Skull shape and the demands of feeding: a biomechanical study of peccaries (Mammalia, Cetartiodactyla)

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A primary requirement of the mammalian skull is to exert forces on different foods and to resist the forces imposed on it during feeding. Skull shape patterns within and among mammals are generally well known, but the biomechanical relevance of this variation remains limited for some groups. By integrating geometric morphometric and biomechanical analyses, we test the hypothesis that skull shape in peccaries reflects biomechanical attributes to generate and dissipate powerful forces, presumably in response to tough foods. We obtained skull shape and size from 213 specimens of the three living peccary species and estimated bite force, bite stress at molars, bending and shear stress on the mandibular corpus, and condylar stress. We found larger estimated bite forces, greater resistance to bending loads, and lower stress emerging from the larger muscle attachment areas and shorter and deeper mandibular corpora for both *Pecari tajacu* and *Tayassu pecari* relative to *Parachoerus wagneri*. Peccaries (*P. tajacu* and *T. pecari*) with more powerful biomechanical attributes feed mainly on tougher foods (e.g., palm fruits). These results support the hypothesis that species eating tough foods tend to have a feeding morphology mechanically adapted to stronger bites and greater biting resistance, which must be closely reflected in their craniomandibular shape.

Um requerimento primário do crânio de um mamífero é exercer forças em diferentes alimentos e resistir às forças impostas nele durante a alimentação. Os padrões de forma do crânio dentro e entre mamíferos são geralmente bem conhecidos, entretanto a relevância biomecânica desta variação permanece limitada a alguns grupos. Integrando análises de morfometria geométrica e de biomecânica nós testamos a hipótese de que a forma do crânio de tayassuídeos reflete atributos biomecânicos para gerar e dissipar forças de grande magnitude, tal como em resposta à alimentos duros. Nós obtivemos a forma e o tamanho do crânio de 213 espécimes das três espécies de tayassuídeos viventes e estimamos a força de mordida e o stress nos molares, no corpo mandibular e no côndilo. Nós encontramos maiores forças de mordida e de resistência e baixo stress emergindo de áreas mais amplas de inserção muscular e de corpos mandibulares mais curtos e altos de *Pecari tajacu* e *Tayassu pecari* em relação a *Parachoerus wagneri*. Tayassuídeos (*P. tajacu* and *T. pecari*) com atributos biomecânicos mais poderosos se alimentam principalmente de alimentos duros (por exemplo, frutos de palmeiras). Estes resultados suportam a hipótese de que espécies que se alimentam de alimentos duros tendem a apresentar uma morfologia do aparato alimentar mecanicamente adaptada a mordidas fortes e grande resistência de mordida, que deve estar intimamente associada as suas formas craniomandibulares.

Key words: biomechanics, Chacoan peccary, collared peccary, functional morphology, geometric morphometrics, mandible, Tayassuidae, white-lipped peccary

The ability to acquire and process foods is essential for animal survival and reproduction. Therefore, it is reasonable to assume that selection acts on the morphology of the feeding apparatus to maintain or improve feeding performance because variation in performance has direct consequences on fitness (Schwenk 2000; Ross and Iriarte-Diaz 2014). The cranium and mandible are complex components of the vertebrate skeleton that are intimately associated with feeding ability and are probable products of adaptation (Herring 1993). Integrating shape and biomechanical analyses can improve our understanding of how the form–function relationships of these phenotypes vary among species and the selective regimes that shaped them (Pérez-Barbería and Gordon 1999; Raia et al. 2010; Cooke and Terhune 2015).

Mammals are distinguished among vertebrates by their mastication mechanisms (Herring 1993). Remarkably, much of their cranial evolution seems to reflect the demands of mastication (Davis 1961; Kemp 2005): the secondary palate, dentary-squamosal jaw articulation, and precise occlusion between lower and upper molars and premolars. However, a primary requirement of the mammalian skull is to exert and resist forces while eating a range of different foods using a variety of feeding behaviors (Thomason 1991; Ross and Iriarte-Diaz 2014). The evolution of the strengthened jaw articulation and increased mass of the adductor musculature allows a combination of extremely powerful but also precisely applied bite forces, whereas the simplification of the mandible to a single pair of dentary bones has implications for its ability to resist associated internal forces and stresses (Davis 1961; Kemp 2005). In feeding biomechanics, force and resistance are important measures of feeding performance (Ross and Iriarte-Diaz 2014).

To serve their biomechanical functions, the form of biological structures should reflect their mechanical attributes (Hylander 1979; Anderson et al. 2008; Ross and Iriarte-Diaz 2014). Recent advances in geometric morphometric methods (GMMs) are opening unprecedented possibilities for investigating shape (Klingenberg 2010; Adams et al. 2013). Mammals, in particular, have been extensively studied and clearly exhibit various patterns of skull shape variation (Marcus et al. 2000; Raia et al. 2010; Cáceres et al. 2014; Cardini and Polly 2013; Meloro et al. 2015; Hendges et al. 2016). The mechanical implications of this variation are a growing topic, and analyses integrating shape and biomechanical features have proven to be powerful tools for understanding form–function relationships in mammals. Correlations between cranial shape and biomechanical variables such as bite force suggest that stronger bites are associated with a shorter rostrum and mandible, wider skull, and more developed muscle attachment areas, whereas elongation of the mandible and rostrum optimize speed during bite (Anderson et al. 2008; Nogueira et al. 2009; Maestri et al. 2016). More comprehensive approaches have provided insights on cranial feeding performance (i.e., force, resistance, and stress magnitudes), which vary within and among species as a function of shape (Taylor 2006; Tanner et al. 2010; Timm-Davis et al. 2015), including in fossils (Cassini and Vizcaíno 2012; Piras et al. 2013; Smith et al. 2015). Demands for feeding

seem to be the major drivers of this variation among species (Hylander 1979, 1988; Nogueira et al. 2009; Cassini and Vizcaíno 2012; Timm-Davis et al. 2015; Maestri et al. 2016). However, important changes in feeding performance may also relate to shared ancestry (Pérez-Barbería and Gordon 1999; Meloro et al. 2008; Piras et al. 2013) and ontogeny (Tanner et al. 2010). The continuing integration of shape and biomechanical methods can expand our understanding also for groups of mammals beyond primates and carnivorans, which are the focuses of most of these studies.

