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VARIAÇÃO ECOGEOGRÁFICA E FUNCIONAL DO CRÂNIO DE TAYASSUIDAE (MAMMALIA: ARTIODACTYLA)

TESE DE DOUTORADO

Carla Deonisia Hendges

Santa Maria, RS, Brasil
2018

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VARIAÇÃO ECOGEOGRÁFICA E FUNCIONAL DO CRÂNIO DE TAYASSUIDAE (MAMMALIA: ARTIODACTYLA)

Tese apresentada ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para a obtenção do título de **Doutora em Biodiversidade Animal**

Orientador: Prof. Dr. Nilton Carlos Cáceres

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“Do or do not. There is no try”.

Master Yoda

RESUMO

VARIAÇÃO ECOGEOGRÁFICA E FUNCIONAL DO CRÂNIO DE TAYASSUIDAE (MAMMALIA: ARTIODACTYLA)

AUTORA: Carla Deonisia Hendges
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Compreender os mecanismos determinantes e os papéis funcionais da variação fenotípica tem sido um tema central da ecogeografia e evolução. Tayassuídeos são excelentes modelos para testar hipóteses ecogeográficas e funcionais dada a extensa distribuição geográfica ao norte e sul do Equador de duas das três espécies atuais e a evolução de algumas características craniais que pressupõe altas performances biomecânicas. Nessa tese nós utilizamos procedimentos de morfometria geométrica e análises de variância uni e multivariadas para descrever a variação geográfica na forma e tamanho do crânio de *Pecari tajacu* e *Tayassu pecari* e testar a influência de fatores ambientais, alométricos e espaciais. Nós também investigamos se a forma do crânio das três espécies atuais reflete seus atributos biomecânicos. No primeiro capítulo, obtivemos a forma do crânio para 294 espécimes de *P. tajacu* e *T. pecari* de 134 diferentes localidades na America do Sul. Utilizando *Partial Least Squares* e análises de partição de variância nós quantificamos o relacionamento entre a forma e fatores ambientais, espaciais e alométricos. Nossos resultados revelaram padrões de variação geográfica na forma do crânio de ambas as espécies, mas a forma de *T. pecari* é mais conservativa. O ambiente explicou a maior parte da variação, enquanto um fraco efeito alométrico e da autocorrelação espacial foi encontrado apenas em *P. tajacu*. No segundo capítulo, nós testamos a variaçao geográfica no tramanho de 426 espécimes destes dois tayassuídeos provenientes de 174 localidades diferentes ao sul do equador e 83 ao norte. Nós testamos o efeito da latitude, temperatura sazonal, precipitação e influência humana no tamanho do crânio com *Generalized Least Squares* incluindo estruturas de autocorrelação espacial. Diferenças de tamanho em regiões de simpatria e alopatria foram exploradas com modelos de ANOVA. Nós encontramos um padrão latitudinal no tamanho do crânio de *P. tajacu* e *T. pecari* inverso a Regra de Bergmann. O tamanho foi positivamente associado à precipitação oferecendo suporte à disponibilidade de recursos como um importante fator selecionando maiores tamanhos corporais em baixas latitudes, especialmente para *T. pecari*. A influência humana afeta negativamente o tamanho das espécies no hemisfério sul. As distribuições de tamanho corporal, em grande parte não sobrepostas, sugerem que as diferenças de tamanho podem ser necessárias para a sobreposição simpátrica dessas espécies. No capitulo 3, combinamos análises de morfometria geométrica e modelos biomecânicos e obtivemos a forma craniomandibular e o tamanho do centróide de 213 espécimes e estimamos força de mordida e estresse nos molares, corpo mandibular e no processo condilar. Nós encontramos que *P. tajacu* e *T. pecari* compartilham traços de forma craniomandibular (corpo mandibular mais curto e profundo e áreas de inserção muscular mais amplas) que lhes permite aplicar maior força durante a mordida e resistir ao risco de fraturas de maiores demandas biomecânicas do que *P. wagneri*. De modo geral, nossos resultados ressaltam o papel da variação ambiental dirigindo clinas na forma e tamanho do crânio, sobretudo a disponibilidade de recursos, e corroboraram a hipótese de que a forma reflete de perto o desempenho biomecânico das espécies.

Palavras-chave: Biomecânica. Macroecologia. Mandibula. Morfometria geométrica. Performance alimentar. Regra de Bergmann. Suiformes. Variação clinal. Variação morfológica.

ABSTRACT

ECOGEOGRAPHICAL AND FUNCTIONAL VARIATION IN SKULL OF TAYASSUIDAE (MAMMALIA: ARTIODACTYA)

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Understanding the determining mechanisms and functional roles of phenotypic variation have been a central topic of ecogeography and evolution. Peccaries are excellent models for testing ecogeographical and functional hypotheses given the extensive geographic distributions ranging across both Northern and Southern hemispheres of two of the three living species as well the evolution of skull features that presuppose high biomechanical performance. In this thesis, we used geometric morphometrics procedures and univariate and multivariate analyses of variance to describe the geographical variation in skull shape and size of *Pecari tajacu* and *Tayassu pecari* and to test the influence of environmental, allometric and spatial factors. We also investigated if skull shape of the three living peccaries reflect their biomechanical attributes. In the first chapter, we obtained the skull shape for 294 specimens of both *P. tajacu* and *T. pecari* from 134 different localities in South America. Using Partial Least Squares and variation partitioning analysis we quantified the relationship between the skull shape and the environmental, spatial and allometric factors. Our results revealed patterns of geographical variation in skull shape of both species, but shape is more conservative in *T. pecari*. The environment explained most of this variation, while a weak allometric and spatial autocorrelation effect was found only in *P. tajacu*. In the second chapter, we tested the geographical variation in skull size of 426 specimens of both species from 174 different localities south of the equator and 83 in the north. We regressed the skull size against latitude. Effects of seasonal temperature, precipitation, and human influence including spatial autocorrelation structures were tested through Generalized Least Squares. Differences in size between sympatric and allopatric areas were explored with ANOVA models. We found a latitudinal pattern in skull size of peccaries, one inverse to Bergmann Rule. Size was positively associated with precipitation, offering support to resource availability as a major mechanism behind increases in lower latitudes, especially for *T. pecari*. Human influence affects negatively the size of peccaries in Southern hemisphere. The largely non-overlapping body-size distributions of the two species suggest that size differences may be necessary for sympatric overlap of these two peccaries. In chapter 3, combining geometric morphometrics and biomechanical analyses we obtained the skull shape and centroid 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 that *P. tajacu* and *T. pecari* share craniomandibular shape traits (shorter and deeper mandibular corpora and wider muscle insertion areas) enabling them to apply stronger forces and resist stress and fractures from higher biomechanical demands than *P. wagneri*. In a broader sense, our results highlight the role of the environmental variation driving clinal variation in skull shape and size, especially the resource availability. The results also corroborate the hypothesis that shape closely reflects the biomechanical performance of species.

Keywords: Biomechanics. Macroecology. Mandible. Geometric morphometrics. Feeding performance. Bergmann's Rule. Suiformes.Clinal variation. Morphological variation.

Sumário

Introdução geral

A variação fenotípica e suas implicações para as populações naturais

Variação fenotípica é característica ubíqua das populações naturais: indivíduos diferem em morfologia, fisiologia e comportamento em suas interações intra e interespecíficas (BOLNICK et al., 2011; SCHREIBER et al., 2011). Charles Darwin e Alfred Wallace foram pioneiros ao reconhecer que essa variação é a matéria-prima para a seleção natural, e assim, um dos principais fatores para a continuidade evolutiva (BOLNICK et al., 2011). Um dos clássicos exemplos de divergência evolutiva moldada pelo ambiente é o caso dos tentilhões que habitam diferentes ilhas em Galápagos e irradiaram em uma variedade de espécies com ecologias e hábitos diferentes, incluindo a variação no tamanho e forma dos bicos, inicialmente observada por Darwin (BEGON et al., 2009). O mecanismo da hereditariedade não era conhecido na época de Darwin, e hoje, sabemos o papel das mutações produzindo novas variações que são transmitidas de uma geração para outra (KARDONG, 2016). A variação herdada, é assim, o que permite respostas evolutivas dos organismos para à seleção (SCHREIBER et al., 2011; KARDONG, 2016). Seleção natural, evolução neutra, deriva genética, migração e restrições filogenéticas são todos mecanismos evolutivos atuando sob a variação (FRECKLETON & JETZ, 2009; MARROIG & CHEVERUD, 2004). Tais processos são a base para a diversificação e/ou adaptação morfológica, funcional e ecológica dos organismos dentro de suas populações ou comunidades biológicas, tanto em escalas temporais quanto espaciais (RIDLEY, 2007).

A adaptação é um conceito fundamental da teoria evolutiva referindo-se àquelas propriedades dos seres vivos que os tornam capazes de sobreviver e de se reproduzir na natureza, ou seja aumentarem sua aptidão (RIDLEY, 2007). A longa probóscide da mariposa *Xanthopan morganii praedicta* é bem adaptada para extrair néctar na base de uma corola de 30 cm de uma espécie de orquídea (ARDITTI et al., 2012). Variação em caracteres morfológicos tradicionais, como o tamanho do corpo, também parecem ter um alto valor adaptativo embutido, com implicações em padrões de uso de recursos, áreas de vida, comportamentos, abundância e riqueza das espécies e até mesmo nas taxas de extinção dos animais (CALDER 2001, SMITH & LYONS 2013). A forma e o tamanho da mandíbula e os dentes de mamíferos geralmente refletem adaptações para as demandas funcionais de suas dietas (UNGAR, 2010; ROSS & IRIARTE-DIAZ, 2014; MELORO et al., 2015). Enquanto, a variação em ossos do crânio

também está associada com sua capacidade auditiva e olfativa (VALKEMBURG et al., 2014). Entretanto, a compreensão destes padrões é ainda um dos tópicos mais desafiadores para a biologia evolutiva, em parte, porque nem sempre é tarefa fácil acessar a variação existente nestes caracteres.

Recentes avanços nos métodos de morfometria geométrica (GM) estão abrindo possibilidades sem precedentes para investigar a forma e o tamanho das estruturas biológicas e suas correlações com outras variáveis (KLINGENBERG, 2010; ADAMS et al., 2013). Adicionalmente, espécimes depositados em coleções científicas dos museus de história natural, no mundo todo, têm possibilitado o registro rápido e bastante acurado de caracteres morfológicos para táxons atuais e extintos (GAUBERT et al., 2006). Comparações dentro e entre espécies tem melhorado nossa compressão sobre a variação fenotípica e seus principais determinantes. Dentro das populações, variação morfológica tem sido identificada entre sexos (ASTUA, 2010) e durante a ontogenia dos indivíduos (TANNER et al., 2010). Variação intraespecífica em traços de forma e tamanho também é prevalente em escalas espaciais (CARDINI et al., 2007; SOUTO-LIMA & MILLIEN, 2014). Em contextos interespecíficos ou de assembleias a diversificação ecomorfológica também tem sido associada com eventos de radiação em alguns grupos mamalianos (CACERES et al., 2014; ASTUA et al., 2015; MELORO et al., 2015), embora estes processos de divergência nem sempre são adaptativos (MARROIG & CHEVERUD, 2004). Algumas variações morfológicas favorecem ainda a coexistência de espécies potencialmente competidoras (ou seja, *character displacement*, BROWN & WILSON, 1956; ADAMS, 2004). Deslocamento de carácter é um fenomeno evolutivo causado por intensas interações competitivas entre espécies ecologicamente similares, cujas distribuições se sobrepõem geograficamente (BROWN & WILSON, 1956 ADAMS, 2004). Para Brown & Wilson (1956) a evolução de diferenças morfológicas em zonas de simpatria diminuiria a sobreposição de recursos e consequentemente a competição inter-especifica entre as espécies. Espera-se, portanto, que duas espécies competidoras tenham suas diferenças morfológicas acentuadas em zonas simpátricas e minimizadas ou perdidas em alopatria. Deslocamento de caracter é um mecanismo evolutivo influenciando variacao mofológica em diferentes táxons (mamíferos carnívoros: DAYAN & SIMBERLOFF, 1998, salamandras: ADAMS, 2004).

De um modo geral, fatores abióticos (temperatura, precipitação, disponibilidade de recursos) e bióticos (competição, predação), deriva genética e restrições filogenéticas são elencadas como as principais forças evolutivas da variação. Variação é assim fonte fundamental

de diversidade biológica, pois é através dela que os seres vivos podem divergir e se adaptar (RIDLEY, 2007; SMITH et al., 2008).

Variação ecogeográfica no tamanho e forma

Durante a sua viagem Darwin também ficou impressionado com as diferenças entre as emas de uma região para outra na América do Sul. É provável que essas observações de variação geográfica tenham levado Darwin a aceitar inicialmente que as espécies podiam mudar (RIDLEY, 2007). Hoje é amplamente conhecido que as morfologias usualmente variam ao longo da distribuição geográfica, sobretudo em animais de ampla distribuição (MAYR, 1956; MILLIEN et al., 2006), padrões geralmente manifestados como clinas (BROWN & LOMOLINO, 2006; RIDLEY, 2007). Um clina é um gradiente contínuo de variação intraespecífica, gerados por gradientes ambientais ou por efeitos de autocorreção espacial, ou seja, quando a seleção natural favorece genótipos diferentes em ambientes distintos e há fluxo gênico (migrações) entre as populações (RIDLEY, 2007).

Padrões espaciais relacionados ao tamanho animal são historicamente bem estudados levando a formulação de diversas generalizações ecogeográficas (SMITH & LYONS, 2013). Uma das primeiras e mais bem conhecidas é a Regra de Bergmann descrita em 1847 por Carl Bergmann. Ao observar que entre animais homeotérmicos, maiores tamanhos corporais eram frequentes em latitudes mais altas e ambientes frios, Bergmann hipotetizou que dentro de um gênero, animais maiores serão encontrados nestes ambientes porque a perda de calor é reduzida pela menor área de superfície em relação ao volume (BERGMANN, 1847). Essa relação positiva entre temperatura e tamanho do corpo tem sido amplamente documentada em mamíferos e aves em contextos intra e interespecíficos (ASHTON ET AL. 2000; MEIRI & DAYAN, 2003; OLSON et al. 2009; MARTINEZ et al. 2013), bem como em alguns organismos ectotérmicos (ASHTON & FELDMAN, 2003). Entretanto, a descrição de padrões opostos tem questionado a universalidade dessa regra sugerindo que podem existir mecanismos mais importantes associados com a eficiência energética e tamanho corpóreo em homeotérmicos (MEIRI et al. 2007; MCNAB 2010). Um grande número de estudos tem mesmo enfatizado a disponibilidade de recursos como um dos principais preditores da variação do tamanho do corpo de mamíferos, principalmente no hemisfério sul (MEDINA et al., 2007; SCHIAFFINI, 2016; CORREL et al., 2016). Neste cenário, a seleção favorece tamanhos reduzidos em altas latitudes, onde as temperaturas e a produtividade tendem a ser mais baixas, porque isso reduz as necessidades energéticas dos organismos (MCNAB, 2010). Para

mamíferos, particularmente, a maior parte deste conhecimento tem emergido de estudos usando medidas lineares ou o tamanho do centroide do crânio como um substituto para o tamanho do corpo (MEIRI & DAYAN, 2003).

A variação geográfica na forma do crânio é também um fenômeno prevalente em mamíferos, geralmente explicado por gradientes ambientais (CARDINI et al., 2007; CÁCERES et al., 2014). De forma geral, crânios mais robustos e com um aumento na área dos molares, do arco zigomático e da bula timpânica são característicos de mamíferos em áreas sazonais da América do Sul (CÁCERES et al., 2014; MELORO et al., 2014; BUBADUE et al., 2016). Embora os métodos de morfometria geométrica separem a forma do tamanho, alguma correlação residual pode permanecer, gerando efeitos alométricos nos padrões de variação da forma (KLINGENBERG, 2016), um fenômeno observado em primatas mesmo em amplas escalas espaciais (CÁCERES et al., 2014; MELORO et al., 2014). De modo geral, a forma é mais conservativa do que o tamanho e assim amplamente influenciada por relacionamentos filogenéticos (FRECKLETON & JETZ, 2009; MAESTRI et al., 2018) e por mecanismos de evolução neutra (por exemplo: deriva genética, fluxo gênico, MARROIG & CHEVERUD, 2004). Uma questão ainda a ser resolvida, é, entretanto, o quanto dessa variação geográfica é genética, uma vez que, a plasticidade fenotípica das espécies pode também ser responsável por parte da variação (SOUTO-LIMA & MILLIEN, 2014). Muito embora, isso não invalida a significância adaptativa dos padrões observados (PIGLIUCCI, 2005; BROWN & LOMOLINO, 2006).

Crânio, forma e função em mamíferos

A forma das estruturas biológicas retém um conjunto importante de “informações” sobre atributos funcionais e adaptação dos animais (ROSS & IRIARTE-DIAZ, 2014). O crânio e a mandíbula dos mamíferos são intimamente associados com a sua ecologia alimentar e óbvios produtos da evolução, sendo assim, especialmente informativos (HERRING, 1993).

Ao longo da evolução, características como: heterodontia, oclusão dental, palato secundário e a articulação do osso dentário diretamente com esquamosal foram importantes para o surgimento dos mecanismos mastigatórios dos mamíferos, e, consequentemente, para a expansão de seus nichos alimentares (KEMP, 2005). A articulação temporomandibular (ATM) reforçada permitiu movimentos à mandíbula e o aumento das áreas de inserção de dois dos principais músculos adutores, o temporal e o masseter. Adicionalmente, ocorreu um processo de simplificação da mandíbula formada por um único osso, o dentário. Este arranjo confere aos

mamíferos a capacidade de exercer poderosas forças de mordida em diferentes alimentos e resistir as forças internas da mastigação (KEMP, 2005), atributos funcionais essenciais para o crânio mamaliano (THOMASON, 1991; ROSS & IRIARTE-DIAZ, 2014).

Em termos de biomecânica, a mandíbula atua como um sistema de alavanca de terceira classe, com a força de entrada (F*i*) cruzando a alavanca entre o pivô e a força de saída (F*o*) (THOMASON, 1991; CASSINI & VIZCAÍNO, 2012). A articulação temporomandibular (ATM) atua como um pivô, os músculos mastigatórios fornecem a força de entrada, enquanto a força de saída é produzida pelos dentes que atuam sobre os alimentos (CASSINI & VIZCAÍNO, 2012). As distâncias perpendiculares entre a linha de ação das forças (força muscular e força de mordida) e o pivô é um segmento da alavanca denominado de braço de momento de entrada (M*i*), enquanto a distância entre o pivô ao ponto onde a mordida é aplicada nas séries dentárias e o braço de momento de saída (M*o*) (Figura 1). A razão entre a força de entrada (F_i M_i) e a força de saída (F_o M_o) representa assim uma estimativa da força de mordida final (THOMASON, 1991). Em outras palavras, a força desenvolvida durante a mastigação pode ser mais ou menos absorvida pela ATM de acordo não apenas com a magnitude da força gerada, mas também com distância entre regiões de resistência (dentes) e o fulcro (ATM). A análise deste sistema de alavanca e do relacionamento entre os braços do momento nos permite avaliar se a performance mecânica do sistema favorece o desenvolvimento de força ou velocidade (CASSINI & VIZCAÍNO, 2012).

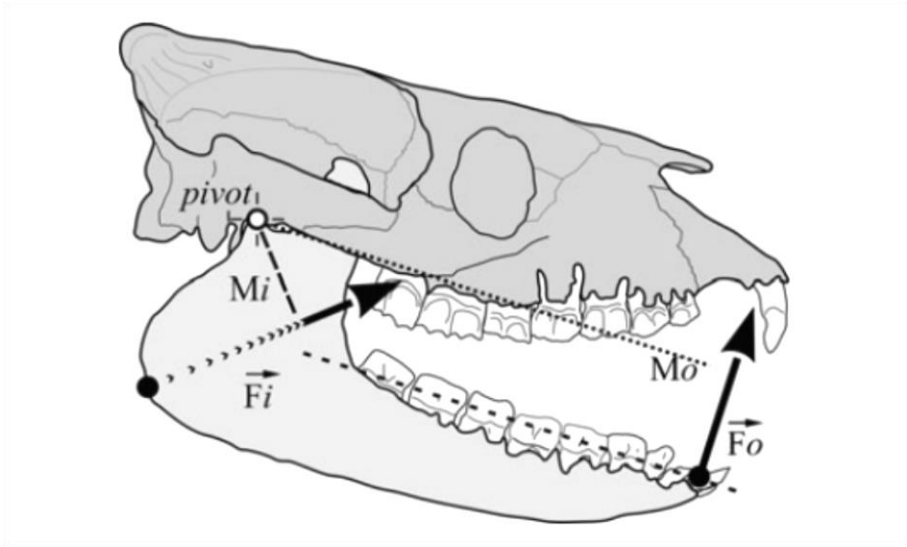

Figura 1. Mandíbula como um sistema de alavanca de terceira classe. F*i* = vetor de força de entrada; F*o* = vetor de força de saída; M*i* = braço de momento de entrada; M*o* = braço de momento de saída. Extraída de Cassini & Vizcaíno (2012, p. 12).

Modelos biomecânicos como este são alternativas às medições de força de mordida *in vivo*, as quais nem sempre são fáceis de obter em mamíferos, especialmente naqueles com amplas distribuições geográficas. Métodos de morfometria geométrica também têm possibilitado a extração fácil e acurada do tamanho do centroide da área de inserção dos músculos adutores, usada como um *proxy* para as forças de entrada. Abordagens integrando estes dois métodos têm sido assim uma maneira eficiente para estimar forças de mordida em mamíferos fósseis e atuais (VIZCAÍNO et al., 1998; CASSINI & VIZCAÍNO, 2012).

Mais importante ainda, estes métodos integrados possibilitado o teste de hipóteses funcionais. Correlações entre a forma craniana e a força de mordida, estão demonstrando, por exemplo, que mordidas mais fortes são geralmente associadas com crânios ou mandíbulas mais curtos e largos com amplas áreas de inserção da musculatura, enquanto o alongamento nesses traços otimiza a velocidade (NOGUEIRA et al., 2009; MAESTRI et al., 2016). Abordagens mais abrangentes também têm mostrado que a performance alimentar (ou seja, força, resistência e magnitudes de estresse) varia dentro e entre espécies em função da forma (HYLANDER, 1979, 1988; TAYLOR, 2006; TANNER et al., 2010; TIMM-DAVIS et al., 2015). Entre os primatas, por exemplo, corpos mandibulares mais profundos são frequentemente interpretados como uma adaptação para resistir aos estresses dorsoventrais ocasionados pela mastigação de folhas ou frutos duros (HYLANDER, 1979, 1988; TAYLOR, 2006). Demandas de alimentação parecem ser os principais fatores dessa variação entre as espécies (HYLANDER, 1979, 1988; NOGUEIRA et al., 2009; CASSINI & VIZCAÍNO, 2012; TIMM-DAVIS et al., 2015; MAESTRI et al., 2016). No entanto, mudanças importantes na performance alimentar também são explicadas pela filogenia (PÉREZ-BARBERIA & GORDON, 1999; PIRAS et al., 2013) e ontogenia (TANNER et al., 2010). A integração contínua desses dois métodos pode expandir nossa compreensão sobre os relacionamentos de forma e função também para outros grupos de mamíferos, além de primatas e carnívoros, os quais são o foco da maioria desses estudos.

Tayassuideos como modelos de estudo de variação ecogeográfica e funcional

Tayassuidae é uma família de mamíferos artiodáctilos onívoros de médio porte popularmente conhecidos como porcos do mato. Atualmente, apenas três espécies representam a diversidade da família: *Pecari tajacu* (Linnaeus 1758) (cateto); *Tayassu pecari* (Link, 1795) (queixada) e *Parachoerus wagneri* (Rusconi, 1930) (tágua) (GASPARINI, 2013; PARISI DUTRA et al., 2017). *Pecari tajacu* é a menor das três espécies pesando aproximadamente de 15 a 30 kg, quando adulto. Uma característica marcante dessa espécie é a presença de uma faixa

de pelos brancos ao redor do pescoço conferindo um aspecto de colar. Em *T. pecari* essa faixa é verificada na região da garganta e distal do rostro, de tamanho intermediário esta espécie pesa em torno de 25 a 40 kg. *Parachoerus wagneri* é a maior espécie pesando em torno de 30 a 40 kg, sua pelagem é cinza acastanhada exibindo pelos brancos ao redor da boca (ver Figura 2) (TABER et al., 2011).

