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SIMOJOVELHYUS IS A PECCARY, NOT A HELOHYID (MAMMALIA, ARTIODACTYLA)

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ABSTRACT—*Simojovelhyus pocitosense* is based on a lower jaw fragment with three molars from the late Oligocene amber mine deposits near the village of Simojovel, Chiapas Province, Mexico. It is the oldest fossil mammal known from Central America. It was described by Ferrusquia-Villafranca in 2006 as a helohyid, a group of primitive artiodactyls known from the Bridgerian and Uintan (older than 49–42 Ma), yet it comes from early Arikareean deposits about 25–27 Ma, suggesting that it was a very late helohyid living more than 10 m.y. after their apparent Uintan extinction. We re-examined the specimen, and compared it to the large collection of recently described peccaries from the Chadronian (*Perchoerus minor*) and Orellan (*Perchoerus nanus*) and Bridgerian helohyids (*Helohyus* sp.). Once the range of variation of characters in helohyids and peccaries is accounted for, *Simojovelhyus* shows derived similarities to early peccaries, especially in the bunodont molars with inflated cusps and the configuration of cristids and accessory cuspulids, and none of the incipient lophodonty and primitive morphology seen in helohyids. In fact, the only real similarity other than symplesiomorphies between *Simojovelhyus* and helohyids is its small size, but it is close to the size range of the tiny Chadronian peccary *P. minor*. Thus, based on both derived tooth characters and its age, it is much more parsimonious to regard *Simojovelhyus* as a tiny Mexican peccary from the Arikareean, not a very late helohyid. This removes the anomalously late occurrence of helohyids from the mammalian fossil record, and forces a re-examination of our view of mammalian evolution in Central America.

INTRODUCTION

FERRUSQUIA-VILLAFRANCA (2006) described a lower jaw fragment with m1–3 from the late Oligocene of Chiapas, Mexico, and named it *Simojovelhyus pocitosense*. It was compared to numerous primitive bunodont artiodactyls, but it was determined to be a very late member of the helohyids, a taxon that is known primarily from the middle Eocene (Uintan and Duchesnean), and unknown after 42 Ma. The specimen came from beds in an amber mine near the town of Simojovel, in Chiapas Province, near the Guatemalan border with Mexico. The only other land mammal found near Simojovel thus far has been a protoceratid, *Paratoceras tedfordi*, which came from upper beds of the early Miocene Balantum Sandstone (Webb et al., 2003). According to Frost and Langenheim (1974), the fossil of *Simojovelhyus* occurred in beds that are correlative with the upper part of the *Globigerina angulisuturalis/Paragloborotalia opima opima* Range Zone and the lowest *Globigerina ciperoensis* Partial Range Zone (Berggren et al., 1995), making it between 24.9 and 26.8 Ma in the current time scale of Luterbacher et al. (2004), or late Oligocene in age. Thus, it would be correlative with early Arikareean strata in the North American mammalian chronology (Tedford et al., 2004), and its occurrence would be at least 10 m.y. younger than the last known occurrence of a helohyid. This age discrepancy, and the fact that it is one of the oldest land mammal fossils known from Central America, makes its identity very important.

MATERIALS AND METHODS

The fossil itself (IHNE 6784) is a left mandibular fragment with m1–3 (Fig. 1.4). As Ferrusquia-Villafranca (2006) explains, the original specimen has since been lost, so all that remain is high-quality casts, but the name remains valid because the type specimen might still be found some day. We took a high-quality cast of the specimen (given to Stucky by Ferrusquia-Villafranca, DMNH 54905) to the American Museum of Natural History in New York and the Denver Museum of Nature and Science in Denver, where we made close side-by-side comparisons and measurements not only with helohyids, but also with a variety of other bunodont artiodactyls, especially primitive peccaries, which have just recently been revised (Prothero, 2009).