It is widely agreed that the cranial morphology of peccaries (Cetartiodactyla: Tayassuidae) has evolved in response to tough or hard diets (Herring 1972; Kiltie 1981; Pérez-Barbería and Gordon 1999). Despite a great diversity of fossil forms (Gasparini 2007, 2013), only three extant species in three genera are currently recognized according to the classification of Parisi Dutra et al. (2017): *Pecari tajacu* (collared peccary), *Tayassu pecari* (white-lipped peccary), and *Parachoerus wagneri* ("*Catagonus*," Chacoan peccary). *Pecari tajacu* is found from the southwestern United States to north-central Argentina, whereas *T. pecari* occurs from southern Mexico to northern Argentina (Altrichter et al. 2012; Gasparini 2013). Throughout their range, these species consume a variety of plant material of different toughness (e.g., fruits, seeds, roots, nuts, grass) and occasionally invertebrates, snakes, and even fishes (Fragoso 1999; Desbiez et al. 2009; Reyna-Hurtado et al. 2009). However, hard fruits and seeds, particularly from palm species, dominate their diets (Beck 2006). The Chacoan peccary has the most restricted range of the three living peccaries and is endemic to the Dry Chaco of north-central Argentina, western Paraguay, and southeastern Bolivia, inhabiting semiarid thorn forests (Wetzel 1977; Gasparini et al. 2013; Torres et al. 2017). Its diet is composed of a large amount of soft vegetable items (e.g., flowers, fleshy fruits), mainly of cactus, but it also feeds on roots, and seeds from other plant species (Taber et al. 1994; Gasparini et al. 2013). Most of these foods require powerful forces during mastication making peccaries especially interesting mammals in which to study relationships between shape variation and biomechanical attributes.

The dental and cranial morphologies of extant peccaries, represented by bunodont cheek teeth, interlocking canines, and well-developed pre- and post-glenoid processes, as well their essentially orthal chewing stroke, are well suited for processing hard foods in a crushing style of mastication (Herring 1972, 1985). The Chacoan peccary, however, has evolved dental grinding mechanisms and possesses mesodont-bunodont teeth with high crowns (= "zygodont"—Gasparini 2007; Prothero and Grenader 2012; Gasparini et al. 2013), and this could imply an unusual design to the feeding system in this taxon (Herring 1985). Peccaries clearly exhibit differences in cranial morphology and probably in bite forces that are reasonably hypothesized to be linked to their feeding habits (Kiltie 1981, 1982, 1985; Sicuro and Oliveria 2002; Gasparini 2007, 2013; Hendges et al. 2016). However, the functional relevance of this variation in terms of feeding biomechanics is still unknown.

In this study, we used geometric morphometric and bio-mechanical techniques to determine how the skull shape of peccaries translates into biomechanical attributes related to generation and dissipation of powerful forces during feeding (Hylander 1979, 1988; Ross and Iriarte-Diaz 2014). In practice, it is difficult or impossible to obtain in vivo biomechanical measures (e.g., bite force and stress) from free-ranging wild animals such as these peccaries. However, important biome-chanical attributes can be estimated using proxies of muscle size and moment-arms based on geometric landmarks (Cassini and Vizcaíno 2012), and this was the method used in our study. We hypothesized that *P. tajacu* and *T. pecari*, which eat tough foods, should have skull shape traits (shorter and deeper crania and mandibles with better developed muscle insertion areas) adapted to higher biomechanical performance during feed-ing (force and resistance), compared to the skull shape traits of *P. wagneri*, which almost exclusively eat the tender parts of cactus. We based this hypothesis on previously documented correlations of bite force with toughness of diet in mammals (Nogueira et al. 2009; Maestri et al. 2016), including studies of *P. tajacu* and *T. pecari* (Kiltie 1982; Pérez-Barbería and Gordon 1999).

MATERIALS AND METHODS

Acquisition of morphological data.—We collected data from 213 crania and mandibles of *P. tajacu* (n = 136), *T. pecari* (n = 69), and *P. wagneri* (n = 8). The ventral view of the cra-nium and lateral view of the mandible of the specimens were photographed at the same distance (1.56 m) using a Nikon Coolpix P530 digital camera. For each specimen, we also took the following measurements on the mandible: condyle length, condyle width, symphysis length, corpus width, and corpus height (Supplementary Data SD1). Measurements were taken using Vernier calipers, with 0.01 mm precision.

All specimens studied are housed in the extant mammal collections of the Field Museum of Natural History, Chicago, Illinois, and American Museum of Natural History, New York, New York (Supplementary Data SD2). Only adult specimens characterized by fully erupted dentition and completely fused cranial sutures were included (Margarido et al. 2007).

Geometric morphometric analyses.—TPSDig2 software was used to digitize 33 landmarks on the cranium images and 20 landmarks and 12 semi-landmarks on the mandibular images (Rohlf 2015; Fig. 1). Landmarks and semi-landmarks were selected to describe the muscle attachment areas, molars areas,
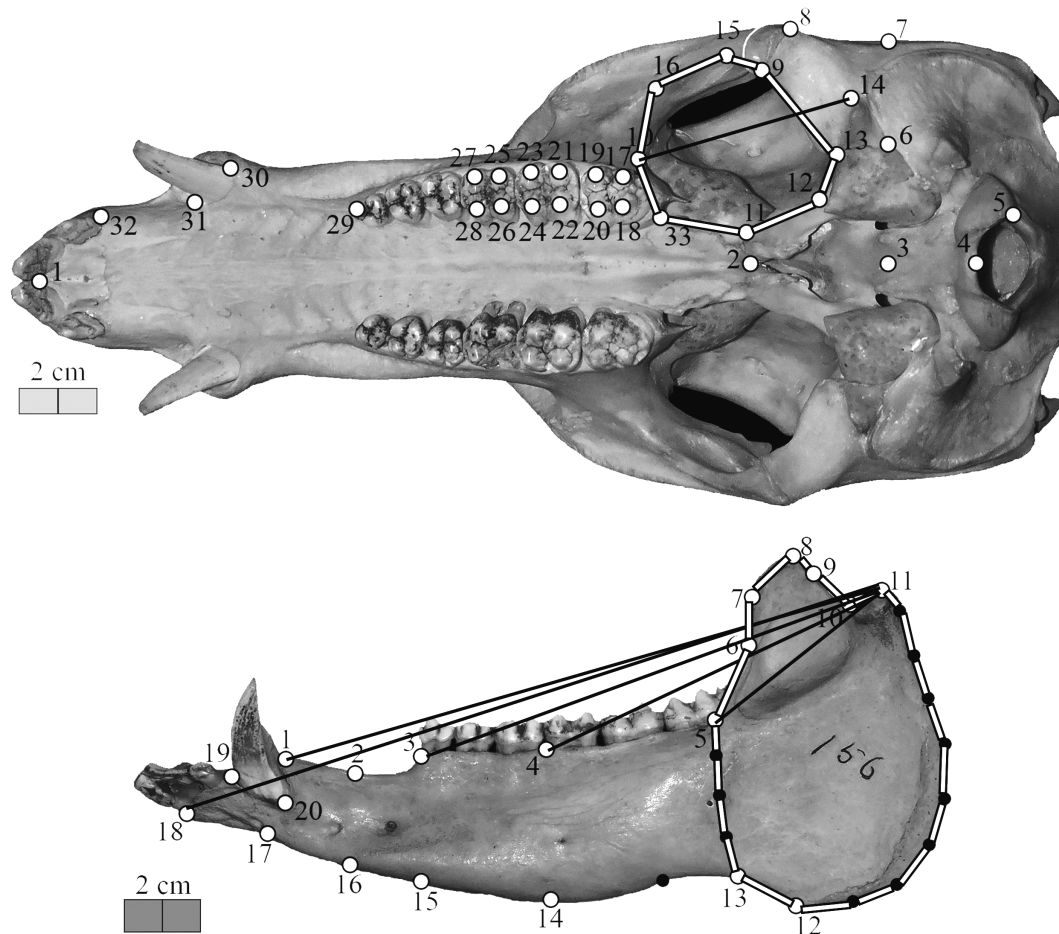
Fig. 1.—Position of the landmarks (white circles) and semi-landmarks (black circles) on the ventral view of the cranium and lateral view on the mandible of peccaries. Landmark descriptions are in Supplementary Data SD1. White line illustrates the temporalis muscle insertion area in the cranium and of the masseter attachment in the mandible. Black lines illustrate the in-lever and out-lever distances estimated from different points.

