EVOLUTION OF THE EARLY MIOCENE HESPERHYNE 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 Hesperhyus (and sometimes Desmat'hys), 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, Luctasyus coombsiae, from the late Arikareean of Wyoming, along with “Cynoraca” (now Marshochoerus socialis) from the late Arikareean of the John Day Formation. Floridachyus olseni from the early Hemingfordian of the Thomas Farm local fauna in Florida is a slightly more derived hesperhyine, as is the new genus Stuckhyus siouensis (replacing the invalid name “Desmat’hyus siouensis”) from the late Arikareean of Wyoming. The most derived taxon is Hesperhyus vagrans (from the late Hemingfordian and early Barstovian). New material demonstrates Hesperhyus a very distinctive large peccary with robust, inflated cheek teeth. Hesperhyus is completely different from the smaller more gracile Desmat’hys 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 Hesperhyus. 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 species 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): Dicotylhes 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 Neogean 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 Stuckhyus simouensis (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; SDM, South Dakota School of Mines, Rapid City, South Dakota; UCMP, 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 Linneaus 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 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—Hesperhyus vagrans Douglass, 1903; Desmat'hys pinensis Matthew, 1907; Wrightohyus yatkolai, new genus and species; Floridachyus olseni White, 1941; Stuckhyus siouensis new genus; Lucasyus coombsiae, new genus and species; Marshochoerus socialis, Dicotylhes tajacu, the collared peccary; Tayassu pecari, the white-lipped peccary; and Catagonus wagneri, the Chacoan peccary;
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 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 = hypoconulid; MT = metacone; MV = median valley; PA = paraconule; PCL = paracrista; 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.

**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.

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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).
common age. What Wright (1998) called the *Hesperhyis*-"Cynorca" *sociale* 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.

### Hesperhyis Douglass, 1903

*Figures 4-8*  
*Tables 1-4*

**Type and only species**—*Hesperhyis 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 *Hesperhyis* 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, Ocolott 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 short temporal 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.

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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*.

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

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

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<td>—</td>
<td>—</td>
<td>160</td>
</tr>
<tr>
<td>Canine-p2 diastema</td>
<td>7.4</td>
<td>13.3</td>
<td>—</td>
<td>15.5</td>
<td>17.8</td>
<td>13.7</td>
</tr>
<tr>
<td>Length, p2-m3</td>
<td>125</td>
<td>112.2</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>109.6</td>
</tr>
<tr>
<td>Ramus depth</td>
<td>44.1</td>
<td>55.9</td>
<td>58.0</td>
<td>39.9</td>
<td>—</td>
<td>39.8</td>
</tr>
<tr>
<td>Ramus width</td>
<td>32</td>
<td>32.2</td>
<td>31.7</td>
<td>—</td>
<td>—</td>
<td>24.5</td>
</tr>
</tbody>
</table>
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*.

