

EVOLUTION OF THE EARLY MIOCENE HESPERHYINE PECCARIES

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Abstract—The Hesperhyinae is a monophyletic group of primitive peccaries that have long been plagued by confused systematics, invalid taxa, incorrect generic assignments, and poor specimens. Even though the currently published literature recognizes only *Hesperhys* (and sometimes *Desmathyus*), previously undescribed fossils show that there are seven distinct genera (four new) and seven species (two new). Hesperhyines are now defined by a distinctive suite of characters in the choanal region of the skull. The earliest hesperhyines include a primitive new genus and species, *Lucashyus coombsae*, from the late Arikareean of Wyoming, along with “*Cynorca*” (now *Marshochoerus*) *socialis* from the late Arikareean of the John Day Formation. *Floridachoerus olseni* from the early Hemingfordian of the Thomas Farm local fauna in Florida is a slightly more derived hesperhyine, as is the new genus *Stuckyhyus siouxensis* (replacing the invalid name “*Desmathyus siouxensis*”) from the late Arikareean of Wyoming. The most derived taxon is *Hesperhys vagrans* (from the late Hemingfordian and early Barstovian). New material demonstrates *Hesperhys* a very distinctive large peccary with robust, inflated cheek teeth. *Hesperhys* is completely different from the smaller more gracile *Desmathyus pinensis* (from the late Arikareean of South Dakota) and the new taxon *Wrightohyus yatkolai*, from the late Arikareean-early Hemingfordian of Nebraska and Wyoming. All of three of these taxa were incorrectly lumped into *Hesperhys*. *Pediohyus ferus* Loomis, 1910, is too fragmentary and incomplete for confident comparison, so it is a *nomen dubium*. This revision of all the new material and mistaken systematic assignments reveals a significant evolutionary radiation and a much greater taxonomic diversity of peccaries in the early to middle Miocene than the older literature had ever suggested. It also substantiates the importance of this large monophyletic clade that was completely unrecognized by earlier scientists.

INTRODUCTION

The peccaries or javelinas (family Tayassuidae) are a uniquely New World family of suiform artiodactyls. Although they superficially resemble pigs (family Suidae), they had a long evolutionary history in the North America since the late Eocene (starting at 37 Ma), independent of suid evolution in the Old World. They eventually spread to South America in the early late Miocene (before 10 Ma) and underwent another evolutionary radiation there (Frailey and Campbell, 2012).

Three living species of peccary still survive in Central and South America (including the southwestern United States): *Dicotyles tajacu*, the collared peccary; *Tayassu pecari*, the white-lipped peccary; and *Catagonus wagneri*, the Chacoan peccary. This last species was first known in 1930 only from fossils until living populations were discovered in the Gran Chaco of Paraguay in 1971. At least 20-25 genera occurred in North America during the last 37 Ma.

Even though they are well represented by fossils in North America, peccaries have long been neglected by published taxonomic studies. Many new and excellent specimens are now available to study in the Frick Collection of the American Museum of Natural History of New York, but most have not yet been studied or published. In 1983, David B. Wright did his master’s thesis at the University of Nebraska on some late Miocene peccaries, and in 1991 he completed a doctoral dissertation at the University of Massachusetts on Neogene peccaries. Except for a few short papers on general topics (e.g., Wright, 1993), and a short summary chapter that provided no detailed descriptions or new names (Wright, 1998), most of Wright’s work has not been published, and it has been more than 20 years since he left the profession. Most of Wright’s descriptions are not widely available to the scientific community since they remain in unpublished theses (although they are now much easier to obtain thanks to online dissertation download services). It is necessary to re-describe the fossils as much as possible, or when necessary, paraphrase from Wright’s unpublished theses, since I found most of his conclusions are sound, but others I disagree with. Because no one else has taken up the task of finishing Wright’s work and properly naming and describing these new fossils, my students and I have begun to take up the task. Prothero (2009) revised the earliest peccaries from the late Eocene and Oligocene, and several other papers on late Miocene peccaries have been recently published (Prothero and Sheets, 2012; Prothero and Grenader, 2012; Prothero and Pollen, 2012).

MATERIALS AND METHODS

Since the beginning of this comprehensive research program of the North American Tayassuidae in 2007, I have visited nearly every museum in the United States that has significant peccary specimens.

Specimens were measured with digital calipers and data entered and statistically analyzed using Excel spreadsheets. Most photos were taken with a Nikon 5700 camera, and edited in Photoshop by Pat Linse and Erik Prothero.

Figure 1 shows the terminology of the upper and lower teeth employed in this paper. Figure 2 shows a detail of the nasal and choanal region of a typical hesperhyine, with a detail of the holotype skull of *Stuckyhyus siouxensis* (CM 1423), showing the major features discussed in this paper. Further details can be found in Wright (1991).

Institutional Abbreviations: ACM, Beneski Museum of Natural History, Amherst College, Amherst, Massachusetts; AMNH, American Museum of Natural History, New York, New York, including the Frick Collection (F:AM); ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; SDSM, South Dakota School of Mines, Rapid City, South Dakota; UCMF, University of California Museum of Paleontology, Berkeley, California; UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; USGS, United States Geological Survey collections, Menlo Park, California (now at USGS Denver); USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM, Yale Peabody Museum, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus 1858

Order Artiodactyla Owen 1848

Family Tayassuidae Palmer 1897

Subfamily Hesperhyinae (new)

Diagnosis—As Wright (1991) discovered, the hesperhyines have a distinctive morphology in their nasal-choanal region (Fig. 2). Instead of the simple broad arcuate choanal margin of most mammals (Fig. 2A), the pterygoids fuse together and push the active choanal opening posteriorly to form a “neochoanal chamber”. The anterior choanal opening thus is left behind as the “plesiochoanal fossa” or “plesiochoanal chamber”. All hesperhyine fossils that adequately preserve this region have this unique plesiochoanal chamber, medially fused pterygoid bones, large pterygoid processes on the alisphenoid, and vertical processes on the palatine bones (see Wright, 1991, 1998).

Included Taxa—*Hesperhys vagrans* Douglass, 1903; *Desmathyus pinensis* Matthew, 1907; *Wrightohyus yatkolai*, new genus and species; *Floridachoerus olseni* White, 1941; *Stuckyhyus siouxensis* new genus; *Lucashyus coombsae*, new genus and species; *Marshochoerus socialis*,

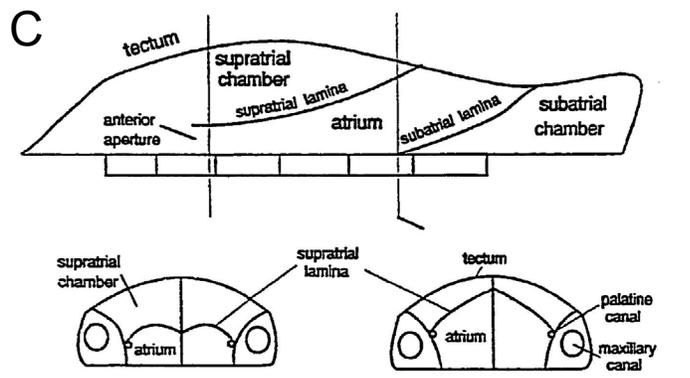
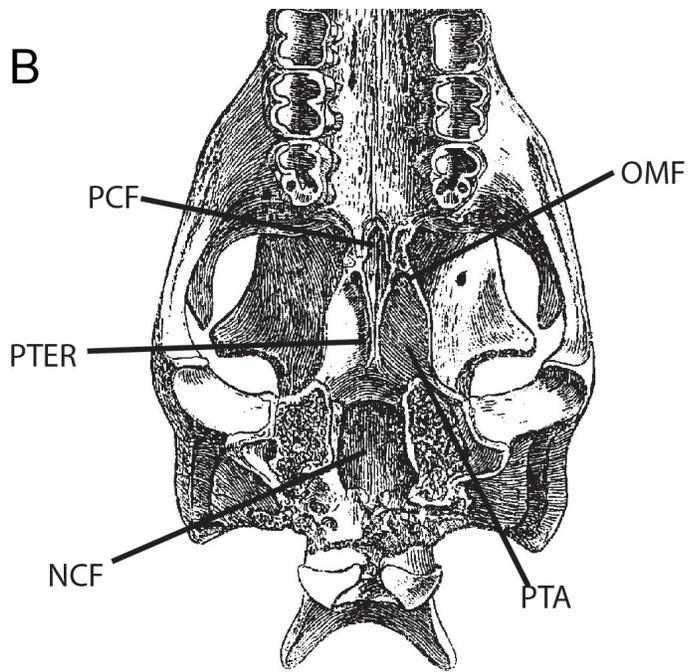
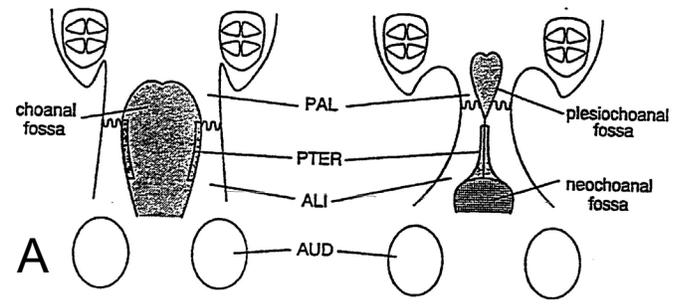
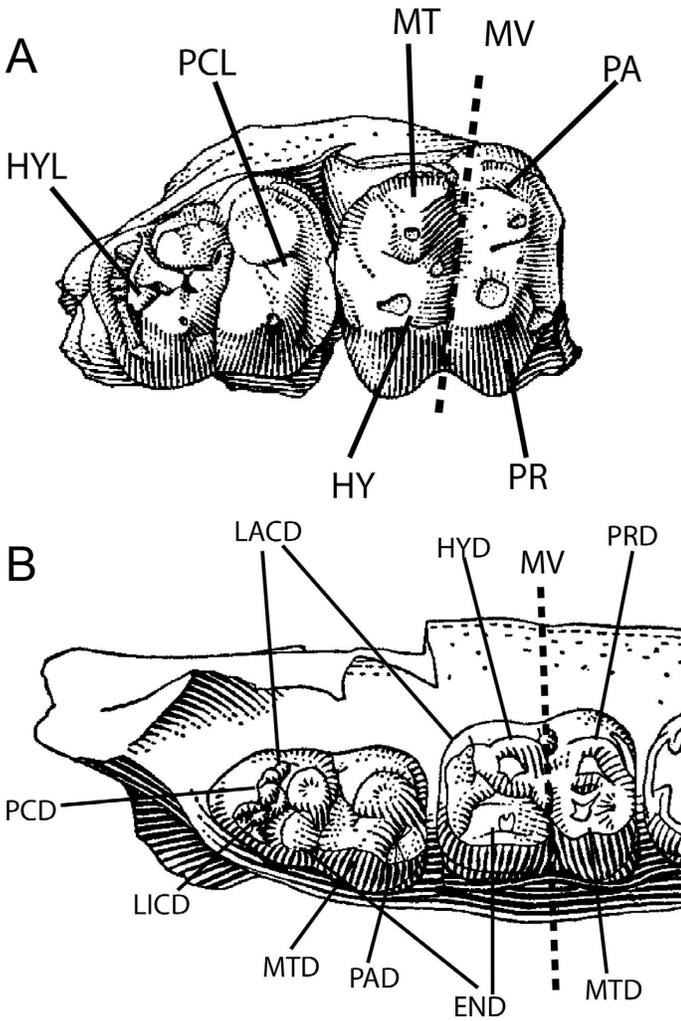


FIGURE 1. Typical peccary molars showing the dental terminology employed in this paper. **A**, holotype right M2-M3 of *Marshochoerus sociale* (after Woodburne, 1969 Fig. 1); **B**, HY= hypocone; HYL = hypoconule; MT = metacone; MV = median valley; PA = paracone; PCL = paraconule; PR = protocone. **B** “*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.

new genus (Fig. 3).

Discussion—The peccaries known as *Hesperhyus*, *Desmathyus*, and *Floridachoerus* have long been described in the literature. It has been over 112 years since *Hesperhyus* was named in 1903. However, their systematic affinities were confused or simply not analyzed. In large part, this was due to the exclusive use of characters which are not very diagnostic, such as the details of their mostly plesiomorphic cheek teeth. As has long been known, the cusps and crests of peccary cheek teeth are highly variable within populations (Colbert, 1938; Simpson, 1949; Wright, 1991, 1998). Except for their similar age range (late Arikareean-Hemingfordian-Barstovian), there seemed to be little to connect these genera other than shared primitive similarity. In some cases, *Desmathyus* was considered the junior synonym of *Hesperhyus*, although in morphology *Hesperhyus* is more distinctively different in its skull and teeth from any other hesperhyine peccary, including *Desmathyus*, *Floridachoerus*, and the others described in this paper.

The breakthrough occurred when Wright (1991, 1998) examined skulls with excellent preservation of their nasal-choanal regions, which had never been described before. Surprisingly, he found a rich set of diverse characters that showed a definite hierarchical structure within the Tayassuidae. As Wright (1998, p. 394) showed, there are numerous synapomorphies that unite the Hesperhyinae besides their symplesiomorphic features of the skulls and the teeth, and their

FIGURE 2. **A**, 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); **B**, detail of the holotype skull of *Stuckyhyus siouxensis* (CM 1423, Peterson, 1905, Plate XXXV) showing the distinctive hesperhyine nasal-choanal characters. Abbreviations: NCF = neochoanal fossa; OMF = orbitomaxillary fossa; PCF = plesiochoanal fossa; PTA = pterygoid wing of alisphenoid; PTER = pterygoid; **C**) Sketch of the anatomical features of the nasal region used in this paper (After Wright, 1991, Fig. 9).

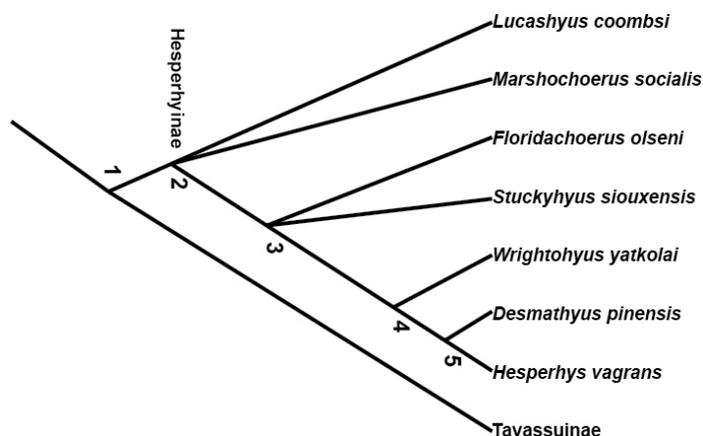


FIGURE 3. Phylogenetic relationships of the taxa discussed in this paper. Characters are (following Wright, 1991, Fig. 88; Wright, 1998): **1**) Tayassuinae-Hesperhyinae clade: Cancellous, anteriorly acuminate auditory bulla; glenoid fossil condyloid, ventral to the level of the basioccipital; tympanic 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.

common age. What Wright (1998) called the *Hesperhys*-“*Cynorca*” *societe* clade (here renamed the Hesperhyinae) is defined by a number of unique features, including medially fused pterygoid bones, pterygoid processes on the alisphenoid, vertical processes on the palatine bones, and the presence of a plesiochoanal chamber. I will not try to redo Wright’s (1991, 1998) phylogenetic analysis in this paper (summarized in Fig. 3), and focus instead on the alpha-systematics of defining and describing the fossils (especially the new taxa) that Wright never finished or published.

Hesperhys Douglass, 1903

Figures 4-8
Tables 1-4

Hesperhys Douglass, 1903

Desmathyus Matthew, 1924 (in part)

Type and only species—*Hesperhys vagrans* Douglass, 1903

Distribution—Late Hemingfordian and early Barstovian, Montana, Nebraska, Wyoming, California.

Diagnosis—Very large hesperhyine with very massive, robust skull and flaring orbits and zygomatic arches, and broad rostrum; cheek teeth more robust and bulbous than in any other hesperhyine. The plesiochoanal fossa is reduced to a shallow pocket. P3 has a large protocone. The i1 and i2 are deep dorsoventrally at the base.

Description—Douglass (1903, p. 175-176) gave a very brief description of CM 748 (Figs. 4-5), a lower jaw from the early Barstovian Flint Creek beds in Montana. He made no comparisons with any other peccary, nor did he diagnose the specimen in a useful fashion. Because the type specimen was only a fragmentary lower jaw with no associated skull or upper teeth, the affinities of *Hesperhys* were long a puzzle. However, there are now a number of good specimens of this taxon in the Frick Collection, including a good skull and jaws (F:AM 143840) from early Barstovian Humbug Quarry, Olcott Formation, Sioux County, Nebraska (Skinner et al., 1977). The jaws of F:AM 143840 (Figs. 6E-F) match closely with the holotype from Montana (Figs. 4A-B) in both morphology and size (Fig. 7, Tables 1-4), allowing us to associate the skull of F:AM 143840 with this genus and species, and provide a full description of this long-missing elements of the taxon.

