988 (Fig. 5). P4 has a prominent paracone and metacone forming a labial crest. The P4 protocone has a crest that curves posterolabially and merges with the posterior cingulum. The posterior cingulum forms a "Y"-shaped juncture with this crest; the other arm of the "Y" curves

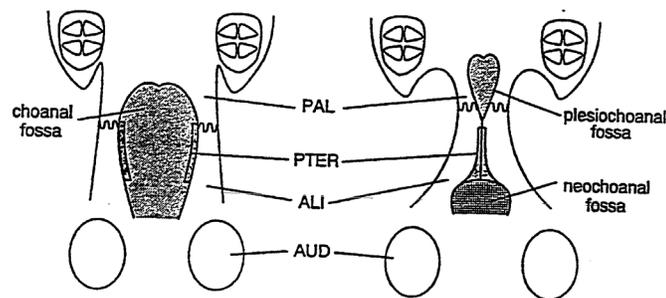


FIGURE 3. Comparison of a primitive tayassuine palate and choanal region (left) with the derived condition in hesperhyines (right). **Abbreviations:** ALI = pterygoid process of alisphenoid; AUD = auditory bulla; PAL = palatine; PTER = pterygoid. (after Wright, 1991, fig. 10).

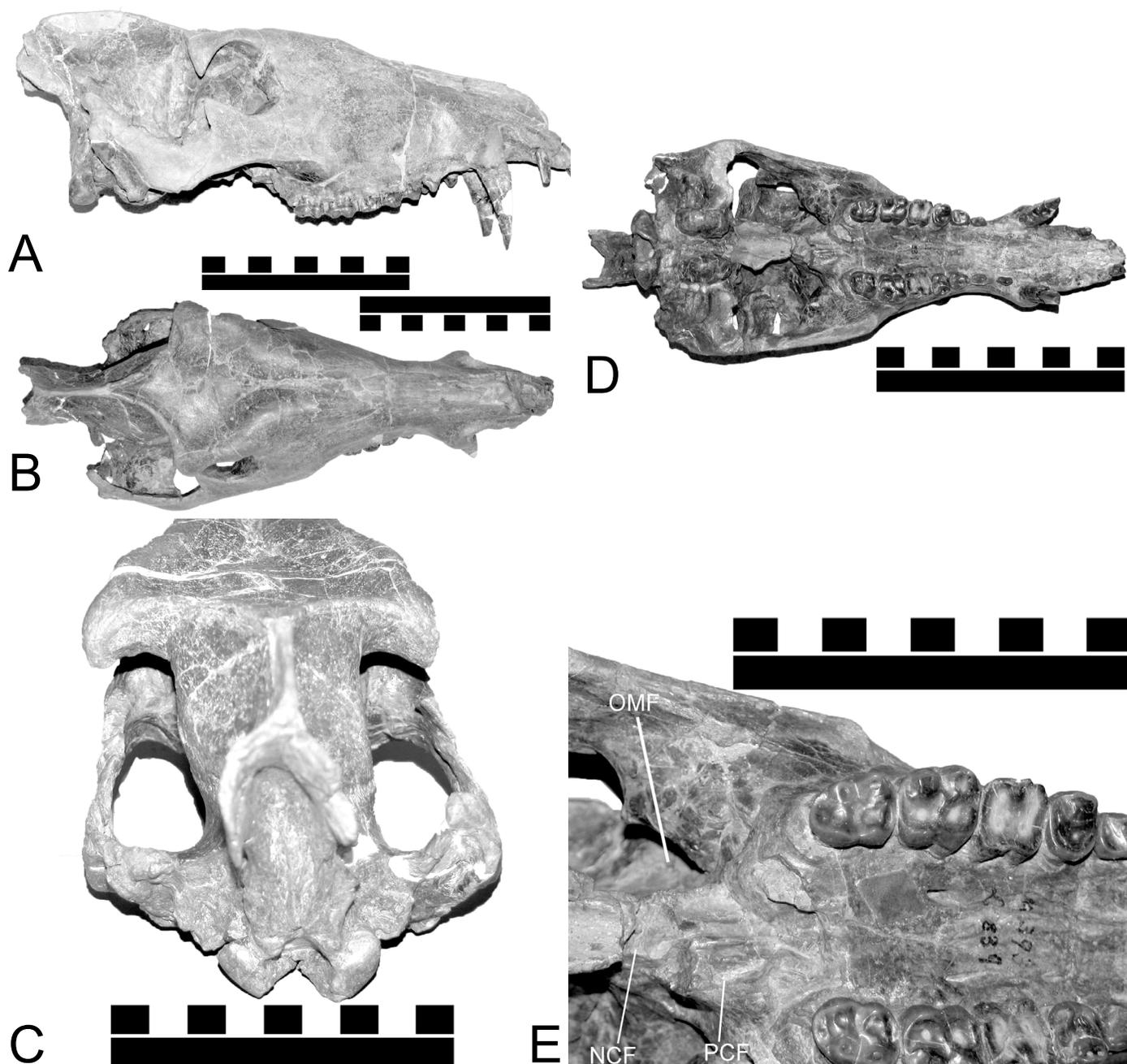


FIGURE 4. *Fremdohyus osmonti*, UCMP 393, holotype skull. **A**, right lateral view. **B**, dorsal view. **C**, posterior view of occiput. **D**, ventral view. **E**, detail of cheek teeth and choanal region. **Abbreviations:** OMF = orbito-maxillary fossa; NCF = neochoanal fossa; and PCF = plesiochoanal fossa.

down on the lingual cingulum. There is also a faint labial cingulum. In both UCMP 393 and UCMP 1988, the M1 is very worn, so only the broad fossettes can be seen where the four cusps would have been in an unworn tooth. In UCMP 1988, M2 has well developed paracones and metacones, although the tip of metacone has been worn into a fossette. The large protocone and hypocone are deeply worn, so they have teardrop-shaped fossettes that trend from the anterolateral to the posterolabial part of the tooth. There is a well-developed anterior cingulum, and a weak posterior cingulum. In UCMP 1988, the M3 is barely worn. The prominent paracones and metacones have strong wear facets on their anterior and