<table>
<thead>
<tr>
<th></th>
<th><em>Hesperhys vagrans</em></th>
<th></th>
<th><em>Desmathyus pinensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N  MEAN   SD  CV</td>
<td>N  MEAN   SD  CV</td>
<td></td>
</tr>
<tr>
<td>Length p2</td>
<td>3  12.3 0.63  5.12</td>
<td>2  10.6 6.2  5.8</td>
<td></td>
</tr>
<tr>
<td>Width p2</td>
<td>3  8.4  0.94  11.19</td>
<td>2  6.9  4.0  5.8</td>
<td></td>
</tr>
<tr>
<td>Length p3</td>
<td>5  16.4 0.58  3.17</td>
<td>3  13.0 1.2  0.9</td>
<td></td>
</tr>
<tr>
<td>Width p3</td>
<td>5  12.3 1.18  9.59</td>
<td>3  9.4  0.9  0.3</td>
<td></td>
</tr>
<tr>
<td>Length p4</td>
<td>7  18.3 0.85  4.65</td>
<td>3  16.5 0.5  0.4</td>
<td></td>
</tr>
<tr>
<td>Width p4</td>
<td>7  15.1 1.06  7.02</td>
<td>3  11.3 0.4  0.3</td>
<td></td>
</tr>
<tr>
<td>Length m1</td>
<td>6  20.9 1.08  5.17</td>
<td>2  18.5 10.7 5.7</td>
<td></td>
</tr>
<tr>
<td>Width m1</td>
<td>6  18.0 1.27  7.06</td>
<td>2  13.8 0.2  0.1</td>
<td></td>
</tr>
<tr>
<td>Length m2</td>
<td>7  22.0 1.50  6.82</td>
<td>3  22.1 0.4  0.2</td>
<td></td>
</tr>
<tr>
<td>Width m2</td>
<td>6  19.7 1.21  6.14</td>
<td>3  16.1 0.9  0.5</td>
<td></td>
</tr>
<tr>
<td>Length m3</td>
<td>5  29.6 2.12  7.16</td>
<td>1  26.6  —   —</td>
<td></td>
</tr>
<tr>
<td>Width m3</td>
<td>5  18.8 1.65  8.78</td>
<td>1  16.5  —   —</td>
<td></td>
</tr>
</tbody>
</table>
The upper cheek teeth of F:AM 143840 are bulbous; these teeth appear in visual inspection, compared to nearly any basal measurements of the cheek teeth does not capture how robust and of any other hesperhyine (Fig. 7). Even more importantly, the simple which show the full range of variation of the upper teeth. The overall fairly worn (Fig. 6C), but there are numerous other specimens in the medioventrally to wall off the posterior auditory bulla. There is a broad posttympanic process on the squamosal, which extends the tip of the dorsoventrally deep tympanic process of the squamosal. The foramen ovale. The large external auditory meatus passes through the cancellous tissue inside them. The alisphenoid complete encloses processs. Although the auditory bullae are broken, it allows us to see the sphenopalatine fossa. The orbitomaxillary fossa is also large and deep, are also fused together, except for a thin bony lamina which separates known peccaries. The symphysis is very broad and U-shaped. These teeth with massive, bulbous crowns that are different from most other and gracile, as in most peccaries. These accompany the large cheek 6E-F) is that they are strikingly massive and robust, rather than slender 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 1l is almost spatulate, with a deeply concave lingual surface surrounded by robust, posteriorly convergent crests. The lingual 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 cuspules. The t2 is very similar to the t1 only smaller.

The dp2 is double-rooted, with a tall protocone 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 posttympanic 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
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, 8). Matthew (1924) made few details of the molar crowns. He made no comparisons to Douglass’ *D. pinensis*, which distinguished it from other similar peccaries by its large size, and a robust cingulum on M1 and M2. The strong cingulum that sometimes bears a protocone, similar to the condition in *H. vagrans*, has three cusps in *D. pinensis*.

**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): 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 basioccipital and area anterior to M2; Prosymphoceros Quarry: F:AM 143843, partial right dentary with p2-m3.

**Hesperhyus vagrans Douglass, 1903**

| Type specimen | BN 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) |
| Diagnoses | Early Barstovian Oclott 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 basioccipital and area anterior to M2; Prosymphoceros Quarry: F:AM 143843, partial right dentary with p2-m3. |

**Hesperhyus vagrans Douglass, 1903**

| Desmathyus validus Matthew, 1924 | Barstov Formation, San Bernardino County, California (early Barstovian): Soder Ridge Quarry: F:AM 143838, juvenile palate with left and right i1-2, dC1, C1, dP1-3, 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-m3, m3-4, p3-4, m3-2. |

**Diagnosis**—Same as for genus

**Distribution**—Same as for genus

**Discussion**—The diagnostic features and description of the known remains of *Hesperhyus* 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 Douglas’ (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 zygochondry seen in *Platygonus* (Prothero and Grenadier, 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*.
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 *Hesperhyus* 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 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).
Desmathyus pinensis Matthew, 1907
Figs. 9-11
Tables 1-4

Desmathyus pinensis Matthew, 1907
Hesperhyx pinensis Simpson, 1945
Hesperhyx pinensis McKenna and Bell, 1997
Hesperhyx pinensis Wright, 1991
Hesperhyx pinensis Wright, 1998 (in part)
Hesperhyx 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 Arikareean (Harrison Formation equivalent).

Hypodigm—“3 mi. e of Porcupine [Shannon County, South Dakota]”, latest Arikareean (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.