Skull—(partially paraphrased from Wright, 1991) The overall impression of the skull of F:AM 143840 (Figs. 6A-D) is that it is robust and massive, with much thicker ridges and arches than in any other hesperhyine. It has broad, flat frontal bones, which have thick postorbital processes on the lateral edges. The skull has sharp temporal

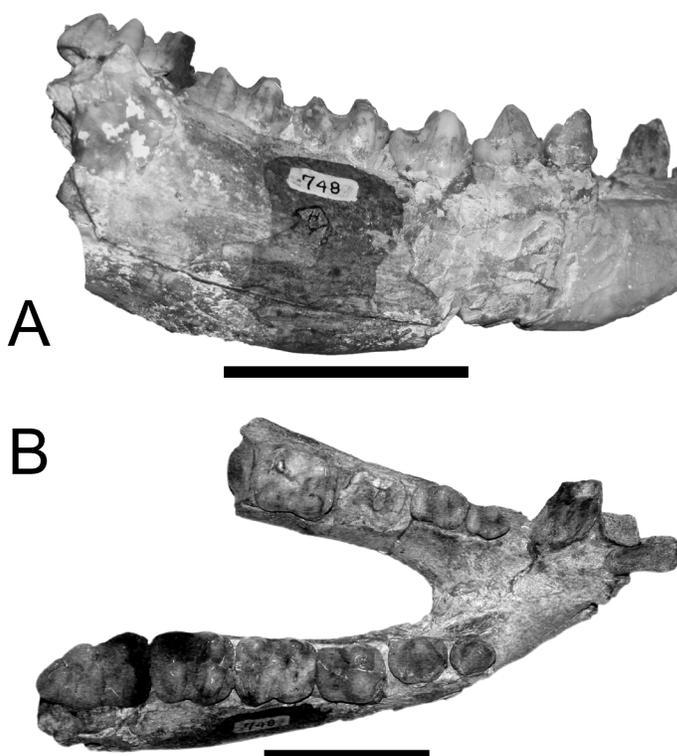


FIGURE 4. CM 748, holotype jaw of *Hesperhys vagrans*, **A**, lateral and **B**, dorsal views. Scale bar = 5 cm.

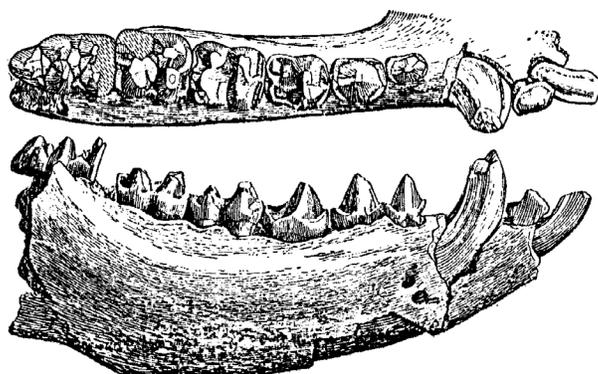


FIGURE 5. Douglass’s (1903) original illustration of CM 748, holotype of *H. vagrans*.

lines that converge posteriorly into a large sagittal crest. In dorsal view, the nuchal crest appears V-shaped, and inclines towards the rear. In lateral view, the dorsal profile is nearly flat. There is a robust lacrimal tuberosity, and the lacrimal foramen is ventral to the tuberosity, embedded in a shallow fossa on the anterior edge of the orbit. The zygomatic arches have broad, flat lateral surfaces, inclined slightly anterolaterally. The zygomatic arch originates above the posterior part of M1, and has a sharp ridge that separates the shallow rostral muscular fossa from the narrow origin of the masseteric muscles on the bottom of the zygomatic arch. There are only small canine buttresses, suggesting that F:AM 148340 was a female individual. This negates the idea the increased skull robustness can be attributed to sexual dimorphism in a male individual, and confirms that they are indeed discrete taxa.

The narrow palatine postdental process extends to the level of the glenoid fossa. There is a deep plesiochoanal fossa which does not extend forward into the palate. There is a narrow spine in this fossa which projects from its anterior margin. The skull has narrow pterygoids which are fused medially. The alisphenoidal pterygoid processes are pressed together in the midline, and are very narrow. The ventral orbitosphenoids, dorsal to the pterygoid processes of the alisphenoid,

TABLE 1. Measurements (in mm) of skulls of *Hesperhys vagrans* and *Desmathyus pinensis*.

	<i>Hesperhys vagrans</i>		<i>Desmathyus pinensis</i>	
	F:AM 143840	USGS M 1009	AMNH 12936	UMCP 23598
Condylobasal length	—	>300	271	280
Premaxilla-M3	—	178	165	175
C1-M3	—	133	126	124.6
C1-P2 diastema	—	13.2	12.2	5.6
P2-M3	—	101.4	98.3	100.6
Palate width	—	79.2	61.6	64
Postorbital width	116.8	102	108	112
Width at glenoid	—	—	150	148
Canine buttress width	—	85.5	81	80
Occipital condyle width	63.3	—	48	—
Occipital condyle height	20.6	—	18.3	—

TABLE 2. Measurements (in mm) of upper teeth of *Hesperhys vagrans* and *Desmathyus pinensis*.

TOOTH	<i>Hesperhys vagrans</i>				<i>Desmathyus pinensis</i>	
	N	MEAN	SD	CV	AMNH12936	UCMP 32598
Length DP2	1	10.2	—	—	—	—
Width DP2	1	9.0	—	—	—	—
Length DP3	2	15.9	0.25	1.57	—	—
Width DP3	2	15.1	0.50	3.31	—	—
Length DP4	3	17.5	0.24	1.37	—	—
Width DP4	3	19.2	0.71	4.06	—	—
Length P2	3	13.5	1.36	10.1	11.5	13.2
Width P2 3	11.8	1.24	10.5	9.5	13.6	
Length P3	2	15.7	0.55	3.5	14.8	14.0
Width P3 2	17.1	1.1	6.43	14.1	15.9	
Width P4 2	14.2	1.25	8.8	13.5	14.2	
Width P4 2	19.4	0.6	3.1	18.3	19.5	
Length M1	4	19.9	0.74	3.72	19.3	18.8
Width M1	4	21.6	0.71	3.29	19.2	19.2
Length M2	4	21.6	1.21	5.6	21.3	20.4
Width M2	4	22.0	0.54	2.46	20.8	20.8
Length M3	2	19.2	1.4	7.29	19.5	20.5
Width M3	2	19.5	0.95	4.87	19.7	21.0

TABLE 3. Measurements (in mm) of mandibles of *Hesperhys vagrans* and *Desmathyus pinensis*.

	<i>Hesperhys vagrans</i>			<i>Desmathyus pinensis</i>		
	CMNH	USGS	F:AM	AMNH	AMNH	UCMP
	748	59-11	143840	12396	12937	32598
Symphysis-condyle	—	240	—	—	—	205
Symphysis length	59	74	62	—	—	63.4
Symphysis width	50	50	50	30	40	45.6
Symphysis to m3	170	163	—	—	—	160
Canine-p2 diastema	7.4	13.3	—	15.5	17.8	13.7
Length, p2-m3	125	112.2	—	—	—	109.6
Ramus depth	44.1	55.9	58.0	39.9	—	39.8
Ramus width	32	32.2	31.7	—	—	24.5

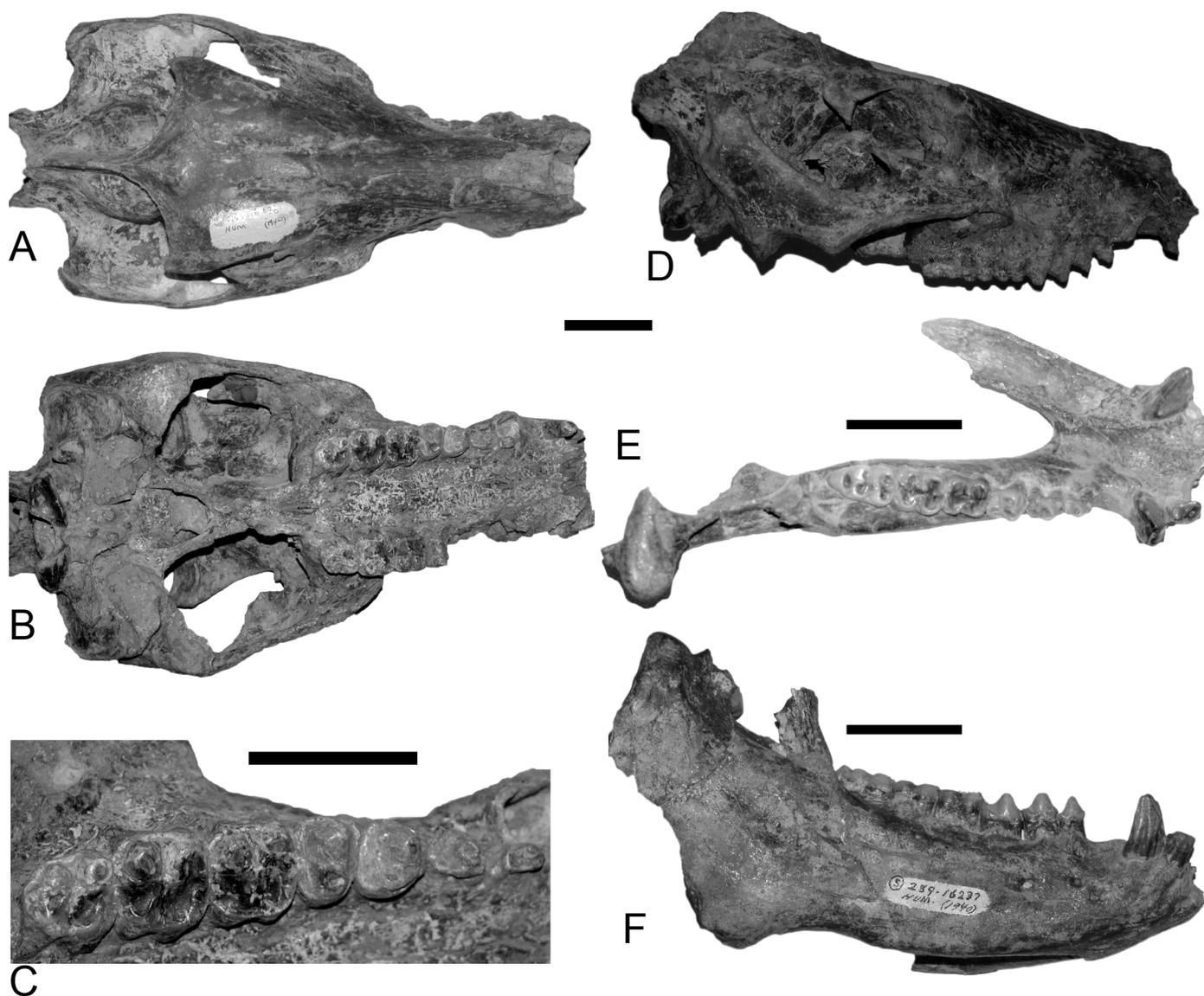


FIGURE 6. *Hesperhys vagrans*, F:AM 143840, referred skull and jaws, from Humbug Quarry, Sioux County, Nebraska. **A**, dorsal view of skull; **B**, ventral view of skull; **C**, close-up of upper cheek teeth; **D**, right lateral view; **E**, crown view of referred lower jaw (compare with the holotype in Fig. 2); and **F**, lateral view of lower jaw. Scale bars = 5 cm.

TABLE 4. Measurements (in mm) of lower cheek teeth of *Hesperhys vagrans* and *Desmathyus pinensis*.

	<i>Hesperhys vagrans</i>				<i>Desmathyus pinensis</i>			
	N	MEAN	SD	CV	N	MEAN	SD	CV
Length p2	3	12.3	0.63	5.12	2	10.6	6.2	5.8
Width p2	3	8.4	0.94	11.19	2	6.9	4.0	5.8
Length p3	5	16.4	0.58	3.17	3	13.0	1.2	0.9
Width p3	5	12.3	1.18	9.59	3	9.4	0.9	0.3
Length p4	7	18.3	0.85	4.65	3	16.5	0.5	0.4
Width p4	7	15.1	1.06	7.02	3	11.3	0.4	0.3
Length m1	6	20.9	1.08	5.17	2	18.5	10.7	5.7
Width m1	6	18.0	1.27	7.06	2	13.8	0.2	0.1
Length m2	7	22.0	1.50	6.82	3	22.1	0.4	0.2
Width m2	6	19.7	1.21	6.14	3	16.1	0.9	0.5
Length m3	5	29.6	2.12	7.16	1	26.6	—	—
Width m3	5	18.8	1.65	8.78	1	16.5	—	—

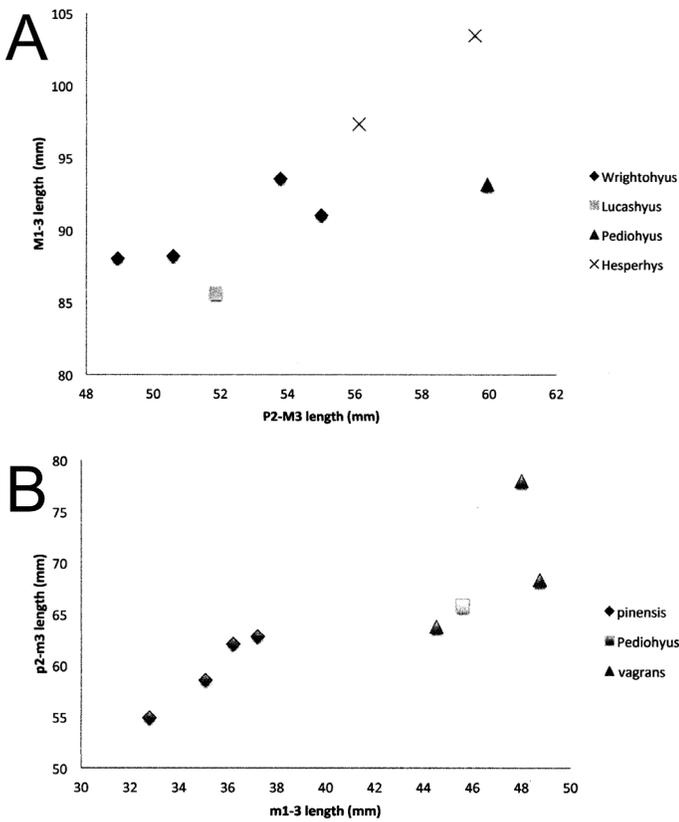


FIGURE 7. Plot showing upper tooth dimensions of hesperhyines. **A**, lower tooth row dimensions; **B**, dimensions of m2. Symbols for taxa indicated on each plot.

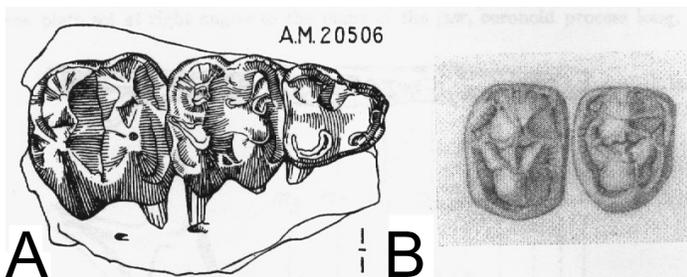


FIGURE 8. AMNH 20506, holotype of “*Desmathyus*” *validus*. **A**, original illustration after Matthew (1924); **B**, sketch of the P3-4 in crypts. Scale bar in cm.

are also fused together, except for a thin bony lamina which separates the left pterygoid fossa from the right. F:AM 143840 has a large, deep sphenopalatine fossa. The orbitomaxillary fossa is also large and deep, occupying all the region between the orbit and the sphenopalatine fossa.

F:AM 143840 has a large glenoid fossa and robust postglenoid process. Although the auditory bullae are broken, it allows us to see the cancellous tissue inside them. The alisphenoid complete encloses the foramen ovale. The large external auditory meatus passes through the tip of the dorsoventrally deep tympanic process of the squamosal. There is a broad posttympanic process on the squamosal, which extends medioventrally to wall off the posterior auditory bulla.

Upper teeth—The upper cheek teeth of F:AM 143840 are fairly worn (Fig. 6C), but there are numerous other specimens in the hypodigm (especially those from the Nebraska and California localities) which show the full range of variation of the upper teeth. The overall impression of all these teeth is that they are distinctly larger than those of any other hesperhyine (Fig. 7). Even more importantly, the simple basal measurements of the cheek teeth does not capture how robust and bulbous these teeth appear in visual inspection, compared to nearly any other peccary. This is the outstanding feature of the holotype lower jaws

of *H. vagrans*, and it is true of the additional referred upper and lower cheek teeth as well.

In addition, the less worn cheek teeth have sharp crests descending from the apices of the main cusps. The lingual cusps often have sharp labial crests. After they are worn down, the crests vanish leaving transversely elongate lingual cusps. This is a zygodont or zygalophodont dentition as seen in more derived peccaries like *Platygonus*. Because these taxa are distant phylogenetically and evolved from completely different branches of the tayassuid phylogeny, the development of zygodonty clearly evolved in parallel (Prothero and Grenader, 2012).

The upper incisors (where preserved) are very robust, with very convex and rounded labial surfaces that have rugose striations on them. The occlusal side of the upper incisors are rounded and slightly serrated, with numerous tiny cuspsules. The lingual surface is slightly concave but mostly flat, with a basal cingulum. It is not as cuplike and spatulate as seen in other hesperhyines.