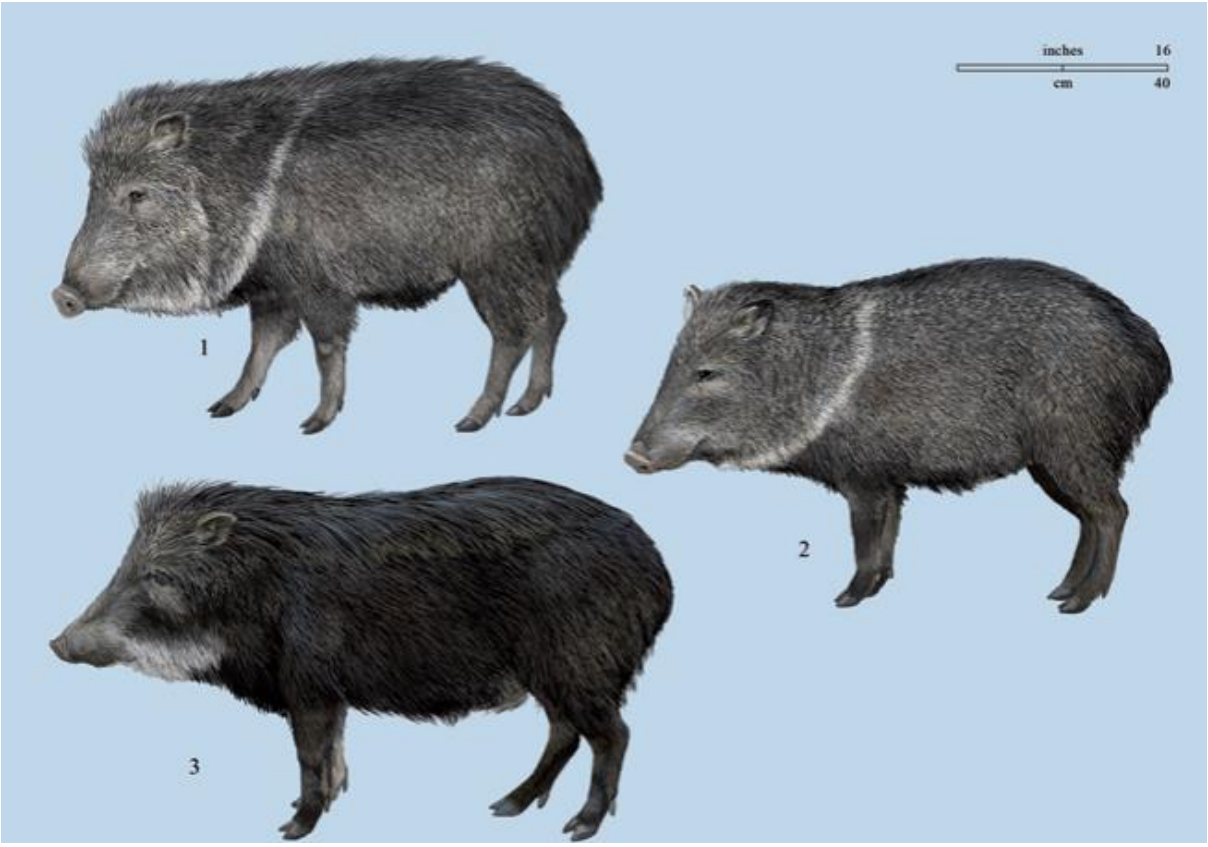

Figura 2. Espécies de tayassuídeos atuais. 1: *Parachoerus wagneri*, 2: *Pecari tajacu* 3: *Tayassu pecari*. Fonte: Taber et al., 2011.

Pecari tajacu tem a maior distribuição geográfica, sendo registrado do sudoeste dos Estados Unidos para o centro-norte da Argentina, em florestas tropicais, desertos, savanas e pastagens. Com uma distribuição um pouco menos extensa, *T. pecari*, ocorre principalmente em florestas tropicais do sul do México até o centro-norte da Argentina (ver Figura 3) (ALTRICHTER et al., 2012; GASPARINI, 2013). A dieta dessas espécies consiste em grande parte de material vegetal (por exemplo, frutas, sementes, raízes, nozes, grama) e ocasionalmente de pequenos animais (FRAGOSO, 1999; KEUROGHLIAN & EATON, 2008). Na região neotropical, onde coexistem amplamente, frutos e sementes das espécies de palmeiras são dominantes nas suas dietas (BECK, 2006). *Parachoerus wagneri* tem a distribuição mais

restrita entre as espécies atuais e é endêmico do Chaco, localizado no centro-norte da Argentina, oeste do Paraguai e do sudeste da Bolívia, habitando florestas de espinhos semi-áridas (ver Figura 3) (WETZEL, 1977; GASPARINI et al., 2013; TORRES et al., 2017). Sua dieta é composta principalmente por cactos, mas também se alimenta de raízes, flores e frutos (TABER et al., 1994). Estas três espécies de porcos são sociais, mas substanciais diferenças são encontradas no tamanho de seus grupos, *P. tajacu* vive em grupos de aproximadamente 30 indivíduos, enquanto grupos de *T. pecari* possuem muitas vezes mais do que 100 indivíduos, em contrapartida, grupos de *P. wagneri* geralmente não ultrapassam 10 indivíduos (TABER et al., 2011).

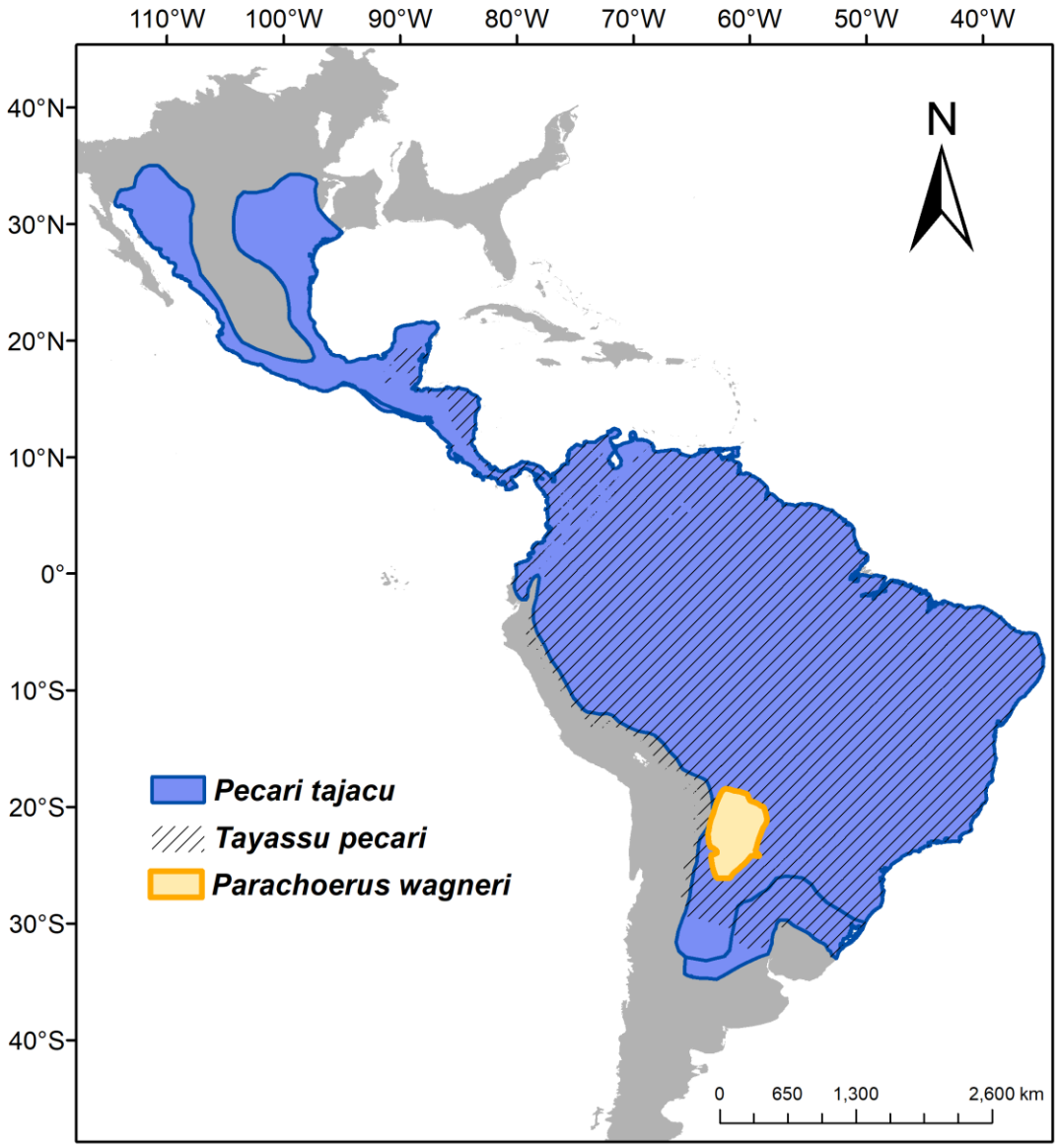

Figura 3. Distribuição geográfica das três espécies de tayassuídeos atuais. *Shapefiles* extraídos de IUCN Red List of Threatened Species. Versão 2017-3. www.iucnredlist.org

A morfologia craniana dos tayassuídeos, caracterizada por dentes bunodontes, caninos interligados, processos pré e pós-glenóides bem desenvolvidos e um movimento mastigatório essencialmente ortogonal (ou, em inglês, orthal) confere a estabilidade mandibular necessária para quebrar alimentos duros (HERRING, 1985). *Parachoerus wagneri*, no entanto, é o único que possui dentes mesodontes-bunodontes com coroas altas (GASPARINI, 2007; GASPARINI et al., 2013). Variação craniomandibular em tayassuídeos tem sido estudada para esclarecer a evolução da morfologia do canino (HERRING, 1972), o crescimento e a fusão de suturas (HERRING, 1974), força de mordida (KILTIE, 1982; SICURO & OLIVEIRA, 2002), dimorfismo sexual (SICURO et al., 2011) e relacionamentos evolutivos (GASPARINI, 2007; PARISI DUTRA et al., 2017). Até o momento, apenas um estudo explorou a variaçao craniomandibular em escalas espaciais, mas além de contemplar poucas amostras (N = 24), também está restrito as populações de *P. tajacu* (KILTIE, 1985).

Duas hipóteses principais são as mais aceitas para explicar os relacionamentos biogeográficos e evolutivos da família Tayassuidae. A primeira, sugere que o ancestral comum mais recente das espécies atuais migrou da América do Norte para a América do Sul, onde diversificou durante o Pleistoceno, com *P. tajacu* e *T. pecari* sendo mais próximos filogeneticamente (WETZEL, 1977). A segunda, sugere que as espécies divergiram na América do Norte no final do Mioceno e colonizaram independentemente a América do Sul, com *P. tajacu* e *P. wagneri* sendo mais próximos (WRIGTH, 1989). Análises filogenéticas baseadas em sequências de citocromo b sugerem ainda que *T. pecari* e *P. wagneri* são mais próximos e a divergência entre eles teria ocorrido antes ou imediamente depois da colonização da América do Sul (THEIMER & KEIM, 1998; GONGORA & MORAN, 2005). Perry et al. (2017) também corroboraram a diversificação sul americana dos tayassuídeos. Mais recentemente, Parisi Dutra et al. (2017) revalidaram a família Tayassuidae como um grupo monofilético e grupo irmão da família Suidae, com as três espécies atuais filogeneticamente próximas. Um novo arranjo taxonômico foi também proposto para o gênero *Catagonus*, verificado como polifilético, e então dividido em dois gêneros (*Brasiliochoerus* e *Parachoerus*). Esta é uma das filogenias mais abrangentes baseada em dados morfológicos e moleculares diponíveis para a família Tayassuidae, e portanto, seguida nessa tese (ver Figura 4).

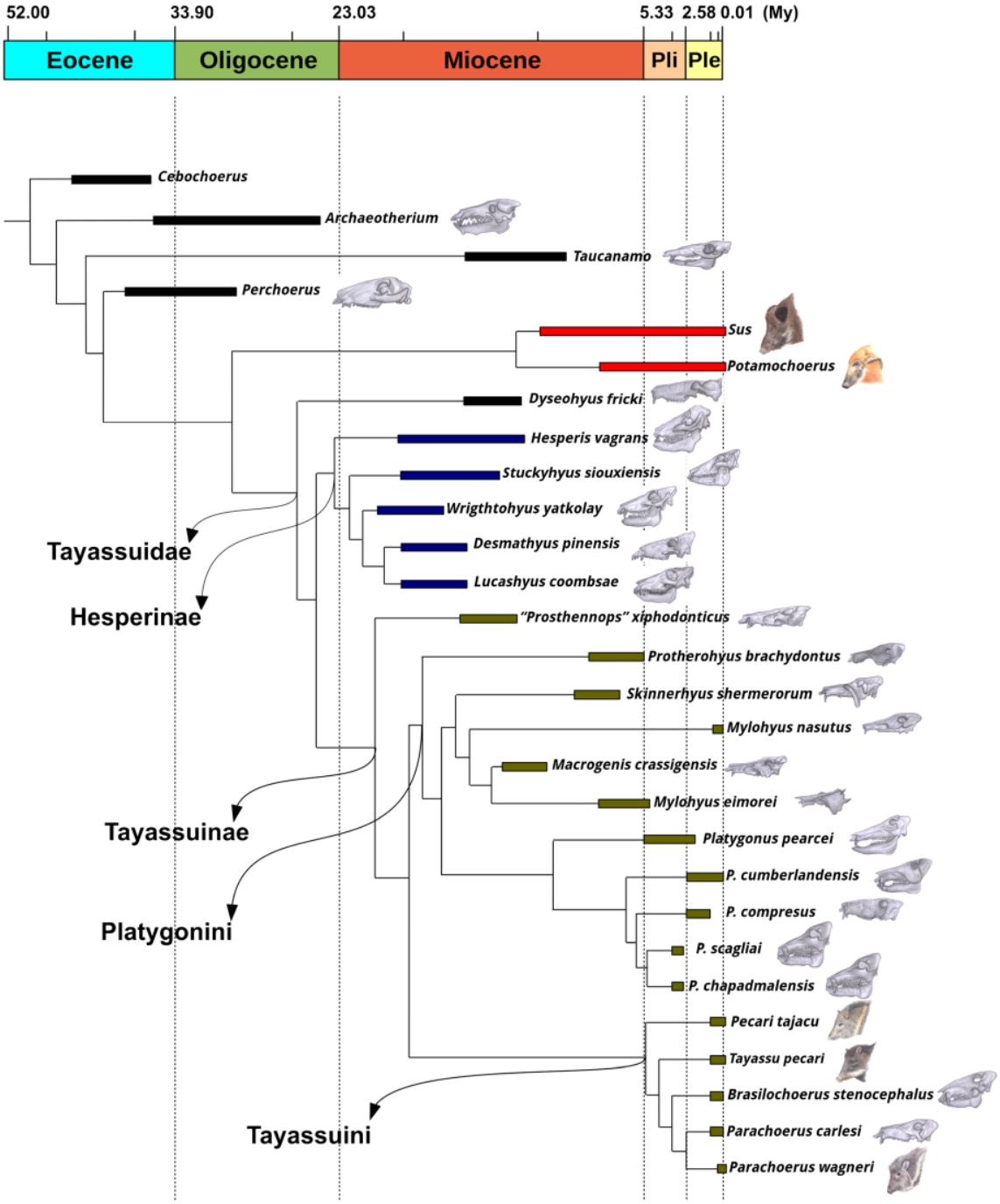

Figura 4. Árvore filogenética proposta para a família Tayassuidae incluindo a distribuição temporal dos táxons. Extraída de Parisi Dutra et al., 2017 e desenhada por Barbara Rossi.

Ao longo da sua história evolutiva e distribuição geográfica atual, os Tayassuídeos estão suscetíveis a intensas forças seletivas resultantes da variabilidade climática, disponibilidade de

recursos alimentares, impactos antrópicos decorrentes da caça e perda de habitat e até mesmo da competição uns com os outros, tendo em vista suas similaridades ecológicas e extensa área de simpatria, sobretudo entre *P. tajacu* e *T. pecari* na região neotropical. Além disso, a sua morfologia craniana parece ter evoluído para dietas biomecanicamente difíceis. Isso faz deles excelentes modelos mamalianos para as hipóteses ecogeográficas e funcionais testadas nesta tese.

A presente tese está estruturada de acordo com as normas do Manual de Teses e Dissertações da UFSM (MDT, 2015). Essa tese é composta por três capítulos em forma de artigos científicos, o primeiro nas normas da revista em que está publicado, e os demais nas normas das revistas nas quais serão submetidos:

Capítulo1: *Environment and space as drivers of variation in skull shape in two widely distributed South-American Tayassuidae, Pecari tajacu and Tayassu pecari (Mammalia: Artiodactyla).*

Neste capítulo, nós usamos procedimentos de morfometria geométrica e análises multivaridas para testar as seguintes hipóteses: 1) o ambiente afeta os padrões de variação da forma do crânio destes tayassuídeos devido a influência do ambiente previamente registrada na variação da forma mandibular de *Sus scrofa* Linnaeus, 1758, uma espécie pertencente a uma família irmã de Tayassuidae (ENDO et al., 2002); 2) alometria explica uma pequena parte da variação da forma nas duas espécies devido às potenciais restrições biomecânicas de ungulados (RAIA et al., 2010); e 3) outros processos espacialmente estruturados tais como a deriva genética e o fluxo gênico devem explicar a variação da forma das duas espécies seja através de um efeito sinérgico com o ambiente ou isoladamente, a forma de *P. tajacu*, cuja mobilidade é comparativamente mais restrita.

Capítulo 2: *Every rule has its exception: ecogeographical patterns in skull size of peccaries (Artiodactyla: Tayassuidae).*

Neste capítulo nós usamos uma medida multivariada de tamanho do crânio, como um substituto para tamanho do corpo, para testar as seguintes hipóteses: (1) a variação intraespecífica no tamanho do crânio de *P. tajacu* e *T. pecari* segue a Regra de Bergmann, exibindo aumentos no tamanho do crânio em latitudes mais altas. Este padrão é amplamente documentado em outros mamíferos (ASHTON 2000; MEIRI & DAYAN 2003); (2) a disponibilidade de recursos alimentares é positivamente correlacionada com a variação latitudinal no tamanho do crânio destes tayassuídeos como também verificado para outros mamíferos (MCNAB, 2010; SCHIAFFINI, 2016); (3) a influência humana é correlacionada com a variação geográfica no tamanho do crânio de tayassuídeos, conforme influência negativa

previamente reportada em outros atributos ecológicos dessas espécies tais como, padrões de abundância e tamanho de grupo (REYNA-HURTADO et al. 2016, MARTÍNEZ-GUTIÉRREZ et al. 2017); (4) a competição interespecífica afeta os padrões de variação do tamanho do crânio, então as diferenças de tamanho entre as espécies serão acentuadas em áreas de simpatria (BROWN & WILSON, 1956; DAYAN et al. 1989).

Capítulo 3: *Skull shape and the demands of mastication: a biomechanical study of peccaries (Mammalia, Artiodactyla).*

Neste capítulo, nós usamos procedimentos de morfometria geométrica e modelos biomecânicos para determinar como a forma do crânio das três espécies de tayassuídeos atuais, *P. tajacu, T. pecari e Parachoerus wagneri* reflete atributos biomecânicos para gerar e dissipar poderosas forças durante a mastigação (HYLANDER 1979, 1988; ROSS & IRIARTE-DIAZ, 2014). *Pecari tajacu* e *T. pecari* compartilham traços morfológicos que refletem um uncurtamento do rostro e um aumento da caixa craniana em comparação com *P. wagneri* (WETZEL 1977; GASPARINI, 2013). Maiores forças de mordida também foram verificadas para *T. pecari* em comparação com *P. tajacu* (KILTIE 1982; SICURO & OLIVEIRA, 2002). Nestas bases, *P. tajacu* and *T. pecari* devem possuir uma forma craniana adaptada para altas performances biomecânicas (força e resitência), enquanto atributos mais relaxados são esperados para *P. wagneri*.

Objetivos

Objetivo Geral

Examinar a variação geográfica na forma e tamanho do crânio de *Pecari tajacu* e *Tayassu pecari* e o papel dos fatores ambientais, alométricos, espaciais e da competição interspecífica como determinantes desta variação. Adicionalmente, verificar se a forma do crânio reflete atributos biomecânicos para gerar e dissipar forças de grande magnitude nos três tayassuídeos atuais, *Pecari tajacu*, *Parachoerus wagneri* e *Tayassu pecari*.

Objetivos específicos

1. Analisar a variação latitudinal na forma do crânio de *Pecari tajacu* e *Tayassu pecari* e a contribuição dos fatores ambientais, alométricos e outros processos espacialmente estruturados (por exemplo, deriva genética e fluxo gênico) na variação da forma.

2. Testar a existência de Regra de Bergmann na variação latitudinal intraespecífica no tamanho do crânio de *Pecari tajacu* e *Tayassu pecari* e os efeitos da sazonalidade, disponibilidade de recurso, influência humana e da competição interespecífica na variação do tamanho do crânio.

3. Investigar se a forma do crânio dos três tayassuídeos atuais (*Pecari tajacu*, *Parachoerus wagneri* e *Tayassu pecari*) reflete atributos biomecânicos para gerar e dissipar poderosas forças durante a mastigação.

CAPÍTULO 1: ENVIRONMENT AND SPACE AS DRIVERS OF VARIATION IN SKULL SHAPE IN TWO WIDELY DISTRIBUTED SOUTH-AMERICAN TAYASSUIDAE, *PECARI TAJACU* AND *TAYASSU PECARI* (MAMMALIA: ARTIODACTYLA)

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Environment and space as drivers of variation in skull shape in two widely distributed South-American Tayassuidae, *Pecari tajacu* and *Tayassu pecari* (Mammalia: Artiodactyla)

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RUNNING HEADLINE: SKULL SHAPE VARIATION IN SOUTH-AMERICAN PECCARIES

ABSTRACT

The influence of the environment on the geographical variation of morphological traits has been recognized in a number of taxa. *Pecari tajacu* and *Tayassu pecari* are ideal models to investigate intraspecific geographic variation in skull because of their wide and heterogeneous geographical distribution in South America. We used geometric morphometric procedures to examine the geographical variation in skull shape of 294 adult specimens of these species from 134 localities. And, we quantified to what extent skull shape variation was explained by environment, skull size and geographical space using Variation Partitioning analysis. We detected a strong pattern of geographic variation for *P. tajacu* skull shape, but not for *T. pecari*. The environment seems to be the major selective force that drives skull shape variation in both species. Nevertheless, other spatially structured processes (e.g. genetic drift, gene flow) might also have affected variation in the skull shape of the more widespread species *P. tajacu*. Allometric relationships might reflect the biomechanical constraints that are thought to be strong enough to limit size-related changes in *T. pecari* skull shape.

ADDITIONAL KEYWORDS: collared peccary - geographic clines – geometric morphometrics – macroenvironmental patterns – Suiformes – ungulates.

INTRODUCTION

Geographical variation in species morphological traits has been strongly influenced by both environmental and historical factors (Freckleton & Jetz, 2009). A large number of macroenvironmental patterns of morphological variation have been described at both the intraspecific (Cardini, Jansson & Elton, 2007; Souto-Lima & Millien, 2014; Kim *et al*., 2015) and interspecific level (Ashton *et al*., 2002; Cáceres *et al*., 2014a; Meloro *et al*., 2014a, b; Bubadué *et al*., 2016). Climatic variables (i.e. temperature and precipitation) have been suggested to account for the patterns observed, through their influence on thermoregulatory mechanisms (Ashton *et al*., 2002; Martinez *et al*., 2013), or on food availability in the environment (Cardini *et al*., 2007). In this respect, morphological variation across the environmental gradient might reflect not only evolutionary adaptations, but also the phenotypic plasticity of species (Peres-Neto & Magnan, 2004; Souto-Lima & Millien, 2014; Jaffe, Campbell-Staton & Losos, 2016). A biotic process such as size can also act as an important source of variation that shapes morphologies (Gould, 1966), even across large spatial scales (Cáceres *et al*., 2014a; Meloro *et al*., 2014a, b). For instance, in Old and New World primates and carnivores, differences in skull size have produced new skull size–shape associations and consequent diversification in the diet (Singleton, 2005; Marroig & Cheverud, 2005; Meloro *et al*., 2008). Furthermore, neutral evolution (e.g. genetic drift, gene flow) might be responsible for the observed morphological variations (Marroig & Cheverud, 2004; Cardini *et al*., 2007), especially in an historical context of changing environmental conditions (Souto-Lima & Millien, 2014: 205).

Despite the vast literature available on the geographic variation in mammalian skulls (Cardini *et al*., 2007; Cáceres *et al*., 2014a; Meloro *et al*., 2014a, b; Bubadué *et al*., 2016), this is still poorly explored for some groups, such as ungulates, although some information is available for Suiformes. Endo *et al*. (2002) suggested that geographic variation in the mandibles of *Sus scrofa*

(Artiodactyla: Suidae; Linnaeus, 1758) is affected by environmental variables (i.e. temperature and altitude). This reflects the strict relationship between the ungulate diet and the environment (Sponheimer *et al.*, 2003). In fact, it is well known that craniomandibular morphologies of ungulates are determined by interactions between adaptations to particular feeding habits and biomechanical and/or phylogenetic constraints (Pérez-Barbería & Gordon, 1999; Mendoza, Janis & Palmqvist, 2002; Mendoza & Palmqvist, 2008; Raia *et al*., 2010; Piras *et al*., 2010). Moreover, a small size effect in craniodental morphology has been recently established (Raia *et al*., 2010; Piras *et al*., 2010) as a consequence of the biomechanical constraints that different digestive strategies exert on them (Raia *et al.*, 2010). Nevertheless, no study has yet explored how and to what extent the skull shape of ungulate species responds to environmental, allometric (skull size) and spatial factors on broad-scales. Therefore, the ecogeographical trend previously found within the Suiformes makes other members of this group, such as the two widely distributed peccaries, *Pecari tajacu* (Linnaeus, 1758) and *Tayassu pecari* (Link, 1795), ideal models with which to investigate intraspecific geographic variation in skull shape.

These peccaries (Aartiodactyla: Tayassuidae) are widespread frugivorous/omnivorous ungulates in the Neotropical region (Keuroghlian & Eaton, 2008a), which extended their distribution into South America during the Great American Biotic Interchange (GABI), in the middle Pliocene (ca. 4.0–3.3 Ma) (Woodburne, 2010; Gasparini, 2013). Except for *Catagonus wagneri* (Rusconi, 1930), which is restricted to the South-American Gran Chaco, *P. tajacu* and *T. pecari* have the widest geographic distribution across South America (Altrichter *et al*., 2012; Gasparini, 2013). *Pecari tajacu* (ca. 22 kg) is a habitat generalist that occupies a wide range of habitats (tropical rainforests, dry forests, xeric thorn forests, deserts, savannas and grasslands) (Eisenberg & Redford, 1999). It lives in small herds that defend their limited home ranges (i.e. 50-700 ha) and exhibit intraspecific territoriality behaviour between herds (Fragoso, 1999; Keuroghlian & Eaton, 2008a, b). In contrast, *T. pecari* (ca. 35 kg) tends to be more selective

and requires large home ranges (i.e. >2.000 ha) in undisturbed environments (i.e., tropical and subtropical moist broad-leaf forests) to meet its food requirements as part of large herds (Keuroghlian & Eaton, 2008a, b). *Tayassu pecari* has even been considered to be migratory, due to its long-distance movements, especially during periods of fruit scarcity (Bodmer, 1990; Fragoso, 1999; Carrillo, Saenz & Fuller, 2002; Keuroghlian, Eaton & Longland, 2004).