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 hesperhymes is discussed below. D. pinensis appears
to be a smaller hespherhyine restricted to the latest Arikareean to early Hemingfordian of South Dakota, and found nowhere else.

**Wrightothyus new genus**

Figures 12-13

Tables 5-8

*Hesperhyus* (in part) Wright, 1991

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

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

**Distribution**—Late Arikareean 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.

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**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 postorbitally to join with a sharp sagittal crest. There are a pair of supraorbital foramina and

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FIGURE 12. UNSM 62604, holotype of *Wrightothyus 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).
shallows which extend posteriorly and laterally from the lacrimal process and extend posteriorly and laterally from the lacrimal process. A small protuberance of bone, known as the lacrimal crest, connects the anterior edge of the lacrimal bone to the nasal bone.

In the orbit, there is a small lacrimal tubercle, which is dorsal to the single large lacrimal foramen. The front of the orbit is extended ventrally and laterally to the lacrimal crest. The nasal septum is also closely associated with the skull of UNSM 62604.

Cranial processes include: the parietal, the squamosal, the postzygomatic, the mandibular, and the zygomatic processes.

In palatal view (Fig. 12C), there are small incisive foramina. The nasofrontal process is dorsal to the single large lacrimal foramen. There is a large, anteriorly placed nasal process, which is dorsally continuous with the nasal bone. The nasofrontal process is anteroposteriorly elongated oval in shape in crown view. There are sharp anterior and posterior crests on the paracone. The strong posteroconulid 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 posterolabial cingulum, resulting in two distinct concentric cingular crests. P4 has three roots as well, two on the labial side and a strong one on the lingual side. The enamel portion of the paracone is partially divided into two cusps. There is a large protocrist with a solid crest that branches anterolabially from the anterior surface. There is a small metaconule, and a robust cingulum around the posterior cingulum. 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 paracone. On UNSM 62604, this configuration describes the right p4, but the left p4 has no paraconid and the anterolabial cingulum merges with the anterior cingulum. The p4 metaconule 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 anterolabial accessory cusp. The metaconid has a posteroconulid accessory cusp, which sits in the median valley. The m1 has a small hypocodid, 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 hypocodid meets the entocodid, forming a weak crest. The m3 is like the m1 and m2, except that it has a large lobed hypocodid.

Discussion—Wright (1991, p. 77-79) was the first to study the Runningwater Formation UNSM specimens (which he called “Hesperhyus cf. pineensis”), 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 *Hesperhyus-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 *Hesperhyus*. 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 *Hesperhyus 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 “*Hesperhyus cf. pinensis*”.

*Wrightohyus yatkolai* new species

Figures 12-13  
Tables 5-8

**Hesperhyus 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*: “Bourdeau 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 occult; “Cottonwood Creek,” Dawes County, Nebraska: FAM 143844, partial mandible with left p3-m3.

**From Runningwater equivalent rocks, Wyoming**: “16-mile District,” near Lusk, Wyoming: FAM 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 *Hesperhyus cf. pinensis*. As discussed above, the cladistic relationships of *D. pinensis*, *H. vagrans*, 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) hesperhyrine (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 Arikareean 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 hesperhyne peccary, as defined by having a long cancellous anteroventral process of the auditory bulla, a large plesiochoanal fossa, broad postamular 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 Arikareean, 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
lacral 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 anterodorsal edge of the bulla stretches an elongate process, almost reaching the plane of the palatine. 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 postzygomatic 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 metaconule, 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 cingulae 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

**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).
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 subpatululate. 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 i4 blades would occlude with it.

The p2 has two roots, one anterior and one posterior. There are faint anterior and posterior crests on the paracoronal 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 protocoonid 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 protocoonid has steep sides, and its anterior crest projects at the base as a small anterocoonid, 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 sides of the p4. This tooth has tall trigonid cusps, especially the protocoonid, with its sharp anterior crest that descends sharply to meet a low paraconid. From the labial side of the protocoonid 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 hypocoonid process and two large cusps on the posterior cingulum.

Discussion—Wright (1991) showed, it is a distinct genus and species, more referable to any other hesperhyine genus known, and required a new diagnosis.