The dp1 has two roots, and a single anteroposteriorly elongate cusp with anterior and posterior crests, and a tiny lingual cingulum. The dp2 has a single large cusp in the labial position. On the lingual base of this cusp is a low enamel ridge, which has a small cusp-like structure on its posterior edge. The entire tooth is surrounded by a cingulum, which is weak on the labial surfaces. On the posterolabial part of the tooth is a small cuspsule. The dp3 has a broad anterior root and two posterior roots. The four principal cusps include a distinct protocone smaller than the paracone, which merge at the base, and are connected to the hypocone by a narrow crest. The dp4 has a very similar cusp pattern to dp3.

P2 has three roots: one anterior, two posterior. It is capped by a single subconical cusp surrounded by a lingual and posterior cingulum. P3 has the same pattern of three roots. It bears a tall protocone with a lower, more arc-shaped protocone. The entire tooth is surrounded by a robust cingulum, which bears a blunt point in the anterolabial corner of the tooth (Figs. 6C-D). P4 has a single lingual root and two labial roots. The crown is compressed anteroposteriorly. It bears two similar-sized cusps, and a robust cingulum around it.

All three upper molars have a similar, plesiomorphic crown pattern (Fig. 6C). The deep median valley separates the anterior from the posterior cusps. When these are worn, they become an anterior and posterior dentin lakes separated by the enamel of the median valley. M3 is slightly smaller than M2 and not as square as M1 or M2. The M3 posterior cusps are very narrow.

Lower jaw and teeth—One of the distinctive features of the holotype lower jaw (CM 748) (Figs. 4-5) and the referred jaws (Figs. 6E-F) is that they are strikingly massive and robust, rather than slender and gracile, as in most peccaries. These accompany the large cheek teeth with massive, bulbous crowns that are different from most other known peccaries. The symphysis is very broad and U-shaped. These similarities, along with those of the teeth, allow us to confidently assign F:AM 143840 and other F:AM jaws to the taxon represented by the holotype, CM 748, thus allowing us to associate the skull of F:AM 143840 with this taxon as well.

The i1 is almost spatulate, with a deeply concave lingual surface surrounded by robust, posteriorly convergent crests. The labial surface is smoothly convex. The tooth is deep dorsoventrally at the base compared to its transverse width. The anterior edge on unworn teeth has several small cuspsules. The i2 is very similar to the i1 only smaller.

The dp2 is double-rooted, with a tall protoconid and a sharp anterior crest descending to the base. The dp3 has a small metaconid cusp, attached to the protoconid. On the anterior surface of the protoconid is a sharp crest that merges with the small anteroconulid. The dp3 has a low talonid with a faint cingulum. The dp4 is very similar to the dp3.

The p2 is double-rooted, and in side view is highly triangular. Its single large cusp is the protoconid, which is transversely compressed with sharp anterior and posterior crests. The entire tooth is surrounded by a strong cingulum, which also enclosed a small talonid basin. The p3 has a large protoconid with a distinct talonid, formed by a strong posterior cingulum. In less worn specimens, the talonid basin bears a single posterolabial cusp (Figs. 4, 6E). This talonid cingulum continues to a strong labial cingulum, which merges with a low but robust anteroconulid.

The p4 is very different from the p2 or p3 and is semi-molariform. There is both a protoconid and a metaconid. The protoconid is connected to a small paraconid by an anterolabial crest. The posterior cingulum surrounds a robust central cusp on the talonid.

M1 and M2 bear four main cusps. The pair of cusps on the

trigonid, and on the talonid, are anteroposteriorly compressed, and separated by a deep median valley. In the paraconid position on the protoconid is a small anterolingual process, while the metaconid bears a posterolabial process. A large metaconid and hypoconid are connected anterolingually. There is a large, sharp vertical posterior cleft on the entoconid, and a large hypoconulid. Most of M3 is similar to the cusp pattern on M1 and M2, but there is a large posterior lobe on the hypoconulid which has three cusps in an arc.

Discussion—*H. vagrans* is the largest and the youngest of all the hesperhyines. It is distinct from all other hesperhyines (and most other peccaries) in its unusually robust and massive skull and jaws, laterally projecting orbit and zygomatic arches, broad blunt (rather than pointed) rostrum, and especially its large, robust bulbous cheek teeth (Figs. 4, 6, 7). With the discovery of all this additional material (including the skull and jaws of F:AM 143840), this distinction becomes even more clear than when we had only the holotype lower jaw. Although most recent authors (including Simpson, 1945; McKenna and Bell, 1997; and Wright, 1991, 1998) have lumped other hesperhyines in with *H. vagrans*, none of these other taxa have the distinctly robust skull and jaws, and massive bulbous cheek teeth unique to *H. vagrans*. Thus, I reject the synonymy of taxa such as *Desmathyus pinensis* and “*Thinohyus (Bothriolabis) siouxensis* with *Hesperhyus*.”

Hesperhyus vagrans Douglass, 1903

Figs. 4-6
Tables 1-4

Hesperhyus vagrans Douglass, 1903

Desmathyus validus Matthew, 1924

Type specimen—CM 748, a broken lower jaw with left i2-3, c1, p2-3; right p2-m3; from the Flint Creek beds, early Barstovian, Montana (Figs. 4-5)

Hypodigm—*Early Barstovian Olcott Formation, Sioux County, Nebraska* (Skinner et al., 1977): Humbug Quarry, F:AM 143840, nearly complete skull and jaws (Fig. 6); F:AM 14184, maxillary fragment; F:AM 143842, partial left dentary with p2-m3; Echo Quarry, F:AM 143831, fragmentary skull with left and right M2-3, lacking basicranium and area anterior to M2; Prosynthetoceras Quarry: F:AM 143843, partial right dentary with p2-m3;

Late Hemingfordian Sheep Creek Formation, Sioux County, Nebraska: Stonehouse Draw Quarry, F:AM 18592, left maxillary fragment with pP4, M1; AMNH 20506 (holotype of *Desmathyus validus* Matthew, 1924), right maxillary fragment with P3-M3 (Fig. 8).

Barstow Formation, San Bernardino County, California (early Barstovian): Sunder Ridge Quarry: F:AM 143838, juvenile palate with left and right I1-2, dC1, C1, dP1-4, M1-2; F:AM 143839, juvenile right dentary with i1, c1, dp2-4, m1-2; Green Hills Quarry, F:AM 143837, partial mandible with left and right i1-2, c1, p2-m3; Quarry 5 mi east of Yermo; F:AM BAR-240, maxillary fragment with dP4, M1.

Caliente Formation, San Luis Obispo County, California (early Barstovian): USGS M109, partial skull with left and right I1-3, C1, dP1, P2-M3, lacking zygomatic arches, parts of rostrum and occiput; partial mandible with left and right i1-3, c1, left p2-4, m2-3, right p3-4, m2-3.

Diagnosis—Same as for genus

Distribution—Same as for genus.

Discussion—The diagnostic features and description of the known remains of *Hesperhyus vagrans* are discussed above.

Matthew (1924) described another new taxon, *Desmathyus validus*, from the Stonehouse Draw, late Hemingfordian Sheep Creek Formation, Sioux County, Nebraska (Skinner et al., 1977). It is based on AMNH 20506 (Fig. 8), a juvenile right maxilla with dP3-M1, and P3-4 in crypts (since excavated). Matthew (1924, p. 3-4) mostly distinguished it from other similar peccaries by its large size, and a few details of the molar crowns. He made no comparisons to Douglass' (1907) *Hesperhyus vagrans*, since the type of that taxon was only a mandible, and no upper teeth were known then. Matthew (1924, p. 3) also noted that it was fairly zygodont, a condition approaching the zygodonty or zygolophodonty seen in *Platygonus* (Prothero and Grenader, 2012). As noted above in the descriptions above, these are all conditions found in the newly described upper cheek teeth of *H. vagrans*. In size, especially, “*Desmathyus validus*” is very large, and appears to be even larger than most specimens of *H. vagrans* (Fig. 14). As there are no longer any valid diagnostic criteria for recognizing “*Desmathyus validus*”, I regard this taxon as a junior synonym of *H. vagrans*.

Desmathyus Matthew, 1907

Figures 9-11

Tables 1-4

Desmathyus Matthew, 1907

Hesperhyus Simpson, 1945 (in part)

Hesperhyus McKenna and Bell, 1997 (in part)

Hesperhyus Wright, 1991 (in part)

Hesperhyus Wright, 1998 (in part)

Hesperhyus Albright, 1999

Type and only species—*Desmathyus pinensis* Matthew, 1907

Diagnosis—Smaller hesperhyine with a long narrow rostrum and gracile zygomatic arches and orbital regions, and smaller less robust and inflated cheek teeth (in contrast to *Hesperhyus*); P3 has a large lingual cingulum which may develop a protocone; i1 and i2 are dorsoventrally shallow at the base; narrow but deep plesiochoanal chamber.

Distribution—Late Arikarean to early Hemingfordian of South Dakota.

Description—(partially paraphrased from Wright, 1991)

Skull: The fossils of *D. pinensis* (Figs. 9A-E) were briefly described but never illustrated by Matthew (1907), and to my knowledge no illustrations of it have ever appeared in print. The skull is significantly smaller than that of *H. vagrans* (Fig. 10, Table 1), but about the same size as some of the other hesperhyines described here. Together with additional skulls (e.g., UCMP 32598, shown in Fig. 11), it is now possible to give a complete description of the taxon and assess its variability.

In addition to the size differences, *D. pinensis* has a much narrower rostrum (Fig. 10) which smoothly tapers and widens posteriorly into a slightly broader orbital and zygomatic region (in contrast to the abrupt posterior extension of the orbitals and zygomatic arches of *H. vagrans*). The sagittal crest is sharp (Fig. 9A), with strong temporal ridges with merge posteriorly at the anterior end of the sagittal crest. The occiput is narrower and much more posteriorly stretched than in *H. vagrans*, with a sharp lamdoid crest lacking the “V-shape” seen in *H. vagrans*. There is only a faint lacrimal tubercle. At the root of the zygomatic arch, a strong ridge divided the rostral muscle fossa from the origin of the masseter, which lies on the ventral surface of the zygomatic arch. The holotype of *D. pinensis* has massive canine buttresses (Fig. 9B), much larger proportionally than in other hesperhyines. On the anterior face of the buttress, is a broad flat surface, and there is also a distinct facet that springs anteroventrally from the dorsal edge of the buttress. AMNH 19236 has a narrow plesiochoanal fossa, whose anterior margin extends to the middle of M3. The alisphenoid pterygoid processes are bent at a low angle, as seen in most hesperhyines. AMNH 19236 has an anteroposteriorly elongated pterygopalatine fossa. It has a large orbitomaxillary fossa, which is not separated from the maxillary canal by a large area of maxillary bone.

Upper dentition (Fig. 9B)—*D. pinensis* has a massive I1 with a strong lingual cingulum. The I2 is short and subconical, and bears sharp anteromedial and posterolateral crests, and a narrow lingual cingulum. The I3 is caniniform, a sharply pointed elongate tooth. The back of the root is exposed and shows a wear facet, suggesting abrasion from the lower canine.

The dP1 is a small, double-rooted, bladelike tooth. P2 is has three roots, and bears a large paracone with a broad postlingual cingulum. P3 has three roots, with a large paracone, and very broad posterolingual cingulum that sometimes bears a protocone, similar to the condition in *H. vagrans*. It also bears strong anterior and lingual cingula. The P4 is often worn down to two small apical ovals of dentin surrounded by ridges of enamel on the tip of the paracone. This suggests there might have been a small metacone, but if so, it is tiny and only slightly separated from the paracone. P4 has a robust protocone, with an anterolabial process, and a small metaconule. The strong cingulum surrounds the entire P4 except for the lingual side.

M1 is so worn on most specimens that there is no cusp anatomy remaining. M2 has the typical hesperhyine pattern, with transversely elongate lingual cusps, and the wear on the cusps beginning to suggest zygodonty. On the M3, the principal cusps are separated by a metaconule and paraconule, with a thick posterior cingulum.

Lower jaw and teeth—There are three jaws or jaw fragments known from this taxon: the holotype specimen, AMNH 12936 (Fig. 9F-G), plus AMNH 12937, and UCMP 32598. None preserve the angle or the coronoid region. The symphysis is very narrow and U-shaped. There are shallow fossae on the medial surfaces of the rami, just next to the symphysis.

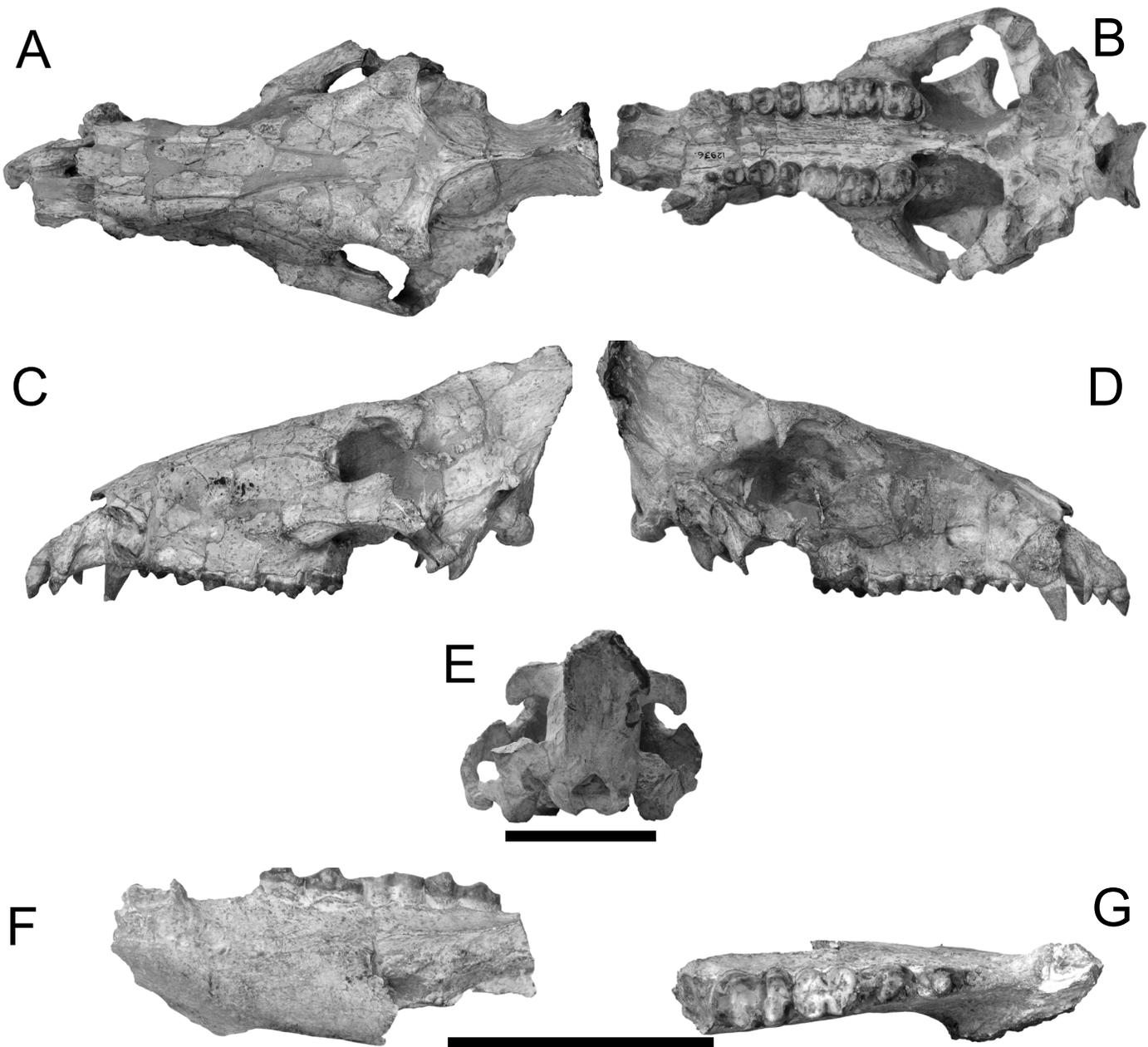


FIGURE 9. AMNH 12936, holotype skull and jaws of *Desmathyus pinensis*. **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, right lateral view; **E**, occipital view; **F**, left ramus, lateral view; and **G**, left ramus, occlusal view. Scale bars = 5 cm. (Photos courtesy of Z. Tseng).

The p2 protoconid is tall and conical, with a strong anterior cingulum. Its talonid has a tiny ridge shaped like a cusp, which is surrounded by a strong cingulum. The p3 is similar to the p2 but larger, with a strong cingulum and a talonid with a small central cusp. The p4 is much like that of other hesperhyines: a distinct paraconid, which can be connected to the protoconid (AMNH 12936) or not (AMNH 12937). The latter specimen has a small cusp placed lingual to the central talonid cusp, while the holotype (AMNH 12936) is too worn to tell.

The M1-3 are very similar to those of *H. vagrans*, in that there are four cusps on M1 and M2. Both the cusps on the trigonid, and on the talonid, are separated by a deep median valley and compressed anteroposteriorly. The cusp pattern of M3 is similar to that on M1 and M2, but with a large posterior lobe on the hypoconulid.