Peccary skulls have been studied in relation to canine morphology (Herring, 1972), suture fusion and growth (Herring, 1974), bite force (Kiltie, 1982; Sicuro & Oliveira, 2002), systematic (Gasparini, 2007) and sexual dimorphism (Sicuro, Neves & Oliveira, 2011). In general, their interlocking canines and craniomandibular joint limit jaw movements in various activities but enable a powerful bite force to crack foods of different hardnesses (Herring, 1972; Kiltie, 1982). In this respect, Kiltie (1982) reported that the bite force in *T. pecari* should be at least 1.3-fold larger than that of *P. tajacu*. In addition, significant differences in craniomandibular dimensions were reported between individuals of *P. tajacu* that inhabit rain-forest and xeric habitats (Kiltie, 1985).

If the environment affects the geographical variation in the *S. scrofa* mandible (Endo *et al*., 2002), a species of a closed related family, we might also expect a strong environmental influence on the variation in skull shape of Neotropical peccaries. However, the same cannot be expected for size due to recent findings by Raia *et al*. (2010) and Piras *et al*. (2010). Furthermore, the effects of geographical space on peccaries are expected to be mainly observed in interaction with the environment since environmental variables tend to be naturally spatially structured (Cáceres *et al*., 2014b). Nevertheless, if other spatially structured processes are also determinants of skull shape variation in mammals (e.g. genetic drift, gene flow; Marroig & Cheverud, 2004; Cardini *et al*., 2007), their effects might be expected to explain variation in *P. tajacu* skull shape due to the territorial behaviour and more restricted mobility of *P. tajacu*

compared with *T. pecari* (Bodmer, 1990; Fragoso, 1999; Carrillo *et al*., 2002; Keuroghlian *et al*., 2004).

Here, we used geometric morphometric procedures to examine the geographical variation in skull shape of *P. tajacu* and *T. pecari* across their extensive geographic range in South America. We also quantified to what extent variation in skull shape is explained by the environment, size and geographical space. More specifically, we tested the following predictions: 1) environmental heterogeneity is an important selective force that drives the variation in skull shape of these peccaries because of the influence of the environment on previously recorded *S. scrofa* mandible. Still, the effect of environment should be stronger on *P. tajacu* due to its higher ecological plasticity; 2) allometry should represent a smaller source of variation in both species due to their potential masticatory biomechanical constraints; and 3) spatial factors might also play an important role, either through interaction with the environment or due to their characteristics of territoriality and more restricted mobility of *P. tajacu*.

MATERIALS AND METHODS

GEOMETRIC MORPHOMETRIC DATA

We photographed the skull ventral view of 294 adult specimens of *P. tajacu* and *T. pecari*, deposited in several South American scientific collections (see Table 1; Fig. 1; Supporting information, Appendix S1). We followed the taxonomy of species proposed by Gongora & Moran (2005), which is one of the most recent and comprehensive phylogenetic relationships available for extant species. We photographed the specimens using a Nikon CoolPix P530 digital camera and applying a standard protocol: each skull was positioned with the palate perpendicular to the camera lens at a fixed distance (3 m). This procedure minimised the deformation due to the lenses and photographic errors between specimens (Zelditch *et al*.,

2004). When taking photos, we positioned a scale bar adjacent to the specimen to transform digital pixels into linear measurements (Zelditch *et al*., 2004).

Thirty-four homologous landmarks were digitised by a single investigator (CH) to describe skull shape (Fig. 2), using TPSDig2 ver. 2.16 (Rohlf, 2015). Intra-observer error was measured by a paired *t*-test using the procrustes distances of four different specimens from each species, after two different routines of landmark digitisation. No significant differences were found between repetitions ($P > 0.05$), demonstrating that the landmark positioning was consistent across successive repetitions. Because we were interested in describing the craniodental morphology of these peccaries, we chose the ventral view of the skulls, where the palate is relatively flat and the teeth can be easily recognised and individualised. We selected the landmarks based on shared characters between *P. tajacu* and *T. pecari*, representing the total skull length and width, temporal muscle area (zygomatic arch), the rostrum (palate), the auditory bulla, and the teeth area (Fig. 2). Landmarks in these regions were also powerful descriptors of skull shape variation in *S. scrofa* (see Owen *et al*., 2014).

After digitisation, we computed a Generalised Procrustes Analysis (GPA, Rohlf & Slice, 1990) to remove coordinate differences in scale, position and orientation from the original landmark. This procedure generated a new set of coordinates, the procrustes coordinates (= skull shape variables), whereas the skull size was directly extracted as centroid size (Bookstein, 1989). The Procrustes coordinates were projected into a weight matrix to characterise shape using affine (Uniform) and non-affine (Partial Warps) components of thin plate spline. A Relative Warp Analysis (RWA) allowed us to graphically view the deformations from the vectors that explained most of the shape variance (Relative Warps or RW) (Zelditch *et al*., 2004). We used the software tpsRelw version 1.49 to compute both GPA and RWA, as well as to extract the weight matrix (Rohlf, 2015). To avoid possible pseudoreplication (Hurlbert, 1984)

and geographic bias, we used the mean values of our Procrustes coordinates and the centroid size per locality in all statistical analyses (see Cáceres *et al*., 2014a).

ENVIRONMENTAL VARIABLES

For each specimen, we recorded the geographic coordinates of its collection locality, resulting in 134 different localities (see Table 1; Fig. 1). We then extracted 22 environmental variables for each site that are important predictors of skull-shape variation in mammals (Cáceres *et al*., 2014a; Meloro *et al*., 2014a, b; Souto-Lima & Millien, 2014). Nineteen bioclimatic variables were taken with 2.5 arc-minutes resolution from the WorldClim raster database (Hijmans *et al*., 2005), and other three variables from the Atlas of the Biosphere (average annual relative humidity, net primary productivity and evapotranspiration, https://nelson.wisc.edu/sage/data-and-models/atlas/maps.php), using DIVA-GIS 7.5 software(http://www.divagis.org/download).

STATISTICAL ANALYSES

SKULL SHAPE

We applied MANOVA and ANOVA to test for differences in skull shape and size between species, also including sex as a factor in an exploratory context. Due to the absence of interaction between species and sex in both skull shape (Pillai's trace = 0.207; $F_{25, 58} = 0.606$; $P = 0.915$) and skull size ($F = 0.388$, d.f = 1, $P = 0.535$), individuals were included in the subsequent analyses regardless of sex. We then repeated MANOVA using the RWs, which explained up to 95% of the total shape variance and species as factor. This test was performed in R environment, version 2.8.1 (R Development Core Team 2013).

SKULL ALLOMETRY

We tested allometry in skull shape through multivariate regressions between the skull shape variables (Procrustes coordinates) and natural log-transformed centroid size (lnCS) in MorphoJ software (Klingenberg, 2011). Additionally, we calculated the common allometric component (CAC) of the shape data using the R package geomorph (Adams & Otarola-Castillo, 2013). The CAC is an estimate of the mean allometric trend within groups or specimens in our case (Mitteroecker *et al*., 2004).

CORRELATION OF SKULL SHAPE WITH THE ENVIRONMENT

We applied Partial Least Squares (PLS, Rohlf & Corti, 2000) to test the correlation between skull shape and the environment. Partial Least Squares is traditionally used in geometric morphometric studies to explore patterns of covariation between two blocks of variables (in our case, Procrustes coordinates as Block 1 and 22 environmental variables as Block 2) taking into account for multicollinearity in the data (Zelditch *et al*., 2004). We implemented PLS for each species, separately, using tpsPLS 1.18 software (Rohlf, 2015). Using the forward.sel function in R package packfor (Dray, Legendre & Blanchet, 2007), we selected the environmental variables that best explained the variance in skull shape, which were subsequently included in variation partitioning.

THE INFLUENCE OF GEOGRAPHICAL SPACE ON SKULL SHAPE

We applied Principal Coordinates of Neighbor Matrices (PCNM) (Dray, Legendre & Peres-Neto, 2006; Borcard, Gillet & Legendre, 2011) to create independent spatial variables that represent the spatial relationship among our sampling-site skulls. For each species, we obtained the PCNM variables from the Principal Coordinate Analysis (PCoA) of the truncated geographic distance matrix between sampling sites (Dray *et al*., 2006). The PCNM generated 44 spatial filters for *P. tajacu* and 28 for *T. pecari*. Because not all spatial filters associated

with the positive eigenvalues are informative, we applied a forward-selection procedure to select only the spatial filters that were significantly correlated with the variation in skull shape (Borcard *et al*., 2011). This procedure then selected two spatial filters as descriptors of skull shape variation for *P. tajacu* (spatial filter 24, $F = 2.210$; $P = 0.027$; spatial filter 7, $F = 1.938$, $P = 0.048$), and one for *T. pecari* (spatial filter 28, $F = 2.301$; $P = 0.039$); we then included these into the variation partitioning analyses. We performed PCNM using the R package vegan 2.0 (Oksanen *et al*., 2012) and forward selection in the R package packfor (Dray *et al*., 2007).

COMPONENTS OF VARIANCE IN SKULL SHAPE

We employed variation partitioning based on redundancy analysis (RDA) (Peres-Neto *et al*., 2006; Borcard *et al*., 2011) to assess the amount of variation in skull shape that could be attributed to the factors: (1) environment (the proportion of variance explained exclusively by the environment described by selected environmental variables); (2) size (the proportion of variance explained by allometric effects described by natural log-transformed centroid size); and (3) geographical space (the proportion of non-environmental variance described by selected spatial filters). These factors were all considered as predictors (X_1, X_2, X_3,) of skull shape (Y, described by RWs that explained up to 95% of the total shape variance). We used adjusted R^2 values to assess the particular contribution of each predictor while controlling for the others, and the fraction of interaction between them (Borcard *et al*., 2011). We computed variation partitioning using the R package vegan 2.0 (Oksanen *et al*., 2012).

RESULTS

SKULL SHAPE

The MANOVA revealed significant differences in skull shape between *P. tajacu* and *T. pecari* (Pillai's trace = 0.894; $F_{26, 107} = 35.052$; $P < 0.001$; N = 134). The first 26 RWs cumulatively

explained 95% of the total variance in skull shape. Mainly, RW1 (33.10% of variance) showed segregation between species, while RW2 (17.91% of variance) showed greater overlap between them (Fig. 3). *Pecari tajacu*, at the extreme negative of RW1, proportionally exhibited a shorter rostrum, larger molars, auditory bulla and occipital condyle, with the temporal muscle area positioned more posteriorly in relation to the molars. On the other hand, *T. pecari*, at the extreme positive of RW1, showed the opposite features. RW2 described shape changes in the muzzle, which was proportionally more elongated in specimens at the extreme positive than at the extreme negative of the axis.

SKULL ALLOMETRY

Variation in skull shape was related with allometry only in *P. tajacu* ($P = 0.024$; $N = 81$; 2.69 % of variance, Fig. 4 a, b). With increasing size in *P. tajacu*, the common allometric component consists of increasing the temporal muscle area, auditory bulla, and palate (Fig. 4a).

CORRELATION OF SKULL SHAPE WITH THE ENVIRONMENT

We detected a strong ($r = 0.693$) and significant ($P < 0.001$) correlation between skull shape and the environment for *P. tajacu.* The first pair of vectors extracted by PLS explained 89.80% of the total covariation. The SW1 environment discriminated between the colder, drier and less productive environments (negative scores) and warm, humid and more productive environments (positive scores) (see Fig. 5; Table 2). Specimens with negative scores, in southern South America, showed a proportionally more robust skull, with an elongated muzzle, larger molars and wider temporal muscle area, positioned closest to the tooth row. The opposite characteristics were exhibited in specimens in northern South America that possessed positive scores (Fig. 5a).

In contrast, the association between the first two pairs of vectors of skull shape and environment was weaker for *T. pecari* (PLS1 var. 80.62%, r = 0.529, P = 0.051; PLS2 var. 11.61%, r = 0.571, P = 0.020). Again, the SW1 environment discriminated between environmental conditions (see Fig. 5; Table 2). Specimens in colder, drier and less productive environments showed proportionally wider skull and temporal muscle areas than specimens in warm, humid and more productive environments. However, little or no variation was observed in the molars of *T. pecari* from southern to northern populations (Fig. 5b).

For *P. tajacu*, the environmental variables with the highest explanatory power were Temperature Annual Range (BIO 7, F = 8.616; P = 0.001) and Precipitation of Wettest Month (BIO 13; F = 2.709; P = 0.008), whereas for *T. pecari*, the most important variables were Temperature Seasonality (BIO 4; F = 3.943; P = 0.002) and Precipitation of Wettest Month (BIO 13; F = 2.221; P = 0.040).

COMPONENTS OF VARIANCE IN SKULL SHAPE

The greater amount of skull shape variation in *P. tajacu* is explained similarly by the interactions between environment and size, and environment and geographical space (adj. R^2 = 0.12; Supporting information, Table S2), followed by the pure fractions of environment, size, and geographical space, respectively (Environment “Pure” Adj. R^2 = 0.10; Size “Pure” Adj. R^2 = 0.02; Geographical space “Pure” Adj. R^2 = 0.02; Fig. 6a; Supporting information, Table S2). When the same variables were considered as pure fractions of skull shape variation in *T. pecari*, only environment showed a significant contribution (Environment “Pure” Adj. R^2 = 0.05, Fig. 6b; Supporting information, Table S2). Also, the environmental variables interacted significantly with geographical space in this species (Adj. R^2 = 0.07, Supporting information, Table S2).

DISCUSSION

The differences in skull shape we observed between *P. tajacu* and *T. pecari* are mainly related to the temporal muscle area, molar area, and muzzle elongation, agreeing with previous data from morphological studies (Kiltie, 1982; Sicuro & Oliveira, 2002; Gasparini, 2007; Sicuro *et al*., 2011). *Pecari tajacu* shows a strong variation in skull shape throughout the environmental gradient. Specimens in colder, drier and less productive environments exhibit characteristics of a less specialised morphology (a proportionally longer muzzle, larger molars, and a temporal muscle positioned closer to the tooth row), commonly found in skulls of frugivorous-omnivorous mammals in less stable environments, such as south of the Amazon Basin (Cáceres *et al*., 2014a; Meloro *et al*., 2014a, b). Particularly, for *P. tajacu*, this morphology is associated with the consumption of a broader range of food items, such as seeds, fruits, roots, tubers, and grass (Olmos, 1993; Keuroghlian & Eaton, 2008b). In turn, specimens distributed in warm, humid and more productive environments showed favourable traits (a proportionally shorter muzzle and narrower molars and temporal muscle) for the consumption of soft and more selective food types, such as freshly fallen fruits, and ripe fruit pulp, which often belong to the diet of *P. tajacu* in tropical forests (Fragoso, 1999).

In contrast, this ecogeographical trend was weaker in the skull shape of *T. pecari*. In colder, drier and less productive environments, the populations showed characteristics linked to a greater masticatory force (a proportionally wider skull and temporal muscle area) (Kiltie, 1982; Sicuro & Oliveira, 2002). However, little or no geographical variation was observed in the molars of *T. pecari*. Given that the main function of teeth is to process food (Souto-Lima & Millien, 2014), this characteristic suggests that *T. pecari* has a more selective feeding habit, especially in relation to the consumption of hard foods. In fact, field studies showed that fruits are more abundant in the diet of *T. pecari* than that in the diet of *P. tajacu* (Keuroghlian & Eaton, 2008b; Desbiez *et al*., 2009). Furthermore, when fruit availability decreases in seasonal

environments, *P. tajacu* alters its diet by including a wide range of other food types, whereas *T. pecari* tends to be more selective, and either includes harder food items such as roots and fibres in its diet (Olmos, 1993; Desbiez *et al*., 2009), or moves over large ranges to search for fruits (Bodmer, 1990; Fragoso, 1999; Carrillo *et al*., 2002; Keuroghlian *et al*., 2004).

Though a significant proportion of the variation in the skull shape of *P. tajacu* and *T. pecari* is explained by a spatially structured environment, the "pure" environmental heterogeneity is clearly the major selective force that drives the variation in skull shape of these peccaries (see Fig. 6). However, the contribution of this factor is weaker in *T. pecari* than in *P. tajacu.* Temperature and precipitation, which are proxies for habitat productivity (Cardini *et al*., 2007), are the best environmental predictors of skull shape variation in both species, this suggests that the environment can influence skull shape through its effects on food resources. Considering the association between skull morphology and diet in ungulates (Pérez-Barbería & Gordon, 1999; Mendoza *et al*., 2002; Mendoza & Palmqvist, 2008), the patterns observed here might be the result of feeding adaptation. However, the skull changes might also reflect phenotypic plasticity, since we detected a stronger impact of the environment on the more plastic species, *P. tajacu.* A wide range of moisture conditions experienced by *P. tajacu* inside and outside forests (Fragoso, 1999; Keuroghlian & Eaton, 2008a), in the present and probably in the past, makes it more susceptible to changes in skull shape due to environmental variation, even in the existence of other spatially structured processes (Cáceres *et al*., 2014b). Conversely, the seasonal affinities of *T. pecari* for humid and more stable environments (Fragoso, 1999; Keuroghlian & Eaton, 2008a) might not have been strong enough to affect skull shape to the same extent as in *P. tajacu.*

Although less important, the effects of "pure" geographical space cannot be completely ruled out, especially on the skull shape of *P. tajacu*. The limited migratory movements of *P. tajacu*, including between herds (Fragoso, 1999), might act as a behavioural barrier by decreasing the

gene flow between geographically distant populations, and consequently, the morphological similarity between them. In fact, some subspecies have been proposed for *P. tajacu* (Grubb & Groves, 1993). More recently, Gongora *et al*., (2006) suggested the existence of two major clades of *P. tajacu*; one representing Northern Central America and the other, South America, with a hybrid zone in Colombia. This result suggests that the variation in skull shape of *P. tajacu* is not exclusively explained by environmental adaptation, but also by other spatially structured processes (e.g. genetic drift, gene flow). Even if speculative, this indicates that both factors might have partly influenced the speciation processes. In this regard, samples from the full geographic distribution of this species might further elucidate this matter.

The small or absent effect of size on the skull shape of these peccaries is consistent with the findings of Piras *et al*., (2010) and Raia *et al*., (2010). However, in these peccaries, this might be connected to possible masticatory biomechanical constraints. To meet the requirements of their interlocking canines, other skull components in these peccaries gradually evolved, to result in a powerful bite force to crack hard foods (Herring, 1972; Kiltie, 1982). Thus, skull size itself might have been subjected to strong anatomical constraints to maintain masticatory strength. Considering that *T. pecari* has a larger body size and bite force than *P. tajacu*, we can suggest that changes occurred in *T. pecari* in relation to size, but not to shape characteristics, whereas some allometric shape changes might have been advantageous for *P. tajacu* (see Fig. 4a). Although we did not test it directly, these traits might have evolved as adaptations against competition, because differences in bite force and body size are important for niche partitioning between these species in sympatric contexts (Kiltie, 1982). In fact, we observed crucial differences in the skull shape of these peccaries in colder and drier environments, to the south of the Amazon Basin, where food items might be scarcer and harder (Souto-Lima & Millien, 2014). *Pecari tajacu* is characterised by a less specialised morphology, at the cost of reducing

bite force (large molars and a lower temporal muscle area), whereas a more conservative morphology and powerful bite force are observed in *T. pecari* (a large temporal muscle area).

From an evolutionary perspective, a more detailed interpretation of these results is difficult, because the origin and diversification of these peccaries remain controversial. Our results appear to be consistent with recent mitochondrial and nuclear DNA sequence findings that suggest an early divergence of *P. tajacu* from the *Tayassu*/*Catagonus* clade during the Pliocene in North America (Theimer & Keim, 1998; Gongora & Moran, 2005). This might have occurred in less productive environments such as savannas and grasslands, which were common in North America during the Miocene and Pliocene periods (Webb, 1991). However, the divergence of *T. pecari* and *C. wagneri* might have occurred during the Pleistocene in South America (Theimer & Keim, 1998; Gongora & Moran, 2005). At this late time, the climatic fluctuations mainly affected the more specialised and larger animals that were adapted to open environments (Gasparini, 2007). In this context, the ancestor of *T. pecari* might have been isolated in the tropical forest (Wetzel, 1977; Frailey & Campbell, 2012) where the climatic conditions have been more stable since the Pleistocene (Mayle, 2004). Alternatively, evidence for the recent evolution of these peccaries in mesic and heavily forested areas in South America is also available (Wetzel, 1977; Gasparini, 2013). In this context, the morphological evolution of both species might occur in more than one step. On a larger time-scale, environmental changes and neutral process might be primarily responsible for variation in skull shape. However, on shorter time-scales, biotic process such as size (and competition, indirectly) might be acting in these peccaries (see Benton, 2009; Bubadué *et al*., 2016).

Here, we detected a strong geographical variation pattern in the skull shape of *P. tajacu*, but, not of *T. pecari*. More importantly, we confirmed that environmental heterogeneity is a major selective force driving the variation in skull shape of these South-American peccaries. Skull changes appear to have been driven either by feeding adaptations or phenotypic plasticity, given

the stronger impact of the environment on the more ecologically plastic *P. tajacu.* Nevertheless, the pure effects of other spatially structured processes (e.g. genetic drift, gene flow), as well as allometric shape variations, were observed only in *P. tajacu*. Allometric relationship might reflect biomechanical constraints, which are thought to be strong enough to limit size-related changes in *T. pecari* skull shape variation. However, a large proportion of skull-shape variation remained unexplained by our analyses, indicating that other factors, such as competition, might influence variation, and therefore, should be considered in future studies.

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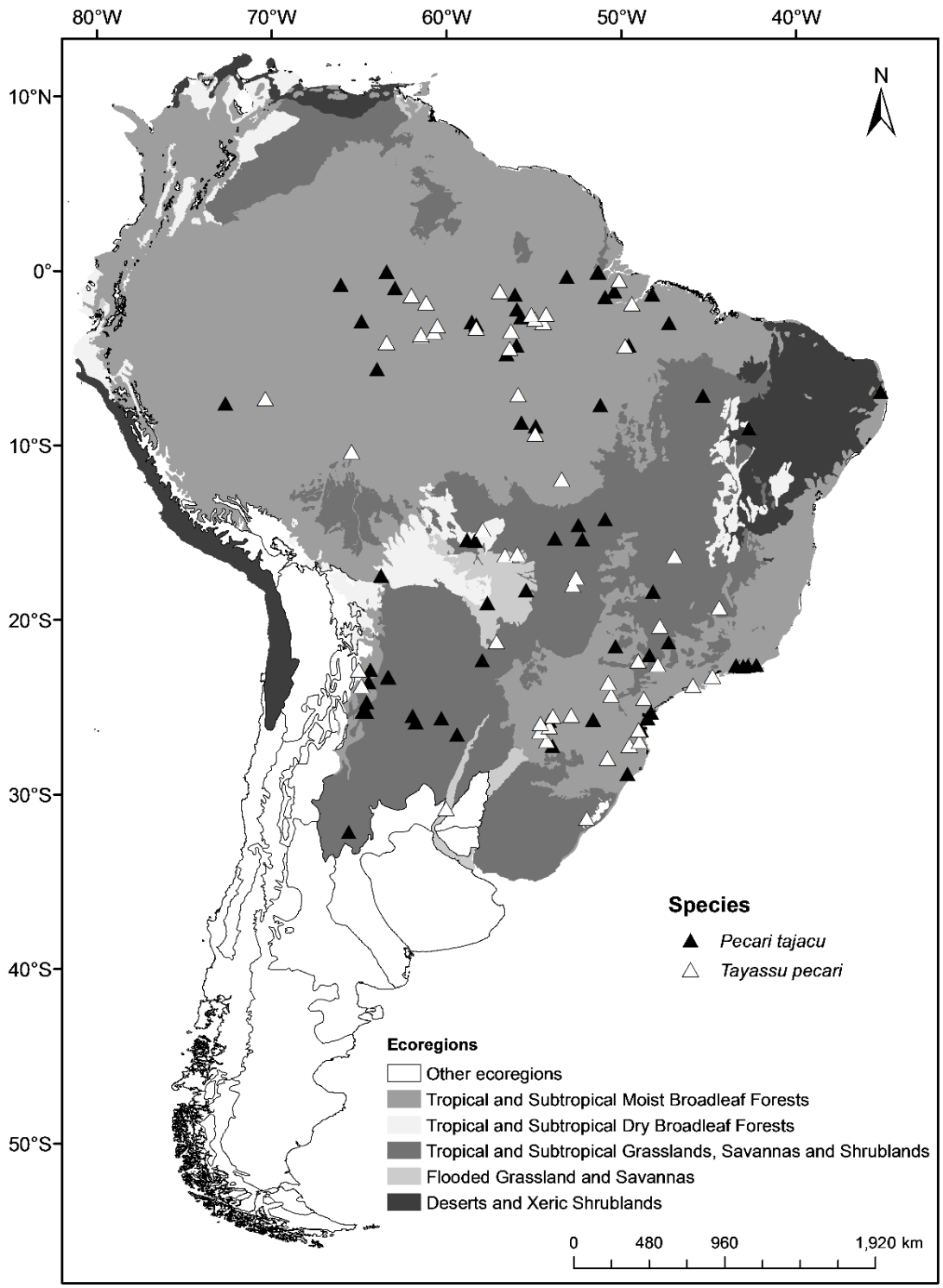

Figure 1. Map of South America showing the geographic distribution of the *Pecari tajacu* and *Tayassu pecari* skull samples. The sampling localities of different species are shown by different symbols. The classification of the ecoregions followed Olson *et al*., (2001).