as well as the mandibular corpus and its cross-sectional areas (Supplementary Data SD1). This configuration is successfully applied to estimate biomechanical variables in the masticatory apparatus of mammals (Cassini and Vizcaíno 2012). After digitization, the landmark coordinates of each view were superimposed applying the generalized Procrustes analysis (GPA—Rohlf and Slice 1990; Adams et al. 2013). Semilandmarks were slid along their tangent directions to minimize bending energy (Perez et al. 2006). GPA was applied to extract both shape and size variables from two-dimensional raw coordinates (*x*, *y*) on the cranium and mandible, separately. Size was obtained as the centroid size: the square root of the sum of squared distances between each landmark and the configuration centroid (Bookstein 1989). From the ventral view of the cranium, we also extracted separately the centroid sizes of the molar teeth (M1, M2, M3) and of the area occupied by the temporalis muscle (Fig. 1). From the mandible view, we extracted the centroid size for the area occupied by the masseter muscle (Fig. 1).

We visualized the patterns of shape variation between species through a principal component analysis (PCA). Procrustes ANOVA was used to test for differences in both shape and size between sex and species. We computed morphological disparity analyses to explore the degree of the shape variation within species, accounting for our unbalanced samples. The metric of morphological disparity obtained for each species (= Procrustes variance) is the same sum of the diagonal elements of the group covariance matrix divided by the number of samples in the group (Zelditch et al. 2012). Although GMMs separate shape from size, both variables can still be correlated generating allometric effects on shape patterns (Klingenberg 2016). Thus, to account for the allometric component, we regressed shape on log-transformed centroid size using a Procrustes ANOVA. In morphometrics, this function uses the sum-of-squared Procrustes distances to assess variation in *y* variable (Procrustes coordinates) modeled by continuous (e.g., centroid size) or categorical factors (e.g., sex, species; see Goodall 1991). These analyses were implemented using the functions procD.lm and morphol.disparity in the R package geomorph

(Adams and Otarola-Castillo 2013; R Development Core Team 2016). Finally, two-block partial least squares (PLS) analysis was applied to explore the maximum covariation between mandible shape variables (partial warps and uniform components) and bite force (size-corrected—Rohlf and Corti 2000). PLS was performed using tpsPLS software (Rohlf 2015).

Biomechanical analyses.—By applying the formula $d = \sqrt{(x2 - x1)^2 + (y2 - y1)^2}$, where *x* and *y* are the raw coordinates for each landmark, we obtained the distance between landmarks located in specific regions of the cranium and mandible (cross-sectional areas). The centroid sizes of temporalis and masseter insertion areas were used as proxies of muscle sizes. Using centroid sizes of muscle attachment areas preserves the dimensionality while providing estimates of relative jaw muscle force using a standard GM measure (see Cassini and Vizcaíno 2012).

Then, we calculated three major sets of biomechanical variables related to feeding biomechanics (Table 1): 1) bite force and bite stress at the molars, 2) bending and shear stress on the mandibular corpus (resistance to bending, stress under bending, resistance to shear, shear stress), and 3) condylar stress (condyle reaction force, condyle stress, relative symphysis length). These variables were estimated for each individual following the approaches proposed by Hylander (1979) and Cassini and Vizcaíno (2012).

Given that some biomechanical variables such as bite force scale with body size in vertebrates (Aguirre et al. 2002), we also calculated size-corrected indices by dividing the absolute values of variables by the average centroid size of the cranium or mandible. According to Vinyard et al. (2003), using mandible or cranium length (in our case centroid size) as a biomechanical standard, it is possible to compare the skulls of different species while holding constant relevant mechanical factors (i.e., size) thought to be significant in influencing skull loading. The means of absolute and size-corrected values of biomechanical performance variables were compared between species using one-way analysis of variance (one-way ANOVA), including Tukey's pairwise comparisons in cases of significant variation. Some variables were log-transformed to meet the assumptions

Table 1.—Descriptions of the formula for each biomechanical variable estimated for peccary species. * = multiplied by; / = divided by.

Biomechanical variables	Formula
Masseter torque	masseter centroid size * the in-lever distance from the tip of the condylar process (L11) to the junction between the ramus and mandibular corpus, at M3 (L5)
Temporalis torque	temporalis centroid size * in-lever distance from the tip of the post-glenoid process (L14) to the curvature between the maxilla and the zygomatic arch (L10).
Jaw muscle torque	masseter torque + temporalis torque
Bite force	jaw muscle torque/out-lever distances at incisor (L11 to L18), canine (L11 to L1), first premolar (L11 to L3), and first molar (L11 to L4)
Bite stress at molars	bite force at the first molar/centroid size of M1, M2, and M3
Resistance to bending	corpus height dividing by mandible length (distance from L11 to L18)
Stress under bending	torque at the incisors (FB * L11 − L1)/corpus height
Resistance to shear	corpus width * corpus height * π
Shear stress	bite force at M1/corpus width * corpus height * π
Condylar reaction force	jaw elevator torque at M1/out-lever distance from the tip of the condylar process (L11) to the anteriormost point of the first molar alveolus (L4)
Condyle stress	condyle reaction force/condylar area (= condyle length * condyle width)
Relative symphysis length	symphysis length/mandible length

of parametric tests. All analyses were performed in the R environment (R Development Core Team 2016).

RESULTS

Shape and size variation.—There were significant interspecific differences in cranial shape ($R^2 = 0.21$, $F_{2,212} = 28.31$, $P < 0.001$). PC1 and PC2 separated the skull shapes of *P. tajacu* and *T. pecari* species, while *P. wagneri* showed overlap with both (Fig. 2). *Pecari tajacu*, with mostly negative scores on PC1, exhibited a shorter maxillary toothrow and a broader temporalis muscle area positioned more posteriorly in relation to the M3 than *T. pecari*, which had more positive scores on PC1.