Discussion—As discussed above, many authors mistakenly assigned *D. pinensis* to *Hesperhys* because the latter taxon was only known from its fragmentary lower jaw and no upper teeth. In particular, the distinctive features of the skull and upper teeth of *H. vagrans* were

unknown until recently, and the striking differences in size, robustness, and inflation of the cheek teeth between the two genera were not apparent. A side-by-side comparison shows (Fig. 10) that these two taxa are strikingly different in many anatomical details, and there is no reason for considering them synonyms or even congeneric.

The possibility exists that the differences might be due to sexual dimorphism. As Wright (1991) showed, this can be ruled out because both the larger male and the smaller female canines are present in samples of both species. In addition, sexual dimorphism commonly occurs in areas of the skull such as the zygomatic arches and sagittal crests, but rarely are the cheek teeth so different in size and cusp inflation between males and females of the same species. Finally, all the known fossils of *D. pinensis* occur in the late Arikareean to early Hemingfordian, while *H. vagrans* is restricted to the late Hemingfordian-Barstovian, so there is a time gap (middle Hemingfordian) with no temporal overlap between the two taxa. If they were male and female morphs, there should be complete temporal overlap between them.

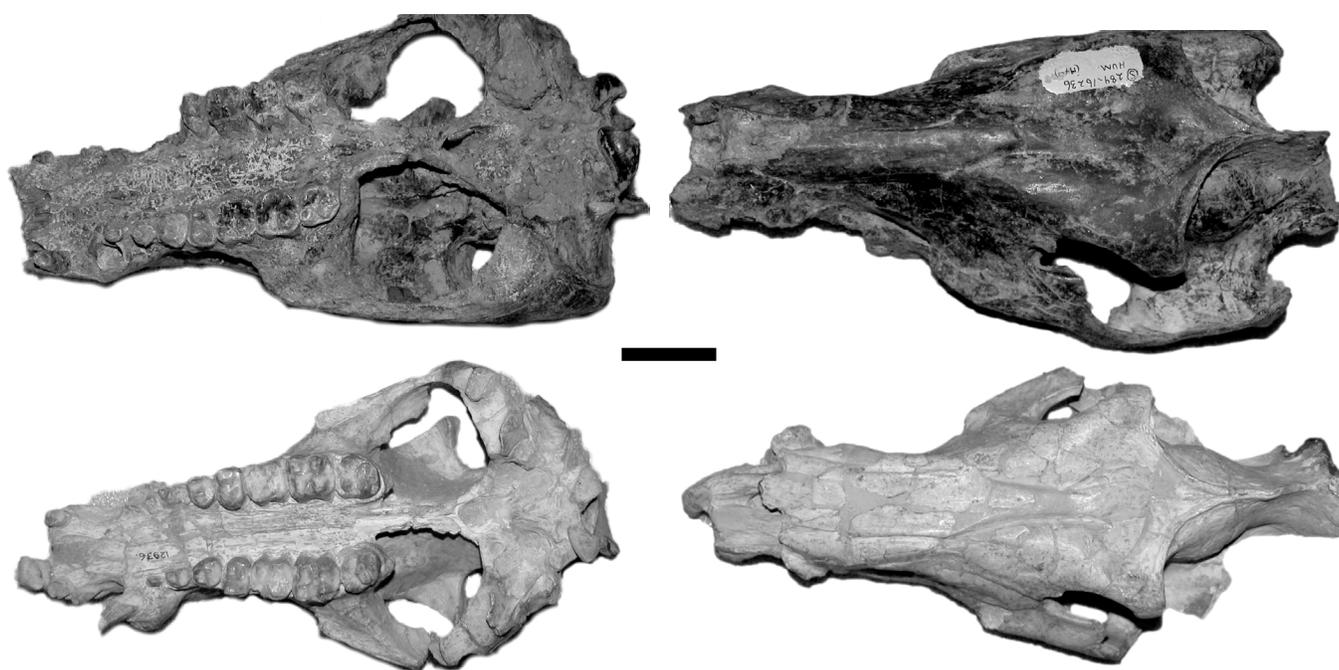


FIGURE 10. Comparison of F:AM 143840, referred skull of *H. vagrans* (top), with AMNH 12936, holotype of *D. pinensis* (bottom). Ventral views left. Dorsal views right. Scale bar = 5 cm.

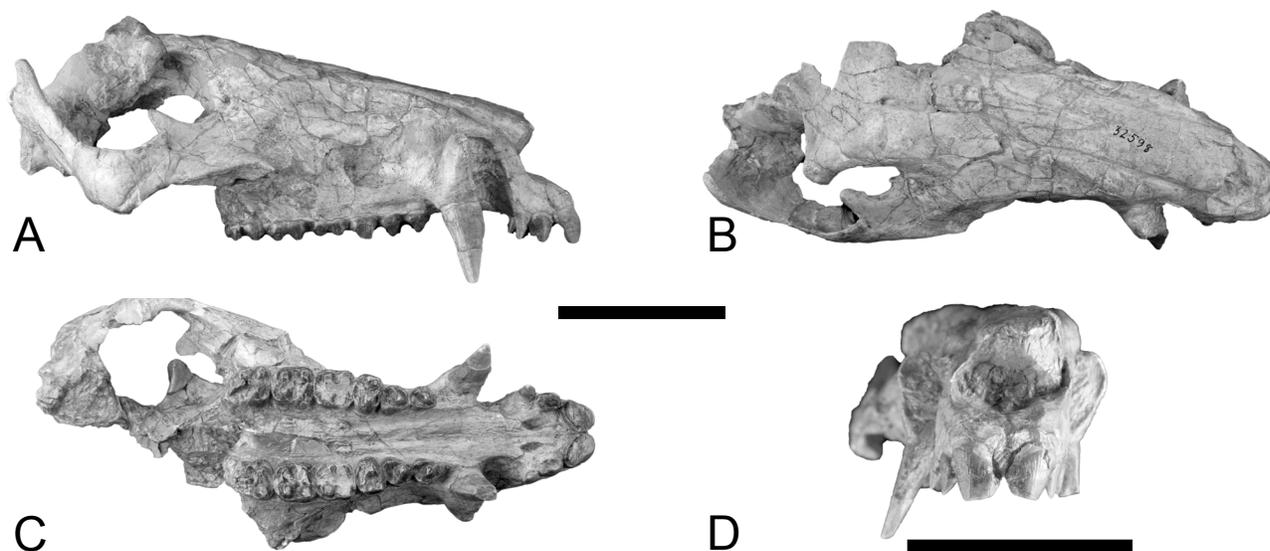


FIGURE 11. UCMP 32598, referred skull of *D. pinensis* from Flint Hill l.f., Batesland Formation, Bennett County, South Dakota. A, lateral view; B, dorsal view; C, ventral view; and D, anterior view. Scale bars = 5 cm. (Photos courtesy P. Holroyd and the UCMP).

***Desmathys pinensis* Matthew, 1907**

Figs. 9-11
Tables 1-4

Desmathys pinensis Matthew, 1907
Hesperhys pinensis Simpson, 1945
Hesperhys pinensis McKenna and Bell, 1997
Hesperhys pinensis Wright, 1991
Hesperhys pinensis Wright, 1998 (in part)
Hesperhys pinensis Albright, 1999

Type specimen—AMNH 12936 (Fig. 9A-G), nearly complete skull with left I2, P3-M3, right I1-3, C1, dP1, P2-m3, missing parts of the zygomatic arch; also partial left dentary with root of c1, p3-m2; from “upper Rosebud, 3 mi. E. of Rosebud [Shannon County, South Dakota]”. Considered to be latest Arikarean (Harrison Formation equivalent).

Hypodigm—“3 mi. e of Porcupine [Shannon County, South Dakota]”, latest Arikarean (may be the same as the type locality):

AMNH 12937, skull fragments including left and right M1, left M3, partial mandible with roots of left and right c1, left p3-4, right p2, m2; AMNH12939, lower jaw.

LACM locality 2003, Brezzina Ranch, Rosebud Formation South Dakota (earliest Hemingfordian): LACM 10977, partial skull with left and right canine, P2-M3, partial mandible with left and right i1-i3, c1, p2-m3. (Macdonald, 1963, p. 229; Macdonald, 1970, p. 74).

Flint Hill, Bennett County, South Dakota (Batesland Formation), earliest Hemingfordian (localities SDSM V-511, UCMP V-3417): UCMP 32598 (Fig. 11), partial skull with complete dentition, lacking braincase, occiput, choanal regions and right zygoma; partial mandible with complete dentition; partial skeleton.

Diagnosis—Same as for genus.

Description—Same as for genus.

Discussion—The distinction between this species and *H. vagrans* is discussed above, and there are many good lines of evidence to suggest that they are different genera and species. The distinction between *D. pinensis* and other hesperhyines is discussed below. *D. pinensis* appears

to be a smaller hesperhyine restricted to the latest Arikarean to early Hemingfordian of South Dakota, and found nowhere else.

***Wrightohyus* new genus**

Figures 12-13

Tables 5-8

Hesperhyus (in part) Wright, 1991

Type and only species—*Wrightohyus yatkolai*, new species

Diagnosis—Skull smaller than *Desmathyus* or *Hesperhyus*, with smaller canine buttresses. Narrower lingual cingula on P3. The p3 has two trigonid cusps, rather than one as in other hesperhyines.

Distribution—Late Arikarean to early Hemingfordian, Nebraska and Wyoming.

Etymology—In honor of David B. Wright, for his contribution to the understanding of peccary evolution. He first identified these specimens in the UNSM collections, and recognized their distinctiveness.

Description—(partially paraphrased from Wright, 1991) UNSM 62604 (Fig. 12A-D) is the most complete and least broken or distorted specimen of this new genus, and serves as the basis for this description. However, there is a sample of nearly complete skulls from the Runningwater Formation (Fig. 13), including UNSM 53620, UNSM 53617, and UNSM 125554, which show the range of variation of specimens from the same formation, and supplement this description.

The skull of UNSM 62604 (Fig. 12A-D) suffers from a slight amount of dorsoventral crushing, but is otherwise undistorted. The dorsal edge of the right zygomatic process, the postorbital process, and the ventral margin of the orbit have subparallel grooves on them that suggest rodent gnawing.

Skull: The skull is marked by a very flat dorsal profile, with sharp temporal crests over the temporal fossae. These temporal crests are perpendicular to the sagittal plane, extending medially from the robust postorbital processes. They then wrap around posteriorly to join with a sharp sagittal crest. There are a pair of supraorbital foramina and

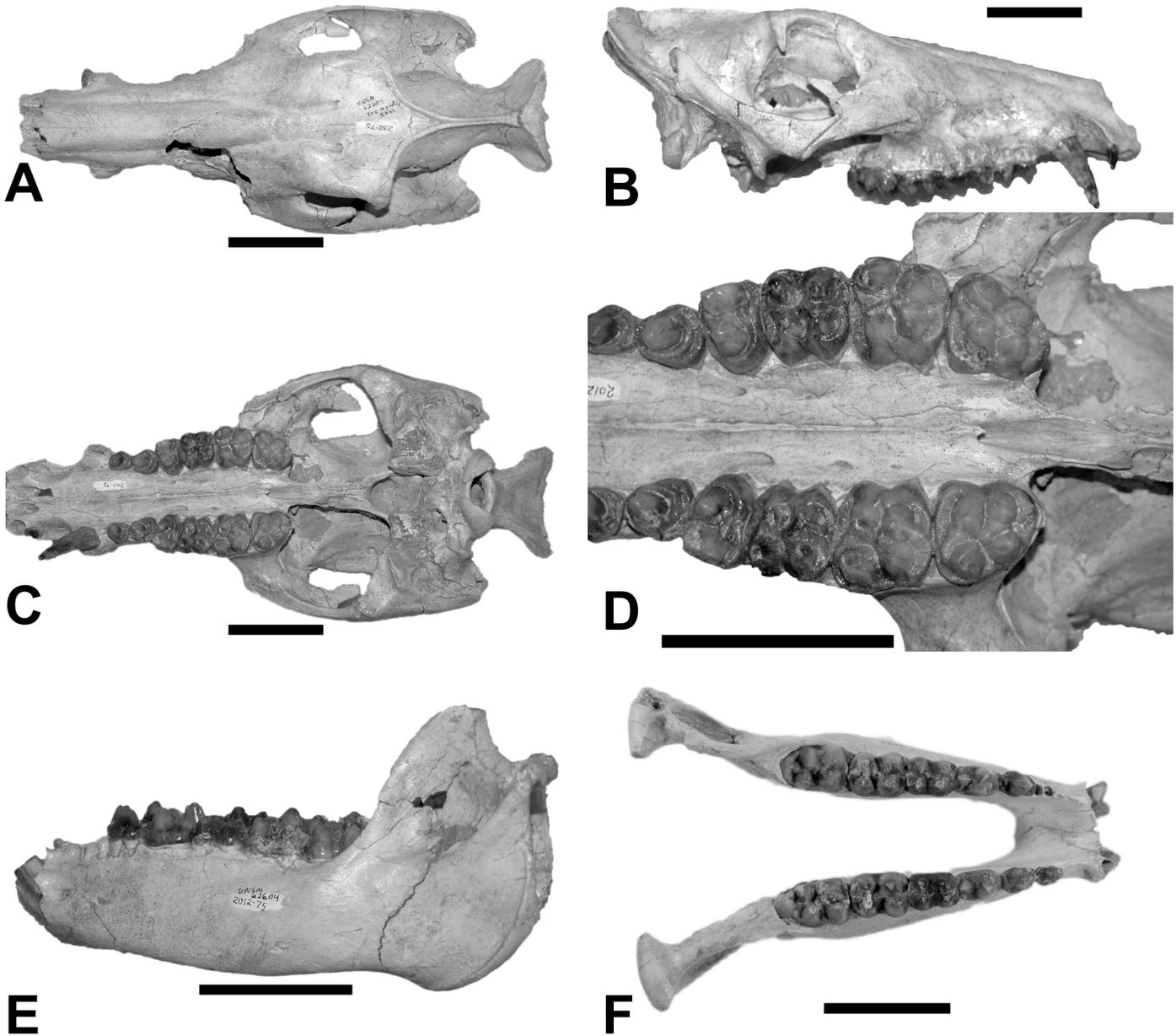


FIGURE 12. UNSM 62604, holotype of *Wrightohyus yatkolai*, new genus, new species. **A**, dorsal view of skull; **B**, lateral view of skull; **C**, ventral view of skull; **D**, close-up of cheek teeth; **E**, lateral view of jaw; and **F**, occlusal view of mandible. Scale bars = 5 cm. (Fig. 10F courtesy R. Secord).

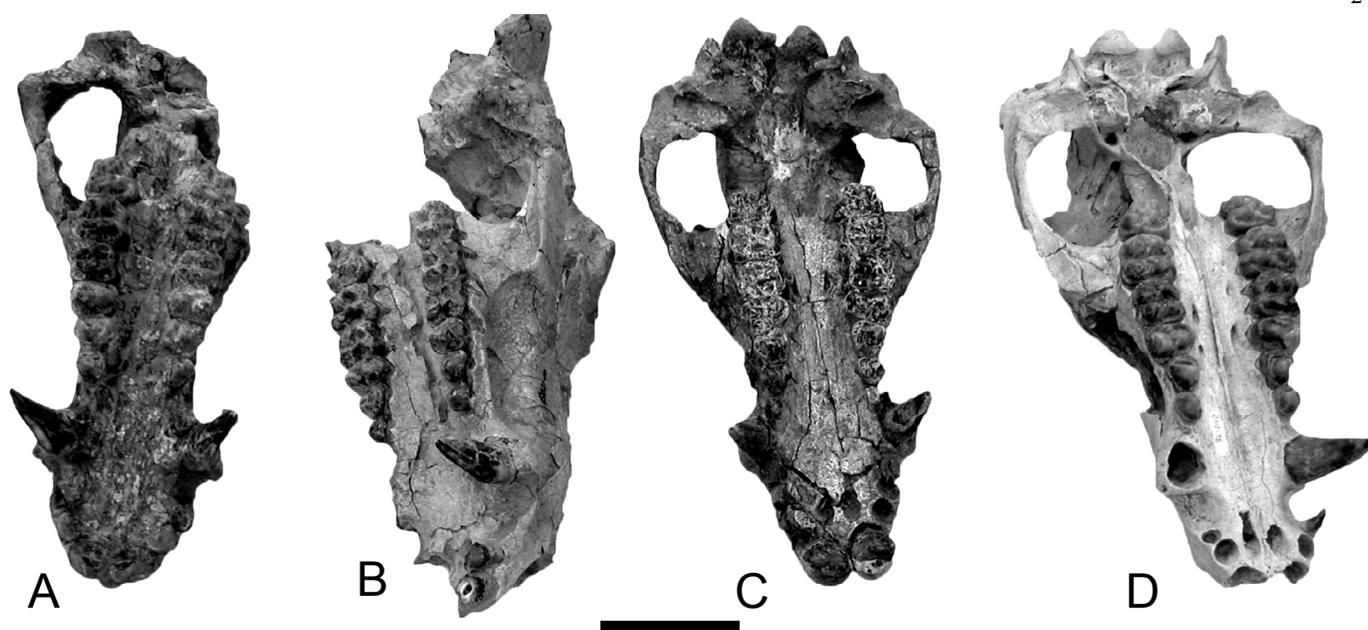


FIGURE 13. Sample of four skulls of *W. yatkolai* from the Runningwater Formation in the UNSM collections: **A**, UNSM 125554; **B**, UNSM 53617; **C**, UNSM 53620; and **D**, UNSM 62604 (holotype). Scale bar = 5 cm.

shallow canals over the orbit. There is a small lacrimal tubercle, which is dorsal to the single large lacrimal foramen. The front of the orbit is embayed ventral and lateral to the lacriman foramen, but not as deeply as in more primitive hesperhyines.