posterior faces. As in the M2, the protocone and hypocone of the M3 are deeply worn, so they have oval-shaped fossettes on their crowns. There is a strong anterior cingulum on the M3, and a very prominent rugose posterior cingulum, with many small cusplules. All the upper premolars and molars have distinct labial cingula, but no lingual cingula.

UCMP 1988 (Fig. 5) also preserves a portion of the post-palatine

part of the skull. The plesiochoanal fossa is not as deep on this specimen as it is on UCMP 393, but it is still present. The well-developed medial ridge in the center of the plesiochoanal fossa is prominent, as it is in UCMP 393. The anterior part of the neochoanal fossa is preserved, together with the anterior part of the fused pterygoids. A narrow but distinct orbitomaxillary fossa can be seen on both sides of the back of the palatine region. The rest of the specimen is broken off posteriorly, as is the part of the skull anterior to the P4, and most of the dorsal roof of the skull.

In lateral view (Fig. 6A), the mandible is roughly the same depth from p2 to m3, but it tapers anteriorly. The long, narrow symphysis is inclined at about a 30° angle to the base of the jaw. There are mental foramina on the lower part of the mandible just below the m1, although they are distorted by breakage. Behind the tooth row on the lateral side of the jaw, there is a prominent masseteric ridge and deep masseteric fossa for the jaw muscles. The back part of the jaw is badly broken and partially restored in plaster, but there seems to be a small angular



FIGURE 5. UCMP 1988, referred partial skull and palate of *F. osmonti* in ventral view.