Type and only species—Stuckyhyus l. coombsae

Type specimen—AMNH 13771, a partial left dentary with p4-m3, collected from the ‘L’t 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.

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

Thinothyus (Bothrolabis) Peterson, 1905

Desmathyus Matthew, 1907 (in part)

Desmathyus Pearson, 1923 (in part)

“Thinothyus” Wright, 1991 (in part)

“Thinothyus” Wright, 1998 (in part)

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

Diagnosis—Hesperhyine with a narrow plesiochoanal fossa, narrow postmaxillary process, and a 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, 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 the same as those in the original papers.

Discussion—Peterson (1905) first described this specimen, and referred it to the John Day genus Thinothyus, which it shares no derived characters with and does not resemble (based on the modern concept of Thinothyus; see Prothero, 2009). He also implied that it was part of a subgenus ‘Bothrolabis’ Cole, even though “Bothrolabis” was never considered a subgenus of Thinothyus, 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 Thinothyus (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 Thinothyus and “Bothrolabis” was very confused. The only other available genus in 1905 was Douglass’s 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 “(F. B.)’s 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 that Lucasathyus (the “Van Tassel” specimen) but less derived than the crown clade of Hesperhyus-Desmathyus-Wrightothyus (Fig. 3).

Lucasathyus 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’t 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.

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 siouxensis (Peterson, 1905)

Figures 16-17

Tables 5-8

Thinothyus (Bothrolabis) Peterson, 1905

Desmathyus siouxensis Matthew, 1907

Desmathyus siouxensis Pearson, 1923

“Thinothyus” siouxensis Wright, 1991

“Thinothyus” 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 Hesperian 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 Farm” (collected by Harold J. Cook), also from the Agate bone bed level, Anderson Ranch Formation (latest Arikareean). Possibly additional material in the USNM 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 *Stuckhyus 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” (= *Stuckhyus*) *siouxensis*. 
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
(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 the 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 lacrimal 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 *Hesperhyus*. 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*.

![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).](image-url)
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 has a pair of roots, judging from the alveoli. P2 has a large paracone, with a broad posterostructural cingulum which has two concentric arc-shaped crests. These extend forward and merge with the front part of the paracone. The P4 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 protocoonid, and moderate anterior cingulum, which meets the weak posterior crest of the protocoonid. 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 posterostructural crest of the protoconid meets the posterostructural crest of the metaconid, forming the beginnings of a transverse lop. 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 Desmathys, as Olsen and MacFadden and Webb (1982) argued, or with Hesperhyus, as McKenna and Bell (1997) suggested. This is especially true now that Desmathys 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. siouensis and the crown clade of Hesperhyus, Desmathys, and Wrightothyus (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
Desmathys olseni Olsen, 1962
Desmathys 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 butresses (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).

Marshochaerus, new genus

Figure 20

Thinohyus Marsh, 1875
Palaeochaerus 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—Marshochaerus socialis (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 maxillolpalatine lacrymal of UCMF 66862 (Fig. 20B,C), so that description also does not need to be repeated.

Distribution—L. John Day Formation, Oregon; early Hemingfordian, Garvin Gulch local fauna, Oakville Formation, Grimes County, Texas; and late Hemingfordian, Phillips Ranch local fauna, Kinnick Formation, Kern County, California (jide 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. socialis.

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 proterus. 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 he 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 proterus Cope, 1867, is an isolated upper canine tooth, ANSP 11543a, and the syntypes includes about nine other ANSP Cope specimens that are clearly tayassuids (Woodburne, 1969, p. 298). Woodburne (1969) then restricted Cynorca proterus 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. proterus 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 UCMP 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. Marshochoerus 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.

**Marshochoerus 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.

**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 *Marshochoerus* 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, possibly 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 *Hesperhyus vagrans* and *Desmathyus pinensis* (Fig. 14). I cannot tell whether *Pediohyus ferus* Loomis, 1910, is a junior synonym of *Hesperhyus 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 (*Hesperhyus*) or two genera (*Hesperhyus* 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
Barstovian rocks yield only one taxon, *Hesperhyus* itself, known only from Nebraska and Montana.

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**REFERENCES**


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**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).