In palatal view (Fig. 12C), there are small incisive foramina. The anterior opening of the vomeronasal duct opens into the anterior wall of the incisive foramina. The anterior palatine foramina lie at the level of P4-M1. UNSM 62604 has a dorsoventrally deep tympanic process, and also a large posttympanic process of the squamosal. The inside of the posttympanic process touches the lateral surface of the auditory bulla. The posttympanic process has a shallow lateral sulcus, which does not connect with the glenoid fossa articular surface. UNSM 62604 has a long and sharply pointed paroccipital process. UNSM 62604 has a fan-shaped occiput. The medial tympanic crest joins with the nuchal crest on its lateral side.

The rest of the details of the nasal-choanal region were described in detail by Wright (1991, p. 69-71), and will not be repeated here.

Upper teeth: Most of the teeth of UNSM 62604 are lightly worn, since this is a subadult individual, allowing the details of crests and cusps to be seen. UNSM 62604 is missing I1 and I2. It has a caniniform I3, and a large C1 with a smooth enamel surface.

There is no evidence of dP1 or its alveolus. P2 has three roots, with an anteroposteriorly elongated oval shape in crown view. There are sharp anterior and posterior crests on the paracone. The strong posterolingual cingulum stretches to the anterior surface of the paracone. The cingulum is broad and lobate on its posterior edge, and it is composed of two concentrically arcuate cingula with sharp edges, with a small basin between them and the paracone. There is also a distinct labial cingulum. The P3 on UNSM 62604 is similar to P2 but larger. It bears a larger posterolingual cingulum, resulting in two distinct concentric circular crests. P4 has three roots as well, two on the labial side and a broad one on the lingual side. The enamel portion of the paracone is partially divided into two cusps. There is a large protocone with a small crest that branches anterolabially from the front surface. There is a small metaconule, and a robust cingulum around the entire P4.

The M1 on UNSM 62604 is nearly square in crown view, with four separate roots. There is slight anteroposterior compression on the lingual cusps, while the labial cusps are nearly conical. There is a paraconule crest extending from the protocone, separating that cusp from the paracone. In the median valley anterolabial to the hypocone lies the metacone. The hypoconule crest stretches posterolabially from the hypocone to the posterior cingulum. Except for the lingual side of the tooth, the cingulum is robust and surrounds the tooth crown. M2 is almost identical to M1 but larger. M3 is also like the other molars,

but narrow posterior crest extends from the back of the tooth. There is a metaconule between the metacone and hypocone, and another cusp anterior to it in the median valley. Compared to the other molars, the paraconule is much larger. The M3 of UNSM 62604 has a small hypocone.

Lower jaw and teeth: Associated with the skull of UNSM 62604 is a partial lower jaw which is nearly complete (Fig. 12E-F). It bears a short coronoid process and a small condyle which is narrow anteroposteriorly. On the temporal fossa there is a sharp ventral ridge. The symphysis is U-shaped and broad. There is a small, deep fossa on the medial surface of the ramus, next to the symphysis.

There are no incisors or canines, just broken roots in their alveoli. The p2 has two roots, with a tall triangular protoconid. From the apex of this cusp, a sharp ridge extends down the front to the base. There is a tiny anterior cingulum on the p2, at the tip of the anterior ridge. On the posterior side of the p2 there are two distinct ridges enclosing a sulcus. The labial ridge is sharp, but the lingual crest is weaker. Both crests connect the posterior cingulum, forming an enclosed basin.

There are two roots on p3 also. Sharp anterior and posterior crests run from the tip of the protoconid, and down to a strong, arcuate anteroicingulum. There is a small metaconid on the lingual surface of the protoconid. The p3 of UNSM 62604 has a low talonid, consisting of an arc-shaped posterior cingulum that encloses a small transverse cusp-like crest on the posterior crest of the protoconid. The p4 has four roots. It bears tall trigonid cusps which tower over the tooth crown. On the protoconid, there is a strong anterior crest that curves to the lingual side and ends in a small basal paraconid. On UNSM 62604, this configuration describes the right p4, but the left p4 has no paraconid and the anterolingual crest merges with the anterior cingulum. The p4 metaconid is pressed tightly against the protoconid. There are sharp narrow grooves on the posterior surfaces of both trigonid cusps. The low talonid bears a large central cusp encircled by an arc-shaped posterior cingulum.

On UNSM 62604, the m1 is four-rooted, with four main cusps. The biggest is the protoconid, with a small anterolingual accessory cusp. The metaconid has a posterolabial accessory cusp, which sits in the median valley. The m1 has a small hypoconulid, strong anterior and posterior cingula, and no labial or lingual cingula. The m2 is very similar to m1. There is a small anterolabial accessory cusp on the metaconid, and posterior grooves on both trigonid cusps. The lingual process of the hypoconid meets the entoconid, forming a weak crest. The m3 is like the m1 and m2, except that it has a large lobed hypoconulid.

Discussion—Wright (1991, p. 77-79) was the first to study the Runningwater Formation UNSM specimens (which he called "*Hesperhys cf. pinensis*"), and recognize that they were distinctly

different from the typical *Desmathyus pinensis* specimens from South Dakota. The sample of skulls (Fig. 13) from Nebraska all had large orbitomaxillary fossae, and pterygoid processes of the alisphenoid that meet the palate with a low angle, both characteristics of *D. pinensis* and *H. vagrans*. The UNSM skulls all have narrow plesiochoanal fossae, a feature found in *D. pinensis*, but a symplesiomorphy compared to the highly reduced fossa in *H. vagrans*. Thus, they are part of the *Hesperhys-Desmathyus* clade.

However, as Wright noted, they are different in several crucial ways. They are disjunctly smaller both in overall skull dimensions and especially in their teeth (Fig. 14). They have smaller canine buttresses (on both presumed male and female skulls, based on canine size), and narrower lingual cingula on P3. The lower jaws have two trigonid cusps on the p3, rather than one. Wright (1991) was unsure whether to distinguish these specimens, but the fact that they are consistently smaller in size, have distinct dental differences, and are found in Nebraska and Wyoming (while all specimens of *D. pinensis* come from South Dakota) supports the idea that they are distinct taxa.

The differences with *D. pinensis* are so slight that Wright (1991) was not inclined to separate it from *D. pinensis*. His solution to the problem was to lump all three morphs into a broadly construed concept of *Hesperhys*. However, as we have already seen, the differences between *H. vagrans* and *D. pinensis* are the most striking and distinctive in the entire subfamily, and the generic distinction is worth maintaining. The Nebraska-Wyoming specimens referred to *W. yatkolai* cannot be assigned to *Desmathyus*, because it has no derived characters shared with *D. pinensis* alone, only shared symplesiomorphies. Cladistically *W. yatkolai* is the sister-taxon of *D. pinensis* plus *Hesperhys vagrans*, and placing them in that same genus would make it paraphyletic (Fig. 3). Thus, a new name is required for the specimens recognized by

Wright as "*Hesperhys cf. pinensis*".

Wrightohyus yatkolai new species

Figures 12-13
Tables 5-8

Hesperhys cf. H. pinensis Wright, 1991

Type specimen—UNSM 62604, a skull and mandible, from UNSM locality Dw-140, Runningwater Formation (early Hemingfordian), Dawes County, Nebraska (Yatkola, 1978).

Hypodigm—(Fig. 13) *From the Runningwater Formation, early Hemingfordian, Dawes County, Nebraska*: "Bourdeaux Creek drainage system", UNSM locality Dw-143, Dawes County, Nebraska: UNSM 53620, skull; *From UNSM locality Dw-142*: UNSM 53617, skull; *From UNSM locality Dw-141*: UNSM 125554, skull; *From unspecified Runningwater-equivalent rocks*: AMNH 73701, partial skull with right M3, but most of skull anterior to M3 is missing, as are the auditory bullae and occiput; "Cottonwood Creek," Dawes County, Nebraska: F:AM 143844, partial mandible with left p3-m3.

From Runningwater equivalent rocks, Wyoming: "16-mile District," near Lusk, Wyoming: F:AM 1177077, partial rostrum with left I2-3, dP1, right I3-dP1; partial mandible with left and right i1-3, c1, p2-m3;

Diagnosis—Same as for genus.

Etymology—In memory of the late Dan Yatkola, who collected the type material, for his many contributions to the understanding of the mammals and stratigraphy of Hemingfordian.

Description—Same as for genus.

Discussion—Wright (1991) referred this material from Nebraska and Wyoming to *Hesperhys cf. pinensis*. As discussed above, the cladistic relationships of *H. vagrans*, *D. pinensis*, and the rest of the crown group dictate that this genus and species be given a new name, since referring these fossils to *Desmathyus* would make that genus paraphyletic, and clearly they are distinct from the species *pinensis* as well.

W. yatkolai was a disjunctly smaller (Fig. 14) hesperhyine (smaller than *D. pinensis* or *H. vagrans*) with narrower lingual cusps on P3, two trigonid cusps on p3, and smaller canine buttresses. It was restricted to Nebraska and Wyoming in the early Hemingfordian, while *D. pinensis* occurred in the late Arikarean and early Hemingfordian of South Dakota. Although these subtle differences from *D. pinensis* are not as dramatic as the differences from *H. vagrans*, nonetheless they seem sufficiently distinct, morphologically, temporally, and geographically, to merit a new genus and species.

Lucashyus new genus

Figure 15
Tables 5-8

Type and only species—*Lucashyus coombsae* new species.

Diagnosis—(modified from Wright, 1991, p. 80) A hesperhyine peccary, as defined by having a long cancellous anteroventral process of the auditory bulla, a large plesiochoanal fossa, broad posthamular part of the pterygoid, broad pterygoid process of the alisphenoid that joins the palate at a high angle, and a shallow orbitomaxillary fossa. It is distinct from other hesperhyines in having a large lacrimal tubercle, a U-shaped margin of the plesiochoanal fossa (V-shaped in more derived hesperhyines), and a narrow lingual cingulum of the P3.

Distribution—Late early Arikarean, eastern Wyoming.

Etymology—In honor of Dr. Spencer G. Lucas, in recognition of his many contributions to the study of Cenozoic mammals.

Description—In the collections of the Beneski Museum of Natural History at Amherst College is a beautiful skull and jaws (ACM 7035) collected in 1920 by Frederic Loomis' Amherst College field crew near Van Tassel, Wyoming (Fig. 15). It was recognized by Wright (1991, p. 80-89) as a distinct taxon, which he informally called the "Van Tassel species", and Wright also mentioned in his 1998 review paper. Since then, others (such as Dr. Robert Hunt of the University of Nebraska) have looked at the specimen, but it has never been described since its first mention in 1991, over 24 years ago.

Skull—(paraphrased from Wright, 1991) The skull of ACM 7035 (Figs. 15A-E) has undergone some lateral compression, and breakage on left side, but the right side is nearly complete and undistorted. It has distinct temporal ridges which converge medially on a sharp sagittal crest. There are distinct supraorbital foramina, with well-defined supraorbital canals. Below a large lacrimal tubercle and a large

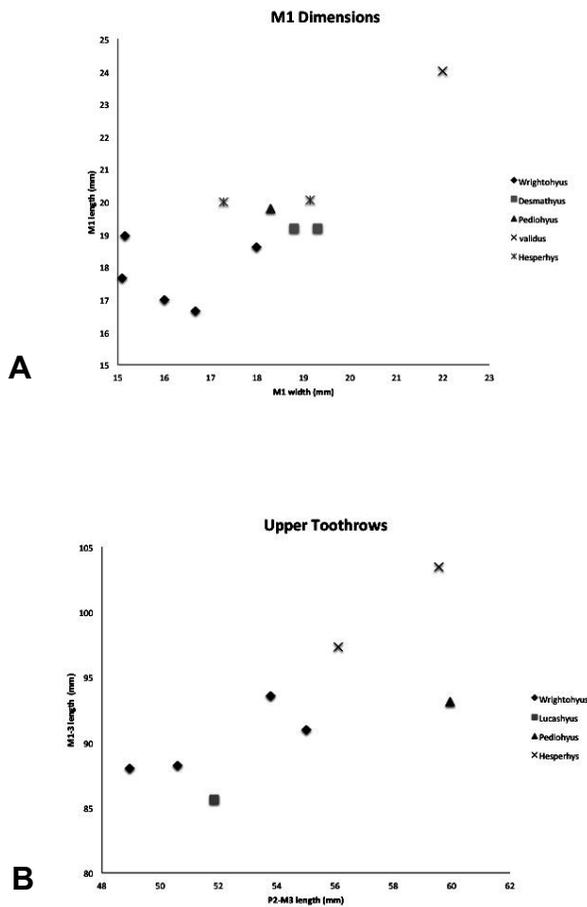


FIGURE 14. Plots of upper tooth dimensions of *Wrightohyus*, *Desmathyus*, *Pediohyus*, "*D.*" *validus*, and *Hesperhys*. **A**, upper M1 dimensions; **B**, plot of M1-3 vs. P2-M3 dimensions.

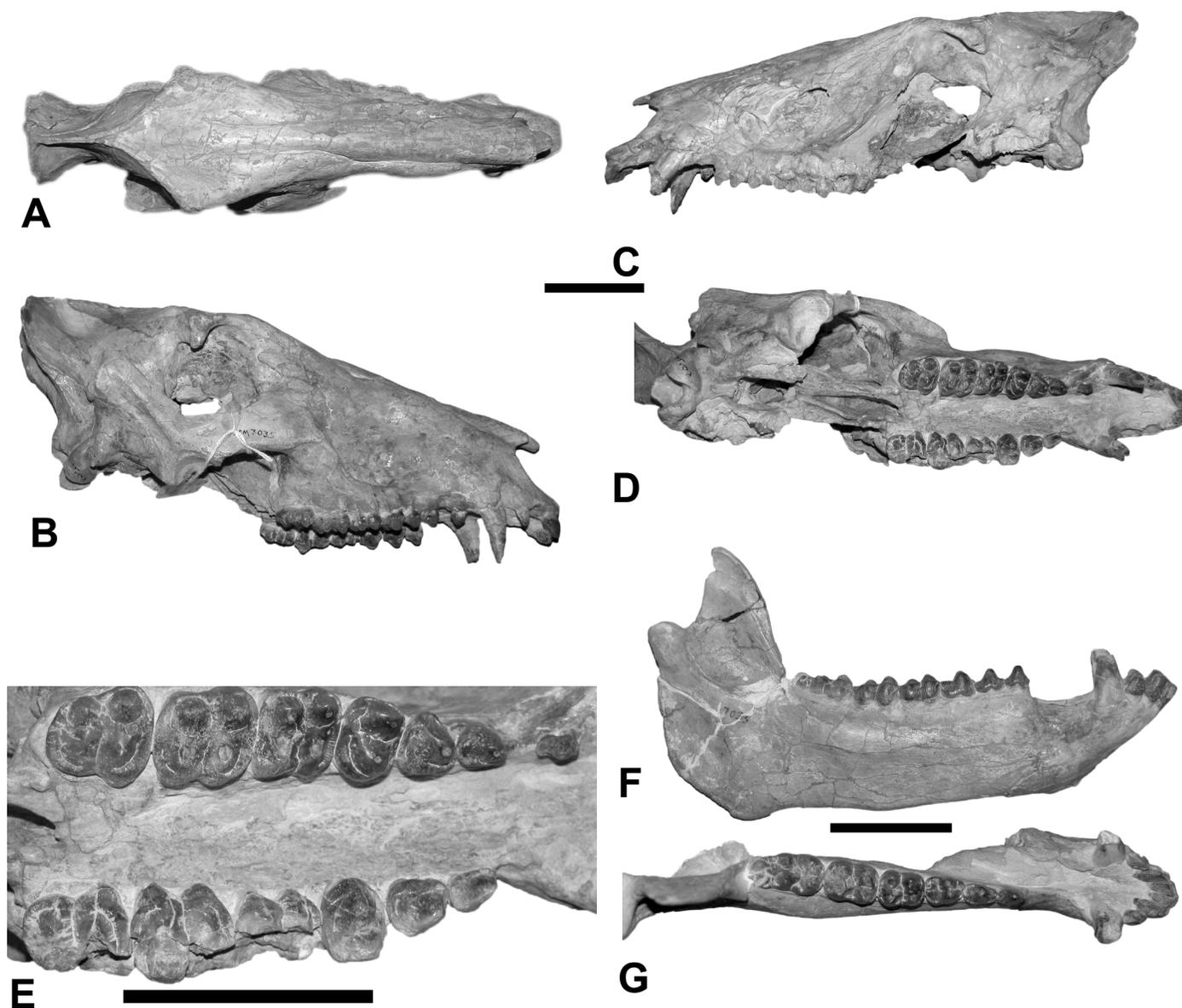


FIGURE 15. ACM 7035, holotype of *Lucashyus coombsae*. **A**, dorsal view; **B**, right lateral view; **C**, left lateral view; **D**, ventral view; **E**, close-up of occlusal view of teeth; **F**, jaw in lateral view; and **G**, occlusal view of lower teeth. Scale bars = 5 cm. (Photo A courtesy K. Wellspring).

lacrimal opening, the anterior margin of the orbit is excavated. ACM 7035 has a narrow zygomatic arch. A spur-like process on the lateral surface of the root of the zygoma separates a shallow pre-orbital fossa (attachment point for the rostral musculature) from a smaller, shallow masseteric muscle fossa on the anterior end of the ventral surface of the zygoma. The nasal incision has a smoothly curved posterior margin, and does not reach as far back as the canine buttress. ACM 7035 has a small canine buttress and precanine fossa. The infraorbital foramen is laterally compressed.

