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Muknalia is a Collared Peccary (*Pecari tajacu*): A Reply to Stinnesbeck et al.

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RESEARCH PAPER

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ABSTRACT

Several years ago, a new genus and species of peccary, "*Muknalia minima*", was described from the Pleistocene of Mexico. We previously examined that specimen and concluded that it was synonymous with the extant collared peccary, *Pecari tajacu*, but that taxonomic revision is rejected by the authors of the original study (this volume). Here, we provide further analysis of "*Muknalia*" and expand on previous evidence from both morphology and taphonomy that support synonymy with *P. tajacu*. We argue that morphological features, both in terms of size and shape, that were used to diagnose "*Muknalia*" all fall within the range of variation of the extant *P. tajacu*, or are a consequence of taphonomic modification, including human handling.

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A new genus and species of Pleistocene peccary (*Muknalia minima*) was recently described by Stinnesbeck et al. (2017, 2018) based on an isolated left dentary from a submerged Yucatán cave. We observed and assessed this specimen and interpreted it to be synonymous with the collared peccary, *Pecari tajacu* (Schubert et al., 2020). Our taxonomic revision is rejected by Stinnesbeck (this volume), and we follow up here with additional comments supporting the synonymy.

First, it is important to note that this dentary (*Figure 1A*) is fragmented and chemically weathered over

the anterior ³⁄₄ of the specimen (Stinnesbeck et al., 2017, 2018). Obvious dissolution pits as well as fractured and missing portions along the anterior and anterodorsal surfaces, particularly the alveolar margins of the canine and premolars, limit morphological interpretations of bone in this region. However, preserved teeth are in good condition, displaying their intact morphology. The posterior ¹⁄₄ of the specimen, beginning along the caudal edge of the m3 displays a different taphonomic history. In contrast to the anterior ³⁄₄, this posterior portion exhibits some intact and uncorroded bone surfaces



Figure 1 *Muknalia minima* holotype **(A)**, overlay of Muknal dentary on top of *Peccary tajacu* specimen **(B)**, and additional modern *P. tajacu* comparisons **(C–H)**. All modern specimens were collected from the wild. **B** and **C** are the same modern specimen, USNM 108514, Cozumel, Mexico; **D**, USNM 108513, Cozumel, Mexico; **E**, USNM 108515, Yucatán, Mexico; **F**, ETMNH-Z 13485, Arizona; **G**, ETMNH-Z 12844, Mojave County, Arizona; **H**, ETMNH-Z 14306, Sonora, Mexico. **G** and **H** are both right dentaries and the images are reversed. Black arrows show an example of the thickened muscle attachment area for the *masseter lateralis superficialis*. Muknal dentary from Stinnesbeck et al. (2017). Catalog numbers added digitally for **F–H**. Scale bar = 2 cm.

that preserve predepositional evidence of human modification in the form of fine striations interpreted to be cut marks (Stinnesbeck et al., 2018), and polishing on cortical and trabecular bone (Schubert et al., 2020). The better preservation of the posterior section may reflect the original *in situ* position of the specimen, where this portion appears to have been buried in sediment (Stinnesbeck et al., 2017, Fig. 1.2; Stinnesbeck et al., 2018, Fig. 2d, e).

According to Stinnesbeck et al. (this volume), Schubert et al. (2020) disagreed with the identification of the new taxon because we interpreted the shape of the specimen to be the result of "anthropological handling (breakage and polishing)" rather than intact morphology. This is not accurate; rather, we interpret the specimen to be Pecari tajacu based on intact morphology and size (Schubert et al., 2020), and consider the taxonomically unique features described by Stinnesbeck et al. (2017) to be misinterpretations of anatomy and altered surfaces. The specimen has multiple breaks that may or may not have been caused by humans. Interestingly though, some of these fractures are polished, a feature that is often associated with human handling, and can be mistaken for intact morphology. Polishing is caused by abrasion and can result in smooth, rounded, and/or shiny surfaces.

Next, it is important to emphasize that *P. tajacu* dentaries express significant morphological and size variation. Schubert et al. (2020) depict some of this variation in tables and supplementary data, as well as Fig. 1. Unfortunately, in examining this figure (Schubert et al., 2020, Fig. 1) as part of our reply, we recognized errors in our scaling. *Figure 1* here corrects the scale errors, adds additional examples of variation in the species, and provides an overlay of the Muknal dentary on top of a modern *P. tajacu* comparative specimen.