We examined all the holotypes of the various named species of *Helohyus* and *Perchoerus*, as well as numerous specimens of all the included species, to get a full sense of the range of variability in the two taxa. Some of the material we examined included: *Helohyus plicodon*: DMNH 6872, right dentary with p2–m3; DMNH 57142, left m3; DMNH 17305, left m1–2; DMNH 6793, left m1–3; DMNH 41492, right m3 and associated postcranial elements; DMNH 31920, left m2; DMNH 34004, left p3–m1; DMNH 25359, right m3; DMNS 17023, left m1–3; AMNH 12149, left p2–m2; AMNH 108123, ramus with p4–m3; AMNH 12148, left m1–3; *H. lentus*: AMNH 12150, right m3; *H. validus*: AMNH 12694, right m3.

Perchoerus minor: From the Chadronian (late Eocene), White River Group, South Dakota and Nebraska: AMNH 86222 (holotype), right and left rami with right p3–m3, left p3–4, m2 and partial m3; AMNH 86221, partial ramus with m3, from the type locality; USNM 206190, partial juvenile skull, isolated maxillae and ramal fragments; UNSM 372193, skull fragment, right ramus with m2–3;YPM-PU 12736, right ramus with p4–m3; YPM-PU 13599, right and left ramal fragments; YPM 14651, left ramus with m2–3; AMNH 12314, right and left rami with m2–3; YPM 14656, right ramus; YPM 14648, right and left rami with m1–3; FMNH PM20802, left m3; FMNH PM22407, right ramus with m1–3.

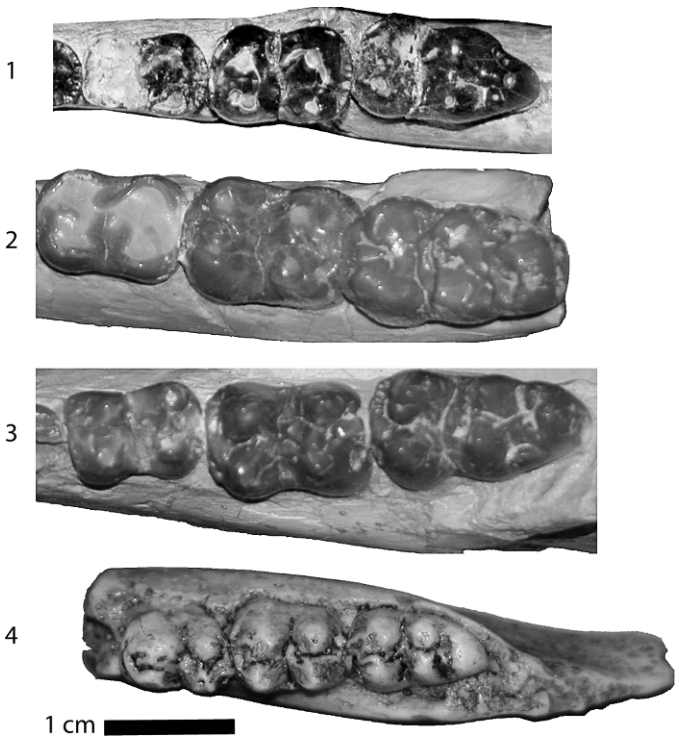

FIGURE 1—Comparison of type specimen of *Simojovelhyus* with the m1–3 of *Perchoerus* and *Helohyus*: *1*, *H. plicodon*, AMNH 108123; *2*, *P. minor*, F:AM 73745; *3*, *P. minor*, F:AM 73715; *4*, type specimen of *Simojovelhyus*.

Perchoerus nanus: From the Orellan (early Oligocene), White River Group, South Dakota and Nebraska:YPM 11784 (holotype), left ramus with p3–4, m1–3; LACM (CIT) 79/90, partial skull with left P3–M3, right P2–M3, and jaws with left p4–m3 and right p3–m3; AMNH 1200, lower jaw; YPM 14648, left m1–3; YPM 14656, part of right ramus with p4–m3; YPM 14654, right and left rami with p4–m3; YPM-PU 10511, left ramus with p4–m3; YPM-PU 12736, left and right rami; F:AM 73731, skull and jaws; YPM 1656, lower jaw; FMNH P12152, skull and jaws; FMNH PM46421, right m2–3.