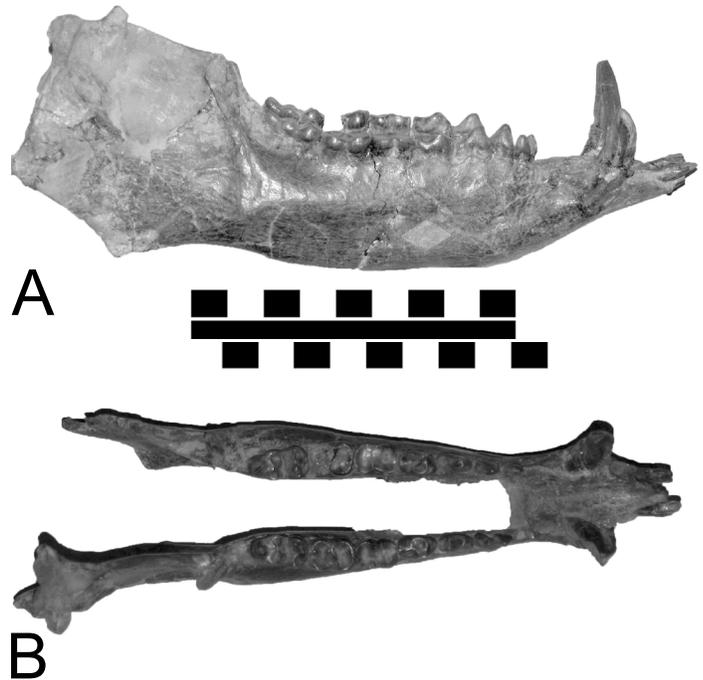


FIGURE 6. *Fremodohyus osmonti* UCMP 393, holotype mandible. **A**, right lateral view. **B**, crown view.

process. The coronoid process and the articular process are too broken to ascertain their shapes.

The lower incisors are all inclined anteriorly parallel to the slope of the symphysis. They are cylindrical teeth with oval wear fossettes on the posterior part of their crowns. The crowns of both first lower incisors are broken off. The lower canines are large and triangular in cross-section, with a strong medial ridge on the external face, and a large wear facet on the posterior side that occluded with the upper canines. There is a long diastema behind the lower canines, but no diastemata between the rest of the lower cheek teeth. The p1 (or dp1) is a simple blunt blade-like cusp, with two roots. It is slightly recurved. The p2 is a larger blade-like cusp, also with two roots. The p3 has a larger blade-like cusp or ridge, with a weak talonid heel. The p4 (Fig. 6B) has a prominent ridge on the trigonid between the protoconid and paraconid, and a ridge curving down from the metaconid down to an antero-posterior ridge in the middle of the talonid. Most of the talonid is badly worn, so very little can be determined of the details of its cusps.

As in the upper molars, the lower molars of UCMP 393 are extremely worn, so very little cusp morphology is left. The m1 is almost completely worn down to the roots and pulp cavity, so there are

large fossettes for the trigonid and talonid, and no cusps left. Likewise, the m2 is almost completely worn down to fossettes for the trigonid and talonid, except for a small cusp in the posterior rim of the talonid fossette. The m3 is less completely worn, so the cusps of the trigonid are still visible, but their tips are worn down to a pair of fossettes for the paraconid and protoconid, and another for the metaconid and entoconid. The talonid has a large heel in the hypoconulid position, with the top worn off to form a large posterior crest surrounding the basin of the hypoconulid.

**Distribution:** Arikareean of the John Day Formation, Oregon.

**Discussion:** Sinclair (1905) only compared UCMP 393 to other John Day specimens he referred to *Thinohyus*, such as *Thinohyus (Bothrolabis) decedens* (now assigned to *Perchoerus probus*—Prothero, 2009), which was published in the same paper in the pages immediately before *Thinohyus (Bothrolabis) osmonti*. At that time, and until 2009, nearly all John Day peccaries were thrown into a wastebasket taxon usage of *Thinohyus*. Prothero (2009) restudied the best material of *Thinohyus* in the YPM and AMNH, redefined *Perchoerus* and *Thinohyus*, and established which species of *Thinohyus* were valid. It was clear at the time that *Thinohyus (Bothrolabis) osmonti* was much



FIGURE 7. Comparison of *F. osmonti* (center) with *Thinohyus lentus* (AMNH 7394) on the right, and UNSM 60604, holotype of *Wrightohyus yatkolai* on the left. *F. osmonti* has the narrow, gracile rostrum with a shallow facial vacuity typical of hesperhyines like *Wrightohyus*, and very different from the convex conical snout of *Thinohyus*. **A**, right lateral view. **B**, dorsal view.