One of the primary morphological features noted to be unique (Stinnesbeck et al., 2017, and this volume) is the 110° angled notch on the mandibular ramus. Stinnesbeck et al. (this volume) state that we (Schubert et al., 2020) argue the angle of the mandibular ramus was removed (broken off) by humans. We actually did not claim that humans broke off the angle of the dentary, but we did note that it was broken, and subsequently modified. The fractured posterior surfaces are shown in Stinnesbeck (this volume, Fig. 1 and Fig. 2) and these figures are used here for discussion.

According to Stinnesbeck et al. (2017, p. 344), "The caudoventral edge of the condylar process includes a 110 degree angle with the caudal edge of the mandibular ramus. Caudal to this angle, the mandibular ramus is almost vertical and 34 mm long. Its caudal margin is majorly preserved and only little material has flaked off." In Fig. 1a (Stinnesbeck et al., this volume), the red arrows mark portions of what is described as the intact angular border, and the small green arrows denote the hypothesized fragmented caudal border of

the mandibular angle (Stinnesbeck et al., this volume). In Fig. 1a, we interpret the margin marked by the higher red arrow and all the green arrows as altered surfaces with varying degrees of polishing. The sheen of polishing is visible along the medial edge of the fracture in Fig. 1a of Stinnesbeck et al. (this volume). In this general view (Fig. 1a), both the red arrows, and all the smaller green arrows point to irregular surfaces that do not reflect intact morphology. The space between the uppermost two green arrows (Fig. 1a) is concave craniocaudally and rounded mediolaterally.

In addition, Stinnesbeck et al. (this volume) state that "the lateral surface of the mandibular angle is mediolaterally convex in the Muknal specimen," but is "flat to even concave in Pecari, due to the masseteric fossa." In this comment the authors refer to Fig. 1a, the posterior view of the Muknal dentary. If the dentary is fragmented as we propose, the same area would appear to be laterally convex in Pecari. Note that the masseteric fossa extends caudally across this surface and terminates with the muscle insertion for the masseter lateralis superficialis, which expands from the base of the condyle along the posterior margin of the mandibular angle to the anterior end of the post-digastric sulcus (Woodburne, 1968, p. 12). This muscle attachment creates a rugose and thickened edge (e.g., see Figure 1H, black arrows) in peccaries that is completely lacking in the Muknal specimen. The relatively vertical mandibular angle proposed for Muknalia lacks evidence of a functional masseter lateralis superficialis.

The location labeled as the "subcondylar area" (Fig. 1a, blue arrows) is interpreted as intact morphology by Stinnesbeck et al. (this volume), and a key feature of *Muknalia*. However, we interpret this smooth and rounded surface to be the result of polishing. In *Pecari* and many other species, bone in this area is relatively thin and solid, with little to no trabecular bone. Thus, wear of a fractured surface in this location can result in a surface that appears to be intact.

In addition, Stinnesbeck et al. (this volume) state that the subcondylar area is thicker (5 mm) in *Muknalia* than the same area in *Pecari* (2 mm). If Stinnesbeck et al. (this volume) are referring to the mediolateral width of their subcondylar area, this statement is inconsistent with our observations, as this area in the Muknal specimen is \sim 2–3 mm thick, not 5 mm. This relative width of 2–3 mm can also be estimated using the scale provided in Stinnesbeck et al. (this volume, Fig. 1a).

Next, the area referred to as the "condylar neck" in Stinnesbeck et al. (this volume, Fig. 1 and Fig. 2) is modified along the posterior surface showing polished trabecular bone that has a sheen. This surface is shown in Schubert et al. (2020, Fig. 1A), but Stinnesbeck (this volume) note that our polishing interpretation "may be the effect of a dark brown shadow" in the figure giving the area an unnatural appearance. Contrary to that interpretation, we note that the figures in Stinnesbeck et al. (this volume, Fig. 1a, c) all evince the same polished trabecular surface.

Stinnesbeck et al. (this volume) agree that the "condylar neck" on the holotype exhibits exposed trabecular bone, but state that this also occurs in extant Pecari, and therefore this exposure is natural and not caused by modification. While trabecular bone can naturally occur at the surface, this is typically the result of abrasion from joint mechanics and/or pathological features. We too have observed natural trabecular bone exposure along the posterior surface of Pecari mandibular condyles, but we interpret this location on the fossil (Schubert et al., 2020, Fig. 1F, G) to be well below (inferior to) the missing condyle. We maintain the interpretation that trabecular bone is exposed and polished in this location on the Muknal specimen, and also suggest that the white arrows in Fig. 2b (Stinnesbeck et al., this volume) point to anatomical positions that are more superior, and are thus non-analogous.