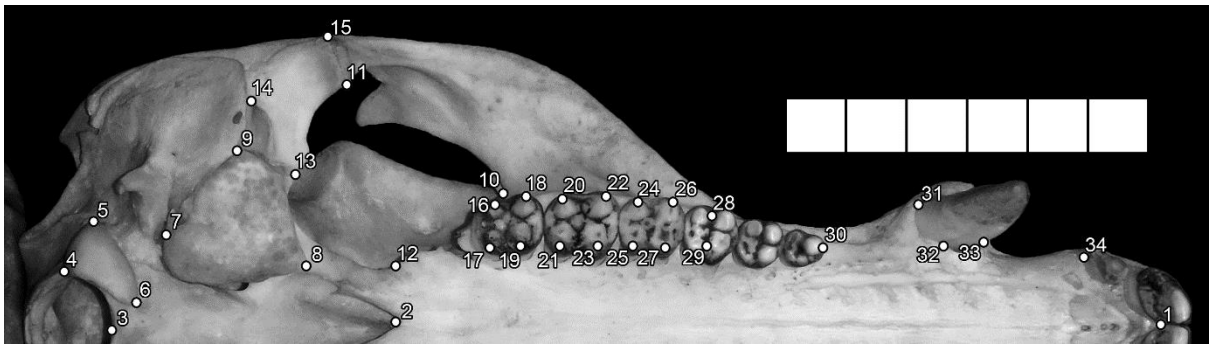

Figure 2. Position of 34 landmarks on a skull of *Pecari tajacu*. 1 = midpoint of central incisors; 2 = most posterior tip of the palatine; 3 = basion: most anterior point of the foramen magnum; 4–6 = occipital condyle area; 7–9 = auditory bulla area; 10–13 = temporal muscle insertion area; 14 = extremity of the postglenoid process; 15 = suture between the zygomatic arch and the glenoid fossa; 16–19 = third molar area; 20–23 = second molar area; 24–27 = first molar area; 28–30 = pre-molar series length; 31–33 = canine area; 34 = posterior-most point of the lateral incisor alveolus.

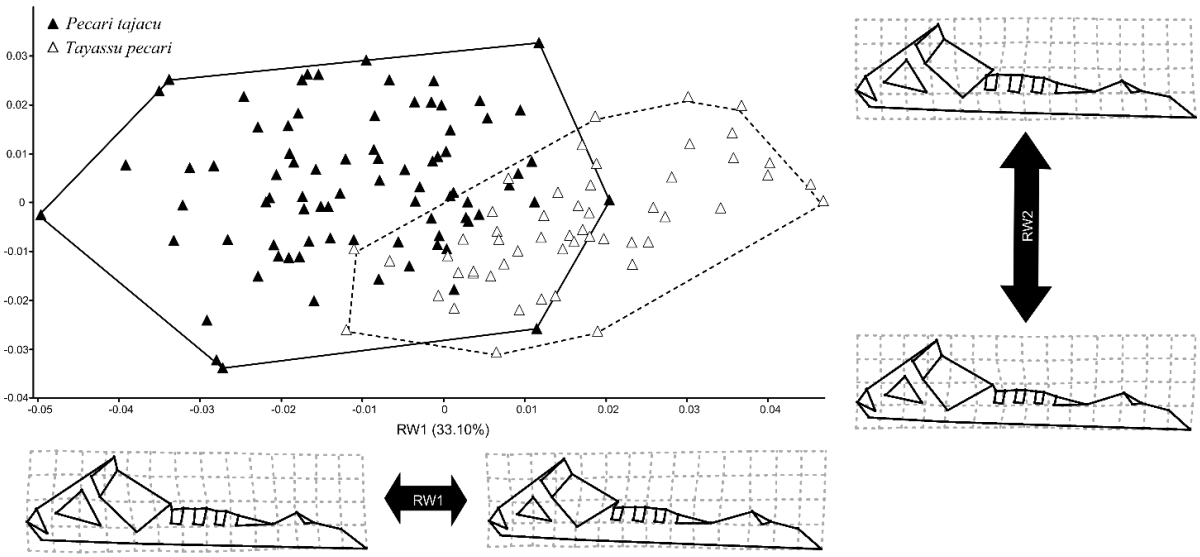

Figure 3. Scatter plot of RW1 vs. RW2. The transformation grids visualise shape deformations relative to the mean at the positive and negative extremes of the Relative Warp axes.

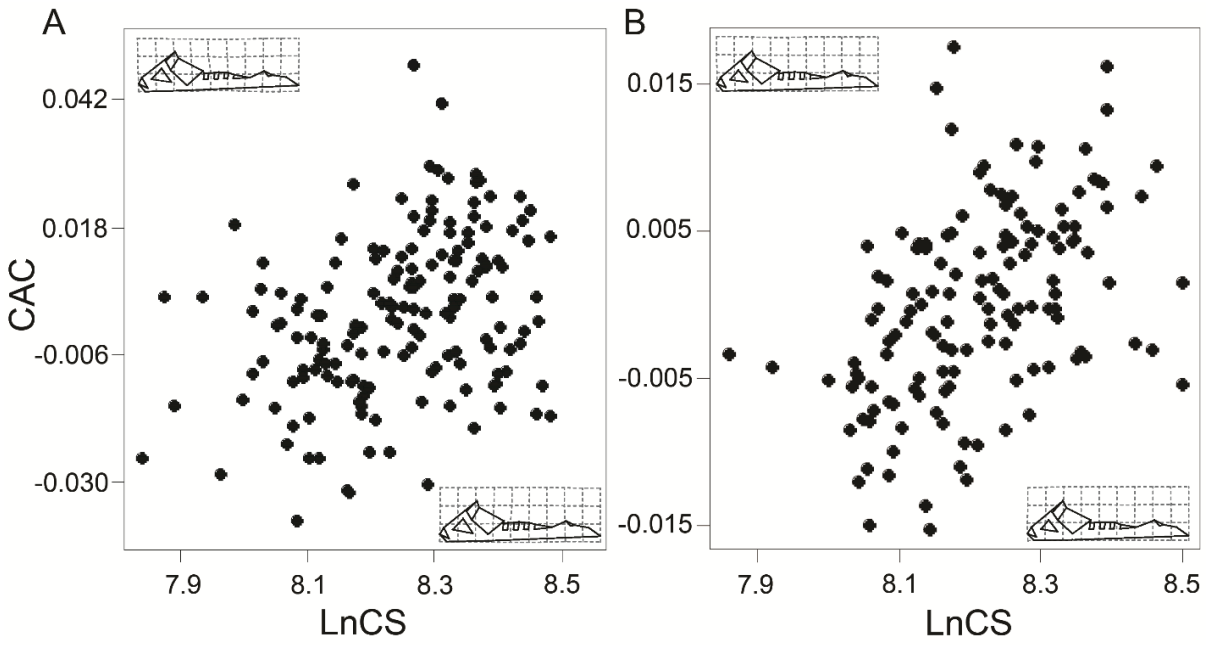

Figure 4. Allometric trajectories viewed as the common allometric component (CAC) versus lnCS for *Pecari tajacu* (A) and *Tayassu pecari* (B).

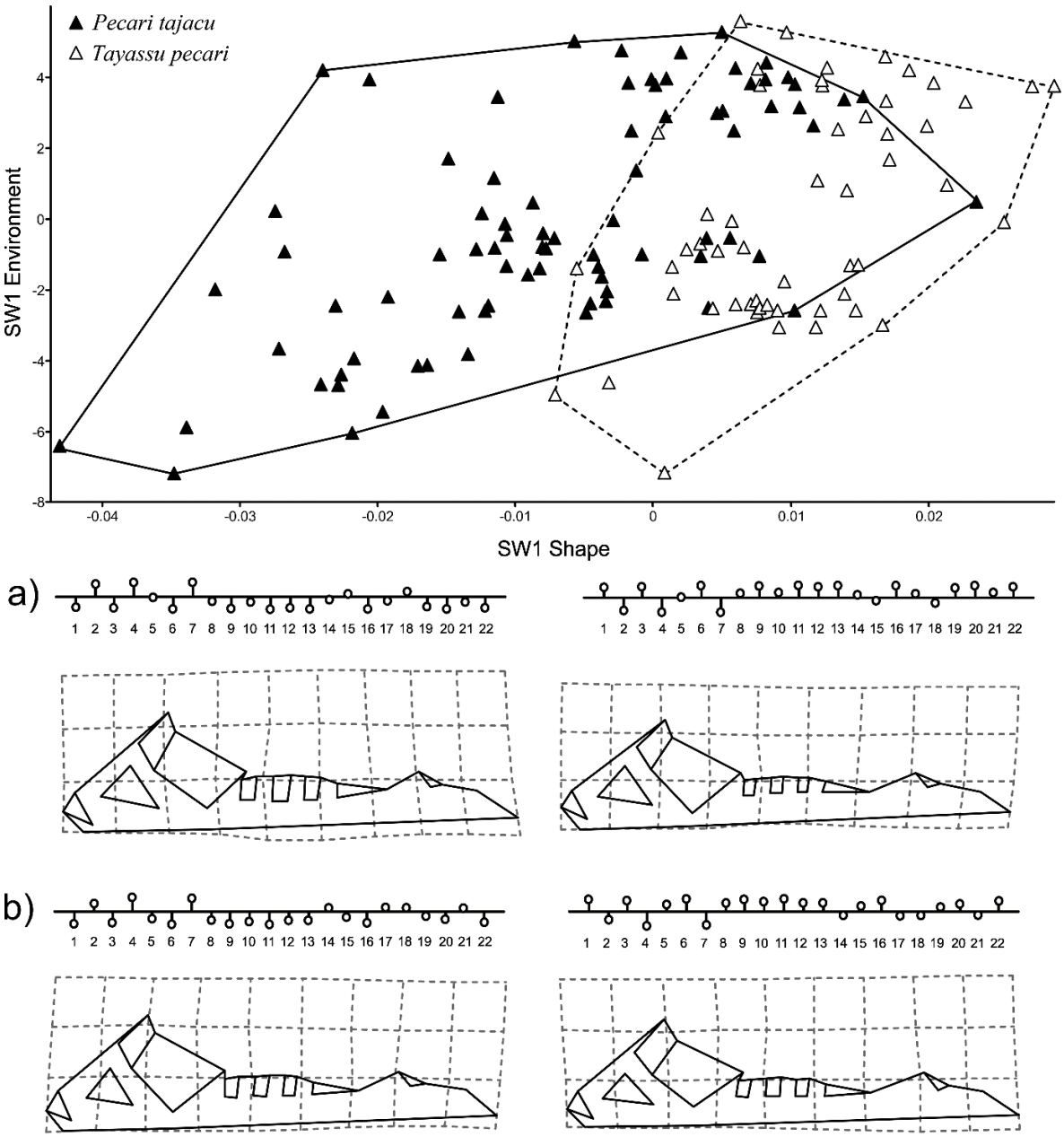

Figure 5. Plot of the first pair of Singular Warps (axis X is block shape, axis Y is block environment). Below, the profile of deformation grids and variables from the most negative to the most positive Singular Warp scores. In **a,** deformations are from 81 geographically averaged *Pecari tajacu* and in **b,** from the 53 geographically averaged *Tayassu pecari.*

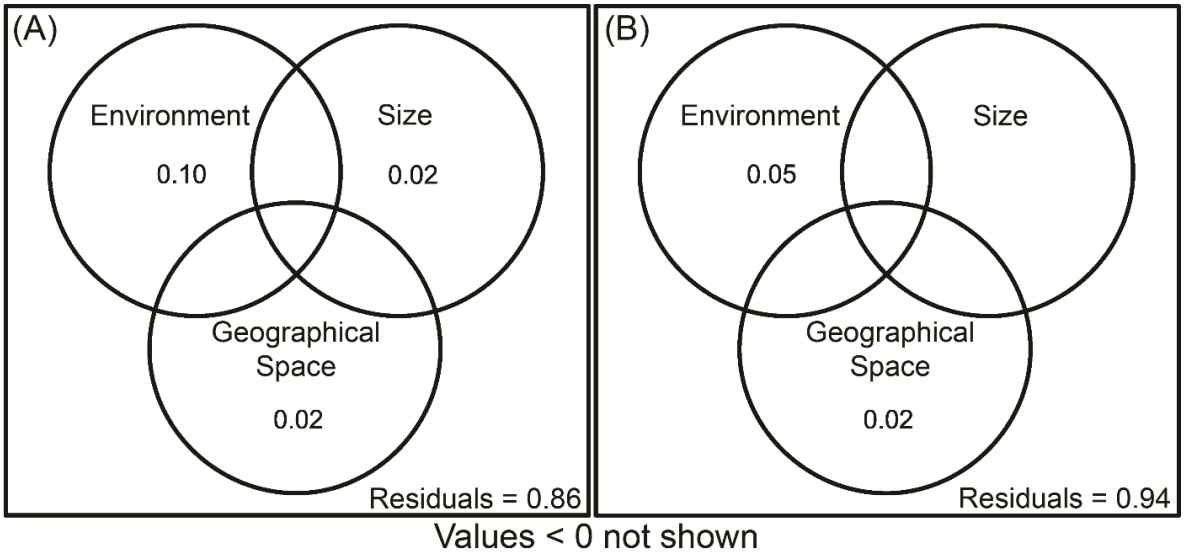

Figure 6. Schematic depiction of the factors analysed in variation partitioning to illustrate both their individual contribution to the skull shape variance and their interacting components for *Pecari tajacu* (A) and *Tayassu pecari* (B).

Table 1. Skull sample size of two species of Tayassuidae included in this study.

Species	Localities	Specimens	females	males	Undet
Pecari tajacu	81	160	43	49	68
Tayassu pecari	53	134	34	42	58
Total	134	294	77	91	126

Table 2. Loading coefficients of environmental variables on the first environmental axis (SW1) obtained from the PLS analysis between shape and the environment. PPT = PLS *Pecari tajacu*; PTP = PLS *Tayassu pecari*. Values higher than the others are highlighted.

Environmental Variables	**PPT**	**PTP**
BIO1 = Annual Mean Temperature	**0.229**	**0.281**
BIO2 = Mean Diurnal Range	**-0.227**	-0.165
BIO3 = Isothermality (BIO2/BIO7) (* 100)	**0.247**	**0.251**
BIO4 = Temperature Seasonality	**-0.289**	**-0.301**
BIO5 = Max Temperature of Warmest Month	0.014	0.169
BIO6 = Min Temperature of Coldest Month	**0.276**	**0.276**
BIO7 = Temperature Annual Range (BIO5-BIO6)	**-0.292**	**-0.264**
BIO8 = Mean Temperature of Wettest Quarter	0.093	**0.214**
BIO9 = Mean Temperature of Driest Quarter	**0.267**	**0.286**
BIO10 = Mean Temperature of Warmest Quarter	0.116	**0.234**
BIO11 = Mean Temperature of Coldest Quarter	**0.267**	**0.294**
BIO12 = Annual Precipitation	**0.239**	**0.205**
BIO13 = Precipitation of Wettest Month	**0.266**	**0.221**
BIO14 = Precipitation of Driest Month	0.080	-0.061
BIO15 = Precipitation Seasonality	-0.053	0.122
BIO16 = Precipitation of Wettest Quarter	**0.263**	**0.251**
BIO17 = Precipitation of Driest Quarter	0.087	-0.057
BIO18 = Precipitation of Warmest Quarter	-0.106	-0.067
BIO19 = Precipitation of Coldest Quarter	**0.227**	0.114
20 = Average Annual Relative Humidity	**0.267**	0.182
21 = Net Primary Productivity – NPP	0.118	-0.042
22 = Evapotranspiration	**0.246**	**0.255**

SUPPORTING INFORMATION

Appendix S1. List of 294 Tayassuidae specimens belonging to species *Pecari tajacu* and *Tayassu pecari*, representing 134 localities in South America, used for morphometric analyses, with data on species, sex (F, female; M, male; or unknown), museum number and geographical coordinates. *Specimens available at Museu Nacional (Rio de Janeiro, Brazil) without a museum number.

Species	Sex	Museum number	Latitude S	Longitude W
Pecari tajacu	Unknown	MACN 20811	32.13 S	65.57 W
Pecari tajacu	Unknown	UFSC 874	28.81 S	49.64 W
Pecari tajacu	Unknown	UFSC 2593	27.20 S	53.92 W
Pecari tajacu	Unknown	MACN 3013	26.54 S	59.40 W
Pecari tajacu	Male	MZUSP 1686	26.31 S	48.87 W
Pecari tajacu	Female	MACN 49319	25.93 S	54.62 W
Pecari tajacu	Unknown	MLP 5.IV.02.7	25.83 S	61.73 W
Pecari tajacu	Unknown	MACN 25793	25.78 S	54.13 W
Pecari tajacu	Unknown	MHNCI 4049	25.69 S	51.61 W
Pecari tajacu	Unknown	MHNCI 4117	25.62 S	48.51 W
Pecari tajacu	Unknown	MACN 24926	25.60 S	60.27 W
Pecari tajacu	Unknown	MHNCI 345	25.49 S	53.92 W
Pecari tajacu	Unknown	MLP 18.XII.02.3	25.47 S	61.91 W
Pecari tajacu	Unknown	MLP 18.XII.02.6	25.47 S	61.91 W
Pecari tajacu	Unknown	MLP 18.XII.02.7	25.47 S	61.91 W
Pecari tajacu	Unknown	MLP 18.XII.02.11	25.47 S	61.91 W
Pecari tajacu	Unknown	MLP 18.XII.02.16	25.47 S	61.91 W
Pecari tajacu	Female	MHNCI 6168	25.45 S	52.87 W
Pecari tajacu	Female	MHNCI 6175	25.45 S	52.87 W
Pecari tajacu	Unknown	MHNCI 3534	25.45 S	52.87 W
Pecari tajacu	Unknown	MHNCI 3535	25.45 S	52.87 W
Pecari tajacu	Unknown	MHNCI 6170	25.30 S	48.30 W
Pecari tajacu	Male	MLP 27.VII.46.1	25.24 S	64.79 W
Pecari tajacu	Male	MACN 30397	25.24 S	64.56 W
Pecari tajacu	Unknown	MACN 25791	24.71 S	64.54 W

Pecari tajacu	Male	MACN 47.407	23.56 S	64.43 W
Pecari tajacu	Unknown	MACN 36693	23.28 S	63.28 W
Pecari tajacu	Unknown	MACN 36690	23.28 S	63.28 W
Pecari tajacu	Unknown	MACN 36-709	23.25 S	63.35 W
Pecari tajacu	Unknown	MACN 36708	23.25 S	63.35 W
Pecari tajacu	Unknown	MACN 36.722	23.25 S	63.35 W
Pecari tajacu	Unknown	MACN 36-697	23.25 S	63.35 W
Pecari tajacu	Unknown	MACN 36707	23.25 S	63.35 W
Pecari tajacu	Unknown	MACN 36.716	23.25 S	63.35 W
Pecari tajacu	Female	MN 5646	23.22 S	44.79 W
Pecari tajacu	Female	MN 8453	23.22 S	44.79 W
Pecari tajacu	Unknown	MLP 4.IV.00.3	22.85 S	64.33 W
Pecari tajacu	Unknown	MACN 35.31	22.84 S	65.00 W
Pecari tajacu	Male	MN 37083	22.65 S	43.03 W
Pecari tajacu	Female	MN 37071	22.61 S	42.75 W
Pecari tajacu	Unknown	MN*	22.60 S	43.44 W
Pecari tajacu	Unknown	MN 47507	22.58 S	42.28 W
Pecari tajacu	Unknown	MN 37016	22.58 S	42.28 W
Pecari tajacu	Male	MZUSP 10344	22.55 S	47.90 W
Pecari tajacu	Male	MZUSP 10345	22.55 S	47.90 W
Pecari tajacu	Female	MZUSP 10347	22.55 S	47.90 W
Pecari tajacu	Male	MZUSP 8880	22.55 S	47.90 W
Pecari tajacu	Male	MZUSP 8468	22.55 S	47.90 W
Pecari tajacu	Male	MZUSP 498	22.35 S	49.02 W
Pecari tajacu	Female	MACN 4520	22.29 S	57.94 W
Pecari tajacu	Unknown	MACN 4527	22.29 S	57.94 W
Pecari tajacu	Female	MZUSP 9013	21.99 S	48.39 W
Pecari tajacu	Female	MZUSP 3759	21.50 S	50.33 W
Pecari tajacu	Unknown	MZUSP 32338	21.28 S	47.30 W
Pecari tajacu	Female	MZUSP 3001	20.34 S	47.79 W
Pecari tajacu	Male	MZUSP 3000	20.34 S	47.79 W
Pecari tajacu	Male	MZUSP 3002	20.34 S	47.79 W
Pecari tajacu	Unknown	MZUSP 3341	19.01 S	57.65 W

Pecari tajacu	Male	MZUSP 2157	18.37 S	48.18 W
Pecari tajacu	Female	MN 42889	18.28 S	55.43 W
Pecari tajacu	Male	MACN 50130	17.47 S	63.72 W
Pecari tajacu	Unknown	MN 42890	16.29 S	56.64 W
Pecari tajacu	Unknown	MN 42892	16.29 S	56.64 W
Pecari tajacu	Unknown	MN 42894	16.29 S	56.64 W
Pecari tajacu	Unknown	MN 64807	16.21 S	55.95 W
Pecari tajacu	Unknown	MN 64168	16.21 S	55.95 W
Pecari tajacu	Unknown	MN 71062	16.21 S	55.95 W
Pecari tajacu	Unknown	MN 71070	16.21 S	55.95 W
Pecari tajacu	Unknown	MN 66675	15.46 S	58.35 W
Pecari tajacu	Unknown	MN 1730	15.40 S	58.82 W
Pecari tajacu	Unknown	MPEG 1330	15.38 S	52.21 W
Pecari tajacu	Female	MZUSP 7016	15.31 S	53.79 W
Pecari tajacu	Male	MZUSP 7014	15.31 S	53.79 W
Pecari tajacu	Male	MZUSP 7012	15.31 S	53.79 W
Pecari tajacu	Female	MZUSP 7013	15.31 S	53.79 W
Pecari tajacu	Unknown	MZUSP 7015	15.31 S	53.79 W
Pecari tajacu	Female	MN 37094	14.56 S	52.45 W
Pecari tajacu	Male	MPEG 17138	14.22 S	50.92 W
Pecari tajacu	Unknown	MN 63492	9.01 S	42.70 W
Pecari tajacu	Unknown	MN 63494	9.01 S	42.70 W
Pecari tajacu	Female	MN 63523	9.01 S	42.70 W
Pecari tajacu	Female	MZUSP 5340	8.89 S	54.89 W
Pecari tajacu	Unknown	MN*	8.70 S	55.72 W
Pecari tajacu	Male	MPEG 1006	7.68 S	51.19 W
Pecari tajacu	Male	MPEG 839	7.61 S	72.63 W
Pecari tajacu	Female	MZUSP 5336	7.32 S	70.34 W
Pecari tajacu	Male	MZUSP 5341	7.32 S	70.34 W
Pecari tajacu	Male	MZUSP 5337	7.32 S	70.34 W
Pecari tajacu	Unknown	MHNCI 4046	7.13 S	45.33 W
Pecari tajacu	Male	MZUSP 8942	6.92 S	35.17 W
Pecari tajacu	Female	MN 37080	5.63 S	63.96 W

Pecari tajacu	Unknown	MZUSP 20022	4.78 S	56.56 W
Pecari tajacu	Unknown	MPEG 26285	4.32 S	49.78 W
Pecari tajacu	Unknown	MZUSP 20019	4.27 S	55.99 W
Pecari tajacu	Unknown	MPEG 11889	4.27 S	49.58 W
Pecari tajacu	Unknown	MPEG 11895	4.27 S	49.58 W
Pecari tajacu	Unknown	MPEG 41069	3.46 S	56.31 W
Pecari tajacu	Female	MN 6010	3.28 S	58.29 W
Pecari tajacu	Male	MN 6026	3.28 S	58.29 W
Pecari tajacu	Male	MPEG 7111	3.09 S	59.97 W
Pecari tajacu	Female	MN 1734	3.09 S	56.63 W
Pecari tajacu	Unknown	MPEG 30681	2.99 S	47.27 W
Pecari tajacu	Unknown	MPEG 30682	2.99 S	47.27 W
Pecari tajacu	Male	MPEG 4497	2.94 S	54.45 W
Pecari tajacu	Female	MN 6008	2.91 S	58.54 W
Pecari tajacu	Female	MN 6009	2.91 S	58.54 W
Pecari tajacu	Female	MN 6011	2.91 S	58.54 W
Pecari tajacu	Male	MN 6025	2.91 S	58.54 W
Pecari tajacu	Male	MZUSP 17551	2.89 S	64.85 W
Pecari tajacu	Male	MN 6019	2.77 S	54.94 W
Pecari tajacu	Female	MZUSP 5339	2.65 S	55.72 W
Pecari tajacu	Male	MPEG 4433	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4437	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4438	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4441	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4442	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4443	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4444	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4445	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4446	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4448	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4452	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4455	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4456	2.49 S	54.30 W