Perchoerus probus: From the Whitneyan (late early Oligocene), White River Group, South Dakota and Nebraska: SDSM 2838, skull and jaws; AMNH 9794, skull and jaws; AMNH 9813, skull and jaws; AMNH 9812, jaws; F:AM 73758, jaws; F:AM 73721, skull and jaws; F:AM 73713, jaws; F:AM 73745, jaws; YPM-PU 10679, jaws; YPM 19048, partial lower jaw with p4–m2.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, U.S.A.; DMNH, Denver Museum of Nature and Science (formerly Denver Museum of Natural History), Denver, CO; FMNH PM, Field Museum of Natural History, Chicago, IL; F:AM, Frick Collection, AMNH; IHNE, Instituto de Historia Natural y Ecologia, Chiapas, Mexico; LACM (CIT), California Institute of Technology Collection, now housed at the Natural History Museum of Los Angeles County, Los Angeles, CA; SDSM, South Dakota School of Mines and Technology Museum, Rapid City, SD; YPM, Yale Peabody Museum, New Haven, CT; YPM-PU, Princeton Collection, now housed at YPM.

COMPARISONS

Ferrusquia-Villafranca (2006) made comparisons with a few individual specimens of the most derived species of the peccary *Perchoerus* (*P. probus* from the Whitneyan), but did not make any comparisons with the tiny, more primitive Chadronian and Orellan species *Perchoerus minor* and *Perchoerus nanus* (recently revised by Prothero, 2009). Even though the smallest Chadronian species of *P. minor* are still a bit larger than *Simojovelhyus* (Table 1), size should not be the only consideration in comparison of something as unusual, and as geographically and temporally isolated, as *Simojovelhyus*. Morphology should be considered much more important, and consideration of its late Oligocene age should be secondary to its clade assignment.

The original comparisons (Ferrusquia-Villafranca, 2006, table 3) do not consider the population variability of *Perchoerus*, and thus rules it out unnecessarily. Ferrusquia-Villafranca's (2006) table 3 discusses the following features (characters).

Size.—*Simojovelhyus* is indeed smaller than any known peccary, but not much smaller than *P. minor* from the Chadronian (Table 1). *Simojovelhyus* was only compared to the much larger Whitneyan taxon *P. probus* (misspelled "*P. lobus*" in his table 3). As Ferrusquia-Villafranca (2006) notes, both *Perchoerus* and *Simojovelhyus* have a slight increase in size from m1 to m2, and a moderate increase in size from m2 to m3. The original comparison (Ferrusquia-Villafranca, 2006, table 1, feature 1) suggests that in peccaries, m2 is much wider than m1, but this is simply not true if one looks at a full range of peccary jaws (Prothero, 2009; Table 1). And there are plenty of individual specimens where the m2 is just barely wider than m1 (e.g., F:AM 73745, *P. probus*).

Occlusal outline and shape.—The original paper (Ferrusquia-Villafranca, 2006, table 3) correctly points out that both *Simojovelhyus* and *Perchoerus* have rectangular or subrectangular m1 and m2, and trapezoidal m3, so this does not distinguish them (contrary to what was written on p. 995).

Trigonid/talonid height and width.—The original description claims that in *Simojovelhyus* the trigonid is taller than the talonid, and the trigonid is wider than the talonid (Ferrusquia-Villafranca, 2006, table 3, feature 3). However, on closer inspection, we find that this difference is extremely subtle or simply not there, or could easily be due to wear in the case of the trigonid/talonid height difference. In figure 4 there is no clear difference in either height or width of the trigonid and talonid. In Ferrusquia-Villafranca's (2006) table 3, feature 3, it is claimed that *Perchoerus* shows a very different trigonid/talonid height and width ratios. In reality, this character is highly variable depending on the wear stage of the tooth, and even relatively unworn teeth show a range of height/width ratios.