Just dorsal to the "condylar neck" of Stinnesbeck (Fig. 1a, Fig. 2a, c) the Muknal dentary is fragmented, with exposed trabecular bone that hasn't been polished. Stinnesbeck et al. place the condylar process of the Muknal specimen directly on top of their proposed "condylar neck" resulting in a relatively low position for that process. In fact, they use this interpretation as another unique characteristic of *Muknalia* (Stinnesbeck et al., 2017; this volume). In contrast, we interpret the missing condylar process to be more dorsal, as in *Pecari*.

Stinnesbeck et al. (this volume) also consider the trapezoidal shape and flat dorsal margin of the coronoid process as a distinguishing feature of *Muknalia*. However, the coronoid is fragmented, particularly on the dorsal surface, and cannot be properly assessed in terms of original shape. Further, the morphology of the coronoid process can vary greatly, even intra-specifically, and some *P. tajacu* comparative specimens do exhibit relatively flat dorsal margins (e.g., *Figure 1G*).

Moving to the anterior end of the Muknal specimen, Stinnesbeck et al. (this volume) interpret a lack of curvature in the diastema between the anterior alveolus of p1 and the posterior margin of the alveolus for the canine to be a characteristic feature of Muknalia. Reference to the p1 is an error or typo here, and should have been listed as the p2 since that is the most anterior premolar position (as in Stinnesbeck et al., 2017). The superior edges of the alveoli for the anterior premolars are fragmented in the Muknal specimen, and what is identified as the superior margin is ventrally skewed in our estimation. The remaining morphology matches that of Pecari. If the missing premolars continued anteriorly in the same vertical alignment with the intact teeth, as in Pecari, then the unmodified alveolar margins of p2 and p3 would be more dorsal than interpreted by Stinnesbeck et al. (this volume, Fig. 1a). The shape of the diastema varies in *Pecari*, ranging from dorsally concave to relatively flat (see *Figure 1*), and the Muknal specimen is within the variation observed in comparative *Pecari*.

The diastema length of 21 mm is also considered to be accurate by Stinnesbeck et al. (this volume) because the "alveolus of the canine is preserved." While it is correct that a portion of the canine alveolus is intact, the posterodorsal margins of the alveolus are broken and missing. Because this section is gone, and since the canine curves and extends posteriorly in the dentary, measurement from the posterior edge of the remaining canine alveolus to the anterior margin of the anterior p2 alveolus results in an erroneously short diastema. As noted previously (Schubert et al., 2020), even though the Muknal measurement is incorrect because of breakage, 21 mm is not outside the range of variation for *P. tajacu*. Stinnesbeck et al. (this volume) also argue that the diastema length to tooth row length (p2 to m3) ratio does not match that of Pecari tajacu they examined, and conclude that the Muknal tooth row is too long (69 mm) for a diastema that short. We examined adult wild peccary specimens in the East Tennessee State University Museum of Natural History zoology collection (ETMNH-Z) and found two P. tajacu specimens (ETMNH-Z 12844, Figure 1G; ETMNH-Z 14306, Figure 1H) that have relatively short diastema lengths (20 mm; 20.9 mm), and compared these to their p2-m3 lengths (75.6 mm; 70 mm). Based on our comparisons, these specimens have shorter diastemas than that proposed for Muknalia, as well as longer p2-m3 lengths.

Stinnesbeck et al. (this volume, Fig. 1) also suggest that a smaller muzzle is supported by "converging dorsal and ventral borders of the mandible seen in lateral view." Once again though, these surfaces are corroded and fragmented. As noted above, the alveolar margins for the anterior premolars are missing. Thus, we interpret the suggested convergence of the dorsal and ventral borders, which is contrasted with comparative examples of *Pecari tajacu*, as due to taphonomically altered morphology. Therefore, the assertion of a smaller or narrower muzzle is not supported if our interpretation based on observed weathering and alignment of the toothrow is correct.

To summarize, we interpret the morphology of "*Muknalia minima*" very differently than Stinnesbeck et al., and contend that the preponderance of anatomical and taphonomic evidence support synonymy with extant *P. tajacu*. In terms of human modification, the only marks that we feel confident in assigning an anthropological origin are those that extend anteriorly from the posterior margin near the 110° angled notch. The most prominent of these marks are shown in Stinnesbeck et al. (this volume, Fig. 1a) and Schubert et al. (2020, Fig. 1B, C). The combination of linear incision marks and polishing attest to the human modification of this important archaeological specimen, albeit representative of an extant genus.

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COMPETING INTERESTS

The authors have no competing interests to declare.

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