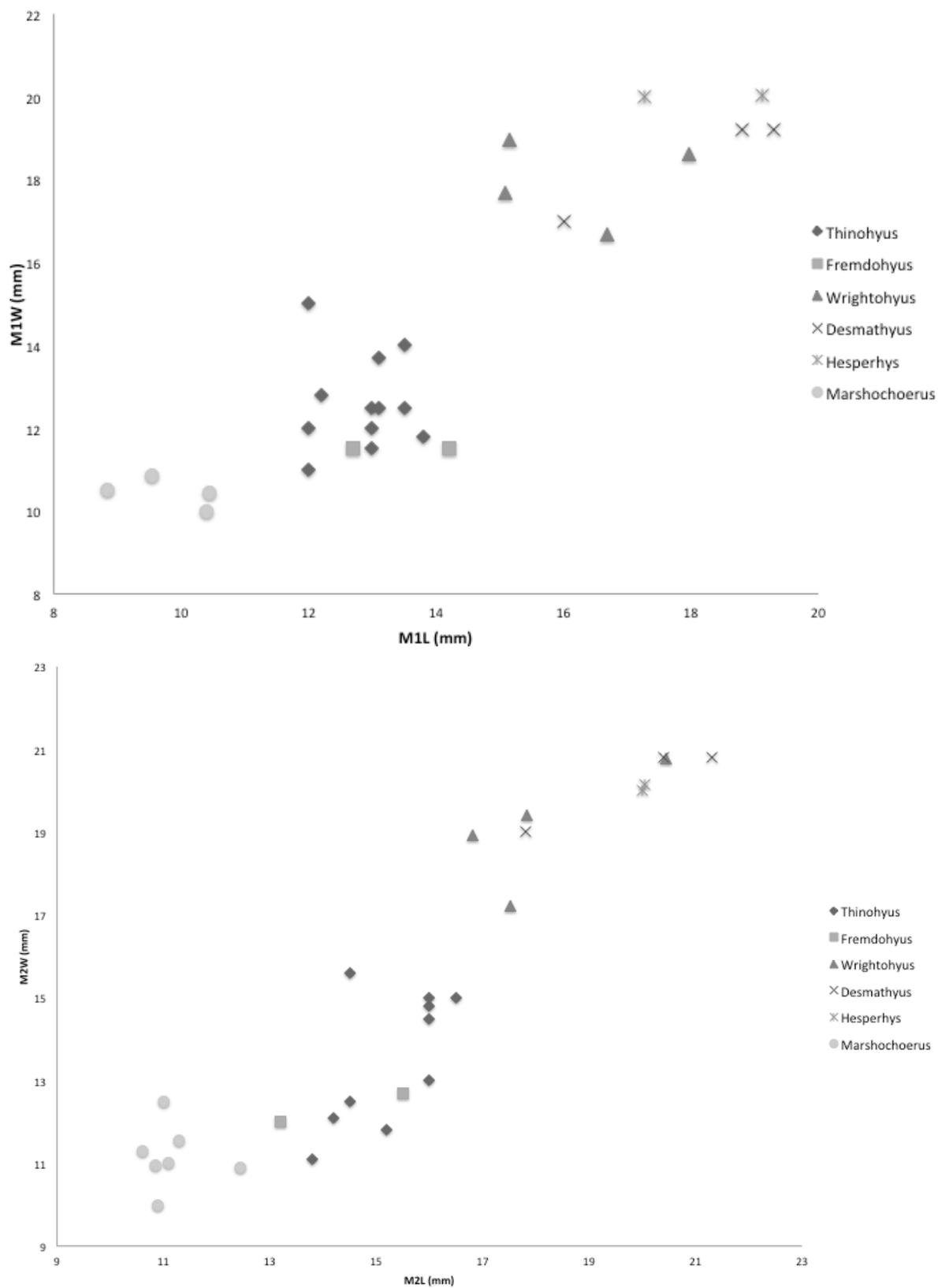


FIGURE 8. Bivariate plot of representative teeth of primitive peccaries. **A**, M1 length vs. M1 width. **B**, M2 length vs. M2 width.