ACM 7035 has a kidney-shaped glenoid fossa, and dorsoventrally deep tympanic process. There is a distinct groove running along the lateral edge of this process, but does not meet the glenoid fossa. ACM 7035 has a massive, cancellous auditory bulla. From the anteroventral edge of the bulla stretches an elongate process, almost reaching the plane of the palate. This process is full of cancellous bone, and its anterior base touches the pterygoid processes of the alisphenoid, and isolates the foramen ovale on its lateral side. ACM 7035 has robust paroccipital processes. On the posttympanic process, the dorsal crest meets the nuchal crest. From the nuchal crest, there are sharp occipital crests than extend downward to the occipital condyles. The rest of the nasal-choanal region was described in detail by Wright (1991, p. 81-82), and will not be repeated here.

Upper teeth: ACM 7035 has a large first upper incisor, with small lingual cingulum. Only the alveolus of I2 remains. I3 seems to be a long, tapered caniniform tooth, although it is partially broken. The dP1 has two roots, and is elongated anteroposteriorly. It consists of a single cusp with sharp anterior and posterior crests, and a distinct lingual cingulum. P2 has two roots: a smaller anterior one, and a broad posterior root. The large paracone is partially surrounded by a cingulum around the base. From the paracone, a posterior crest reaches a raised process on the posterior cingulum. P3 has three roots: one anterior, and two posterior. It is very similar to P2 except that the posterolingual lobe of the cingulum is broader than it is in P2. This posterior cingulum has two concentric arcs, with the lingual one of these merging with the rest of the cingulum. P4 has three roots: two in the labial position, and a broad one on the lingual side. The P4 has a large paracone, protocone, and metacone, and a complete cingulum around the entire tooth.

The M1 and M2 of ACM 7035 are moderately worn, with transversely broad lingual cusps and conical labial cusps. The paraconule and metaconule are not between the bases of the paracone and metacone, but slightly posterior in position. The anterior and posterior cingula are strong, while the labial cingulum is faint and there is no lingual cingulum whatsoever. M3 is also somewhat worn, and similar to other molars, except the posterior part is narrower than the

anterior portion. Between the metacone and the hypocone is a small metaconule. It has a thick posterior cingulum, but no real basin or cusps in that area as some other peccaries have.

Lower jaw: The lower jaw of ACM 7035 consists of the right ramus and most of the symphysis, but missing the left ramus at the level of p2 (Fig. 13E). The right ramus is deep, narrow and bears a tall coronoid process. It has a deep temporal fossa, which is deeply excavated on the ventral edge, with a sharp ridge bounding it. The condyle is robust, and the symphysis is broken but broadly U-shaped.

The i1 and i2 are long and subspatulate. Unlike the condition in *Hesperhyus*, their bases are not deep dorsoventrally. The i3 is a triangular blade with weak lingual cingula. The c1 is a long tusk with a triangular cross section, showing wear on both its anterior and posterior surfaces where the upper I3 and canines would occlude with it.

The p2 has two roots, one anterior and one posterior. There are faint anterior and posterior crests on the paraconid of the p2 that slope steeply downward and outward to the bottom of the tooth. These produce concave curved profiles on the anterior and posterior surfaces of the p2. The protoconid bears a posterior crest which ends on a tiny talonid cusp. The anterior and posterior cingula are strong, but the labial and lingual cingula are weak. The p3 also has two roots. Its protoconid has steep sides, and its anterior crest projects at the base as a small anteroconulid, encircled by a weak anterior cingulum. The talonid on p3 bears a small transversely elongate cusp, surrounded by the posterior cingulum. The p3 has a robust labial cingulum, but a weak lingual cingulum. The p4 has anterior and posterior roots which are broader than those of the other premolars, and show varied degrees of separation on the labial and lingual side of the p4. This tooth has tall trigonid cusps, especially the protoconid, with its sharp anterior crest that descends sharply to meet a low paraconid. From the labial side of the protoconid extends a small anterior cingulum. The p4 has a low, transversely broad talonid, with a single large central cusp surrounded by a strong posterior cingulum. There are no cingula on the labial and lingual sides of the trigonid of p4.

The m1 and m2 show moderate wear in ACM 7035, with the typical arrangement of four principal cusps seen in most hesperhyines. The m3 is much like the m1 and m2, only it has a large hypoconulid process and two large cusps on the posterior cingulum.

Discussion—Wright (1991, 1998) recognized that ACM 7035 was a very primitive hesperhyine, distinct from any other named taxon in that it lacked many of the derived features of the more advanced hesperhyines, yet still had the unique conditions of the hesperhyine nasal-choanal region. Thus, it is the sister taxon to all the rest of the hesperhyines for which adequate skull material is known. According to Loomis' records, it was collected from the "Harrison Formation" in Van Tassel, Wyoming, making it early late Arikareean, and slightly older than most other hesperhyines which are known from the latest Arikareean (Anderson Ranch Formation of Hunt, 2002, formerly the "Upper Harrison" beds). This suggests that *L. coombsae* is slightly younger than *Stuckyhyus siouxensis* or specimens of *Desmathyus pinensis* from the latest Arikareean.

Lucashyus coombsae new species

Figure 15
Tables 5-8

Type specimen—ACM 7035 (Fig. 15), nearly complete skull and mandible with complete dentition. According to Loomis' records, it comes from the "Harrison Formation [early late Arikareean] near Van Tassel, Wyoming."

Referred specimens—AMNH 13771, a partial left dentary with p4-m3, collected from "the L'r Harrison, S. side Niobrara R., Van Tassel" by Olcott in 1908, may also be referable to *L. coombsae*. It is slightly smaller than the dentary of *L. coombsae* (ACM 7035) and *Stuckyhyus siouxensis*, but otherwise similar to ACM 7035. Since it comes from the same locality and same beds, it is likely that it is referable to *L. coombsae*.

Diagnosis—Same as for genus.

Etymology—In honor of Dr. Margery Chalifoux Coombs, for her many contributions to the study of fossil artiodactyls and other large mammals (especially those of the Miocene of North America), and her curation of the Amherst College collection that includes the material of this taxon.

Description—Same as for genus.

Discussion—As shown by Wright (1991), ACM 7035 is a distinct genus and species which had never been described or recognized

before. Thus, new generic and trivial names are required.

Stuckyhyus new genus

Figures 16-17
Tables 5-8

Thinohyus (*Bothrolabis*) Peterson, 1905

Desmathyus Matthew, 1907 (in part)

Desmathyus Pearson, 1923 (in part)

"*Thinohyus*" Wright, 1991 (in part)

"*Thinohyus*" Wright, 1998 (in part)

Type and only species—*S. siouxensis* (Peterson, 1905)

Diagnosis—Hesperhyine with a narrow plesiochoanal fossa, narrow posthamular part of the pterygoid, broad pterygoid process of the alisphenoid that joins the palate at a high angle, shallow orbitomaxillary fossa. It can be distinguished from other hesperhyines by its large lacrimal tubercle, and narrow lingual cingulum on P3.

Distribution—Early late Arikareean, Nebraska.

Etymology—In honor of Dr. Richard Stucky, for his contributions to the study of early artiodactyls (including peccaries), and for his long association with the Carnegie Museum, which houses the material of this taxon.

Description—Peterson (1905) provided a complete description of the skull and jaws of the holotype (Figs. 16-17). Wright (1991, p. 90-93) gave a more detailed description of the naso-maxillary region of CM 1423 (further diagrammed in Fig. 2). There is no need to reprint these descriptions, as they are more than adequate.

Discussion—Peterson (1905) first described this specimen, and referred it to the John Day genus *Thinohyus* Marsh, which it shares no derived characters with and does not resemble (based on the modern concept of *Thinohyus*; see Prothero, 2009). He also implied that it was part of a subgenus "*Bothrolabis*" Cope, even though "*Bothrolabis*" was never considered a subgenus of *Thinohyus*, it was regarded as invalid in Peterson's time, and hasn't been used since. Not only is this genus invalid, but it is based on material of *Thinohyus* (and some *Perchoerus*) which in no way resemble this specimen. Peterson's comparisons may have been so inappropriate because few other early peccary genera were known at the time, and the content of *Thinohyus* and "*Bothrolabis*" was very confused. The only other available genus in 1905 was Douglass' recently proposed (1903) taxon *Hesperhyus*. Although it was in the same collection, it was known only from a lower jaw, so Peterson did not compare skulls to it. After Matthew (1907) proposed the name *Desmathyus*, later authors shoehorned "*T. (B.) siouxensis* into *Desmathyus*, making that genus a taxonomic wastebasket. Finally, Wright (1991, p. 97; 1998) correctly argued that this taxon is not referable to any other hesperhyine genus known, and required a new genus, but he never got around to proposing a name for this taxon. As Wright (1991, 1998) showed, it is a distinct genus and species, more derived than *Lucashyus* (the "Van Tassel" specimen) but less derived than the crown clade of *Hesperhyus-Desmathyus-Wrightohyus* (Fig. 3).

Stuckyhyus siouxensis (Peterson, 1905)

Figures 16-17
Tables 5-8

Thinohyus (*Bothrolabis*) Peterson, 1905

Desmathyus siouxensis Matthew, 1907

Desmathyus siouxensis Pearson, 1923

"*Thinohyus*" *siouxensis* Wright, 1991

"*Thinohyus*" *siouxensis* Wright, 1998

Type specimen—CM 1423 (Figs. 16-17), a nearly complete skull with left and right P3-M3, missing parts of the auditory region and orbit; mandible with left p2-m3 and right c1, p2-m3. From "Upper part of the Harrison horizon on the upper Niobrara River, Sioux County, Nebraska" (Peterson, 1905, p. 308). Probably Anderson Ranch Formation of Hunt (2002) (= old "Upper Harrison beds"), latest Arikareean.

Hypodigm—CM 1418, partial skull, from "the Agate Spring Stock Farm" (collected by Harold J. Cook), also from the Agate bone bed level, Anderson Ranch Formation (latest Arikareean). Possibly additional material in the UNSM collections from the "Marsland Formation" *sensu* C.B. Schultz (early Hemingfordian).

Diagnosis—Same as for genus.

Description—Same as for genus.

Discussion—Even though it has been referred to many different incorrect genera in the past 110 years, the species *siouxensis* is valid, and there is no question that it is a distinct species, different from any

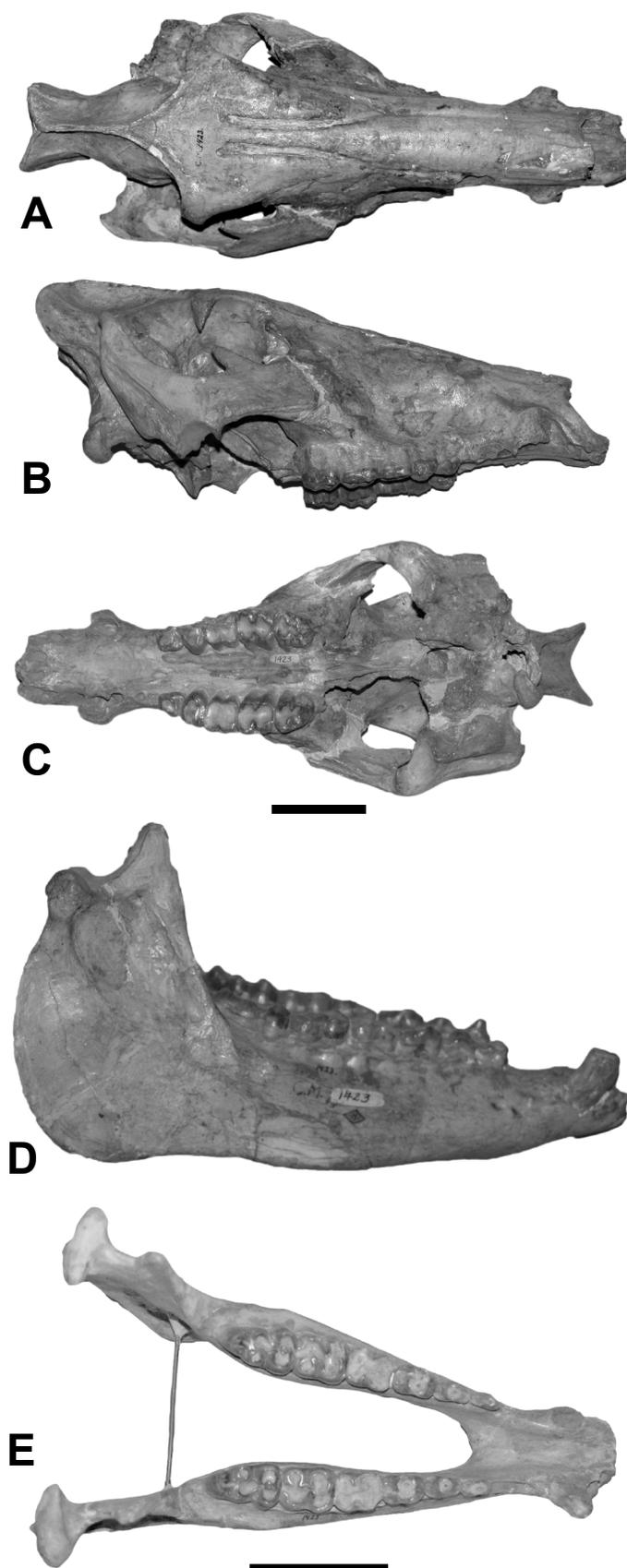


FIGURE 16. CM 1423, holotype of *Stuckyhyus siouxensis*. A, dorsal view; B, lateral view; C, ventral view; D, jaw in lateral view; and E, occlusal view of lower teeth. Scale bars = 5 cm.

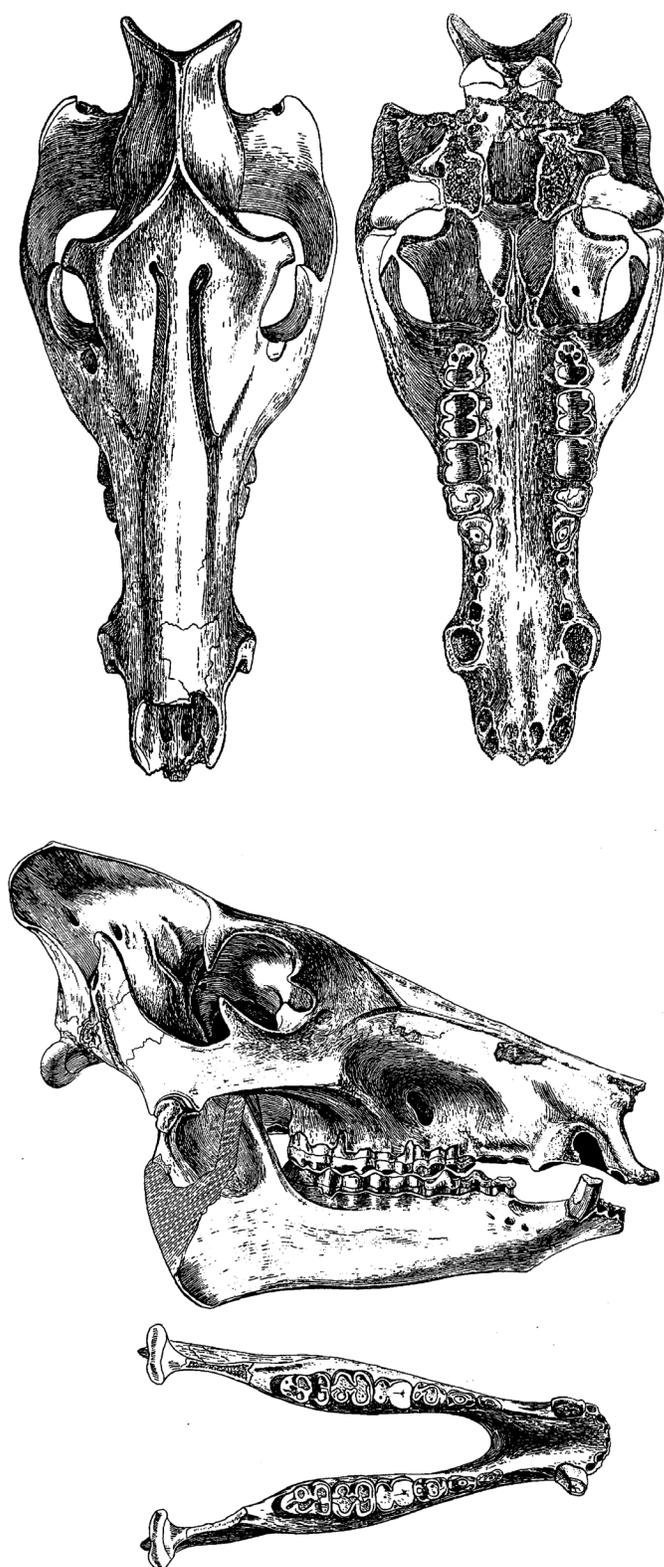


FIGURE 17. CM 1423, Peterson's (1905, Plates XXXIV and XXXV) original illustrations of the holotype of "*Thinohyus*" (= *Stuckyhyus*) *siouxensis*.