Bunodonty.—It was claimed that *Simojovelhyus* has very slight bunodonty, and very slight lophodonty (Ferrusquia-Villafranca, 2006, table 4, feature 4). In fact, as the specimen and figure 3

TABLE 1—Measurements of *Simojovelhyus* and *Perchoerus minor* in mm.

	m1L	m1W	m2L	m2W	m3L	m3W	m1–3
P. minor							
Mean	11.2	8	12.07	9.1	15.56	8.52	38.3
SD	0.28	0	0.94	0.24	1.03	0.91	
CV	2.52	0	7.8	2.69	6.65	10.73	
n	2	2	3	4	5	5	1
Simojovelhyus	8.29	4.37	8.92	6.29	10.24	5.95	27.08

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TABLE 2—Comparison of primitive and derived character states in *Helohyus, Simojovelhyus*, and *Perchoerus*. Derived characters are indicated in **bold face** type. Most characters discussed by Ferrusquia-Villafranca (2006) are symplesiomorphic or highly variable. No derived characters other than small size unite *Simojovelhyus* with *Helohyus*, but numerous derived characters link *Simojovelhyus* with peccaries like *Perchoerus*.

Helohyus	*Simojovelhyus*	*Perchoerus*
Cusps sublophodont	**Cusps inflated/bunodont**	**Cusps inflated/bunodont**
Strong m1–2 paraconid	**m1–2 paraconid absent**	**m1–2 paraconid absent**
Simple paracristid/no protocristid	**Preprotocristid/preparacristid loop**	**Preprotocristid/preparacristid loop**
Simple metaconid with no cristids	**Metaconid cristid in loop**	**Metaconid cristid in loop**
Postvallid on m1–3 continuous	**Postvallid on m1–3 notched**	**Postvallid on m1–3 notched**
Small hypoconid, entoconid	**Large entoconid, hypoconid**	**Large entoconid, hypoconid**
Deeply basined talonid	**No talonid basin**	**No talonid basin**
No cristids on hypoconid	**Complex hypoconid cristids**	**Complex hypoconid cristids**
Small m1–2 hypoconulid	Small m1–2 hypoconulid	Small m1–2 hypoconulid
2–4 cuspules on m3 hypoconulid	2–3 cuspules on m3 hypoconulid	Cuspules variable
Tiny paraconid	Tiny paraconid	Tiny paraconid
Weak, discontinuous cingulids	Weak, discontinuous cingulids	Weak, discontinuous cingulids
Small mesocingulid	Small mesocingulid	Small mesocingulid
Strong postcingulid	Strong postcingulid	Strong postcingulid
2 cuspulids on m1–2	2 cuspulids on m1–2	m1–2 cuspulids variable
2 cristids on the trigonid	2 cristids on the trigonid	Trigonid cristids variable (1–2)
2 cristids on the talonid	2 cristids on the talonid	2 cristids on the talonid
Small open V-shaped ectoflexid	Small open V-shaped ectoflexid	Ectoflexid variable
Distinct paraconid on metaconid	No distinct paraconid	Weak paraconid
Tiny size	**Tiny size**	Slightly larger size

show, it is actually quite bunodont with almost no lophodonty, just as in *Perchoerus* (Table 2). By comparison, helohyids like *H. plicodon* (AMNH 12148 and 108123) are considerably less bunodont with more pyramidal shaped cusps and intervalli between the lingual and labial cusps that represents incipient lophodonty or the kind of zygolophodonty seen in advanced peccaries like *Platygonus*. More worn specimens of *H. plicodon* (e.g., AMNH 10123) are sublophodont.

The m1–2 hypoconulid.—The original paper (Ferrusquia-Villafranca, 2006, table 3, feature 5) pointed out that both *Simojovelhyus* and *Perchoerus* have small m1–2 hypoconulids, so this does not distinguish them. It was also suggested that *Simojovelhyus* has the m1–2 hypoconulid anterior to the postcingulid while peccaries have it on the postcingulid. In fact, several specimens of *Perchoerus* (e.g., AMNH 7392; F:AM 73715) have it in exactly the same configuration as does *Simojovelhyus*.