Pecari tajacu	Male	MPEG 4460	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4466	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4473	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4476	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4483	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4495	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 4504	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 4510	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 8833	2.49 S	54.30 W
Pecari tajacu	Female	MPEG 8834	2.49 S	54.30 W
Pecari tajacu	Male	MPEG 8838	2.49 S	54.30 W
Pecari tajacu	Unknown	MPEG 6472	2.22 S	55.96 W
Pecari tajacu	Unknown	MPEG 28688	1.50 S	50.91 W
Pecari tajacu	Male	MPEG 1258	1.37 S	56.08 W
Pecari tajacu	Female	MPEG 1259	1.37 S	56.08 W
Pecari tajacu	Male	MPEG 1260	1.37 S	56.08 W
Pecari tajacu	Female	MPEG 769	1.34 S	48.22 W
Pecari tajacu	Female	MPEG 2689	1.34 S	48.22 W
Pecari tajacu	Female	MPEG 1109	1.34 S	48.22 W
Pecari tajacu	Male	MPEG 6474	1.15 S	50.39 W
Pecari tajacu	Male	MPEG 1304	1.15 S	50.39 W
Pecari tajacu	Male	MPEG 1305	1.15 S	50.39 W
Pecari tajacu	Female	MPEG 1973	1.15 S	50.39 W
Pecari tajacu	Male	MPEG 1306	1.15 S	50.39 W
Pecari tajacu	Male	MN 69374	0.97 S	62.93 W
Pecari tajacu	Male	MN 1724	0.81 S	66.03 W
Pecari tajacu	Female	MN 1725	0.81 S	66.03 W
Pecari tajacu	Unknown	MPEG 21801	0.33 S	53.10 W
Pecari tajacu	Female	MPEG 1515	0.10 S	51.29 W
Pecari tajacu	Unknown	MPEG 1618	0.10 S	51.29 W
Pecari tajacu	Unknown	MPEG 1663	0.10 S	51.29 W
Pecari tajacu	Unknown	MPEG 2156	0.08 S	51.35 W
Pecari tajacu	Unknown	MPEG 2157	0.08 S	51.35 W

Pecari tajacu	Unknown	MPEG 2158	0.08 S	51.35 W
Pecari tajacu	Unknown	MPEG 2159	0.08 S	51.35 W
Pecari tajacu	Unknown	MN 50295	0.05 S	63.40 W
Tayassu pecari	Unknown	MZUSP 108	31.37 S	51.98 W
Tayassu pecari	Unknown	MZUSP 107	31.37 S	51.98 W
Tayassu pecari	Unknown	MACN 3.55	30.80 S	60.02 W
Tayassu pecari	Unknown	UFSC 4768	27.90 S	50.79 W
Tayassu pecari	Unknown	UFSC 405	27.17 S	49.53 W
Tayassu pecari	Unknown	UFSC 403	26.95 S	48.97 W
Tayassu pecari	Unknown	MLP 1073	26.92 S	54.25 W
Tayassu pecari	Male	MACN 48350	26.36 S	54.65 W
Tayassu pecari	Unknown	UFSC 326	26.30 S	48.99 W
Tayassu pecari	Unknown	UFSC 327	26.30 S	48.99 W
Tayassu pecari	Unknown	MACN 25790	26.11 S	54.11 W
Tayassu pecari	Unknown	MACN 49-340	25.93 S	54.62 W
Tayassu pecari	Unknown	MACN 49342	25.93 S	54.62 W
Tayassu pecari	Unknown	MHNCI 3788	25.49 S	53.92 W
Tayassu pecari	Unknown	MHNCI 3789	25.49 S	53.92 W
Tayassu pecari	Unknown	MHNCI 3790	25.49 S	53.92 W
Tayassu pecari	Unknown	MHNCI 3791	25.49 S	53.92 W
Tayassu pecari	Male	MHNCI 3525	25.45 S	52.87 W
Tayassu pecari	Unknown	MHNCI 3527	25.45 S	52.87 W
Tayassu pecari	Unknown	MHNCI 3528	25.45 S	52.87 W
Tayassu pecari	Female	MHNCI 4154	25.45 S	52.87 W
Tayassu pecari	Female	MHNCI 4140	25.45 S	52.87 W
Tayassu pecari	Unknown	MZUSP 20025	24.49 S	48.71 W
Tayassu pecari	Unknown	UFSC 968	24.30 S	50.57 W
Tayassu pecari	Male	MHNCI 4116	24.30 S	50.57 W
Tayassu pecari	Unknown	MLP 1925	23.76 S	64.85 W
Tayassu pecari	Male	MZUSP 9597	23.74 S	45.90 W
Tayassu pecari	Female	MZUSP 9639	23.74 S	45.90 W
Tayassu pecari	Male	MHNCI 92	23.59 S	50.73 W
Tayassu pecari	Male	MHNCI 135	23.59 S	50.73 W

Tayassu pecari	Female	MHNCI 136	23.59 S	50.73 W
Tayassu pecari	Female	MN 8455	23.22 S	44.79 W
Tayassu pecari	Female	MN 8456	23.22 S	44.79 W
Tayassu pecari	Female	MN 8462	23.22 S	44.79 W
Tayassu pecari	Male	MN 8463	23.22 S	44.79 W
Tayassu pecari	Male	MN 37018	23.22 S	44.79 W
Tayassu pecari	Male	MN 37019	23.22 S	44.79 W
Tayassu pecari	Unknown	MACN 3532	22.84 S	65.00 W
Tayassu pecari	Male	MZUSP 10350	22.55 S	47.90 W
Tayassu pecari	Male	MZUSP 8881	22.55 S	47.90 W
Tayassu pecari	Male	MZUSP 8882	22.55 S	47.90 W
Tayassu pecari	Male	MZUSP 10346	22.55 S	47.90 W
Tayassu pecari	Female	MZUSP 8029	22.55 S	47.90 W
Tayassu pecari	Female	MZUSP 497	22.35 S	49.02 W
Tayassu pecari	Male	MN 3827	21.23 S	57.13 W
Tayassu pecari	Female	MZUSP 2998	20.34 S	47.79 W
Tayassu pecari	Unknown	MN 1608	19.27 S	44.40 W
Tayassu pecari	Unknown	MN 1609	19.27 S	44.40 W
Tayassu pecari	Unknown	MN 67141	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67142	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67143	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67145	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67152	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67160	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67147	18.00 S	52.78 W
Tayassu pecari	Male	MN 67149	18.00 S	52.78 W
Tayassu pecari	Male	MN 67150	18.00 S	52.78 W
Tayassu pecari	Male	MN 67158	18.00 S	52.78 W
Tayassu pecari	Male	MN 67165	18.00 S	52.78 W
Tayassu pecari	Female	MN 67140	18.00 S	52.78 W
Tayassu pecari	Female	MN 67170	18.00 S	52.78 W
Tayassu pecari	Female	MN 67171	18.00 S	52.78 W
Tayassu pecari	Unknown	MN 67146	17.56 S	52.59 W

Tayassu pecari	Unknown	MN 68182	17.56 S	52.59 W
Tayassu pecari	Unknown	UFSC 359	16.34 S	46.94 W
Tayassu pecari	Unknown	MN 42898	16.29 S	56.64 W
Tayassu pecari	Unknown	MN 42901	16.29 S	56.64 W
Tayassu pecari	Unknown	MN 42902	16.29 S	56.64 W
Tayassu pecari	Unknown	MN 42904	16.29 S	56.64 W
Tayassu pecari	Unknown	MN 64004	16.21 S	55.95 W
Tayassu pecari	Unknown	MN 64662	16.21 S	55.95 W
Tayassu pecari	Unknown	MN 71151	14.82 S	57.93 W
Tayassu pecari	Unknown	MZUSP 20027	11.94 S	53.41 W
Tayassu pecari	Unknown	MACN 25-57	10.36 S	65.43 W
Tayassu pecari	Female	MZUSP 8087	9.36 S	54.92 W
Tayassu pecari	Male	MZUSP 25240	7.33 S	70.34 W
Tayassu pecari	Unknown	MHNCI 6171	7.09 S	55.89 W
Tayassu pecari	Unknown	MZUSP 20016	4.46 S	56.37 W
Tayassu pecari	Unknown	MPEG 26226	4.32 S	49.78 W
Tayassu pecari	Unknown	MPEG 26270	4.32 S	49.78 W
Tayassu pecari	Unknown	MPEG 26219	4.32 S	49.78 W
Tayassu pecari	Unknown	MZUSP 20028	4.12 S	63.42 W
Tayassu pecari	Female	MN 37013	3.72 S	61.44 W
Tayassu pecari	Unknown	MZUSP 21607	3.64 S	61.44 W
Tayassu pecari	Female	MN 1723	3.50 S	60.69 W
Tayassu pecari	Male	MN 1726	3.50 S	60.69 W
Tayassu pecari	Unknown	MPEG 41056	3.46 S	56.31 W
Tayassu pecari	Male	MN 6018	3.28 S	58.29 W
Tayassu pecari	Female	MN 6028	3.28 S	58.29 W
Tayassu pecari	Female	MZUSP 5596	3.15 S	60.50 W
Tayassu pecari	Male	MZUSP 5593	3.15 S	60.50 W
Tayassu pecari	Male	MPEG 4568	2.94 S	54.45 W
Tayassu pecari	Male	MPEG 8831	2.94 S	54.45 W
Tayassu pecari	Female	MPEG 8805	2.94 S	54.45 W
Tayassu pecari	Male	MZUSP 5437	2.77 S	54.94 W
Tayassu pecari	Male	MZUSP 5599	2.77 S	54.94 W

Tayassu pecari	Male	MZUSP 5597	2.77 S	54.94 W
Tayassu pecari	Unknown	MZUSP 20023	2.50 S	55.15 W
Tayassu pecari	Male	MPEG 8800	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8801	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8804	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8806	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8809	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8810	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8812	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8813	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8814	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 8815	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8816	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8817	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8819	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8820	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8821	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8824	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 8829	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 4528	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 4534	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 4549	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 4552	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 4579	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 4580	2.49 S	54.30 W
Tayassu pecari	Male	MPEG 4581	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 4585	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 22489	2.49 S	54.30 W
Tayassu pecari	Female	MPEG 22488	2.49 S	54.30 W
Tayassu pecari	Unknown	MPEG 11892	1.89 S	49.39 W
Tayassu pecari	Female	MZUSP 13491	1.89 S	49.39 W
Tayassu pecari	Unknown	MZUSP 13487	1.89 S	49.39 W
Tayassu pecari	Unknown	MZUSP 13489	1.89 S	49.39 W

Tayassu pecari	Unknown	MN 70692	1.82 S	61.15 W
Tayassu pecari	Unknown	MN 70693	1.82 S	61.15 W
Tayassu pecari	Female	MZUSP 20015	1.41 S	61.98 W
Tayassu pecari	Unknown	MZUSP 20024	1.19 S	56.94 W
Tayassu pecari	Female	MN 32709	0.55 S	50.13 W

Appendix S2. Environmental and spatial variables used in the statistical analysis from 81 *Pecari tajacu* and 53 *Tayassu pecari* specimens geographically averaged.

Available in: bij12859-sup-0002-AppendixS2.xls

Table S2. Variation partitioning of the skull shape of *Pecari tajacu* and *Tayassu pecari* onto environment, size, and geographical space components. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

Pecari tajacu	**Df**	**R^2**	**Adj. R^2**	**F**	**P**
Environment	2	0.12861	0.10627	5.7562	**0.001**
Size	1	0.02753	0.01522	2.2363	**0.024**
Geographical space	2	0.04831	0.02391	1.9797	**0.015**
Environment * Size	3	0.15761	0.12479	3.3308	**0.001**
Environment * Geographical space	4	0.16662	0.12275	2.4055	**0.001**
Size * Geographical space	3	0.07602	0.04002	1.8205	**0.005**
All	5	0.19367	0.13992	1.7204	**0.001**
Environment “Pure”	2		0.09999	5.4719	**0.001**
Size “Pure”	1		0.01717	2.5168	**0.014**
Geographical space “Pure”	2		0.01513	1.6772	**0.045**
Residuals			0.86008		
Controlling 1 table x					
Environment | geographical space	2		0.09885	5.3945	**0.001**
Environment | size	2		0.10957	5.9452	**0.001**
Size | geographical space	1		0.1611	2.3091	**0.018**
Size | environment	1		0.1852	2.6507	**0.014**
Geographical space | environment	2		0.1649	1.7329	**0.035**
Geographical space | size	2		0.2480	2.0204	**0.014**
Tayassu pecari	**Df**	**R^2**	**Adj. R^2**	**F**	**P**
Environment	2	0.08783	0.05135	2.4073	**0.011**
Size	1	0.01124	-0.0081	0.5798	0.783
Geographical space	1	0.0383	0.01944	2.0311	0.067
Environment * Size	3	0.10065	0.04558	1.2644	0.158
Environment * Geographical space	3	0.12335	0.06967	1.579	**0.045**
Size * Geographical space	2	0.0502	0.01221	1.282	0.191
All	4	0.13648	0.06452	1.2455	0.127
Environment “Pure”	2		0.05231	2.3979	**0.006**
Size “Pure”	1		-0.0051	0.7298	0.633
Geographical space “Pure”	1		0.01893	1.9916	0.068

Residuals		0.93548		
Controlling 1 table x				
Environment | geographical space	2	0.05023	2.3768	**0.01**
Environment | size	2	0.05373	2.4356	**0.014**
Size | geographical space	1	- 0.0072	0.6264	0.752
Size | environment	1	- 0.0057	0.6981	0.65
Geographical space | environment	1	0.01833	1.9849	0.072
Geographical space | size	1	0.02036	2.051	**0.049**

CAPITULO 2: EVERY RULE HAS ITS EXCEPTION: ECOGEOGRAPHICAL PATTERNS IN SKULL SIZE OF PECCARIES (ARTIODACTYLA: TAYASSUIDAE)

Este manuscrito está em preparação para ser submetido à revista Ecography

Every rule has its exception: ecogeographical patterns in skull size of peccaries (Artiodactyla: Tayassuidae)

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ABSTRACT

Body size is a fundamental determinant of biological properties, and geographic patterns in body size are prevalent in nature. Larger size at higher latitudes (Bergmann's pattern) have long been recognized. Most of the empirical evidence however comes from temperate climates or from taxa in the Northern Hemisphere. Very few investigations have assessed Bergmann's patterns in widespread mammals with distributions both north and south of the equator. We evaluated intraspecific variation in skull size of *Pecari tajacu* and *Tayassu pecari*, two of the widest-ranging tropical mammals, each with distributions spanning more than 50 degrees of latitude. Using geometric morphometrics, we obtained the skull size for 426 adult specimens of both species from 174 different localities south of the equator and 83 in the north. We regressed skull size against latitude using linear regression. Effects of seasonal temperature, precipitation and human influence including autocorrelation spatial structures were tested through Generalized Least Squares (GLS). Differences in size where the species are sympatric or allopatric were explored with ANOVA models. We found a significant latitudinal pattern in skull size of peccaries, one inverse to Bergmann Rule. Size is positively associated with precipitation, offering support to resource availability as a major mechanism behind increases at lower latitudes, especially for *T. pecari*. Human influence affects negatively the size of peccaries in Southern hemisphere. The largely non-overlapping body-size distributions of the two species suggest that size differences may be necessary for sympatric overlap of these two peccaries. In the tropics, resource availability might better predict size clines than temperature for mammals like these peccaries, as well as other social animals whose resource utilization patterns are shaped by group-living.

Keywords: Bergmann's Rule, collared peccary, geometric morphometrics, Resource Rule, size variation, white-lipped peccary.

INTRODUCTION

Animals' lives are influenced more by body size than by any other characteristic (Calder 2001). Adult body size directly influences their metabolic rates, reproductive success, longevity, home ranges, resource use, lifestyle, abundance, species richness, and even their extinction rates (Calder 2001, Smith and Lyons 2013). In essence, size determines how a species fits into its ecological communities or populations (West 1997, Calder 2001). Not surprising, body size patterns have long been a topic of interest, leading to the formulation of several evolutionary and ecogeographical hypotheses (Smith and Lyons 2013).

Spatial patterns in animal size have been studied at least since 1847, when Carl Bergmann described a positive relationship between body size of homoeothermic animals and latitude. This pattern, known as Bergmann's rule, hypothesized that, within a genus, larger animals are found in colder environments and at higher latitudes because heat loss is reduced by their smaller body surface area relative to volume (Bergmann 1847). Mayr (1956) subsequently restricted Bergmann's rule to variation at the intraspecific level, but both intra- and interspecific patterns are currently widespread among mammals and birds (Ashton et al. 2000, Meiri and Dayan 2003, Olson et al. 2009, Martinez et al. 2013), as well in some ectothermic organisms (nonavian reptiles: Ashton and Feldman 2003, turtles: Werner et al. 2016). Nevertheless, conflicting patterns have been described for some mammals (Ashton et al. 2000, Medina et al. 2007, Schiaffini 2016) and birds (Meiri and Dayan 2003, Brumfield and Remsen Jr. 1996), casting doubt on the universality of Bergmann's Rule (and temperature) driving geographical clines in size.

Clines in size can evolve in response to additional selective forces besides temperature (Millien et al. 2006). Seasonality can select for larger body size because larger individuals have greater fasting endurance during periods of food shortage (Boyce 1978, Lindstedt and Boyce 1985). Because colder areas tend also to be more seasonal, this hypothesis has been considered an alternative mechanism to explain patterns consistent with Bergmann's Rule (Ashton et al.

2000). Additionally, there is mounting evidence that body size increases with primary productivity or annual precipitation, both of which often serve as proxies for resource availability (Yom-Tov and Geffen 2006, Meiri et al. 2007, McNab 2010, Schiaffini 2016, Correl et al. 2016). Resource availability could thus constrain Bergmann's Rule patterns (Meiri et al. 2007, McNab 2010, Schiaffini 2016) or even offer a complementary mechanism interacting with temperature (Correll et al. 2016). Human-induced environmental conditions such as habitat fragmentation and hunting also seem to direct affect body size variation (see Millien et al. 2006). Although, unexplored in broad-scale spatial, temporal increases in the body size of carnivoran groups has been attributed to improved food availability due to human influence (Yom-Tov 2003, Yom-Tov et al. 2003).

Biotic factors such as interspecific competition constitute another selective pressure generating geographical shifts in body size via character displacement (Brown and Wilson 1956). Overall, two closely related or ecologically similar species with overlapping geographical ranges will often have their differences accentuated in sympatric zones, and this effect is weakened or lost in allopatry (Brown and Wilson 1956, Dayan and Simberloff 1998). The smaller numbers of species at higher latitudes (i.e. less competition) may permit species to become larger farther from the equator in a manner consistent with Bergmann's Rule (Dayan et al. 1989, Ashton et al. 2000).

Most of the empirical evidence for Bergmann's Rule comes from the Nearctic and Palearctic Regions, mainly from temperate climates where the classic mechanism related to heat conservation seems to fit well (Blackburn and Hawkins 2004, Rodríguez et al. 2008). Tropical taxa, however, do not follow this same pattern as often as temperate species (Rodríguez et al. 2008). Indeed, in the Southern Hemisphere, temperature is considered a poor predictor of size variation in some mammalian taxa (Medina et al. 2007, Maestri et al. 2016, Schiaffini 2016, Correl et al. 2016; Bubadue et al., 2018), although exceptions exist (Gay and

Best 1996, Martinez et al. 2013). The narrow latitudinal ranges of many Southern Hemisphere taxa may contribute to the poor support of observed patterns (Meiri et al. 2007). Few investigations have assessed Bergmann's patterns in widespread mammals with distributions in the north and south of the equator (but see Gay and Best 1996, Martinez et al. 2013). Methodology has also clouded this question, as organism size has been variously estimated (Meiri and Thomas 2007). In many analyses of interspecific variation, phylogenetic affinities explain a large part of size variation, with environmental factors playing a more ancillary role (Olson et al. 2009, Maestri et al. 2016). In this regard, analyzing intraspecific variation is particularly meaningful because it removes the dominant effects of phylogeny to focus on associations between an organism's size and its environment (Angilletta and Dunham 2003).

Peccaries (Artiodactyla: Tayassuidae) are excellent candidates for testing hypotheses surrounding geographical size variation. Two of the three living species, *Pecari tajacu* (Linnaeus 1758) (collared peccary) and *Tayassu pecari* (Link, 1795) (white-lipped peccary) have huge geographic distributions spanning 65 and 50 degrees of latitude (respectively), ranging across both Northern and Southern hemispheres. These two species occupy various habitats from tropical rainforests to deserts and deciduous forests to savannas and grasslands (Eisenberg and Redford 1999). Their diets are mainly composed of plant resources (i.e. palm fruits, seeds, roots, and nuts) and occasionally small animals (Fragoso 1999, Keuroghlian and Eaton 2008b, Desbiez et al. 2009). *Tayassu pecari* is a bit more selective, preferentially living in forested environments and eating fruits (Keuroghlian and Eaton 2008a, b, Altrichter et al. 2012). Over their entire geographic range, populations of these two peccaries may encounter intense selective forces resulting from climatic variability, food resource availability, and even by competition with each other, given their strong ecological similarities and extensive co-occurrence in the Neotropical Region. Environmental effects have been recently identified as important drivers of their skull shape variation (Hendges et al. 2016). Moreover, their broad

distributions bring them into proximity with humans, making peccaries vulnerable to anthropogenic impact, which is already reflected in declines in their abundances and group-size patterns (Altrichter et al. 2012, Reyna-Hurtado et al. 2016, Martínez-Gutiérrez et al. 2017). Each of these selective pressures could also influence geographical size patterns.

Here, we used a multivariate measure of skull size as a surrogate for body size to test the following hypotheses: (1) intraspecific variation of peccaries follows Bergmann's rule, exhibiting increasing skull size with latitude (i.e. in colder and more seasonal environments). This pattern is widely documented in other mammals, including *Sus scrofa* Linnaeus, 1758, a species belonging to the peccaries' sister family (Ashton 2000, Meiri and Dayan 2003); (2) resource availability is positively correlated with clines in peccary size as it is for other mammals (Yom-Tov and Geffen 2006, McNab 2010, Schiaffini 2016, Correl et al. 2016); (3) human influence is correlated with geographical variation in size of peccaries, in accord with previous reports for peccary abundance and group-size patterns (Reyna-Hurtado et al. 2016, Martínez-Gutiérrez et al. 2017); (4) interspecific competition affects their size variation patterns, so that differences are larger in areas of sympatry (Brown and Wilson 1956, Dayan et al. 1989). Some field evidence shows that white-lipped peccaries can be twice the weight of collared peccaries in areas where they co-occur (e.g. Fragoso 1998).

MATERIALS AND METHODS

Data acquisition

We obtained 2D images of the ventral view from 426 skulls of *P. tajacu* (n = 257) and *T. pecari* (n = 169). Samples covering the entire geographic distributions of these species (see Fig. 1) are housed in the collections of the Field Museum of Natural History (Chicago, USA), American Museum of Natural History (New York, USA), Museu Nacional (Rio de Janeiro, Brazil), Museu de Zoologia da Universidade de São Paulo (Sao Paulo, Brazil), Museu Paraense

Emilio Goeldi (Belém, Brazil), Museu de História Natural Capão da Imbuia (Curitiba, Brazil), Coleção Cientifica do Laboratório de Mamíferos Aquáticos da Universidade Federal de Santa Catarina (Florianópolis, Brazil), the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires, Argentina), and Museo de Ciencias Naturales de La Plata (La Plata, Argentina). A list of specimens examined can be found in the Supplementary material Appendix S1.

Ventral views of skulls were photographed in the same plane and at the same distance using a Nikon Coolpix P530 digital camera. Only adult specimens, i.e., those with fully erupted dentition and completely fused sutures were included (Margarido et al. 2007). Eleven landmarks were digitized on each photograph to describe the length and width of the skull, using TPSDig2 software (Rohlf 2015, Fig. 2). We positioned the landmarks only on the left side to avoid redundancies in bilaterally symmetric structures (see Cardini et al. 2007).

After digitization, we superimposed the landmark coordinates by applying a generalized Procrustes analysis (GPA, Rohlf and Slice 1990, Adams et al. 2013). GPA allowed us to extract the centroid size, a proxy for size obtained as the square root of the sum of squared distances between each landmark and the configuration's centroid (Bookstein 1989). The log-transformed centroid size (log Cs) was used as the dependent variable in the analyses of geographic variation. GPA was implemented using the R package geomorph (Adams and Otarola-Castillo 2013, R Core Team 2016).

We also assembled the geographic coordinates of the collecting locality for each specimen. We included only specimens of known provenance. Temperature seasonality (Bio 4) and annual precipitation (Bio 12), as a proxy for food availability (Yom-Tov and Geffen 2006, McNab 2010), were then extracted at spatial resolution of 30" (c.a. 1 km) from the WorldClim raster database (www.worldclim.org/version2, Fick and Hijmans 2017). For analyzing the anthropogenic influence, we used the Human Influence Index (HII) dataset of the Last of the

Wild Project (WCS, CIESIN, Columbia University 2005). This dataset of 1 km grid cells integrates information on human population densities, land use, infrastructure, and human access from nine global data layers. We extracted these predictors using the raster, sp and rgdal R packages (R Core Team 2016).

Statistical analyses

First, we tested the effects of sexual size dimorphism, applying ANOVA to test for differences between males, females, and genderless individuals, using an alpha of 0.05 to gauge statistical significance.

Because peccaries have extensive latitudinal distributions both north and south of the equator, and Bergmann's Rule makes contrasting predictions for their variation, each species was divided into two groups: (i) peccaries from south of the equator (*P. tajacu* = 160 individuals from 99 localities; *T. pecari* = 128 individuals from 75 localities); and (ii) peccaries from north of the equator (*P. tajacu* = 97 individuals from 59 localities; *T. pecari* = 41 individuals from 24 localities).

In order to assess geographic variation in skull size of each species, we applied linear regressions of log Cs on latitude.

Generalized Least Squares (GLS) were applied to evaluate the influence of temperature seasonality, annual precipitation, and human influence on peccary skull size. In cases of positive and significant spatial autocorrelation as assessed by the Moran's Test (Semivariograms can be seen in Supplementary material Appendix S2), we fitted the GLS models to include spherical, exponential, Gaussian, and linear autocorrelation structures (see Legendre and Legendre 2012). The best model (assuming a model lacking autocorrelation structures and those including it) was selected using Akaike information criterion (AIC). Models with $\Delta AIC < 2$ are considered equally good and equally plausible (Burnham and Anderson 2002). These analyses were conducted using the nlme, ape and MuMIn R packages (R Core Team 2016).