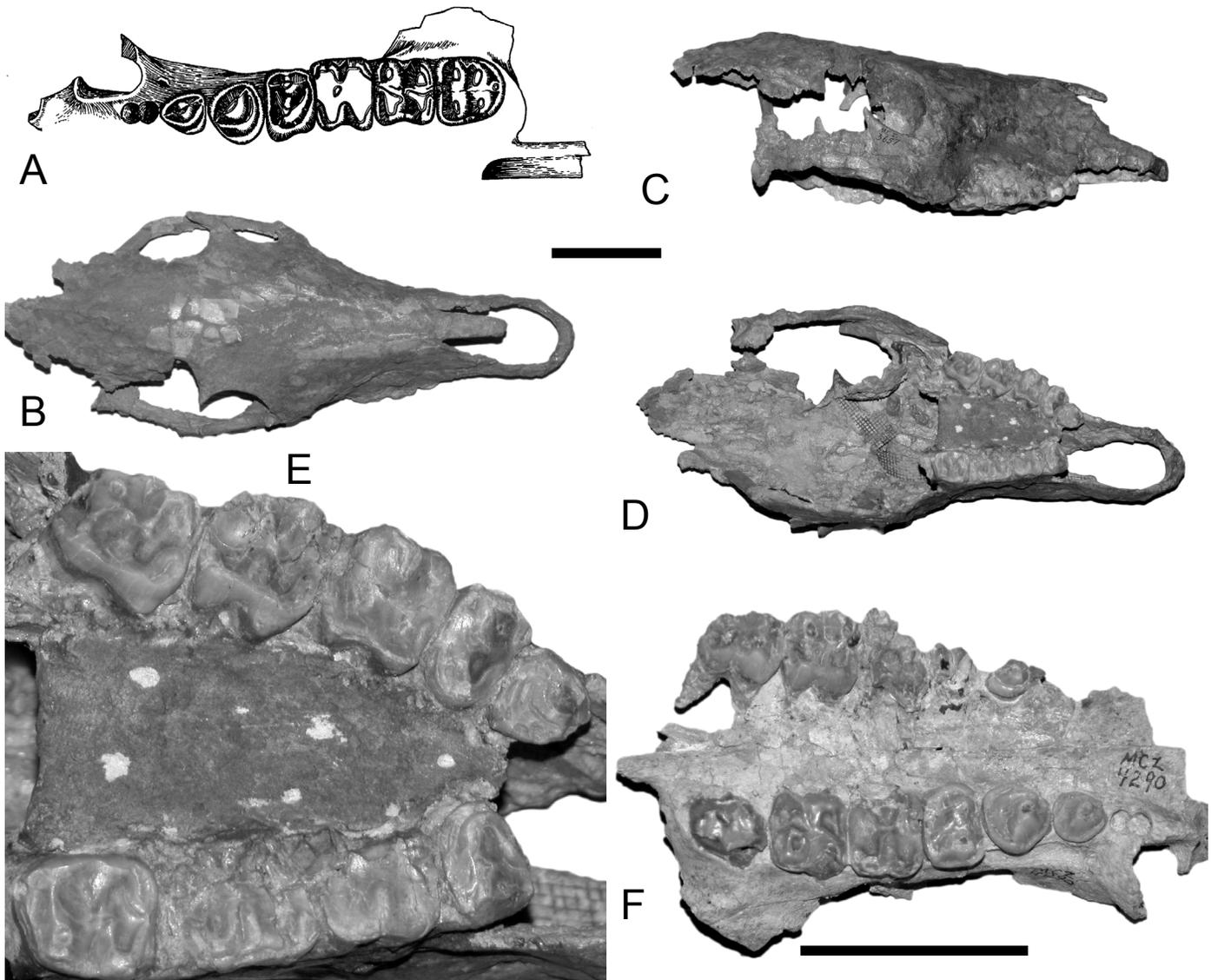


FIGURE 18. *Floridachoerus olseni* White, 1941. A, White's original illustration of the teeth of the holotype, MCZ 3657; B, holotype in dorsal view; C, lateral view; D, ventral view; E, close-up of cheek teeth; and F, MCZ 4290, referred palate (not the holotype). Scale bars = 5 cm.

other hesperhyine known.

***Floridachoerus* White, 1941**

Figures 18-19
Table 9

Floridachoerus White, 1941

Desmathyus Olsen, 1962

Desmathyus MacFadden and Webb, 1982

Floridachoerus Albright, 1999

Floridachoerus Wright, 1991

Hesperhyus McKenna and Bell, 1997

Floridachoerus Wright, 1998

Type and only species—*Floridachoerus olseni* White, 1941

Diagnosis—(Modified from Wright, 1991, 1998) A hesperhyine (as indicated by the narrow plesiochoanal fossa), having a P3 with a large lingual crescent in the protocone position, retaining the the broad pterygoid processes of the alisphenoid that join the palate at a high angle.

Distribution—Early Hemingfordian, Thomas Farm local fauna, Hawthorne Formation, Gilchrist County, Florida; late Arikareean, Toledo Bend local fauna, Newton County, Texas.

Description—White's (1941, p. 96) original diagnosis of the genus and species was as follows: "P3 as wide as long and more complex than in *Desmathyus*; P4 one and one half times as wide as

long; M1+2 as wide as long; M3 slightly longer than wide." Clearly, this definition is inadequate by modern standards, with no mention of the tooth crown morphology, and only relative tooth dimensions that are generally plesiomorphic and non-diagnostic.

Wright (1991) redescribed the MCZ material from White's Thomas Farm collection. Oddly though, he lists the wrong specimen as the holotype. It is MCZ 3657, a partial skull (Fig. 18A-E), not MCZ 4290, a crushed palate (Fig. 18F), as Wright (1991, 1998) claimed. In fact, Wright (1991) never mentions MCZ 3657 at all. I am not sure why a normally careful scientist such as David Wright would make this mistake. White (1941, p. 96) clearly stated that the holotype was MCZ 3657, and the Harvard specimen is clearly labeled as the holotype with the large red square as all MCZ holotypes are marked. In addition, MCZ 3657 is the largest and most complete of all the peccary specimens from the Thomas Farm drawers in the MCZ collections. Wright (1991) included photographs of other MCZ specimens, so he visited the collections. Those fossils have not been actively studied in a long time, so it's unlikely that MCZ 3657 was on display or on loan or otherwise missing from the collections. Wright (1991, p. 100) even calls another specimen, MCZ 7301, the "only skull." For whatever reasons, Wright's (1991) description is incomplete because he never mentions the features of the actual holotype.

White (1941, plate XIV, fig. 4, p. 99) published a tiny line sketch of the cheek teeth of the holotype, but did not show the rest of the specimen (Fig. 18A). MCZ 3657 actually consists of a partial skull

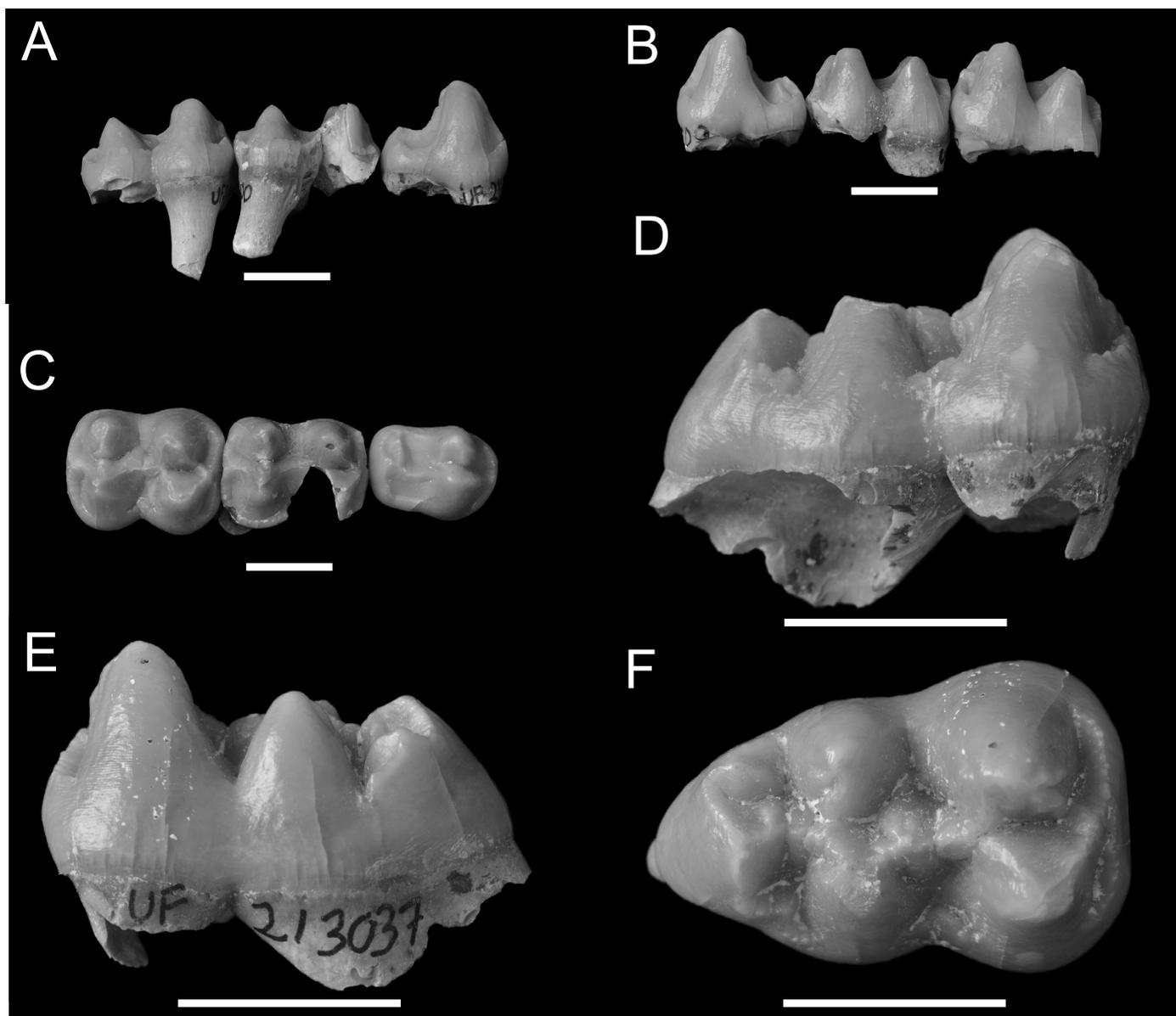


FIGURE 19. *Floridachoerus olseni*. Referred lower teeth in the UF collections. **A**, UF211500, p4-m2 in lateral view; **B**, same specimen in medial view; **C**, same specimen in occlusal view; **D**, UF 213037, isolated m3 in lateral view; **E**, same specimen in medial view; and **F**, same specimen in occlusal view. Scale bars = 1 cm. (Photos courtesy R. Hulbert and the UF Museum).

(Fig. 18B-D) that was apparently crushed flat (like most Thomas Farm specimens). It was then reconstructed with some kind of wire mesh reinforcement on the inside and a lot of plaster and paint, so the cranium looks like a distorted balloon. It's hard to tell what is original bone and what is reconstructed. The frontal, temporal and nasal regions are apparently mostly real bone, but it is clear that they were highly broken and distorted, so it is difficult to say much about their anatomy with confidence.

There is a distinct short pair of nasals broken at the tip, and a short nasal incision that apparently reaches back to the level of the I3 or canine. The premaxillaries have been mostly reconstructed, and reinforced with a lot of wire and plaster, so they now form a looping pattern across the front of the rostrum that is not based on real fossil bone. The orbital region was also badly broken and reconstructed, but there is a clear pointed postorbital process rising from the mostly reconstructed zygomatic arch, and portions of the temporal part of the skull curving posterolaterally behind the orbit on its posterodorsal edge. The rest of the orbit and the lacrimar region are too poorly preserved to interpret with any confidence.

In ventral view (Fig. 18D), all of the basicranium and occipital region are missing from the holotype. The bulk of the premaxillary

region and all the anterior teeth are missing as well. Only the palate and cheek teeth are adequately preserved. These are described below.

Wright (1991, p. 100) mentioned another skull (MCZ 7301) which is completely crushed laterally, so only a few parts of the anatomy can be interpreted. There are also a few skull features preserved in MCZ 4290, a crushed palate (Fig. 18F), which Wright (1991, p. 99-100) mistakenly identified as the holotype. Most of the preserved features are those found in the rest of the Hesperhyinae. The temporal lines merge posteriorly onto what would have been a sagittal crest. The canine buttresses are small in MCZ 7301, but slightly larger in MCZ 4290, a crushed palate. MCZ 7301 has a narrow plesiochoanal fossa, which begins at the level of posterior M3, although that is tricky to judge given the poor preservation. In MCZ 4290, the plesiochoanal fossa opens at the level of M3, and the plesiochoanal chamber does not extend beyond the anterior margin. In MCZ 7301, the pterygoid processes of the alisphenoid are relatively broad, such as in *S. siouxensis* but not like the condition in *Hesperhys*. There are no pterygoid bones preserved, but the glenoid fossa is on the level with the ventral side of the auditory bulla. MCZ 4290 has a robust postglenoid process, but the lateral sulcus for the tympanic process is not sharply distinct from the articular surface of the glenoid fossa, a condition seen in *S. siouxensis*.

The upper dentition can be described from the holotype, MCZ 3657 (with very worn teeth), the crushed palate, MCZ 4290 (the specimen with the least worn teeth), as well as the teeth on the laterally crushed skull, MCZ 7301. None of the incisors or canines are preserved on any specimen, but dP1 had a pair of roots, judging from the alveoli. P2 has a large paracone, with a broad posterolingual cingulum which has two concentric arc-shaped crests. These extend forward and merge with the front part of the paracone. The P2 has a robust labial cingulum, with a small transverse crest in the basin formed by the cingulum. P3 is also dominated by a large paracone, with a shallow groove on the posterior side which borders a small cusp-like metacone. On the lingual lobe of the tooth, there are two concentric arc-shaped crests of the cingulum. The labial crest is thicker and taller than the lingual crest. There is also a robust labial cingulum. The P4 has a large paracone and protocone, the latter with strong anterolabial and posterolabial crests. The P4 is completely surrounded by a robust cingulum. All three molars are very similar to the standard condition found in all hesperhyines, with four discrete cusps in a square, the lingual cusps being more transversely elongate than the labial cusps, and a strong valley between the anterior and posterior rows of cusps.

The lower teeth are preserved in a few broken ramal fragments in the MCZ collection, plus in some isolated teeth in the UF collection (Fig. 19). No incisors are known, nor is p2, but the lower canines have the classic triangular tusk-like shape. The p3 has a tall protoconid, and moderate anterior cingulum, which meets the weak posterior crest of the protoconid. The p4 in all cases is usually very worn, so it is difficult to interpret. It apparently had a small paraconid, and a talonid with a single central cusp.

The m1 is well preserved on MCZ 7302, and it approaches the zygodont morphology seen in some other hesperhyines, as well as other genera of peccaries, such as *Platygonus* (Prothero and Grenader, 2012). As in other zygodont peccaries, the posterolingual crest of the protoconid meets the posterolabial crest of the metaconid, forming the beginnings of a transverse loph. The metaconid is transformed into an anteroposteriorly elongated cusp, which connects the hypoconid to the trigonid cusps. The m2 is similar, as is the m3. On the m3, there is a large hypoconulid lobe bearing two cusps.

Discussion—Even though White's (1941) description was inadequate, the type specimen and enough other specimens clearly show that *Floridachoerus* is a well-defined genus that can be distinguished from any other peccary. There is no justification for reducing it to synonymy with *Desmathyus*, as Olsen (1962) and MacFadden and Webb (1982) argued, or with *Hesperhyus*, as McKenna and Bell (1997) suggested. This is especially true now that *Desmathyus* is clearly defined, and distinguished from all the other hesperhyines lumped into this genus. *Floridachoerus* is a much more primitive genus, part of a trichotomy with *S. siouxiensis* and the crown clade of *Hesperhyus*, *Desmathyus*, and *Wrightohyus* (Fig. 3). Yet it has derived features which distinguish it from *Lucashyus* and other more primitive hesperhyines.

Floridachoerus olseni White, 1941

Floridachoerus olseni White, 1941

Desmathyus olseni Olsen, 1962

Desmathyus olseni MacFadden and Webb, 1982

Floridachoerus olseni Albright, 1999

Floridachoerus olseni Wright, 1991

Floridachoerus olseni Wright, 1998

Type specimen—MCZ 3657, a partial skull (Fig. 18B-E), from the Thomas Farm locality, Gilchrist County, Florida (early Hemingfordian) (*contra* Wright, 1991, 1998).