Mandible shape also showed significant variation between the three species ($R^2 = 0.20$; $F_{2,212} = 26.50$, $P = 0.001$),

characterized by differences in mandibular corpus and masseter muscle area. PC1 primarily segregated the mandible shape of *P. wagneri* from that of the other two peccaries. *Parachoerus wagneri*, with positive scores on PC1 (23.32%), had a more elongated and shallower mandibular corpus, with markedly decreased masseter muscle area compared to the other two species, which had negative scores on PC1. PC2 (16.10%) contrasts variation in the mandibular corpus of *P. tajacu* and *T. pecari*. With negative scores, *P. tajacu* exhibited a proportionally shorter and deeper mandibular corpus than *T. pecari*, which had positive scores on PC2 (Fig. 2).

The morphological disparity analysis showed the highest Procrustes variation in the skull shape of *P. tajacu* (PV mandible = 0.00181; PV cranium = 0.00156) followed by *T. pecari* (PV mandible = 0.00143; PV cranium = 0.00114) and *P. wagneri* (PV mandible = 0.00116; PV cranium = 0.00093).
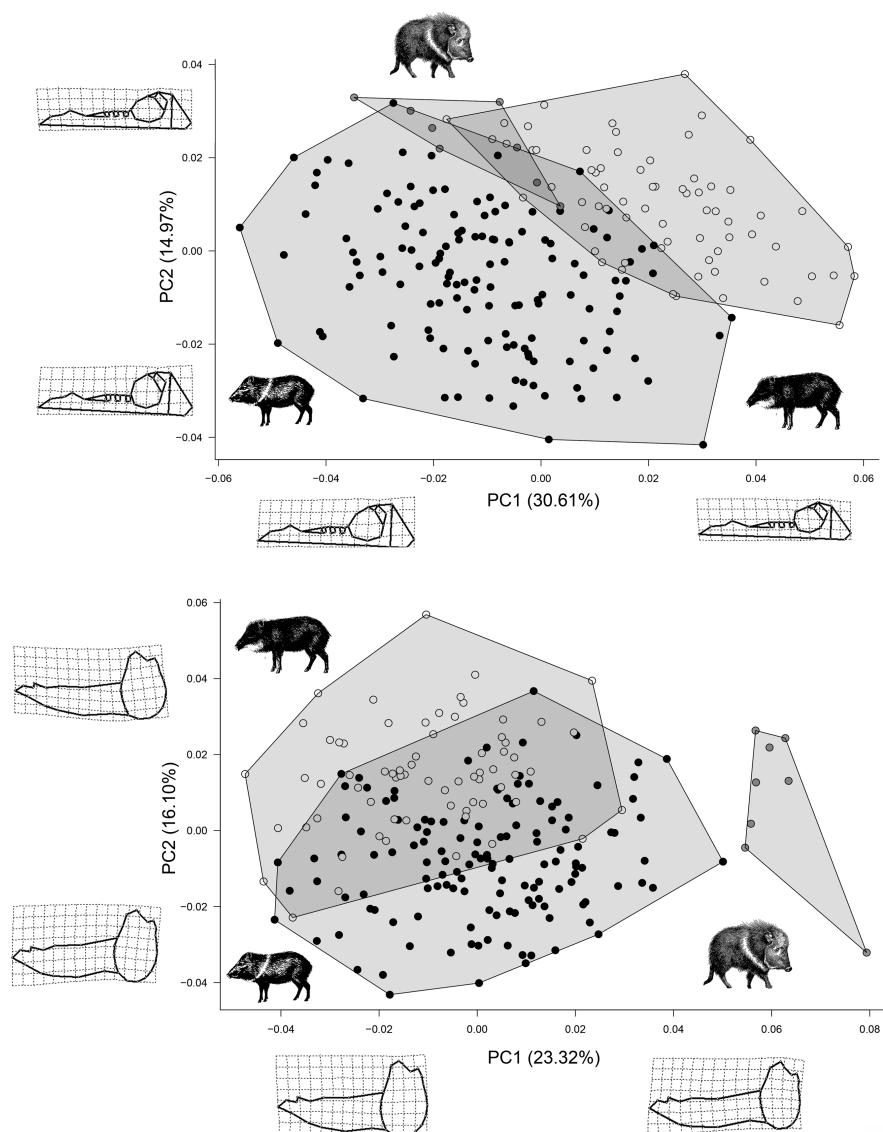
Fig. 2.—Cranial and mandibular morphospace identified for peccaries by the principal component analysis. Transformation grids show the shape deformations relative to the mean at the positive and negative extremes of the first two principal component axes. Solid circles = *Pecari tajacu* (collared peccary); open circles = *Tayassu pecari* (white-lipped peccary); gray circles = *Parachoerus wagneri* (Chacoan peccary).

Nevertheless, this variation was not significantly different between *T. pecari* and *P. wagneri* ($P > 0.05$).

There were no sex differences in the shapes of *T. pecari* (cranium: $F_{1,46} = 0.72$, $P = 0.70$; mandible: $F_{1,46} = 1.67$, $P = 0.07$) and *P. wagneri* (cranium: $F_{1,3} = 1.09$, $P = 0.36$; mandible: $F_{1,3} = 0.52$, $P = 0.73$). Slight sexual dimorphism was apparent in the shape of the skull of *P. tajacu* (cranium: $F_{1,94} = 2.33$, $P < 0.01$; mandible: $F_{1,94} = 2.10$, $P < 0.03$). However, the PCA projections did not show segregation between males and females, suggesting that collared peccaries are also not sexually dimorphic in shape (Supplementary Data SD3).

The size of both cranium ($F_{2,212} = 646.62$, $P < 0.001$) and mandible ($F_{2,212} = 843.15$, $P < 0.001$) also differed between these species. *Parachoerus wagneri* had the largest cranium and mandibles, while *P. tajacu* had the smallest. Size showed a weak influence on the shape variation of cranium and mandible in *P. tajacu* (cranium: $R^2 = 0.05$, $F = 7.61$, $P < 0.01$; mandible: $R^2 = 0.02$, $F = 2.82$, $P < 0.01$) and on cranial shape of *T. pecari* ($R^2 = 0.05$; $F = 4.18$; $P < 0.01$). There were no significant differences between sexes in size of the cranium (*P. tajacu*: $F_{1,94} = 0.38$, $P = 0.52$; *T. pecari*: $F_{1,46} = 1.39$, $P = 0.27$; *P. wagneri*: $F_{1,3} = 0.02$, $P = 0.99$) and mandible (*P. tajacu*: $F_{1,94} = 0.15$, $P = 0.70$; *T. pecari*: $F_{1,46} = 1.33$, $P = 0.25$; *P. wagneri*: $F_{1,3} = 0.20$, $P = 0.87$) in the three species.