Finally, to evaluate skull size differences between species and between sites (*P. tajacu* allopatric vs. sympatric with *T. pecari*), we performed ANOVA analyses. We also compared the slopes of the regressions of size with latitude between *P. tajacu* allopatric and sympatric with *T. pecari* in north, and between the two peccaries coexisting in south using ANCOVA models. Significant interaction between the regressor (correlated variable) and categorical factors (sites and species) indicates differences in slopes, i.e., in the rate of change in size.

RESULTS

Neither peccary species nor their hemispheric groupings presented sexual differences in size (Northern: *P. tajacu* = F = 1.99, d.f. = 2, 94; P > 0.05; *T. pecari* = F = 2.27, d.f. = 2,38; P > 0.05; Southern: *P. tajacu* = F = 1.42, d.f. = 2, 157; P > 0.05; *T. pecari* = F = 1.39, d.f. = 2, 125; P > 0.05). Consequently, we pooled males, females, and genderless individuals in all ensuing analyses.

Skull size variation of peccaries varied significantly with latitude, except in northern populations of *P. tajacu*. Peccaries showed decreasing skull size with increasing latitude, contrary to the expectations of Bergmann´s Rule (Table 1; Fig. 3).

Temperature seasonality, annual precipitation, and human influence are all significantly reflected in skull size variation only for peccaries in the southern hemisphere. Temperature seasonality and human influence were negatively related with skull size of both species. However, after correcting for spatial autocorrelation, only the effect of human influence remains significant for *P. tajacu* (Table 1; Fig. 4a and c). Annual precipitation was positively correlated with skull size, but when spatial autocorrelation is taken into account, this relationship is significant only for *T. pecari* (Table 1; Fig. 4b).

Significant differences in skull size are evident between species, with *T. pecari* consistently larger than *P. tajacu* in both southern (F = 1576, d.f. = 1, 287; P < 0.001) and northern hemispheres (F = 696.4, d.f. = 1, 137; P < 0.001). ANOVA also revealed that *P. tajacu*

have larger skulls in areas where they are sympatric with *T. pecari* than in allopatric areas (F = 4.21; d.f. = 1, 94; P = 0.04; Fig. 5). The slopes of regressions between *P. tajacu* allopatric vs. sympatric (latitude: slopes -0.00051 and -0.00055, respectively) and between *P. tajacu* and *T. pecari* sympatric in south (latitude: slopes 0.0018 and 0.0015, respectively) do not differ significantly (P > 0.5), revealing similar degree of size variation between sympatric and allopatric *P. tajacu* populations and between both peccaries where they are found together in south. This means that there is a constant size difference between them.

DISCUSSION

Peccaries vary substantially in size across their enormous ranges, but this variation is complicated and has no single determinant. The latitudinal gradient in skull size of peccaries does not support Bergmann's Rule. Skull size, and by extension body size, increases at lower latitudes and in less seasonal areas near the equator, and does so for both species and in both hemispheres. On the other hand, the positive association between skull size and precipitation provides support for resource availability as a determinant of clines in size of peccaries, at least in Southern Hemisphere (Yom-Tov and Geffen 2006, McNab 2010, Schiaffini 2016). Clines in size of southern peccaries are also negatively correlated with human influence. The variable but largely non overlapping body-size distributions throughout their ranges suggest that size differences may contribute to the sympatry of these two peccaries (Brown and Wilson 1956, Dayan et al. 1989).

The negative latitudinal relationship with size suggests that temperature does not select for larger size for peccaries in colder environments as predicted by Bergmann`s Rule. Species-specific life-history traits are commonly used as explanations for deviations from Bergmann patterns in mammals (see Ashton et al. 2000, Medina et al. 2007). Indeed, both peccaries appear to use a variety of strategies to deal with extremes environmental temperatures. During the

winter or wet season, peccaries exhibit higher diurnal activity, whereas in dry season, they shift their activity towards dawn and dusk and into the night (Taber et al. 2011, Hofmann et al. 2015). Herds of *T. pecari* are often found in areas close to water such as lakes, rivers, and wetlands (Fragoso 1999, Carrillo et al. 2002, Taber et al. 2011). Herds of *P. tajacu* typically rest in burrows, caves, or in cavities excavated at the bases of large trees during the hottest hours of day (Taber et al. 2011). At its northern range limits, *P. tajacu* individuals sometimes huddle together to decrease heat loss in winter nights (Zervanos and Hadley 1973, Bissonette 1978). The larger groups of *T. pecari* also maintain strong cohesion (Fragoso 1999). Individual and social behaviors must contribute to the thermoregulation of these peccaries to its environments, offsetting their smaller body size in colder and more seasonal areas (disadvantageous in heat conservation) and larger size in warmer areas (interfering with heat loss).

Precipitation is positively associated with skull size variation of peccaries in the Southern Hemisphere, although this relationship is significant only for *T. pecari* when spatial autocorrelation is taken into account. These results corroborate the role of resource availability in determining size increases in peccaries (McNab 2010, Schiaffini 2016). Several additional studies have shown the influence of resource availability in other southern mammals (Medina et al. 2007, Schiaffini 2016, Correl et al. 2016). Effects of productivity are also pronounced in the body size of several omnivorous mammals (Yom-Tov and Geffen 2006), including those group-foraging mammals, such as primates (Cardini et al. 2007; Bubadue et al., 2018). Serving to determine clines in size for *T. pecari*, size correlations with productivity represent deviations from Bergmann's Rule. Peccaries and most of these other mammals consume plant foods, whose abundance and availability of is directly correlated with precipitation in tropical forests (Murphy and Lugo 1986) as well as in drier biomes (Fay 2009). Fruits, dominant in the diet of peccaries, especially for *T. pecari*, are even more ephemeral and patchy resources (Keuroghlian and Eaton 2008a, b). Meeting food requirements is not thus a simple task for frugivorous

species, especially for those living in groups like peccaries and primates (Cardini et al. 2007). Shifts in fruits availability, for instance, affect habitat use, home ranges, and group size of *T. pecari* and lead to substantial alterations in the diet of *P. tajacu* (Fragoso 1999, Carrillo et al. 2002, Desbiez et al. 2009, Reyna-Hurtado et al. 2015). Resource availability and water itself may thus exert strong selective pressures on body size of these species, even more than temperature. Evidence that the ancestors of these modern peccaries evolved in tropical forest environments suggest even the optimality of these habitats for them (Wetzel 1977, Gasparini 2013).

Human influence affects peccary size clines only in the Southern Hemisphere and its effect is negative. Peccaries are larger in areas with less human influence. Contrasting patterns are found in some carnivores, which show body size increases due to food supplementation provided by humans (Yom-Tov 2003, Yom-Tov et al. 2003). For peccaries, higher human influence is generally synonymous with intense habitat loss and hunting (Keuroglian and Eaton 2008a, Taber et al. 2011). Human impacts are already known to negatively affect their abundance and group-size patterns (Reyna-Hurtado et al. 2015, Martínez-Gutiérrez et al. 2017). Adult body size of animals appears to be a function of time that growing individuals have unhindered access to high-quality food (Geist 1987). In this context, disturbed fragments may not offer the same energetic requirements (mainly fruits) needed by peccaries to achieve their maximum body size as undisturbed environments do (Keuroglian and Eaton 2008a). Reports that hunters select bigger adult animals are also available (Gabor and Hellgren 2000). For peccaries, human influence leads to smaller individuals in resource-poor areas and those with additional hunting pressures.

Tayassu pecari is consistently larger than *P. tajacu* in both hemispheres. In contrast with our expectations, *P. tajacu* did not exhibit significant shifts in either size or size-latitude relationships between allopatric and sympatric areas. This suggests that interspecific

exploitative competition for food resources does not determine variation in body size of *P. tajacu* fitting with character displacement (Brown and Wilson 1956). Rainforests comprise a large part of sympatric range of these two peccaries are rainforests, where the food supply may be not a limiting condition preceding competitive exclusion (Brown and Wilson 1956). Unlike carnivorans with a very specialized meat diet that often display character displacement (Dayan et al. 1989, Dayan and Simberloff 1998), more generalist consumer can minimize competition with dominant species by expanding into alternative and less-contested resources (Pfennig et al. 2006). Lowered levels of dietary overlap between *P. tajacu* and *T. pecari* are indeed verified during food shortages (Olmos 1993, Galetti et al. 2015).

Nevertheless, the variable but largely non overlapping body-size distributions of these peccaries suggests that size differences may be needed for sympatric overlap and coexistence of these species. Functional profiles emerging from biomechanical models have demonstrated the similar performance capabilities of these two peccary species to exploit foods (Hendges et al. 2018, unpublished). The generally high overlap in their diets also confirm this (Fragoso 1999, Desbiez et al. 2009). However, larger body size and larger group size offers *T. pecari* (the behaviorally dominant species) some advantages over *P. tajacu* (subordinate species) on the same foods. Interference competition has even been suggested as a mechanism behind their temporal and habitat segregation (Fragoso 1999, Keuroglian and Eaton 2004, Hofmann et al. 2015). More specific reports reveal that *P. tajacu* herds rapidly vacate resource areas when they encounter herds of *T. pecari* (Galetti et al. 2015). Thus, if body size differences reflect competitive interactions between peccaries, it highlights a role for competition by interference rather than exploitative competition in depressing resource levels.

In conclusion, the size-latitudinal relationships in these two widely distributed peccaries do not support Bergmann's rule, but instead suggest that resource availability may be an important selective mechanism behind increased body size at lower latitudes areas with higher

precipitation, greater primary productivity, and lower human influence. The higher thermoregulatory costs and lowered resources availability (e.g. foods and water) could be leading to smaller body sizes in more marginal habitats. The non-overlapping and parallel variation in body sizes of these peccaries across their huge sympatric ranges suggests that size could contribute to the stable coexistence of these species.

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Table 1 Results from the Linear Regressions and Generalized Least Squares including autocorrelation structures when significant autocorrelation was detected.

Models without autocorrelation structure						**Models with autocorrelation structures**					
Species/variables	T	F	R^2 adj	P	Moran's I	Selected Model	AICc	delta	Weight	T	P
Northern P. tajacu											
Latitude	- 0.98	0.97	- 0.00	0.327	-	-	-	-	-	-	-
Longitude	- 2.13	4.56	0.05	**< 0.05**	-	-	-	-	-	-	-
Temperature Seasonality	- 0.49	0.24	-0.01	0.622	**< 0.001**	exponential.autocor	-192.6	0.00	0.31	0.16	0.87
Annual precipitation	0.99	0.98	- 0.00	0.324	**< 0.001**	spherical.autocor	-193.8	0.00	0.24	1.09	0.27
Human Influence	-0.89	0.98	-0.00	0.377	0.10	-	-	-	-	-	-
Northern T. pecari											
Latitude	- 4.29	18.48	0.43	**< 0.001**	-	-	-	-	-	-	-
Longitude	- 2.28	5.20	0.15	**< 0.05**	-	-	-	-	-	-	-
Temperature Seasonality	-1.57	2.46	0.05	0.131	**< 0.001**	spherical.autocor	-75.5	0.00	0.35	-0.45	0.65
Annual precipitation	1.26	1.60	0.02	0.219	**< 0.001**	ratio.autocor	-74.6	0.00	0.55	0.72	0.47
Human Influence	0.19	0.03	-0.04	0.851	**< 0.05**	linear.autocor	-63.7	0.00	0.26	0.76	0.45
Southern P. tajacu											
Latitude	-4.42	19.62	0.16	**< 0.001**	-	-	-	-	-	-	-
Longitude	3.38	11.46	0.09	**< 0.001**	-	-	-	-	-	-	-
Temperature Seasonality	-4.14	17.15	0.14	**< 0.001**	**< 0.001**	ratio.autocor	-350.2	0.00	0.65	-1.18	0.23
Annual precipitation	2.93	8.59	0.07	**< 0.001**	**< 0.001**	ratio.autocor	-351.2	0.00	0.67	1.28	0.20
Human Influence	-4.42	19.6	0.16	**< 0.001**	**< 0.001**	exponential.autocor	-345.3	0.00	0.99	-2.28	**< 0.05**
Southern T.pecari											
Latitude	-4.18	17.52	0.18	**< 0.001**	-	-	-	-	-		-
Longitude	3.19	10.19	0.11	**< 0.001**	-	-	-	-	-		-
Temperature Seasonality	-3.73	13.96	0.15	**< 0.001**	**< 0.001**	Temp. season. model	-281.6	0.0	0.70	-3.73	**<0.001**
Annual precipitation	2.65	7.03	0.07	**< 0.001**	**< 0.001**	Annual precip. model	-277.5	0.0	0.70	2.65	**<0.01**
Human Influence	-4.15	17.29	0.18	**< 0.001**	**< 0.001**	Human Influence model	-278.7	0.0	0.70	-4.15	**< 0.001**

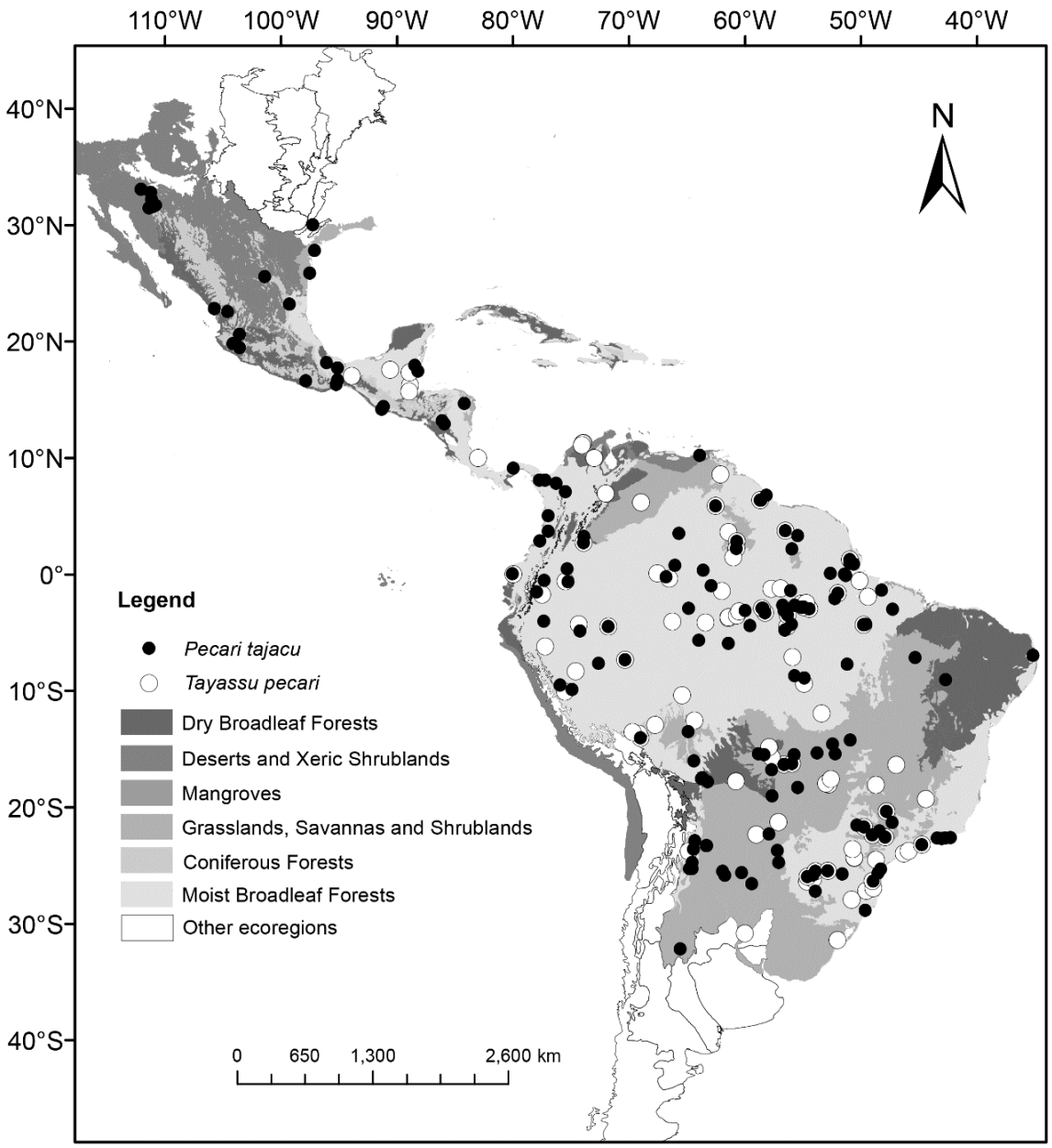


Figure 1 Geographical distribution of *Pecari tajacu* and *Tayassu pecari* skull samples across northern and southern hemispheres. The classification of the ecoregions follows Dinerstein et al. 2017. Deserts and Xeric Shrublands and Coniferous Forests are located in Neartic Region.

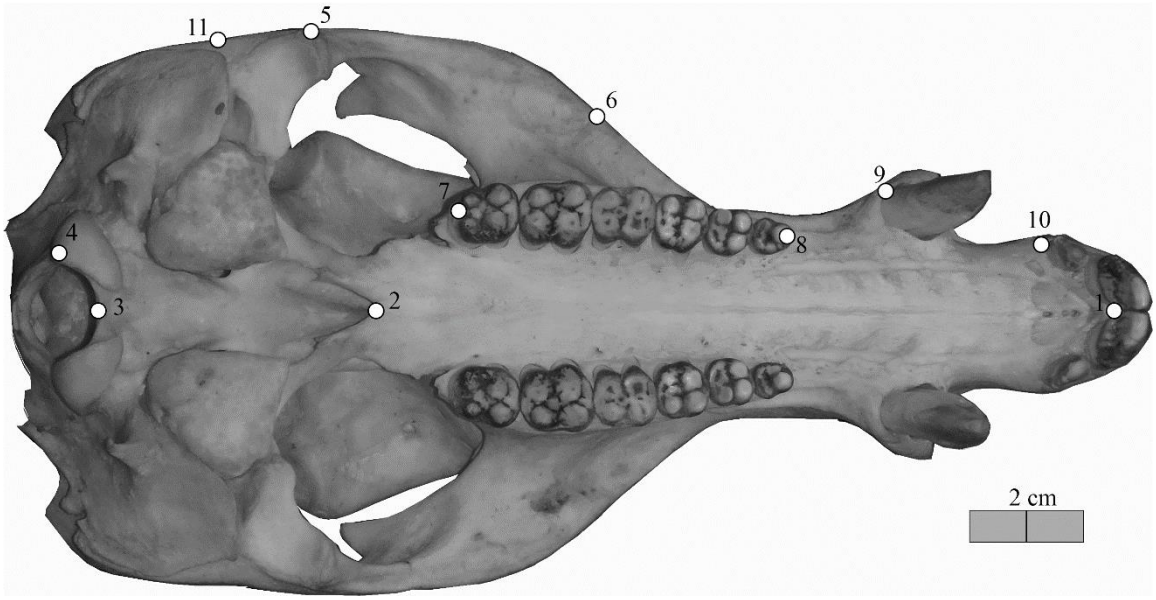


Figure 2 Position of the 11 landmarks on the ventral view of the skull in a peccary specimen (MZUSP 10345). 1 = midpoint of central incisors, 2 = posteriormost point of interpalatine suture, 3 = anteriormost point of the foramen magnum along the midline, 4 = posteriormost margin of the occipital condyle, 5 = suture between jugal and squamosal in the zygomatic arch, 6 = suture between maxilla and zygomatic arch, 7 – 8 = maxillary tooth row, 9 = posteriormost point of the lateral canine, 10 = posteriormost point of the lateral incisor, 11 = lateral point of the skull at the region of post-glenoid process.

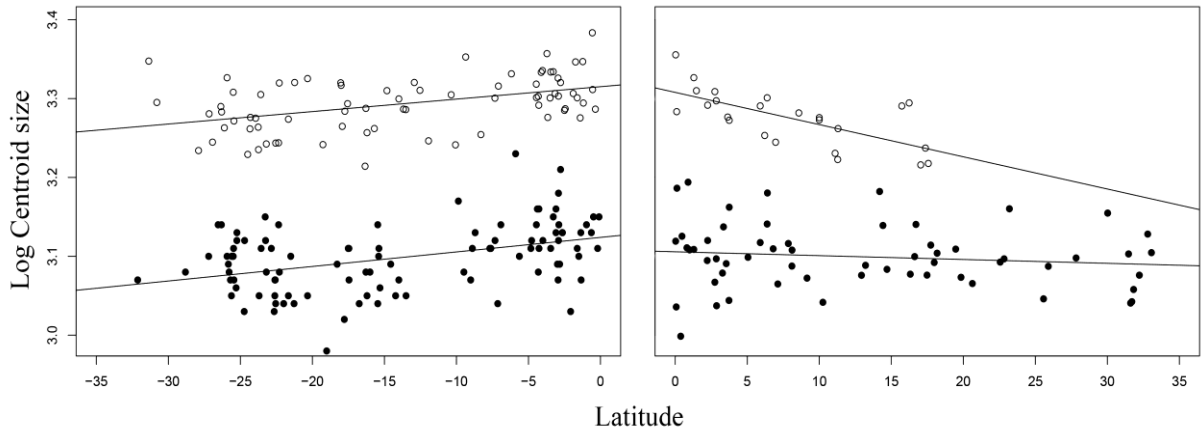


Figure 3 Variation in skull size of peccaries in relation to latitude for Southern (left) and Northern (right) hemispheres. Solid circles = *Pecari tajacu* (collared peccary); Open circles = *Tayassu pecari* (white-lipped peccary).

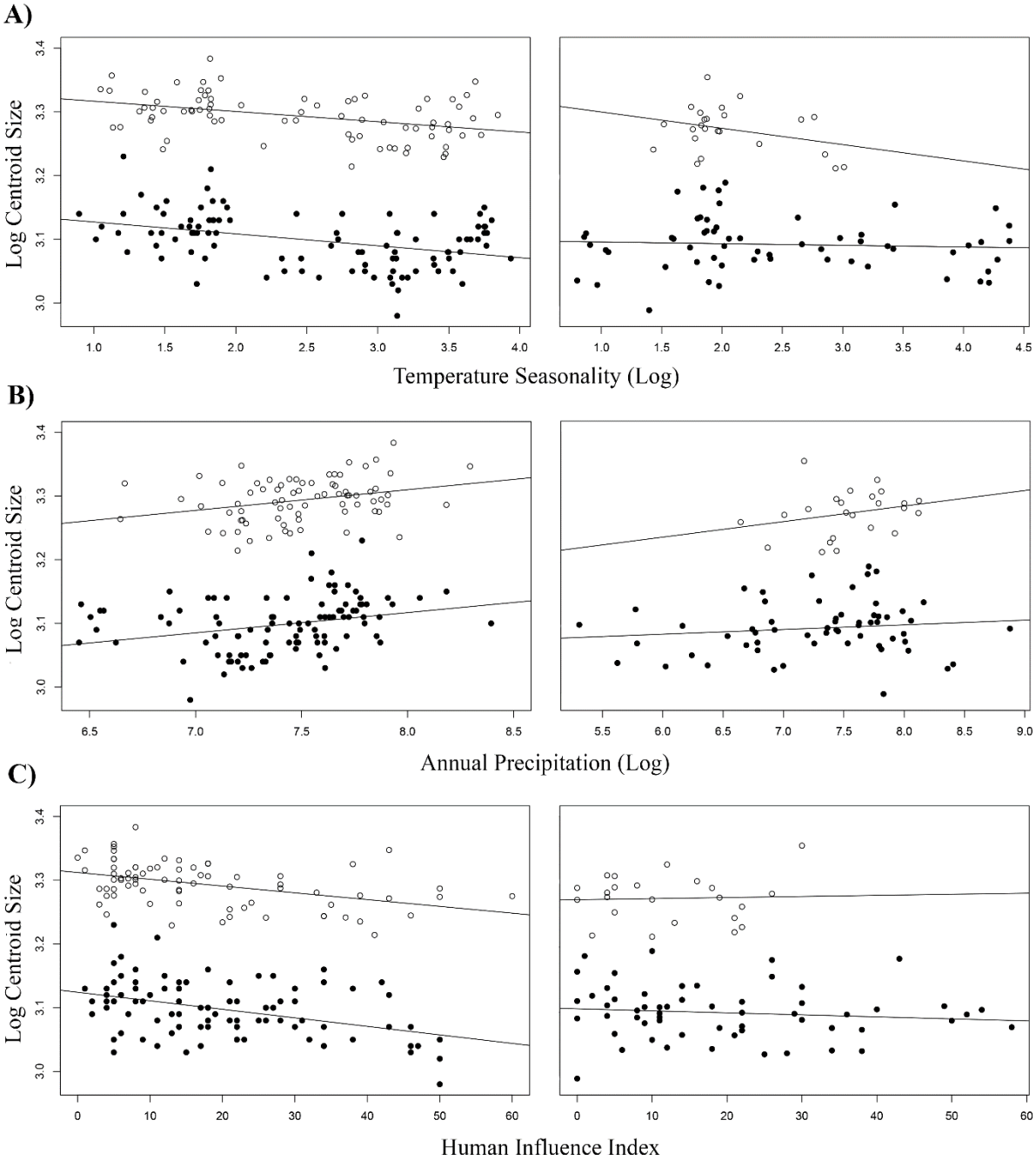


Figure 4 Variation in skull size of peccaries in relation to temperature seasonality (A), annual precipitation (B) and human influence index (C) for Southern (left) and Northern (right) hemispheres. Solid circles = *Pecari tajacu* (collared peccary); Open circles = *Tayassu pecari* (white-lipped peccary).