The m3 hypoconulid.—In the original publication, it was claimed that *Simojovelhyus* has a large m3 hypoconulid with only two cuspules while peccaries have a large m3 hypoconulid with five or more cuspules (Ferrusquia-Villafranca, 2006, table 3, feature 6). In fact, this is highly variable among peccaries, and some specimens (e.g., AMNH 86222, the type of *P. minor*) have only two to three cuspules. Even more advanced peccaries (e.g., "*Cynorca*" *occidentalis*, AMNH 73660) have an almost identical m3 hypoconulid to *Simojovelhyus*, with a single large cusp and possibly one or two cuspules anterior to it. In addition, the m3 hypoconulid of some helohyids (e.g., *H. plicodon*, AMNH 108123) show at least three and possibly five cuspules, so this character is too variable to be diagnostic.

Paraconid.—It was pointed out that both *Simojovelhyus* and peccaries have a tiny paraconid, so this does not distinguish them (Ferrusquia-Villafranca, 2006, table 3, feature 7).

Cingulids.—The original paper showed that both *Simojovelhyus* and peccaries have weak, discontinuous cingulids (Ferrusquia-Villafranca, 2006, table 3, feature 8). The borders of the teeth are smooth in *Simojovelhyus*, but supposedly crenulated in peccaries. However, this is not true of the smallest, most primitive peccaries like the type specimen of *P. minor* (AMNH 86222), which is smooth on the "crenulated" labial side as well as the lingual side, especially on the m3. The original paper (Ferrusquia-Villafranca, 2006, table 3, feature 8) points out that both *Simojovelhyus* and peccaries have a small mesocingulid, and a well developed postcingulid, so there is no difference between them in this regard (Table 2).

Other cuspulids.—The original description claimed that *Simojovelhyus* has two cuspulids on m1–2, but there is only one on peccaries (Ferrusquia-Villafranca, 2006, table 3, feature 9). However, on less worn specimens of *Perchoerus* (F:AM 73745) the number of cuspulids on m1–2 are highly variable. Likewise, it was claimed that there were multiple cuspulids on m3, but as pointed out above, this is highly variable in peccaries.

Cristids.—The original article claimed there are two cristids in the trigonid of *Simojovelhyus* and only one on *Perchoerus* (Ferrusquia-Villafranca, 2006, table 3, feature 10), but this is highly variable in peccaries. In reality, a close examination of the cast of *Simojovelhyus* shows very little development of cristids. The original illustration of the specimen (Ferrusquia-Villafranca, 2006, fig. 4) exaggerates the development of cristids between the illustration and the photograph of the cast. In addition, AMNH 9813 (*P. probus*) shows more than one cristid on the lower molars. As previously demonstrated (Ferrusquia-Villafranca, 2004, table 3, feature 10), both peccaries and *Simojovelhyus* have two cristids on the talonid, so this does not distinguish them (Table 2).

Ectoflexid/entoflexid.—The original description (Ferrusquia-Villafranca, 2006, table 3, feature 11) claimed that *Simojovelhyus* has a moderate ectoflexid (small cusp in the intervallid on the labial side of the tooth) that is open and V-shaped, while peccaries have a shallow ectoflexid that is open and U-shaped. In reality, we find this character highly variable within peccaries, with some specimens (e.g., F:AM 73715) showing the same condition as in *Simojovelhyus*.