Biomechanical attributes.—Estimates of absolute bite force differed between species: *T. pecari* showed higher estimated bite forces than *P. wagneri* and *P. tajacu* at the canine, PM1, and M1. Bite force at the incisor was larger in *T. pecari* than in *P. tajacu* but did not differ significantly from *P. wagneri* (Table 2). However, the size-corrected ANOVA with bite force clearly showed that the differences between *T. pecari* and *P. tajacu* were no longer apparent, instead indicating that these two peccaries had larger bite forces than *P. wagneri* (Table 2; Fig. 3). Bite stress at the molars also differed significantly among the three species, except at the first molar of *P. tajacu* and *T. pecari*. During biting, *T. pecari* and *P. tajacu* generate higher stress at the molars than do *P. wagneri* (Table 2; Fig. 4).

Absolute resistance to bending was greater in the mandibular corpora of *T. pecari* and *P. tajacu* than in *P. wagneri* (Table 2). However, the size-corrected analysis revealed the strongest resistance to dorsoventral loads in the mandible of *P. tajacu* (Table 2; Fig. 5). *Parachoerus wagneri* presented greater absolute and size-corrected stress under bending than either *P. tajacu* or *T. pecari* (Table 2; Fig. 5). Absolute and size-corrected resistance to shear was larger in the mandible of *T. pecari* than *P. wagneri* and *P. tajacu*, while the highest shear stress occurred in the mandibular corpus of *P. tajacu* (Table 2; Fig. 5). Overall, the mandibular morphology of *T. pecari* was stronger than that of the other two peccaries.

Absolute and size-corrected condyle reaction force was larger in *P. tajacu* and *T. pecari* than in *P. wagneri* (Table 2; Fig. 6). The largest condyle stress, however, occurred in *P. tajacu* (Table 2). *Tayassu pecari* and *P. tajacu* also showed larger relative symphysis length than *P. wagneri* (Table 2; Fig. 6).

Partial least squares showed a strong and significant covariation between mandible shape and size-corrected bite force ($R^2 = 0.78$; $P < 0.001$; PLS1 var. 97.15%). The visualization of shape variation described by the PLS shape vector of mandible showed that lower estimated bite force is associated with

Table 2.—Results from the absolute and size-corrected analyses of ANOVA and Tukey's tests comparing biomechanical performance-related variables among peccary species. PW: *Parachoerus wagneri*, Chacoan peccary; PT: *Pecari tajacu*, collared peccary; TP: *Tayassu pecari*, white-lipped peccary. * indicates statistical significance.