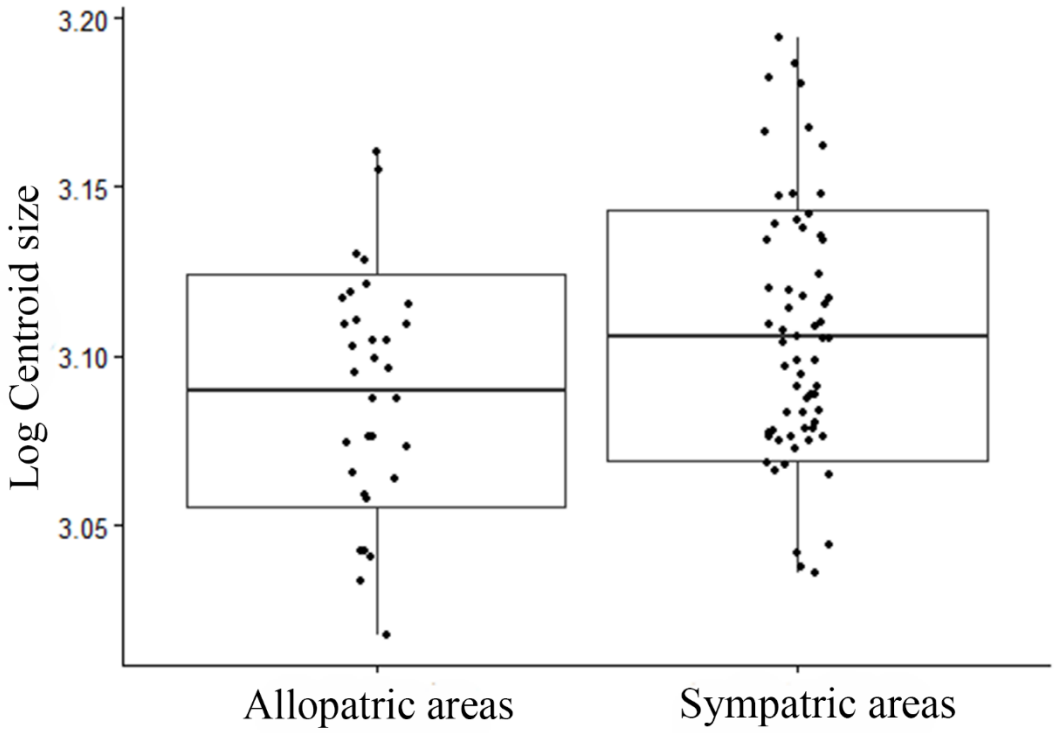


Figure 5 Boxplot representing variation in skull size of collared peccaries in allopatric areas and in areas where they co-occur with white-lipped peccaries. Black string represents mean values, white box the standard deviations and vertical bar the upper and lower limits.

Appendix S1. List of specimens belonging to *Pecari tajacu* and *Tayassu pecari* included in the analyses of geographical variation. Positive latitudes = Northern hemisphere, Negative latitudes = Southern hemisphere.

Species	Museum Number	Sex	Locality	Latitude	Longitude
Pecari tajacu	AMNH 184217	undetermined	1	33.06	-112.05
Pecari tajacu	AMNH 399	undetermined	2	32.80	-111.22
Pecari tajacu	AMNH 184219	undetermined	3	32.22	-111.14
Pecari tajacu	AMNH 184220	male	4	31.82	-111.13
Pecari tajacu	AMNH 174311	undetermined	5	31.70	-110.79
Pecari tajacu	FMNH 52861	undetermined	6	31.61	-111.05
Pecari tajacu	AMNH 184218	female	7	31.47	-111.36
Pecari tajacu	FMNH 134434	undetermined	8	30.02	-97.27
Pecari tajacu	FMNH 53023	undetermined	9	27.83	-97.11
Pecari tajacu	FMNH 53024	undetermined	9	27.83	-97.11
Pecari tajacu	FMNH 53030	undetermined	9	27.83	-97.11
Pecari tajacu	FMNH 53032	undetermined	9	27.83	-97.11
Pecari tajacu	FMNH 53033	undetermined	9	27.83	-97.11
Pecari tajacu	AMNH 22674	female	10	25.90	-97.51
Pecari tajacu	FMNH 14039	female	11	25.57	-101.42
Pecari tajacu	FMNH 16011	male	11	25.57	-101.42
Pecari tajacu	FMNH 16012	male	11	25.57	-101.42
Pecari tajacu	AMNH 165013	undetermined	12	23.20	-99.28
Pecari tajacu	AMNH 24587	male	13	22.83	-105.73
Pecari tajacu	AMNH 24593	male	13	22.83	-105.73
Pecari tajacu	AMNH 24586	undetermined	13	22.83	-105.73
Pecari tajacu	AMNH 23874	female	13	22.83	-105.73
Pecari tajacu	AMNH 24592	female	13	22.83	-105.73
Pecari tajacu	AMNH 24584	male	13	22.83	-105.73
Pecari tajacu	FMNH 14032	male	14	22.56	-104.62
Pecari tajacu	FMNH 14033	male	14	22.56	-104.62
Pecari tajacu	FMNH 14034	female	14	22.56	-104.62
Pecari tajacu	FMNH 14035	male	14	22.56	-104.62
Pecari tajacu	FMNH 14037	male	14	22.56	-104.62
Pecari tajacu	AMNH 25782	female	15	20.63	-103.57
Pecari tajacu	AMNH 25951	male	16	19.84	-104.15
Pecari tajacu	AMNH 26004	male	17	19.47	-103.58
Pecari tajacu	AMNH 17266	male	18	18.18	-96.06
Pecari tajacu	AMNH 17267	male	18	18.18	-96.06
Pecari tajacu	AMNH 17268	female	18	18.18	-96.06
Pecari tajacu	FMNH 63922	male	19	17.98	-88.47
Pecari tajacu	FMNH 63923	female	19	17.98	-88.47
Pecari tajacu	FMNH 15992	male	20	17.74	-95.13
Pecari tajacu	FMNH 22400	undetermined	21	17.48	-88.18
Pecari tajacu	AMNH 206835	undetermined	22	16.71	-95.13

Pecari tajacu	FMNH 15996	male	23	16.62	-97.85
Pecari tajacu	FMNH 15997	female	23	16.62	-97.85
Pecari tajacu	AMNH 145963	female	24	16.32	-95.25
Pecari tajacu	AMNH 29442	undetermined	25	14.70	-84.20
Pecari tajacu	FMNH 15932	undetermined	26	14.42	-91.17
Pecari tajacu	FMNH 41622	undetermined	27	14.19	-91.32
Pecari tajacu	AMNH 29443	male	28	13.21	-86.11
Pecari tajacu	AMNH 28954	male	29	12.93	-85.91
Pecari tajacu	AMNH 69600	female	30	10.25	-63.91
Pecari tajacu	AMNH 36701	male	31	9.15	-79.97
Pecari tajacu	AMNH 37613	female	32	8.11	-77.74
Pecari tajacu	FMNH 69638	female	33	8.10	-77.22
Pecari tajacu	FMNH 69639	female	33	8.10	-77.22
Pecari tajacu	FMNH 69641	male	33	8.10	-77.22
Pecari tajacu	FMNH 69642	female	33	8.10	-77.22
Pecari tajacu	FMNH 69643	male	33	8.10	-77.22
Pecari tajacu	FMNH 69644	male	33	8.10	-77.22
Pecari tajacu	FMNH 68803	female	34	7.85	-76.28
Pecari tajacu	FMNH 68802	male	34	7.85	-76.28
Pecari tajacu	AMNH 37789	male	35	7.12	-75.46
Pecari tajacu	AMNH 80300	undetermined	36	6.80	-58.16
Pecari tajacu	AMNH 41937	undetermined	37	6.40	-58.63
Pecari tajacu	AMNH 48145	undetermined	38	6.38	-58.68
Pecari tajacu	AMNH 48223	undetermined	38	6.38	-58.68
Pecari tajacu	AMNH 130458	male	39	5.90	-62.54
Pecari tajacu	FMNH 90032	female	40	5.05	-76.95
Pecari tajacu	FMNH 95802	female	41	3.75	-56.50
Pecari tajacu	FMNH 86744	male	42	3.73	-76.95
Pecari tajacu	AMNH 76903	female	43	3.54	-65.68
Pecari tajacu	FMNH 95534	male	44	3.35	-55.45
Pecari tajacu	FMNH 95800	male	44	3.35	-55.45
Pecari tajacu	FMNH 95801	male	44	3.35	-55.45
Pecari tajacu	FMNH 87876	female	45	3.28	-73.88
Pecari tajacu	FMNH 90028	male	46	2.87	-77.68
Pecari tajacu	AMNH 95822	female	47	2.85	-60.71
Pecari tajacu	AMNH 95823	female	47	2.85	-60.71
Pecari tajacu	FMNH 87874	female	48	2.75	-73.92
Pecari tajacu	FMNH 87875	male	48	2.75	-73.92
Pecari tajacu	FMNH 20024	undetermined	49	2.25	-60.75
Pecari tajacu	MPEG 6472	undetermined	50	2.22	-55.96
Pecari tajacu	MPEG 28688	undetermined	51	1.29	-50.95
Pecari tajacu	MPEG 1304	male	52	1.00	-50.96
Pecari tajacu	MPEG 1305	male	52	1.00	-50.96
Pecari tajacu	MPEG 1973	female	52	1.00	-50.96

Pecari tajacu	MPEG 1306	male	52	1.00	-50.96
Pecari tajacu	MPEG 6474	male	53	0.89	-50.60
Pecari tajacu	MN 1724	male	54	0.81	-66.03
Pecari tajacu	MN 1725	female	54	0.81	-66.03
Pecari tajacu	FMNH 70565	male	55	0.47	-75.33
Pecari tajacu	FMNH 72412	undetermined	55	0.47	-75.33
Pecari tajacu	MN 50295	undetermined	56	0.38	-63.59
Pecari tajacu	MPEG 21801	undetermined	57	0.12	-52.62
Pecari tajacu	AMNH 66749	male	58	0.07	-80.03
Pecari tajacu	MPEG 2156	undetermined	59	0.03	-51.41
Pecari tajacu	MPEG 2157	undetermined	59	0.03	-51.41
Pecari tajacu	MPEG 2158	undetermined	59	0.03	-51.41
Pecari tajacu	MPEG 2159	undetermined	59	0.03	-51.41
Pecari tajacu	MPEG 1515	female	1	-0.10	-51.29
Pecari tajacu	MPEG 1618	undetermined	1	-0.10	-51.29
Pecari tajacu	MPEG 1663	undetermined	1	-0.10	-51.29
Pecari tajacu	AMNH 79523	female	2	-0.20	-66.81
Pecari tajacu	AMNH 64001	female	3	-0.49	-77.29
Pecari tajacu	FMNH 125121	undetermined	4	-0.63	-75.27
Pecari tajacu	MN 69374	male	5	-0.97	-62.93
Pecari tajacu	MPEG 769	female	6	-1.34	-48.22
Pecari tajacu	MPEG 2689	female	6	-1.34	-48.22
Pecari tajacu	MPEG 1109	female	6	-1.34	-48.22
Pecari tajacu	MPEG 1258	male	7	-1.37	-56.08
Pecari tajacu	MPEG 1259	female	7	-1.37	-56.08
Pecari tajacu	MPEG 1260	male	7	-1.37	-56.08
Pecari tajacu	AMNH 67723	male	8	-1.51	-77.95
Pecari tajacu	AMNH 67722	female	8	-1.51	-77.95
Pecari tajacu	AMNH 95828	male	9	-1.62	-51.99
Pecari tajacu	AMNH 96142	female	10	-2.07	-52.27
Pecari tajacu	AMNH 93100	male	11	-2.64	-56.76
Pecari tajacu	MZUSP 5339	female	12	-2.65	-55.72
Pecari tajacu	MN 6019	male	13	-2.77	-54.94
Pecari tajacu	FMNH 50889	male	14	-2.83	-55.13
Pecari tajacu	FMNH 51087	female	14	-2.83	-55.13
Pecari tajacu	MZUSP 17551	male	15	-2.89	-64.85
Pecari tajacu	MN 6008	female	16	-2.91	-58.54
Pecari tajacu	MN 6009	female	16	-2.91	-58.54
Pecari tajacu	MN 6011	female	16	-2.91	-58.54
Pecari tajacu	MN 6025	male	16	-2.91	-58.54
Pecari tajacu	FMNH 51088	female	17	-2.92	-58.42
Pecari tajacu	MPEG 4497	male	18	-2.94	-54.45
Pecari tajacu	MPEG 30681	undetermined	19	-2.99	-47.27
Pecari tajacu	MPEG 30682	undetermined	19	-2.99	-47.27

Pecari tajacu	MPEG 7111	male	20	-3.09	-59.97
Pecari tajacu	MN 1734	female	20	-3.09	-56.63
Pecari tajacu	MN 6010	female	21	-3.28	-58.29
Pecari tajacu	MN 6026	male	21	-3.28	-58.29
Pecari tajacu	MPEG 41069	undetermined	22	-3.46	-56.31
Pecari tajacu	FMNH 89175	male	24	-4.00	-77.33
Pecari tajacu	MPEG 11889	undetermined	25	-4.27	-49.58
Pecari tajacu	MPEG 11895	undetermined	25	-4.27	-49.58
Pecari tajacu	MZUSP 20019	undetermined	26	-4.27	-55.99
Pecari tajacu	MPEG 26285	undetermined	27	-4.32	-49.78
Pecari tajacu	AMNH 91721	female	28	-4.39	-59.58
Pecari tajacu	FMNH 88799	female	29	-4.45	-71.78
Pecari tajacu	FMNH 88800	female	29	-4.45	-71.78
Pecari tajacu	FMNH 88802	female	29	-4.45	-71.78
Pecari tajacu	FMNH 89176	male	29	-4.45	-71.78
Pecari tajacu	FMNH 89177	male	29	-4.45	-71.78
Pecari tajacu	FMNH 88803	male	29	-4.45	-71.78
Pecari tajacu	MZUSP 20022	undetermined	30	-4.78	-56.56
Pecari tajacu	FMNH 86897	female	31	-4.83	-74.22
Pecari tajacu	MN 37080	female	32	-5.63	-63.96
Pecari tajacu	AMNH 92843	male	33	-5.89	-61.43
Pecari tajacu	MZUSP 8942	male	34	-6.92	-35.17
Pecari tajacu	MHNCI 4046	undetermined	35	-7.13	-45.33
Pecari tajacu	MZUSP 5336	female	36	-7.32	-70.34
Pecari tajacu	MZUSP 5341	male	36	-7.32	-70.34
Pecari tajacu	MZUSP 5337	male	36	-7.32	-70.34
Pecari tajacu	MPEG 839	male	37	-7.61	-72.63
Pecari tajacu	MPEG 1006	male	38	-7.68	-51.19
Pecari tajacu	MN semnum2	undetermined	39	-8.70	-55.72
Pecari tajacu	MZUSP 5340	female	40	-8.89	-54.89
Pecari tajacu	MN 63492	undetermined	41	-9.01	-42.70
Pecari tajacu	MN 63494	undetermined	41	-9.01	-42.70
Pecari tajacu	MN 63523	female	41	-9.01	-42.70
Pecari tajacu	FMNH 34298	undetermined	42	-9.48	-75.92
Pecari tajacu	FMNH 34305	male	43	-9.87	-74.92
Pecari tajacu	AMNH 215157	male	44	-13.50	-64.91
Pecari tajacu	AMNH 215154	male	44	-13.50	-64.91
Pecari tajacu	FMNH 79926	female	45	-14.00	-69.00
Pecari tajacu	FMNH 79929	female	45	-14.00	-69.00
Pecari tajacu	MPEG 17138	male	46	-14.22	-50.92
Pecari tajacu	MN 37094	female	47	-14.56	-52.45
Pecari tajacu	MZUSP 7016	female	48	-15.31	-53.79
Pecari tajacu	MZUSP 7014	male	48	-15.31	-53.79
Pecari tajacu	MZUSP 7012	male	48	-15.31	-53.79

Pecari tajacu	MZUSP 7013	female	48	-15.31	-53.79
Pecari tajacu	MZUSP 7015	undetermined	48	-15.31	-53.79
Pecari tajacu	MPEG 1330	undetermined	49	-15.38	-52.21
Pecari tajacu	MN 1730	undetermined	50	-15.40	-58.82
Pecari tajacu	AMNH 324	undetermined	51	-15.46	-55.77
Pecari tajacu	AMNH 323	undetermined	51	-15.46	-55.77
Pecari tajacu	MN 66675	undetermined	52	-15.46	-58.35
Pecari tajacu	FMNH 21384	male	53	-16.00	-64.42
Pecari tajacu	MN 64807	undetermined	54	-16.21	-55.95
Pecari tajacu	MN 64168	undetermined	54	-16.21	-55.95
Pecari tajacu	MN 71062	undetermined	54	-16.21	-55.95
Pecari tajacu	MN 71070	undetermined	54	-16.21	-55.95
Pecari tajacu	MN 42890	undetermined	55	-16.29	-56.64
Pecari tajacu	MN 42892	undetermined	55	-16.29	-56.64
Pecari tajacu	MN 42894	undetermined	55	-16.29	-56.64
Pecari tajacu	FMNH 28314	male	56	-16.75	-57.70
Pecari tajacu	FMNH 28315	male	56	-16.75	-57.70
Pecari tajacu	FMNH 28316	male	56	-16.75	-57.70
Pecari tajacu	FMNH 28317	female	56	-16.75	-57.70
Pecari tajacu	FMNH 34332	male	57	-17.46	-63.67
Pecari tajacu	AMNH 61796	male	57	-17.46	-63.67
Pecari tajacu	MACN 50130	male	58	-17.47	-63.72
Pecari tajacu	AMNH 214749	undetermined	59	-17.51	-63.77
Pecari tajacu	AMNH 263363	undetermined	60	-17.78	-63.22
Pecari tajacu	MN 42889	female	61	-18.28	-55.43
Pecari tajacu	MZUSP 3341	undetermined	62	-19.01	-57.65
Pecari tajacu	MZUSP 3001	female	63	-20.34	-47.79
Pecari tajacu	MZUSP 3000	male	63	-20.34	-47.79
Pecari tajacu	MZUSP 3002	male	63	-20.34	-47.79
Pecari tajacu	MZUSP 32338	undetermined	64	-21.28	-47.30
Pecari tajacu	MZUSP 3759	female	65	-21.50	-50.33
Pecari tajacu	FMNH 52330	male	66	-21.67	-49.75
Pecari tajacu	MZUSP 9013	female	67	-21.99	-48.39
Pecari tajacu	MACN 4520	female	68	-22.29	-57.94
Pecari tajacu	MACN 4527	undetermined	68	-22.29	-57.94
Pecari tajacu	MZUSP 498	male	69	-22.35	-49.02
Pecari tajacu	MZUSP 10347	female	70	-22.55	-47.90
Pecari tajacu	MZUSP 8880	male	70	-22.55	-47.90
Pecari tajacu	MZUSP 8468	male	70	-22.55	-47.90
Pecari tajacu	MZUSP 10344	male	70	-22.55	-47.90
Pecari tajacu	MZUSP 10345	male	70	-22.55	-47.90
Pecari tajacu	MN 47507	undetermined	71	-22.58	-42.28
Pecari tajacu	MN 37016	undetermined	71	-22.58	-42.28
Pecari tajacu	MN semnum1	undetermined	72	-22.60	-43.44

Pecari tajacu	MN 37071	undetermined	73	-22.61	-42.75
Pecari tajacu	MN 37083	male	74	-22.65	-43.03
Pecari tajacu	MLP 4.IV.00.3	undetermined	75	-22.85	-64.33
Pecari tajacu	MN 5646	female	76	-23.20	-44.76
Pecari tajacu	MN 8453	female	76	-23.20	-44.76
Pecari tajacu	MACN 36.709	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.708	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.722	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.697	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.707	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.716	undetermined	77	-23.25	-63.35
Pecari tajacu	MACN 36.693	undetermined	78	-23.28	-63.28
Pecari tajacu	MACN 36.690	undetermined	78	-23.28	-63.28
Pecari tajacu	MACN 47407	male	79	-23.56	-64.43
Pecari tajacu	FMNH 26647	undetermined	80	-23.70	-57.20
Pecari tajacu	MACN 25791	undetermined	81	-24.71	-64.54
Pecari tajacu	FMNH 26646	female	82	-24.73	-57.08
Pecari tajacu	MACN 30397	male	83	-25.24	-64.56
Pecari tajacu	MLP 27.VII.46.1	male	84	-25.24	-64.79
Pecari tajacu	MHNCI 6170	undetermined	85	-25.30	-48.30
Pecari tajacu	MHNCI 6168	female	86	-25.45	-52.87
Pecari tajacu	MHNCI 6175	female	86	-25.45	-52.87
Pecari tajacu	MHNCI 3534	undetermined	86	-25.45	-52.87
Pecari tajacu	MHNCI 3535	undetermined	86	-25.45	-52.87
Pecari tajacu	MLP 18.XII.02.3	undetermined	87	-25.47	-61.91
Pecari tajacu	MLP 18.XII.02.6	undetermined	87	-25.47	-61.91
Pecari tajacu	MLP 18.XII.02.7	undetermined	87	-25.47	-61.91
Pecari tajacu	MLP 18.XII.02.11	undetermined	87	-25.47	-61.91
Pecari tajacu	MLP 18.XII.02.16	undetermined	87	-25.47	-61.91
Pecari tajacu	MHNCI 0345	undetermined	88	-25.49	-53.92
Pecari tajacu	MACN 24926	undetermined	89	-25.60	-60.27
Pecari tajacu	MHNCI 4117	undetermined	90	-25.62	-48.51
Pecari tajacu	MHNCI 4049	undetermined	91	-25.69	-51.61
Pecari tajacu	MACN 25793	undetermined	92	-25.78	-54.13
Pecari tajacu	MLP 5.IV.02.7	undetermined	93	-25.83	-61.73
Pecari tajacu	MACN 49319	female	94	-25.93	-54.62
Pecari tajacu	MZUSP 1686	male	95	-26.32	-48.96
Pecari tajacu	MACN 3013	undetermined	96	-26.54	-59.40
Pecari tajacu	UFSC 2593	undetermined	97	-27.20	-53.92
Pecari tajacu	UFSC 874	undetermined	98	-28.81	-49.64
Pecari tajacu	MACN 20811	undetermined	99	-32.13	-65.57
Tayassu pecari	AMNH 149363	undetermined	1	17.57	-90.59
Tayassu pecari	FMNH 22401	undetermined	2	16.24	-88.87
Tayassu pecari	FMNH 121193	undetermined	3	17.37	-88.93

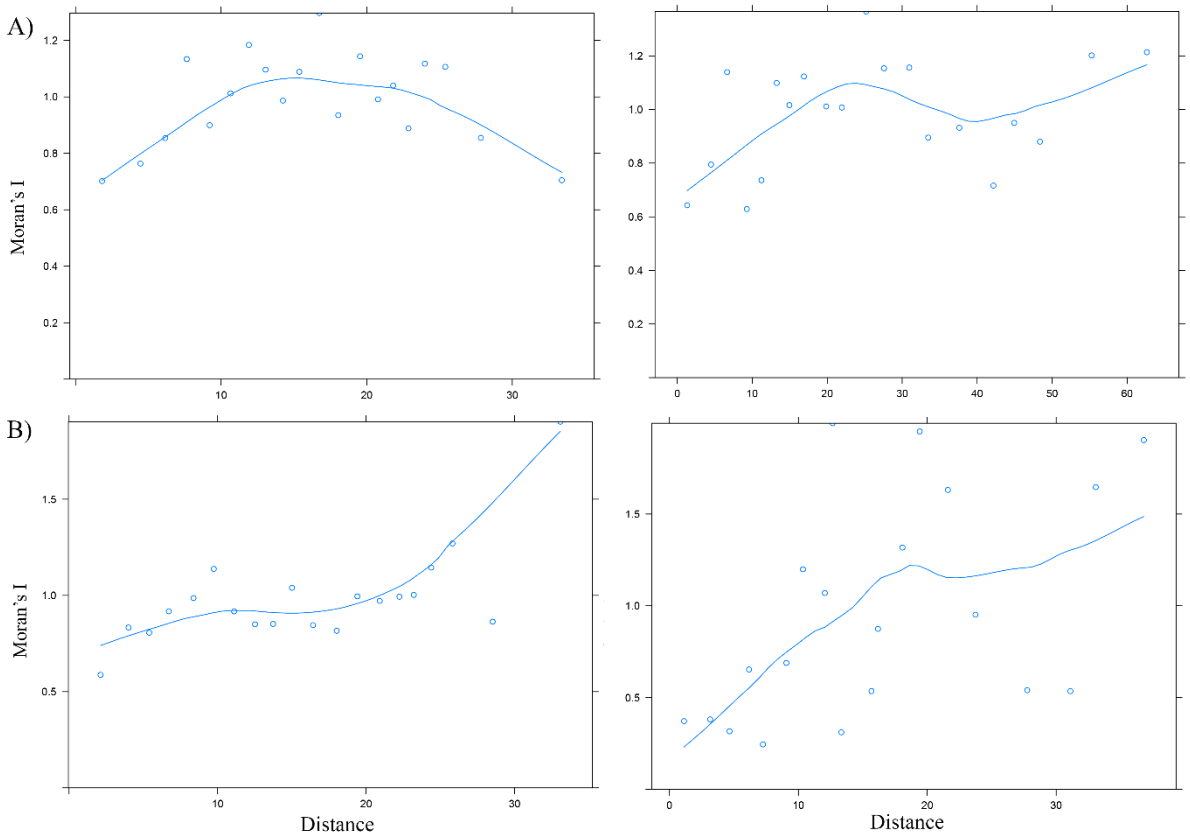
Tayassu pecari	AMNH 207423	undetermined	4	17.04	-93.92
Tayassu pecari	FMNH 15971	female	5	15.73	-88.94
Tayassu pecari	FMNH 15972	female	5	15.73	-88.94
Tayassu pecari	FMNH 15973	female	5	15.73	-88.94
Tayassu pecari	FMNH 15974	male	5	15.73	-88.94
Tayassu pecari	FMNH 13167	undetermined	6	11.30	-73.90
Tayassu pecari	AMNH 15464	female	7	11.28	-73.98
Tayassu pecari	AMNH 32675	female	8	11.10	-74.08
Tayassu pecari	AMNH 32673	male	8	11.10	-74.08
Tayassu pecari	AMNH 32674	female	8	11.10	-74.08
Tayassu pecari	FMNH 18286	male	9	10.00	-83.03
Tayassu pecari	FMNH 21924	female	10	10.00	-73.00
Tayassu pecari	FMNH 36102	undetermined	11	8.58	-62.12
Tayassu pecari	FMNH 92368	male	12	6.97	-72.00
Tayassu pecari	FMNH 92369	male	12	6.97	-72.00
Tayassu pecari	AMNH M-64097	male	13	6.38	-58.68
Tayassu pecari	AMNH M-42876	undetermined	13	6.38	-58.68
Tayassu pecari	AMNH M-64098	male	13	6.38	-58.68
Tayassu pecari	AMNH M-42410	male	13	6.38	-58.68
Tayassu pecari	FMNH 92370	female	14	6.21	-68.97
Tayassu pecari	AMNH M-130451	male	15	5.90	-62.54
Tayassu pecari	AMNH M-130455	male	15	5.90	-62.54
Tayassu pecari	AMNH M-130456	female	15	5.90	-62.54
Tayassu pecari	AMNH M-130457	female	15	5.90	-62.54
Tayassu pecari	FMNH 95536	female	16	3.75	-56.50
Tayassu pecari	FMNH 95803	male	16	3.75	-56.50
Tayassu pecari	MZUSP 21607	undetermined	17	3.64	-61.44
Tayassu pecari	AMNH M-96134	female	18	2.85	-60.71
Tayassu pecari	AMNH M-96132	male	18	2.85	-60.71
Tayassu pecari	AMNH M-96140	female	18	2.85	-60.71
Tayassu pecari	FMNH 87878	male	19	2.75	-73.92
Tayassu pecari	FMNH 87879	female	19	2.75	-73.92
Tayassu pecari	FMNH 20025	undetermined	20	2.25	-60.75
Tayassu pecari	MN 70692	undetermined	21	1.47	-61.00
Tayassu pecari	MN 70693	undetermined	21	1.47	-61.00
Tayassu pecari	MPEG 34150	undetermined	22	1.29	-50.95
Tayassu pecari	AMNH M-78553	female	23	0.10	-67.55
Tayassu pecari	AMNH M-66750	male	24	0.03	-79.98
Tayassu pecari	AMNH 78551	male	1	-0.36	-66.53
Tayassu pecari	MN 32709	female	2	-0.55	-50.13
Tayassu pecari	FMNH 125120	undetermined	3	-0.57	-75.48
Tayassu pecari	MZUSP 20024	undetermined	4	-1.19	-56.94
Tayassu pecari	AMNH 94172	female	5	-1.23	-57.74
Tayassu pecari	MZUSP 20015	female	6	-1.41	-61.98