DISCUSSION

The following characters help to distinguish *Simojovelhyus, Helohyus*, and *Perchoerus*: *Helohyus* is the sister taxon of *Hexacodus* and is part of the early clade that includes *Hexacodus uintensis* and *H. pelodes* (a virtual carbon copy except for inflation of the p4 in *Hexacodus*, a taller trigonid and more prominent paraconid, and much larger size), *Homacodon vagans, Microsus cuspidatus*, and a new genus currently under study by Stucky. *Simojovelhyus* lacks a distinct paraconid on the lower molars; *Helohyus* has a distinct paraconid that is high on the anterior face of the metaconid. *Simojovelhyus* has a prominent preprotoconid cristid that descends directly down the anterior face of the protoconid and then has an extension of this crest which is directed toward the medial part of the tooth. *Simojovelhyus* has a prominent notch between the protoconid

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and metaconid. *Helohyus* has a strong postvallid with only a slight notch that is high on the trigonid. *Simojovelhyus* has three prominent ridges extending off of the apex of the hypoconid. The cristid oblique is directed to the metaconid but is separated by a deep notch on m1–2 between the trigonid and talonid; a crest descends directly down the lingual face of the hypoconid toward the entoconid but is not connected because of a deep valley between the very prominent and conical entoconid and hypoconid. The posthypoconid cristid is directed posteriorly to the hypoconulid. *Simojovelhyus* has no labial cingulid. *Helohyus* often has a prominent cingulid and that is always developed on the anterior face of the protoconid and the posterior area of the hypoconid. *Simojovelhyus* has a weakly developed post cingulid on m1–2 and *Helohyus* has a prominent postcingulid.

Simojovelhyus has the following characteristics of the lower dentition that are derived relative to the morphology of *Helohyus* and ally it to the peccaries: 1) the paraconid is absent on m1–2; 2) the preprotocristid and preparacristid form an anterior loop; 3) the metaconid has an additional cristid that is directed anteriorly into the preprotocristid and preparacristid loop; 4) the postvallid has a distinctive notch between the protoconid and metaconid on m1–3; 5) the entoconid and hypoconid are hypertrophied and there is no talonid basin; and 6) the cristids that come from the hypoconid are trefoiled and complex.

Helohyus on the other hand possesses a number of plesiomorphies including 1) a distinctive paraconid that is high and on the anterior face of the metaconid; 2) a simple and low paracristid that connects to the paraconid (there is no protocristid); 3) a simple bulbous metaconid with no accessory cristid; 4) a continuous postvallid on m1–3 (a small non-inflated hypoconid and entoconid and a deeply basined talonid; and 6) no accessory cristids from the hypoconid. All of these characteristics are shared with *Hexacodus* and other homacodontids.

In summary, we find no important anatomical derived features that rule out the tayassuid affinities of *Simojovelhyus*, since most of the distinctions alleged by Ferrusquia-Villafranca (2006) are encompassed by the range of variation of typical *Perchoerus* teeth. Instead, the derived features such as the inflation of the cusps, the degree of bunodonty, the lack of lophodonty, and numerous features of the cuspulids and cristids support the tayassuid affinities of *Simojovelhyus*. In contrast, a close comparison of *Simojovelhyus* to *Helohyus plicodon* exhibits numerous differences, most strikingly the peccary-like inflation of the cusps in *Simojovelhyus* that is not seen in *Helohyus*, and the incipient lophodonty in *Helohyus* that is not seen in *Simojovelhyus* nor in *Perchoerus*. In fact the only similarity between *Simojovelhyus* and helohyids is their size, which we do not consider to be a synapomorphy between the two taxa. Indeed, arguing that a late Oligocene taxon like *Simojovelhyus* is related to a Bridgerian or Duchesnean (early to late middle Eocene) group like helohyids, rather than to contemporaneous group like peccaries (known from the Chadronian to present) is very unparsimonious. Based on the derived morphology shared with peccaries, and their age overlap, we argue that *Simojovelhyus* is simply a small peccary, similar in size to *Helohyus plicodon*, but from the late Oligocene of Mexico. It is slightly smaller than the Chadronian *P. minor*, while peccaries in more northerly latitudes like *P. nanus* and *P. probus* from the Orellan and Whitneyan increased in size.

Peccaries of early to middle Miocene age are known from Panama (MacFadden et al., 2010), and it is likely that *Simojovelhyus* is merely a precursor to an abundant fossil record of peccaries in the Tertiary and Quaternary of Central America.

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