Hypodigm—*Thomas Farm local fauna*: MCZ 4290, palate; MCZ 7301, crushed skull; MCZ 7303, right M3; MCZ 7306, right lower canine; MCZ 7305, right p3-4, m1; MCZ 7302, right dentary fragment with left m1; MCZ 7304, right m3. Further collection of the Thomas Farm locality by the Florida Museum of Natural History over the decades since White worked the locality for Harvard produced 53 additional specimens, mostly isolated teeth and postcranial fragments (e.g., Fig. 19). The complete listing can be uploaded at the Florida Museum of Natural History online catalogue (http://www.flmnh.ufl.edu/scripts/DBs/vp_uf_pub.asp).

Diagnosis—Same as for genus.

Description—Same as for genus.

Discussion—As Wright (1991, p. 103) noted, the Thomas Farm quarry sample is all from a restricted geographic location and probably a limited temporal interval, so it gives us some idea of variation within

a population or a species. Thus, we have presumed sexual dimorphism in the canine buttresses (large in MCZ 4290, small in MCZ 7301), and some other variations in the cusp morphology between samples as well. However, the sample is still very small compared to the samples and their individual variability, as discussed by Colbert (1938), Simpson (1949), Wright (1991), and Prothero and Grenader (2012).

Marshochoerus, new genus

Figure 20

Thinohyus Marsh, 1875

Palaeochoerus Cope, 1879

Thinohyus (*Bothrolabis*) Merriam and Sinclair, 1907

Perchoerus Matthew, 1909 (in part)

Cynorca Woodburne, 1969

"*Cynorca*" Wright, 1991

"*Cynorca*" Wright, 1998

Type and only species—*Marshochoerus sociale* (Marsh, 1875)

Diagnosis—Smallest of all the hesperhyines (see Tables 5-8); narrow plesiochoanal fossa; retains P3 with a narrow lingual cingulum.

Description—Descriptions and illustrations of nearly all the known material of this taxon were given by Woodburne (1969, p. 289-297), and need not be repeated here. Some of the most important images for reference are shown in Fig. 20. Wright (1991, p. 104-106) described the maxillopalatine labyrinth of UCMP 66862 (Fig. 20B,C), so that description also does not need to be repeated.

Distribution—Late Arikareean, John Day Formation, Oregon; early Hemingfordian, Garvin Gully local fauna, Oakville Formation, Grimes County, Texas; and late Hemingfordian, Phillips Ranch local fauna, Kinnick Formation, Kern County, California (*vide* Woodburne, 1969, p. 289). Wright (1991) regarded only the John Day specimens as referable to this taxon, and the others as indeterminate.

Etymology—In honor of Othniel Charles Marsh, who first recognized and named *M. sociale*.

Discussion—The genus *Cynorca* was proposed by Cope (1867) for a motley collection of fragmentary fossils collected by James T. Thomas from the "Yorktown beds" (probably early Miocene) near the Patuxent River, Charles County, Maryland. As Gazin and Collins (1950, p. 17-18), Woodburne (1969, p. 287-289) and Spamer et al. (1995, p. 244-245) have documented, the genus has been a taxonomic nightmare.

Thinking the upper canine was referable to a cetacean, Cope (1867) originally and incorrectly referred it to the whale genus *Squalodon*, as *Squalodon proterva*. Then he renamed it "*Cynorca*" (dog-orca) as a replacement for *Squalodon*, still thinking he had an orca or "killer whale". But in the same collection he had obvious peccary cheek teeth, which Cope referred to the modern genus *Dicotyles*, and called those specimens *D. torquatus*. Unfortunately, the type collection includes specimens that are not tayassuids (sharks, teleosts, turtles, crocodiles, and cetaceans). For many years, there was confusion about which specimen is the holotype, and other problems associated with basing a taxon on isolated tooth fragments of unknown association. If the name *Cynorca* can be made valid at all, Woodburne (1969) concluded that the lectotype specimen of *Cynorca proterva* Cope, 1867, is an isolated upper canine tusk, ANSP 11543a, and the syntypes includes about nine other ANSP Cope specimens that are clearly tayassuid (Woodburne, 1969, p. 298). Woodburne (1969) then restricted *Cynorca proterva* to similar-sized fragments of tiny peccaries from all the coastal plain Miocene beds of the Chesapeake Bay region. Since then, *Cynorca* became a taxonomic wastebasket for all tiny peccaries from the Arikareean and Hemingfordian anywhere in North America (and now even in Panama, according to MacFadden et al., 2010). In most cases, the only criterion for calling a specimen "*Cynorca*" is shared primitive similarity of cusp morphology, and tiny size.

However, Wright and Eshelman (1987) argued that this type material of *C. proterva* is not diagnostic of a single taxon, and that it could represent any one of four tayassuid taxa known from that time period. Thus, "*Cynorca*" is now considered a *nomen dubium*, a point further emphasized by Wright (1991, 1998). All of the tiny peccaries that were lumped into "*Cynorca*" based on their tiny size and shared plesiomorphic cusp features must be given new genera. In his papers, Wright (1991, 1998) indicated this by placing "*Cynorca*" in quotation marks as an invalid taxon, and pointed out that the species of "*Cynorca*" all needed new generic assignments, since they are a polyphyletic assemblage.

Wright (1991) also showed that the best material of Marsh's species referred to "*Cynorca*" *socialis* is part of the hesperhyine clade,

based on derived features of the maxillo-palatine region of UCMF 66862 (Fig. 20B, C). On the other hand, Wright (1991, 1998) argued that the new material of the skull region of specimens referred to other peccaries, such as "*Cynorca*" *occidentale*, show they are not hesperhyines. "*Cynorca*" *occidentale* is a sister-taxon to the crown group of the Tayassuinae. Thus, it is time to finally break up the polyphyletic wastebasket of "*Cynorca*" and get rid of the name for good, even though people have resisted abandoning this old and popular name which became a convenient taxonomic wastebasket for any tiny early Miocene peccary. Marsh's species *socialis* is a hesperhyine, and thus relevant to this paper. I will deal with the other material called "*Cynorca*" in future papers.

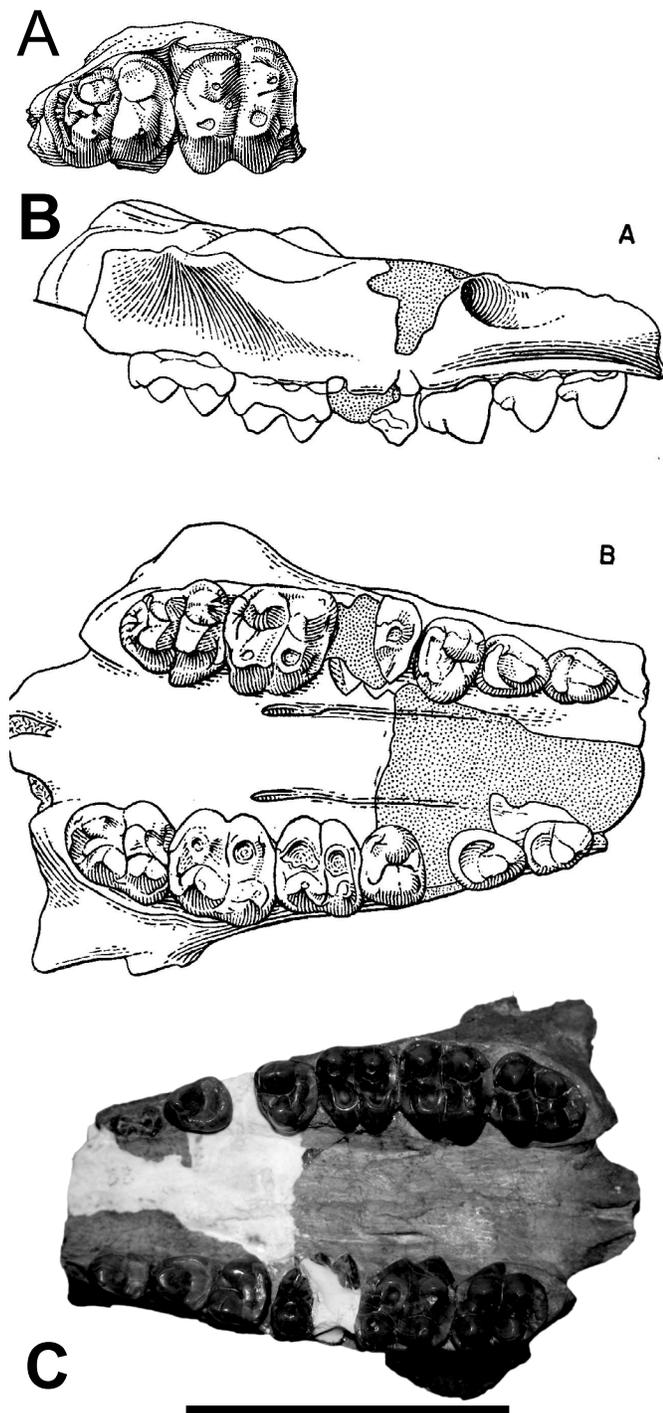


FIGURE 20. *Marchochoerus socialis*. A, YPM 11785, holotype M1 and M2. (From Woodburne, 1969, Fig. 1); B, Drawings of the UCMP 66862, a nearly complete referred palate (From, Woodburne, 1969, Fig. 2); and C, Photograph of UCMP 66862. Scale bar = 5 cm.

Marchochoerus socialis (Marsh, 1875)

Figure 20

Thinohyus socialis Marsh, 1875
Palaeochoerus socialis Cope, 1879
Thinohyus socialis Stehlin, 1899
Thinohyus socialis Sinclair, 1905
Thinohyus (Bothrolabis) socialis Merriam and Sinclair, 1907
Perchoerus socialis Matthew, 1909
Cynorca sociale Woodburne, 1969
"*Cynorca*" *sociale* Wright, 1991
"*Cynorca*" *sociale* Wright, 1998

Type specimen— YPM 11785, associated right and left M2-M3 (Fig. 20A), from the John Day beds (level unknown, but presumed to be late Arikareean).

Hypodigm—John Day material listed by Woodburne (1969, p. 289). Woodburne also included material from the early Hemingfordian Garvin Gully local fauna of Texas, and the late Hemingfordian Phillips Ranch local fauna of California in his hypodigm. Wright (1991) rejected these latter specimens as undiagnostic.

Diagnosis—Same as for genus.

Description—All the known material was well described by Woodburne (1969, p. 289-297), and need not be repeated here. The measurements of these specimens are also given by Woodburne (1969), so they will not be repeated, either.

Discussion—As outlined above, Marsh's (1875) *Thinohyus socialis* has had a complex history, most recently being referred to the now-invalid genus "*Cynorca*". The more diagnostic material of Marsh's species cannot be referred to the much more primitive early Arikareean genus *Thinohyus*, nor to the White River genus *Perchoerus*, nor to the invalid combination *Thinohyus (Bothrolabis)* (see above). No other valid generic name has been proposed for this material, so a new name is required (as Wright, 1991, 1998, noted). Thus, this species is assigned to the new genus *Marchochoerus* in honor of the man who first named and recognized it

TAXA OF UNKNOWN AFFINITIES

Pediohyus ferus Loomis, 1910

Figure 21

Loomis (1910) described a badly broken skull and right ramus (ACM 2047) as *Pediohyus ferus* (Fig. 21). It was reportedly from "The Breaks" about two miles south of Rawhide Buttes in Converse County, Wyoming, and supposedly from the "Sandstone of the Upper Harrison beds". This locality information suggests that it is late Arikareean, either from the Harrison Formation *sensu stricto*, or from the latest Arikareean Anderson Ranch Formation of Hunt (2002) (formerly known as the "Upper Harrison beds" of most authors, and the unit which yields the famous Agate Springs fauna).

ACM 2047 consists of a badly crushed skull with only the right P2-M3, all of which are highly worn down to the roots, and the incisors and canine (Fig. 21A), and associated right ramus. The skull is so distorted and cracked and crushed that almost nothing can be said about its anatomy, and the crown pattern of the cheek teeth is completely worn away, so there are almost no diagnostic characters that would separate it from other hesperhyines. About the only criterion available is the size of the teeth, and in that regard, it falls between the cluster of other large peccaries here referred to *Hesperhys vagrans* and *Desmathyus pinensis* (Fig. 14). I cannot tell whether *Pediohyus ferus* Loomis, 1910, is a junior synonym of *Hesperhys vagrans* Douglass (1903), or a senior synonym of *Desmathyus pinensis* Matthew (1924). Thus, *Pediohyus ferus* is best regarded as a *nomen dubium*. It cannot be clearly assigned to any of the other hesperhyines described in this paper.

CONCLUSIONS

A phylogenetic tree of the hesperhyine peccaries is shown in Fig. 22. Contrary to the old notion of one genus (*Hesperhys*) or two genera (*Hesperhys* and *Desmathyus*) of peccaries during the late Arikareean-Hemingfordian, this research now shows that they were actually quite diverse, with numerous overlapping genera and species through this time interval. Four of the genera overlap in the late Arikareean, three of which are known from the High Plains of South Dakota and Nebraska and one which is found mostly in the John Day beds of Oregon. Three taxa also overlap in the early Hemingfordian, two from the High Plains, and one from Florida. Finally, the late Hemingfordian and early

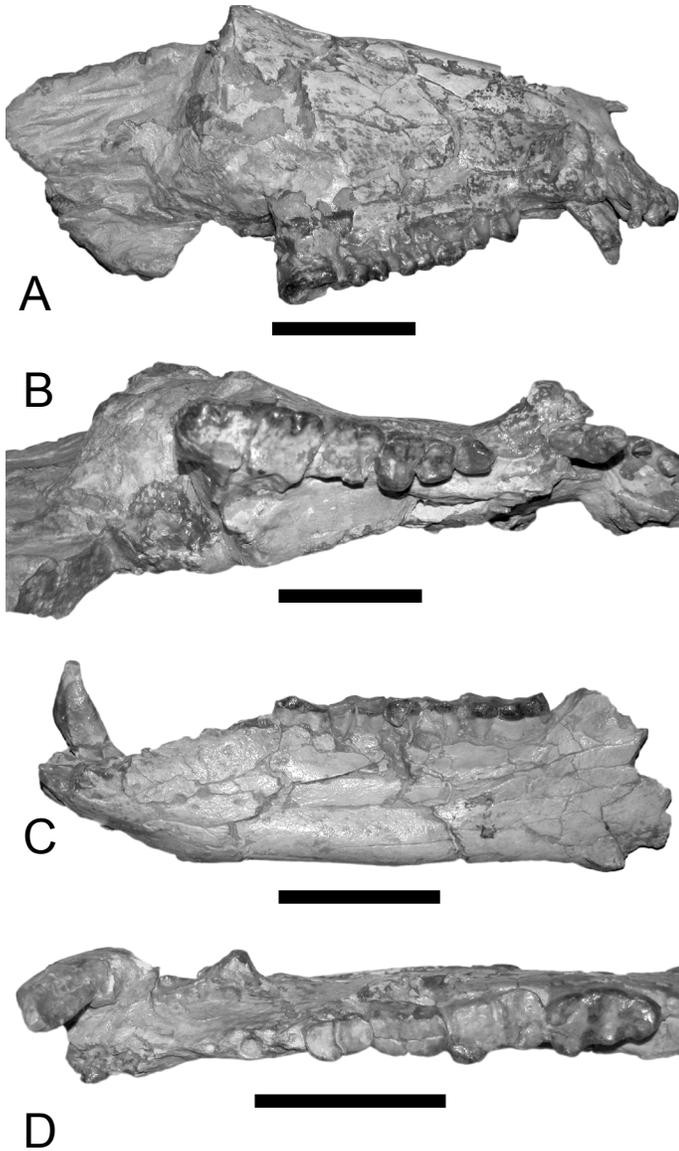


FIGURE 21. *Pediohyus ferus*, ACM 2047, holotype. **A**, lateral view of skull; **B**, ventral view of skull; and **C-D**, lower ramus. Scale bars= 5 cm.

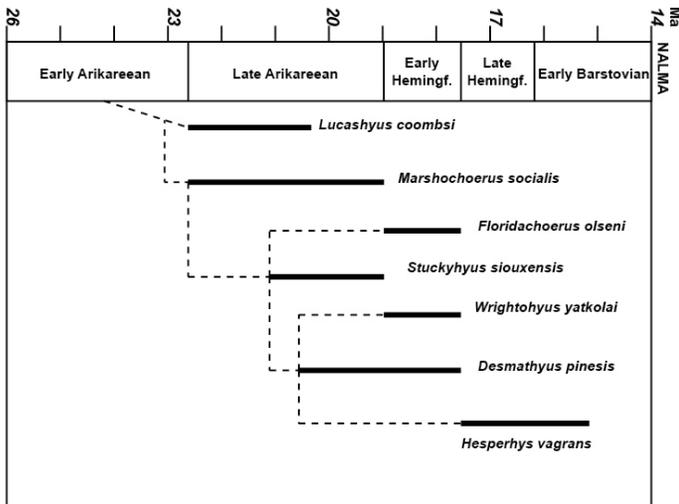


FIGURE 22. Phylogenetic tree of the hesperhyine peccaries. Time scale after Wright (1998).

Barstovian rocks yield only one taxon, *Hesperhyus* itself, known only from Nebraska and Montana.

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