| | Absolute analyses | | | | | Size-corrected analyses | | | | |
| | ANOVA | | Significance level of Tukey's test | | | ANOVA | | Significance level of Tukey's test | | |
	F	P	PW versus PT	PW versus TP	PT versus TP	F	P	PW versus PT	PW versus TP	PT versus TP
Bite force										
M1	249.7	< 0.001*	< 0.001*	< 0.001*	< 0.001*	26	< 0.001*	< 0.01*	< 0.01*	0.635
PM1	237.3	< 0.001*	< 0.01*	< 0.001*	< 0.001*	26.38	< 0.001*	< 0.01*	< 0.01*	0.208
Canine	208.9	< 0.001*	< 0.001*	0.030 *	< 0.001*	13.85	< 0.001*	< 0.001*	< 0.001*	0.656
Incisor	188.3	< 0.001*	< 0.001*	0.180	< 0.001*	9.91	< 0.001*	< 0.001*	< 0.001*	0.603
Bite stress at molars										
M1	23.72	< 0.001*	< 0.001*	< 0.001*	0.194					
M2	57.2	< 0.001*	< 0.001*	< 0.001*	< 0.01*					
M3	46.04	< 0.001*	< 0.001*	< 0.001*	< 0.001*					
Resistance to bending										
	42.36	< 0.001*	< 0.001*	< 0.001*	0.053	184.7	< 0.001*	< 0.001*	< 0.001*	0.001*
Stress under bending										
	173.3	< 0.001*	< 0.001*	< 0.001*	0.438	12.87	< 0.001*	< 0.001*	< 0.001*	0.697
Resistance to shear										
	516.9	< 0.001*	< 0.001*	< 0.001*	< 0.001*	252.1	< 0.001*	0.532	< 0.001*	< 0.001*
Shear stress										
	138.3	< 0.001*	< 0.001*	0.067	< 0.001*	257.9	< 0.001*	< 0.001*	0.568	< 0.001*
Condyle reaction force										
	13.96	< 0.001*	< 0.001*	< 0.01*	< 0.01*	235.7	< 0.001*	< 0.001*	< 0.001*	< 0.001*
Condyle stress										
	207.8	< 0.001*	< 0.001*	0.912	< 0.001*					
Relative symphysis length										
	40.74	< 0.001*	< 0.001*	< 0.001*	< 0.001*	237	< 0.001*	< 0.001*	< 0.001*	< 0.001*
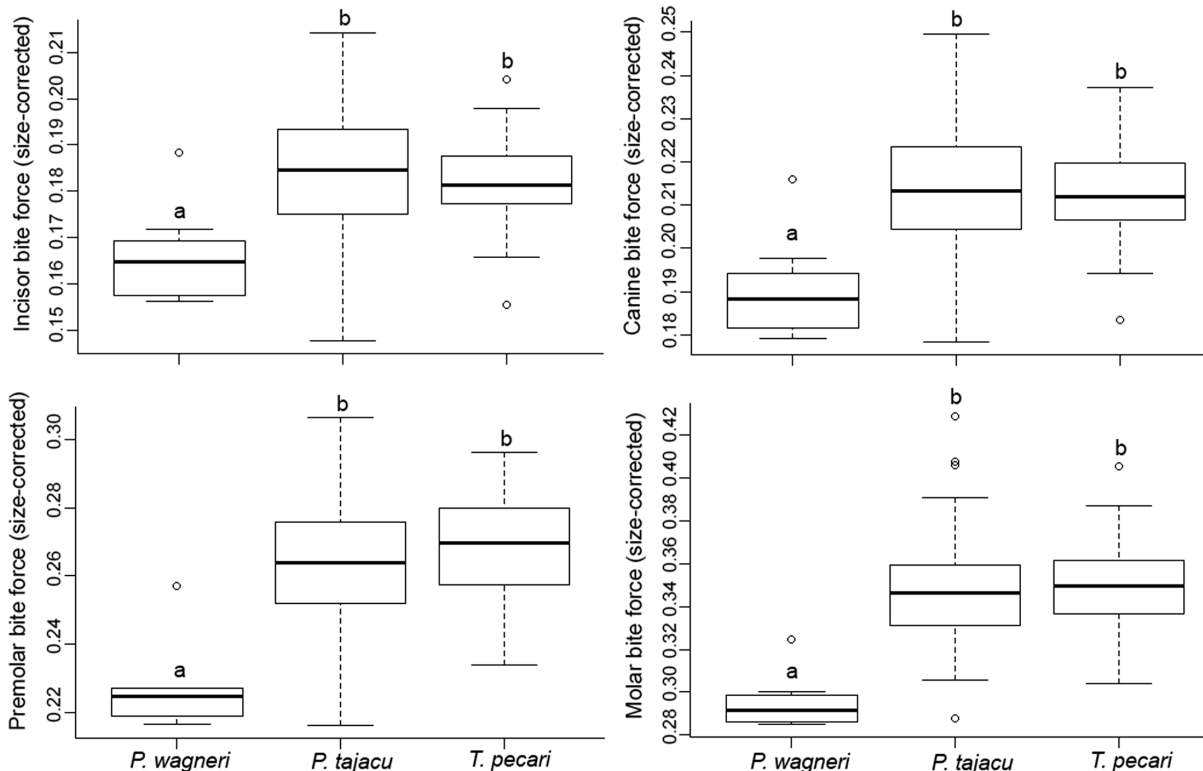
Fig. 3.—Variation in bite forces at incisors, canine, premolars, and molars among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey's pairwise comparisons between species (equal letters mean no significance, different letters mean significance).
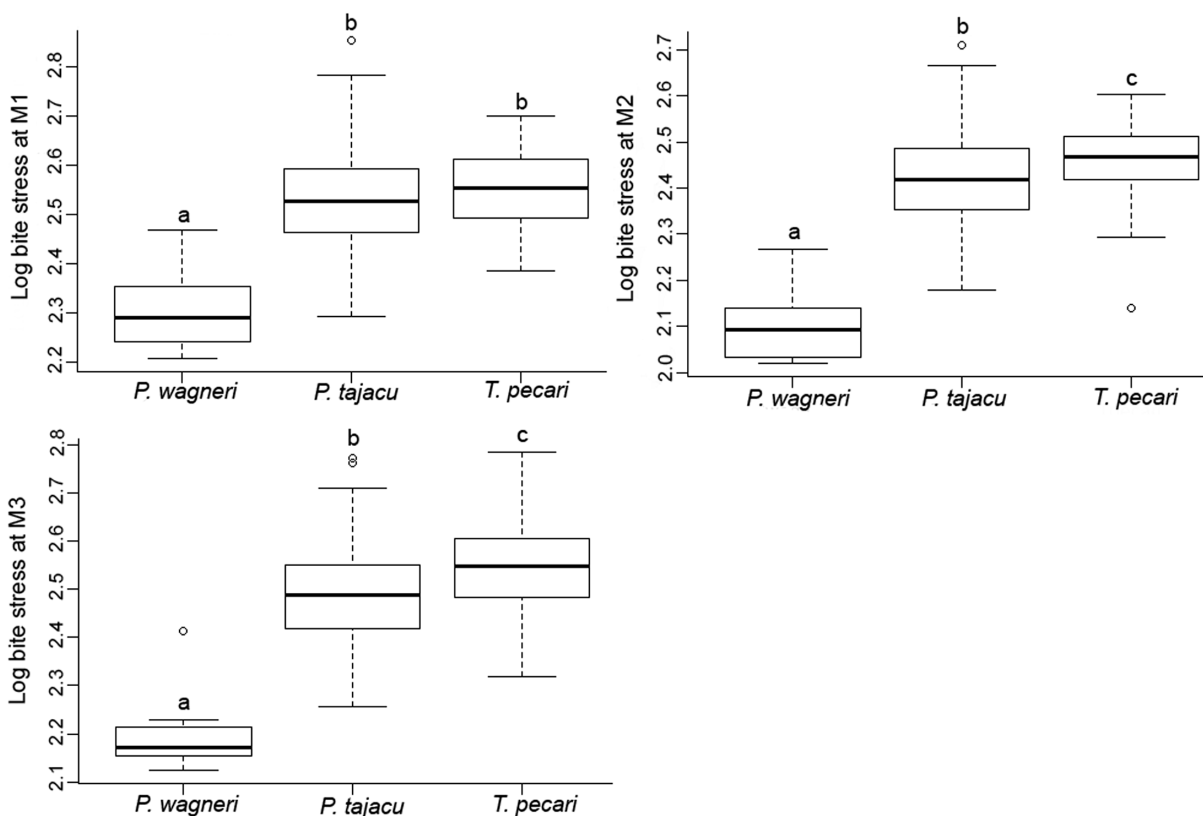
Fig. 4.—Variation in bite stress at the first molar (M1), second molar (M2), and third molar (M3) among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey's pairwise comparisons between species (equal letters mean no significance, different letters mean significance).
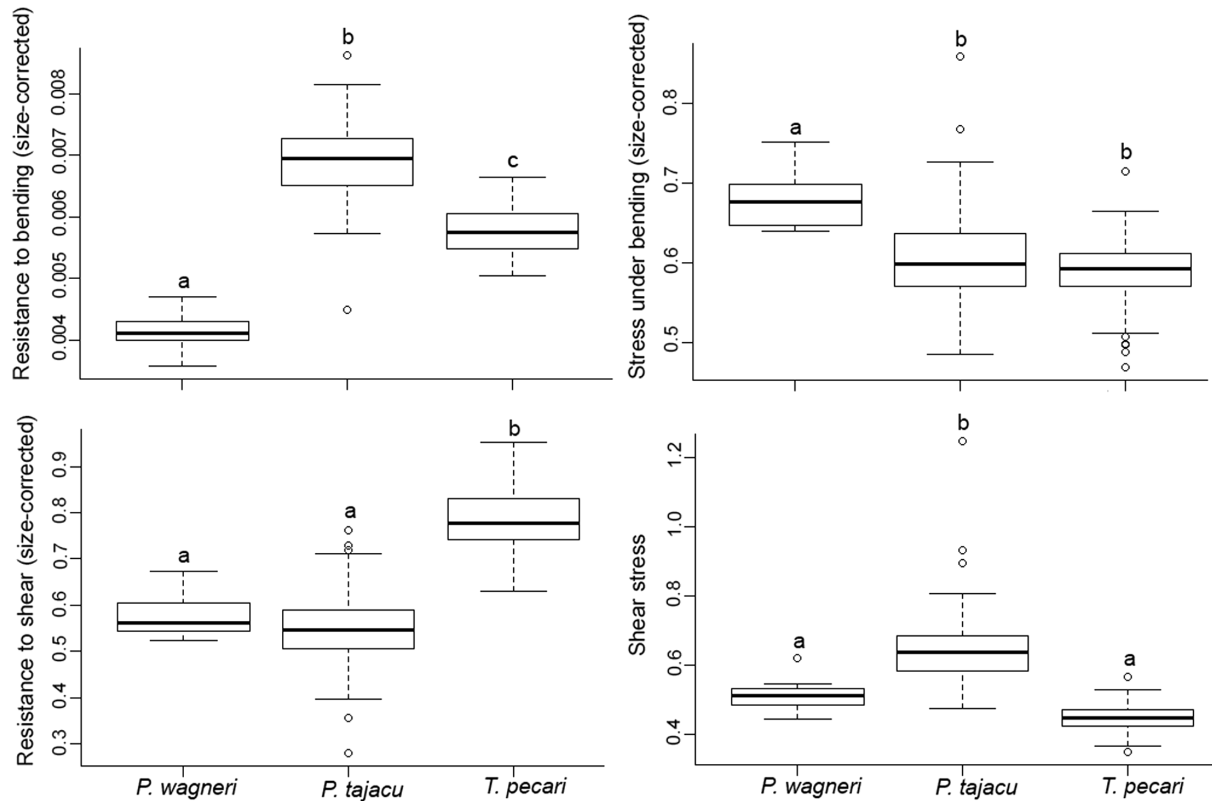
Fig. 5.—Variation in bending and shear stress on the mandibular corpus among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey's pairwise comparisons between species (equal letters mean no significance; different letters mean significance).

an elongation of the mandibular corpus and narrowing of the muscle area exhibited for *P. wagneri*, while high values of bite force are associated with a shortening of the mandibular corpus and relative increase in masseter muscle area, features of both *P. tajacu* and *T. pecari* (Fig. 7).