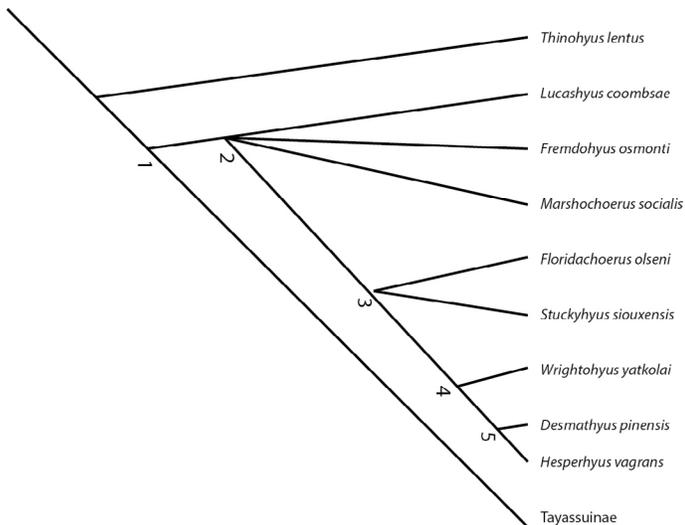


FIGURE 9. Phylogenetic relationships of the taxa discussed in this paper. Characters are (following Wright, 1991, fig. 88; Wright, 1998): 1) Tayassuinae-Hesperhyinae clade: Cancellous, anteriorly acuminate auditory bulla; glenoid fossa condyloid, ventral to the level of the basioccipital; tympanic process very deep dorsoventrally; premaxilla overlaps incisive foramina; M1-2 principal cusps not separated by accessory cusps; P2 with a lingual cingulum; 2) Hesperhyinae: plesiochoanal chamber present; medially fused pterygoid bones; pterygoid processes on the alisphenoid; vertical processes on the palatine bones 3) Plesiochoanal chamber narrow; orbitomaxillary fossa present; 4) large orbitomaxillary fossa; narrow pterygoid process of the alisphenoid; p2 with a broad talonid and cingulum; 5) P3 with large crescentic protocone.

more derived than true *Thinohyus*, but further study of the hesperhyine peccaries (Prothero, 2015) finally clarified how to distinguish these primitive genera of peccaries.

This distinction becomes even clearer when *Thinohyus osmonti* is compared to true *Thinohyus* (Fig. 7, right), side by side. Typical John Day *Thinohyus* has a shorter, rounder, and much more convex, conical rostrum, compared to the long, narrow, gracile rostrum of *F. osmonti*. There is no real facial vacuity in *Thinohyus*, but it is noticeable in *F. osmonti* (Fig. 7A). Instead, the skull of *F. osmonti* very closely resembles those of many of the primitive hesperhyines (Fig. 7, left) described by Prothero (2015).

The only other reason for referring the specimen to *Thinohyus* besides its John Day provenance is size, which is within the cluster of sizes for other John Day specimens (Fig. 8). A plot of almost any dimension of Whitneyan or Arikarean or later peccaries show that *F. osmonti* falls completely within the cluster of John Day *Thinohyus*. Despite the similarity in teeth, however, the skull of *F. osmonti* is distinctly larger and very different in shape from *Thinohyus* (Fig. 7). Likewise, the teeth of nearly all the other hesperhyines (e.g., *Wrightohyus*, *Desmathyus*, *Hesperhyus*) are noticeably larger than *F. osmonti* (Fig. 8), as are the skulls (Fig. 7). The exception is the tiny hesperhyine peccary *Marshochoerus socialis* (formerly *Cynorca sociale*), which is much smaller than any of the peccaries discussed in this study (Fig. 8).

#### *Fremdohyus osmonti* (Sinclair, 1905)

*Thinohyus* (*Bothrolabis*) *osmonti* Sinclair, 1905

*Thinohyus* (*Bothrolabis*) *osmonti* Merriam and Sinclair, 1907

**Type specimen:** UCMP 393, a nearly complete skull and mandible, from the “*Diceratherium* beds, Middle John Day, West side of the John Day Valley, about six miles north of Clarno’s Ferry, Gilliam County, Oregon” (UCMP locality 839, Black Rock 3).

**Referred specimen:** UCMP1988, a skull fragment with palate, from UCMP locality 892, McCallister’s Ranch, “about 150 feet above the top of the Lower John Day”

**Diagnosis:** Same as for genus.

**Description:** Same as for genus.

#### CONCLUSIONS

TABLE 1. Measurements (in mm) of skull and upper teeth of *Fremdohyus osmonti*.