DISCUSSION

Our combined geometric morphometric and biomechanical approach provides meaningful insights on form–function relationships in peccaries. We found a similar pattern of shape variation in the masticatory apparatus, mainly in mandible shape, in *P. tajacu* and *T. pecari*, which both differ from *P. wagneri*. The larger muscle attachment areas and shorter and deeper mandibular corpora reflect larger bite forces and greater resistance to loads in the mandibular corpus of both *P. tajacu* and *T. pecari* relative to *P. wagneri*. In a broader sense, these results indeed suggest that the mandible shape of *P. tajacu* and *T. pecari* enables them to apply stronger forces and resist risk of fracture from higher biomechanical demands of hard foods than does *P. wagneri*.

Peccaries exhibit significant interspecific differences in cranial and mandibular shape. Cranial shape space (Fig. 2) mainly emphasizes the variation between *P. tajacu* and *T. pecari*. The shape variation associated with maxillary toothrow and temporalis insertion area corroborates the pattern recently observed for these two peccaries (Hendges et al. 2016). Shape variation

also reveals the slightly more elongated rostrum in *T. pecari* than in *P. tajacu*, documenting a previously noted morphological pattern (Wetzel 1977; Gasparini 2013). In contrast, mandible shape differentiates *P. tajacu* and *T. pecari* (which overlap) from *P. wagneri*. *Pecari tajacu* and *T. pecari* have shorter and deeper mandibular corpora with a greatly enlarged area of adductor musculature compared to *P. wagneri* (Fig. 2). These shape traits are associated with larger estimated bite forces, greater resistance to ventral bending loads, and lower stress (except at molars) for *P. tajacu* and *T. pecari*, in contrast with the mandible shape of *P. wagneri* (Fig. 7; Table 2). Unfortunately, diet data are not available for the localities of the individuals included in our analyses and this prevented us from making correlations between diet and the biomechanical variables. Nevertheless, the previously documented correlations of diet and bite force offer support for our hypothesis that the two peccaries with tougher diets (*Pecari* and *Tayassu*) possess stronger bites and higher resistance to loads (Kiltie 1982; Pérez-Barbería and Gordon 1999).

Diet is an important selective force acting on the craniomandibular morphologies of mammals, including peccaries (Kiltie 1985; Pérez-Barbería and Gordon 1999). Its effects could be even more pronounced on mandible shape given the more precise functional role of mandibles in feeding (Raia et al. 2010; Ross and Iriarte-Diaz 2014). The pattern we found for *P. tajacu* and *T. pecari* is characteristic of omnivorous mammals relying on hard foods (Pérez-Barbería and Gordon 1999; Ravosa et al.
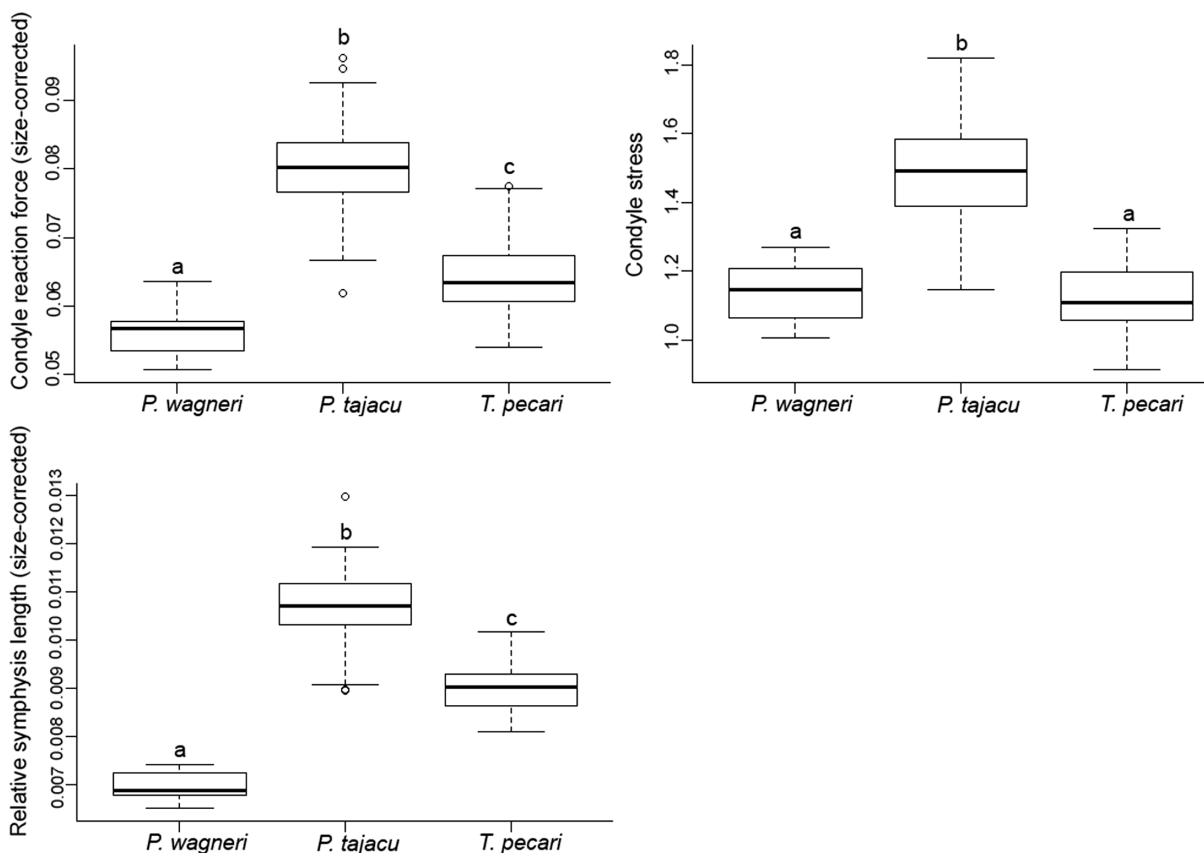
Fig. 6.—Variation in condylar stress among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey's pairwise comparisons between species (equal letters mean no significance; different letters mean significance).
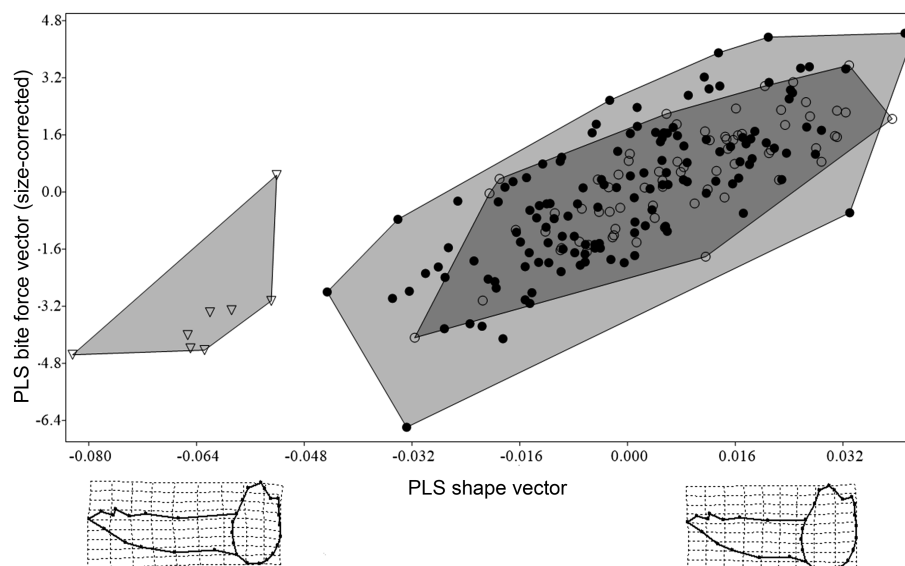
Fig. 7.—Covariation between partial least squares (PLS) mandible shape vector and the size-corrected bite force. Grids depict shape changes associated with negative (a) and positive (b) scores of the PLS vector. Solid circles = *Pecari tajacu* (collared peccary); open circles = *Tayassu pecari* (white-lipped peccary); inverted triangles = *Parachoerus wagneri* (Chacoan peccary).

2000; Taylor 2006; Nogueira et al. 2009; Maestri et al. 2016). In turn, shape and biomechanical traits seen in *P. wagneri* are common features in some browsing ungulates (Pérez-Barbería and Gordon 1999; Mendoza et al. 2002; Raia et al. 2010), and even in extinct peccaries of the genus *Platygonus* (Wetzel 1977; Gasparini 2013). Browsers include ungulates feeding

predominantly on dicotyledonous plants (Mendoza et al. 2002). Fruits, flowers, and roots of dicots, mainly Cactaceae, are indeed predominant in the diet of *P. wagneri* (Taber et al. 1994; Gasparini et al. 2013). These foods can be also tough, but they are likely less tough than palm fruits, seeds, and nuts, which dominate the diets of *P. tajacu* and *T. pecari* (Pérez-Barbería and Gordon 1999). Loads ranging between 100 and 1,260 kg have been suggested to break the nuts and seeds ingested by these two peccaries (Kiltie 1982). Thus, the more relaxed biomechanical attributes (bite force and stress) emerging from the mandible shape of *P. wagneri* seem to be an adaptation to a browsing diet, one presumably less tough than the omnivorous diet of *P. tajacu* and *T. pecari*.

Further comparative support emerges from the differences in the feeding behavior of peccaries. On one hand, the powerful bite and reaction forces shared by *P. tajacu* and *T. pecari* support the hypothesis that they are better adapted to employ similar crushing mechanisms (Kiltie 1981; Herring 1985). Since transverse excursion during the power stroke is small or absent, the vertically deep mandible corpora of these two peccaries are likely an adaptation to resist large bending moments mainly in sagittal planes (Hylander 1979). The vertically deep and transversely thicker mandibular corpora confer an even more efficient design in *T. pecari*, additionally enabling greater dorsoventral shear resistance (Hylander 1979, 1988; Ravosa et al. 2000). Primates engaged in chewing foods that require extensive amounts of incisal preparation also have similar functional profiles in their jaws (Hylander 1979, 1988; Taylor 2006). The mandible shape of *P. tajacu* and *T. pecari* may thus be better adapted to resist higher bending moments generated during crushing mastication or even during incisor biting of tough foods. On the other hand, a smaller condyle area and a slender mandible can result in the lower bite force and decreased vertical bending loads verified in *P. wagneri* (Kiltie 1981; Herring 1985). Lower bite forces and stresses at the molars, however, could be compensated by the enlarged, high-crowned molars of *P. wagneri*, as during chewing, crests in perpetual contact maintain high occlusal pressure on foods even with reduced occlusal force (Herring 1985). However, our stress measures do not take dental topography into account as we measured the whole tooth surface area.

The emergence of similar functional profiles for *P. tajacu* and *T. pecari* complement their greater dietary and phylogenetic affinities (Wetzel 1977; Gasparini 2007; Parisi Dutra et al. 2017). However, molecular evidence showing that *T. pecari* and *P. wagneri* are more closely related is increasing (Theimer and Keim 1998; Gongora and Moran 2005; Perry et al. 2017), which would make similarities between *Pecari* and *Tayassu* a result of convergence. Under any scenario, the mandibular shape and biomechanical traits of *P. wagneri* appear more conservative, retaining a browsing pattern verified in extinct peccaries of the genus *Platygonus*, which were likely well adapted to open, arid environments like those where *P. wagneri* is currently restricted (Wetzel 1977; Gasparini et al. 2013). Improved feeding biomechanics may have been a key factor in the expansion of the dietary niches of *P. tajacu* and *T. pecari* enabling them to exploit food items with a wide range of toughness over a variety of habitats, from tropical forest to arid open environments (Wetzel 1977).

In summary, our results show that *P. tajacu* and *T. pecari* share craniomandibular shape traits enabling them to apply stronger forces and better resist stress and fractures from the mastication of hard foods than does *P. wagneri*. Our analysis and corroborative ecological observations support the hypothesis that species eating tough foods tend to have a feeding morphology that is mechanically adapted to stronger bites and greater biting resistance, which must be closely reflected in their craniomandibular shape traits. Although we need to be cautious about attributing these outcomes solely to feeding adaptations, at some level the functional implications of this variation must reflect the demands of diet and feeding behavior in these peccaries.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Definition of landmarks and semi-landmarks placed on the cranium and mandible, and caliper measurements.

Supplementary Data SD2.—List of specimens of the peccary species *Pecari tajacu*, *Tayassu pecari*, and *Parachoerus wagneri*.

Supplementary Data SD3.—Principal component projections of cranium and mandibular landmarks for males and females of *Pecari tajacu*.

ACKNOWLEDGMENTS

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