	UCMP 393	UCMP 1988
Condylbasal length	225	—
I1-M3	137	—
C1-P3	28	—
C1-M1	47.5	—
P2-M3	81.2	—
M1-3	40.5	41.5
Canine length	38.0	—
Canine width	9.9	—
Palate width at P2	33.0	—
Palate width at M1	26.0	—
Postorbital width	116.8	—
Skull width at zygoma	101.0	—
Skull width at occipital	63.3	—
Length P4	10.0	9.0
Width P4	10.5	11.0
Length M1	14.2	12.7
Width M1	11.5	11.5
Length M2	15.5	13.2
Width M2	12.7	12.0
Length M3	14.8	15.1
Width M3	11.3	11.8

TABLE 2. Measurements (in mm) of mandible and lower teeth of *Fremdohyus osmonti*.

	UCMP 393
Canine-p2 diastema	81.0
Length, p2-m3	88.8
Length, m1-3	43.2
Ramus depth at p2	33.5
Ramus depth at m3	33.5
Canine length	38.0
Canine width	9.9
Length p4	12.0
Width p4	7.0
Length m1	12.0
Width m1	8.0
Length m2	14.0
Width m2	9.3
Length m3	18.3
Width m3	9.5

The long misunderstood taxon “*Thinohyus*” *osmonti* has been nearly forgotten since its description in 1905. If mentioned at all, it has been given an incorrect name based on taxonomy that is a century out of date. It is clearly not a typical John Day *Thinohyus* (with the convex conical rostrum) but a very early and primitive hesperhyine peccary, here referred to a new genus *Fremdohyus*. Even though its teeth are the same size as those of John Day *Thinohyus*, the skull is larger and the rostrum has the narrow, gracile shape with concave facial vacuities typical of other hesperhyines. It is distinct from all known hesperhyines in its smaller size and more primitive features, except for the tiny peccary *Marshochoerus socialis* (= *Cynorca sociale*), which is much smaller still. This now makes eight genera (five of them new since 2015) and eight species (two of them new since 2015) described in this large and diverse but previously unnamed subfamily (Fig. 9), first called the “*Hesperhyus*-*Cynorca*” *sociale* clade” by Wright (1998). None of these taxa (except for *Hesperhyus*) was recognized in any of the existing paleobiological databases (MIOMAP, PBDB), or some of them are mentioned but misassigned. Such hidden diversity, especially in poorly studied groups with lots of undescribed specimens, reveals a level of taxonomic diversity that is underestimated or misassigned in paleobiological databases, and seriously compromises their credibility.

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#### REFERENCES

- Alroy, J., 2016, Fossilworks database page on "*Thinohyus (Bothrolabis) osmonti*" [http://fossilworks.org/bridge.pl?a=taxonInfo&taxon\\_no=319835](http://fossilworks.org/bridge.pl?a=taxonInfo&taxon_no=319835). Accessed 8/8/16.
- Merriam, J.C., and Sinclair, W.J., 1907, Tertiary faunas of the John Day region: University of California Publications, Bulletin of the Department of Geology, v. 5, p. 171-205.
- Prothero, D.R., 2009, The early evolution of North American peccaries (Tayassuidae): Museum of Northern Arizona Bulletin, v. 65, p. 509-542.
- Prothero, D.R., 2015, Systematics of the early Miocene hesperhyine peccaries (*Artiodactyla*, Tayassuidae). New Mexico Museum of Natural History, Bulletin 65, p. 235-255.
- Sinclair, W.J., 1905, New or imperfectly known rodents and ungulates from the John Day series: University of California Publications, Bulletin of the Department of Geology, v. 4, p. 125-143.
- Woodburne, M.O., 1969, Systematics, biogeography, and evolution of *Cynorca* and *Dyseohyus* (Tayassuidae): Bulletin of the American Museum of Natural History, v. 141, p. 273-355.
- Wright, D.B. 1991. Cranial morphology, systematics and evolution of Neogene Tayassuidae (Mammalia) [Ph.D. dissertation]: University of Massachusetts, Amherst, MA.
- Wright, D.B., 1998. Tayassuidae; in Janis, C.M., Scott, K.M., and Jacobs, L.L. eds., Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, p. 389-401.