Tayassu pecari	AMNH 96151	male	7	-1.62	-51.99
Tayassu pecari	AMNH 96154	male	7	-1.62	-51.99
Tayassu pecari	AMNH 67731	undetermined	8	-1.73	-77.48
Tayassu pecari	MPEG 11892	undetermined	9	-1.89	-49.39
Tayassu pecari	MZUSP 13491	female	9	-1.89	-49.39
Tayassu pecari	MZUSP 13487	undetermined	9	-1.89	-49.39
Tayassu pecari	MZUSP 13489	undetermined	9	-1.89	-49.39
Tayassu pecari	MPEG 8070	male	10	-2.45	-54.73
Tayassu pecari	MZUSP 20023	undetermined	11	-2.50	-55.15
Tayassu pecari	MZUSP 5437	male	12	-2.77	-54.94
Tayassu pecari	MZUSP 5599	male	12	-2.77	-54.94
Tayassu pecari	MZUSP 5597	male	12	-2.77	-54.94
Tayassu pecari	FMNH 51086	undetermined	13	-2.92	-58.55
Tayassu pecari	MPEG 4568	male	14	-2.94	-54.45
Tayassu pecari	MPEG 8831	male	14	-2.94	-54.45
Tayassu pecari	MPEG 8805	female	14	-2.94	-54.45
Tayassu pecari	MZUSP 5596	female	15	-3.15	-60.50
Tayassu pecari	MZUSP 5593	male	15	-3.15	-60.50
Tayassu pecari	MN 6018	male	16	-3.28	-58.29
Tayassu pecari	MN 6028	female	16	-3.28	-58.29
Tayassu pecari	MPEG 41056	undetermined	17	-3.46	-56.31
Tayassu pecari	MN 1723	female	18	-3.50	-60.69
Tayassu pecari	MN 1726	male	18	-3.50	-60.69
Tayassu pecari	MZUSP 21607	undetermined	19	-3.66	-61.43
Tayassu pecari	MN 37013	female	20	-3.72	-61.44
Tayassu pecari	AMNH 93727	female	21	-4.03	-66.25
Tayassu pecari	AMNH 93728	female	21	-4.03	-66.25
Tayassu pecari	MZUSP 20028	undetermined	22	-4.12	-63.42
Tayassu pecari	FMNH 123027	undetermined	23	-4.28	-74.32
Tayassu pecari	MPEG 26226	undetermined	24	-4.32	-49.78
Tayassu pecari	MPEG 26270	undetermined	24	-4.32	-49.78
Tayassu pecari	MPEG 26219	undetermined	24	-4.32	-49.78
Tayassu pecari	FMNH 88795	female	25	-4.45	-71.78
Tayassu pecari	FMNH 88796	female	25	-4.45	-71.78
Tayassu pecari	FMNH 88797	male	25	-4.45	-71.78
Tayassu pecari	FMNH 88798	male	25	-4.45	-71.78
Tayassu pecari	MZUSP 20016	undetermined	26	-4.46	-56.37
Tayassu pecari	FMNH 19549	female	27	-6.18	-77.22
Tayassu pecari	MHNCI 6171	undetermined	28	-7.09	-55.89
Tayassu pecari	MZUSP 25240	male	29	-7.33	-70.34
Tayassu pecari	FMNH 62081	male	30	-8.30	-74.60
Tayassu pecari	MZUSP 8087	female	31	-9.36	-54.92
Tayassu pecari	FMNH 34300	undetermined	32	-10.07	-75.53
Tayassu pecari	MACN 2557	undetermined	33	-10.36	-65.43

Tayassu pecari	MZUSP 20027	undetermined	34	-11.94	-53.41
Tayassu pecari	AMNH 209143	undetermined	35	-12.53	-64.37
Tayassu pecari	AMNH 247728	undetermined	36	-12.93	-67.76
Tayassu pecari	FMNH 52498	female	37	-13.52	-69.68
Tayassu pecari	FMNH 79930	male	38	-13.68	-69.16
Tayassu pecari	FMNH 79927	male	39	-14.00	-69.00
Tayassu pecari	FMNH 79928	female	39	-14.00	-69.00
Tayassu pecari	MN 71151	undetermined	40	-14.82	-57.93
Tayassu pecari	AMNH 36656	female	41	-15.70	-57.70
Tayassu pecari	MN 64004	undetermined	42	-16.21	-55.95
Tayassu pecari	MN 64662	undetermined	42	-16.21	-55.95
Tayassu pecari	MN 42898	undetermined	43	-16.29	-56.64
Tayassu pecari	MN 42901	undetermined	43	-16.29	-56.64
Tayassu pecari	MN 42902	undetermined	43	-16.29	-56.64
Tayassu pecari	MN 42904	undetermined	43	-16.29	-56.64
Tayassu pecari	UFSC 359	undetermined	44	-16.34	-46.94
Tayassu pecari	MN 67146	undetermined	45	-17.56	-52.59
Tayassu pecari	MN 68182	undetermined	45	-17.56	-52.59
Tayassu pecari	AMNH 260332	undetermined	46	-17.75	-60.77
Tayassu pecari	MN 67149	male	47	-17.93	-53.02
Tayassu pecari	MN 67150	male	47	-17.93	-53.02
Tayassu pecari	MN 67158	male	47	-17.93	-53.02
Tayassu pecari	MN 67152	undetermined	48	-18.00	-52.78
Tayassu pecari	MN 67147	undetermined	48	-18.00	-52.78
Tayassu pecari	MN 67165	male	48	-18.00	-52.78
Tayassu pecari	MN 67140	female	48	-18.00	-52.78
Tayassu pecari	MN 67170	female	48	-18.00	-52.78
Tayassu pecari	MN 67171	female	49	-18.03	-48.70
Tayassu pecari	MN 1608	undetermined	50	-19.27	-44.40
Tayassu pecari	MN 1609	undetermined	50	-19.27	-44.40
Tayassu pecari	MZUSP 2998	female	51	-20.34	-47.79
Tayassu pecari	MN 3827	male	52	-21.23	-57.13
Tayassu pecari	FMNH 52331	male	53	-21.67	-49.75
Tayassu pecari	FMNH 145320	undetermined	54	-22.30	-59.02
Tayassu pecari	MZUSP 497	female	55	-22.35	-49.02
Tayassu pecari	MZUSP 10350	male	56	-22.55	-47.90
Tayassu pecari	MZUSP 8881	male	56	-22.55	-47.90
Tayassu pecari	MZUSP 8882	male	56	-22.55	-47.90
Tayassu pecari	MZUSP 10346	male	56	-22.55	-47.90
Tayassu pecari	MZUSP 8029	female	56	-22.55	-47.90
Tayassu pecari	MN 8455	female	57	-23.20	-44.76
Tayassu pecari	MN 8456	female	57	-23.20	-44.76
Tayassu pecari	MN 8462	female	57	-23.20	-44.76
Tayassu pecari	MN 8463	male	57	-23.20	-44.76

Tayassu pecari	MN 37018	male	57	-23.20	-44.76
Tayassu pecari	MN 37019	male	57	-23.20	-44.76
Tayassu pecari	MHNCI 0092	male	58	-23.59	-50.73
Tayassu pecari	MHNCI 0135	male	58	-23.59	-50.73
Tayassu pecari	MHNCI 0136	female	58	-23.59	-50.73
Tayassu pecari	MZUSP 9597	male	59	-23.74	-45.90
Tayassu pecari	MZUSP 9639	female	59	-23.74	-45.90
Tayassu pecari	MLP 1925	undetermined	60	-23.76	-64.85
Tayassu pecari	AMNH 61537	female	61	-23.94	-46.33
Tayassu pecari	AMNH 61538	female	61	-23.94	-46.33
Tayassu pecari	MHNCI 4116	male	62	-24.30	-50.57
Tayassu pecari	UFSC 968	undetermined	63	-24.34	-50.56
Tayassu pecari	MZUSP 20025	undetermined	64	-24.49	-48.71
Tayassu pecari	MNHCI 3525	male	65	-25.45	-52.87
Tayassu pecari	MNHCI 3527	undetermined	65	-25.45	-52.87
Tayassu pecari	MNHCI 3528	undetermined	65	-25.45	-52.87
Tayassu pecari	MHNCI 4154	female	65	-25.45	-52.87
Tayassu pecari	MHNCI 4140	female	65	-25.45	-52.87
Tayassu pecari	MNHCI 3788	undetermined	66	-25.49	-53.92
Tayassu pecari	MNHCI 3789	undetermined	66	-25.49	-53.92
Tayassu pecari	MNHCI 3790	undetermined	66	-25.49	-53.92
Tayassu pecari	MNHCI 3791	undetermined	66	-25.49	-53.92
Tayassu pecari	MACN 49.340	undetermined	67	-25.93	-54.62
Tayassu pecari	MACN 49.342	undetermined	67	-25.93	-54.62
Tayassu pecari	MACN 25.790	undetermined	68	-26.11	-54.11
Tayassu pecari	UFSC 326	undetermined	69	-26.30	-49.02
Tayassu pecari	UFSC 327	undetermined	69	-26.30	-49.02
Tayassu pecari	MACN 48350	male	70	-26.36	-54.65
Tayassu pecari	UFSC 403	undetermined	71	-26.93	-48.96
Tayassu pecari	UFSC 405	undetermined	72	-27.17	-49.53
Tayassu pecari	UFSC 4768	undetermined	73	-27.90	-50.79
Tayassu pecari	MACN 3.55	undetermined	74	-30.80	-60.02
Tayassu pecari	MZUSP 108	undetermined	75	-31.36	-52.01
Tayassu pecari	MZUSP 107	undetermined	75	-31.36	-52.01

Appendix S2. Moran's semivariogram for skull size of (A) *Pecari tajacu* and (B) *Tayassu pecari* in Southern (left) and Northern (right) hemispheres



CAPITULO 3: SKULL SHAPE AND THE DEMANDS OF MASTICATION: A BIOMECHANICAL STUDY OF PECCARIES (MAMMALIA, ARTIODACTYLA)

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Skull shape and the demands of mastication: a biomechanical study of peccaries (Mammalia, Artiodactyla)

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Running heading: Biomechanics of skull in peccaries

Selection favors feeding morphologies that more effectively perform fitness-related functions. A primary requirement of the mammalian skull is to exert forces on different foods and to resist the forces imposed on it during mastication. Not surprising, their skull shape patterns of mammals are well known, but the biomechanical relevance of this variation is still limited for some groups. Combining geometric morphometrics and biomechanical analyses, we test the hypothesis that skull shape reflects biomechanical attributes to generate and dissipate powerful forces in peccaries, which presumably evolved towards tough diets. We obtained the skull shape and centroid 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 bite forces, greater resistance to bending loads, and lower stress emerging from the shorter and deeper mandibular corpora and wider muscle insertion areas of both *Pecari tajacu* and *Tayassu pecari* relative to *Parachoerus wagneri*. The shape traits shared by *P. tajacu* and *T. pecari* enable them to apply stronger forces and resist stress and fractures from higher biomechanical demands than *P. wagneri*. Our results support the hypothesis that shape closely reflects the biomechanical performance of species.

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

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Introduction

The ability to acquire and process foods is essential for animal survival and reproduction. It is reasonable, therefore, to presume that selection acts on feeding system morphology to maintain or improve feeding performance because those variations in performance have direct fitness consequences (Schwenk 2000; Ross and Iriarte-Diaz 2014). The cranium and mandible are complexly shaped elements of the vertebrate phenotype that are intimately associated with feeding ability and obvious products of adaptive evolution (Herring 1993). By combining shape and biomechanics analyses, we can improve our understanding about how the form and function (i.e. performance) of these phenotypes varies between the species, and the selective regimes that shaped them (Pérez-Barberia and Gordon 1999; Raia et al. 2010; Piras et al. 2013).

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). The secondary palate, the dentary-squamosal jaw articulation, and the occlusion between lower and upper molars are exclusive features associated with mammalian mastication (Kemp 2005). A primary requirement of the mammalian skull is, however, to exert forces on different foods and to resist the forces imposed on it during mastication (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 (i.e., 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; Ross and Iriarte-Diaz 2014). Recent advances in

geometric morphometric methods (GM) are opening unprecedented possibilities for investigating shape (Klingenberg 2010; Adams et al. 2013). Mammals, in particular, have been extensively studied and clearly exhibit various shape variation patterns (Raia et al. 2010; Caceres et al. 2013; Meloro et al. 2015; Hendges et al. 2016). Understanding the mechanical implications of this variation is growing, and analyses integrating shape and biomechanics have proven to be a powerful tool for understanding the form and function relationships in mammals. Correlations between cranial shape and performance variables such as bite force are demonstrating that stronger bites are generally associated with a shorter rostrum and mandible, wider skull, and more developed muscle attachment areas, whereas elongation in these traits optimizes speed (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 generally vary within and between species (Taylor 2006; Tanner et al. 2010; Timm-Davis et al. 2015), including fossils (Cassini *and* Vizcaíno 2012; Piras et al. 2013; Smith et al. 2015) as a function of shape. Among primates, for instance, deeper mandibular corpora are often seen as an adaptation to counter bending loads during leaf or fruit mastication (Hylander 1979, 1988; Taylor, 2006). Demands for feeding indeed seem 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 phylogeny (Piras et al. 2013; Pérez-Barberia and Gordon 1999) and ontogeny (Tanner et al. 2010). The continuing integration of these two methods can expand our understanding also for other groups of mammals besides primates and carnivorans, which are focus of most of these studies.

It is generally agreed that the cranial morphology of peccaries (Artiodactyla: Tayassuidae) has evolved in response to tough/hard diets (Herring 1972; Kiltie 1981; Pérez-Barberia and Gordon 1999). Currently, only three species represent the family´s diversity:

Pecari tajacu (Linnaeus 1758) (collared peccary), *Tayassu pecari* (Link, 1795) (white-lipped peccary), and *Parachoerus wagneri* (Rusconi, 1930) (Chacoan peccary) (Gasparini 2013; Parisi Dutra et al. 2017). *Pecari tajacu* is found from southern United States to Argentina, whereas *T. pecari* occurs from southern Mexico to northern Argentina (Altrichter et al. 2012; Gasparini 2013). The diet of these species consists in large part of plant material (i.e. fruits, seeds, roots, nuts, grass) and occasionally small animals (Fragoso 1999, Keuroghlian and Eaton 2008b, Desbiez *et al*. 2009). In the Neotropical Region, where they widely coexist, fruits and seeds from palm species are dominant in 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 mainly composed by cactus, but it also feeds on roots, flowers, and fruits (Taber et al. 1994; Gasparini et al. 2013). Most of these foods require powerful forces during mastication, which makes peccaries especially interesting mammals to study if shape variation reflects their biomechanical attributes.

The cranial morphology of extant peccaries, represented by bunodont cheek teeth, interlocking canines, well developed pre- and post-glenoid processes, and an essentially orthal chewing stroke, is well suited for shattering hard foods in a crushing style of mastication (Herring 1972; Herring 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). This could imply an unusual functional profiles in this taxon (Herring 1985). Peccaries clearly exhibit differences in cranial morphology and in bite forces, and this is often linked to their feeding habits (Kiltie 1981, 1982, 1985; Gasparini 2013; Sicuro and Oliveria 2002; Hendges et al. 2016). However, the functional relevance of this variation in terms of feeding performance is still unknown.

In this study, we used geometric morphometric techniques and biomechanics to determine how the skull shape of peccaries translates into biomechanical attributes to generate and dissipate powerful forces during mastication (Hylander 1979, 1988; Ross and Iriarte-Diaz 2014). The largest bite forces should arise from the shorter crania and mandibles with better developed muscle insertion areas (Tanner et al. 2010; Nogueira et al. 2009; Maestri et al. 2016). Additionally, high resistance to bending loads could be the result of deeper mandibular corpora (Hylander 1979, 1988; Taylor 2006). *Pecari tajacu* and *T. pecari* share morphological traits that reflect shortening of the rostrum and enlarged braincase relative to the *P. wagneri* (Wetzel 1977; Gasparini 2013). These two peccaries rely on crushing mastication, whereas grinding mechanisms reliant on decreased forces are apparent for *P. wagneri* (Herring 1985). Stronger bites are also demonstrated for *T. pecari* compared to *P. tajacu* (Kiltie 1982; Sicuro and Oliveira 2002). On these bases, *P. tajacu* and *T. pecari* should possess a skull shape adapted to highest biomechanical performance (force and resistance), whereas more relaxed attributes are expected for *P. wagneri*.

Materials and Methods

Morphological data acquisition

We collected data from 213 crania and mandibles of *Pecari tajacu* (n = 136), *Tayassu pecari* (n = 69) *and Parachoerus wagneri* (n = 8). The taxonomy used here follows the classification proposed by Parisi Dutra et al. (2017). The ventral view of the cranium and lateral view of the mandible of the specimens were photographed at the same distance using a Nikon Coolpix P530 digital camera (distance = 1.56 m). For each specimen, we also took the following measurements on the mandible: condyle length, condyle width, symphysis length, corpus width

and corpus height (see Supplementary Data S1). Measurements were taken using Vernier calipers, with 0.01 mm precision.

All specimens studied are housed in the Recent mammal collections of the Field Museum of Natural History, Chicago, USA, and American Museum of Natural History, New York, USA (a list of specimens can be found in Supplementary Data S2). 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 thirty-three landmarks on the cranium views and 20 landmarks and 12 semilandmarks on the mandibular ones (Rohlf 2015; Fig. 1). 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 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 (see Fig. 1). On the mandible, we also extracted the centroid size for the area occupied by the masseter muscle (see Fig. 1).

We visualized the shape variation patterns between species through a Principal Component Analysis (PCA). Procrustes ANOVA analysis was used to test for differences in both shape and size between sex and species. Although geometric morphometric methods 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 centroid size using a Procrustes ANOVA. In morphometrics this function uses the sum-of-squared Procrustes distances to assess variation in y (Procrustes coordinates) modeled by continuous (e.g. centroid size) or categorical factors (e.g. sex, species) (see Goodall 1991). These geometric morphometric analyses were implemented using the R package geomorph (Adams and Otarola-Castillo 2013; R Core Team 2016).

Biomechanical analyses

By applying the formula $d = \sqrt{(x2 - x1)^2 + (y2 - y1)^2}$, we obtained the distance between landmarks located in specific regions of cranium and mandible to calculate three major sets of variables related to biomechanical performance: 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).

To estimate bite force, the jaw muscle torque was calculated as the sum of masseter torque (masseter centroid size multiplied by (*) in-lever distance from tip of the condylar process (L11) to junction between ramus and mandibular corpus, at M3 (L5), and temporalis torque (temporalis centroid size * in-lever distance from extremity of the post-glenoid process (L14) to curvature between the maxilla and the zygomatic arch (L10). Then bite force was estimated at several bite points by dividing the jaw muscle torque by the out-lever distances at incisor (L11 to L18), canine (L11 to L1), first premolar (L11 to L3), and first molar (L11 to L4). Dividing bite force at the first molar by the centroid size of each molar we obtained the bite stress at molars M1, M2 and M3.

Resistance to bending was estimated by dividing corpus height by mandible length (distance from L11 to L18), and stress under bending by dividing the torque at the incisors by

corpus height. Resistance to shear was calculated as corpus width * corpus height * π, and shear stress as bite force at M1 divided by corpus width * corpus height * π.

Condylar reaction force was calculated as jaw elevator torque at M1 divided by out-lever distance from rom tip of the condylar process (L11) to the anteriormost point of the first molar alveolus (L4).

By dividing the condyle reaction force by condylar area (= condyle length * condyle width), we obtained the condyle stress. Finally, relative symphysis length was calculated as symphysis length divided by mandible length.

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. 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 when we found significant variation. Some variables were log-transformed to meet the assumptions of parametric tests. All analyses were performed in the R environment (R Core Team 2016).

Results

Shape and size variation

There are no sex differences in the shapes of *T. pecari* (cranium: F = 0.72, d.f. = 1, 46; P = 0.70, mandible: F = 1.67, d.f. = 1, 46; P = 0.07) and *P. wagneri* (cranium: F = 1.09, d.f. = 1, 3; P = 0.36, mandible: F = 0.52, d.f. = 1, 3; P = 0.73). Slight sexual dimorphism exists in the shape of the skull of *P. tajacu* (cranium = F = 2.33, d.f. = 1, 94; P < 0.01, mandible = F = 2.10, d.f. = 1, 94; 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 (see

Supplementary Data S3). There are no significant differences between sexes in size of the cranium (F = 1.00, d.f. = 1, 147; P = 0.33) and mandible (F = 0.86, d.f. = 1, 147; P = 0.37) in the three species.

There are significant inter-specific differences in cranial shape (R^2 = 0.21, F = 28.31, P < 0.001). PC1 and PC2 separate the skull shapes of *P. tajacu* and *T. pecari* species, while *P. wagneri* shows overlap with both (Fig. 2). *Pecari tajacu*, with mostly negative scores on PC1, exhibits a shorter maxillary toothrow and a broader temporalis muscle area positioned more posteriorly in relation to the M3 than *Tayassu pecari*, which had more positive scores on PC1.

Mandible shape also shows significant variation between the three species (R^2 = 0.20, F = 26.50, P = 0.001), characterized by differences in mandibular corpus and masseter muscle area. PC1 primarily separates the mandible shape of *P. wagneri* from that of the other two peccaries. *P. wagneri*, with positive scores on PC1 (23.32%), has a more elongated and shallower mandibular corpus, with a markedly decreased masseter muscle area compared to the other two species, with negative scores on PC1. PC2 (16.10%) contrasts variation in the mandibular corpus of *P. tajacu* and *T. pecari*. With negative scores, *P. tajacu* exhibits a proportionally shorter and deeper mandibular corpus than *T. pecari*, with positive scores (Fig. 2).

Size of both cranium (*F* = 646.62, d.f = 2, 212; *P*< 0.001) and mandible (*F* = 843.15, d.f = 2, 212; *P*< 0.001) also differs between these species. *Parachoerus wagneri* has the largest crania and mandibles, while *P. tajacu* has the smallest. Size has 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).

Biomechanical performance

Estimates of absolute bite force differ between species: *T. pecari* has higher bite forces than *P. wagneri* and *P. tajacu* at the canine, PM1, and M1. Bite force at the incisor is larger in *T. pecari* than in *P. tajacu* but does not differ significantly from *P. wagneri* (Table 1). However, the ANOVA with size-corrected bite force clearly shows that the differences between *T. pecari* and *P. tajacu* are no longer apparent, instead indicating that these two peccaries have larger bite forces than *P. wagneri* (Table 1; Fig. 3). Bite stress at the molars also differs 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 1; Fig. 4).

Absolute resistance to bending is greater in the mandibular corpora of *T. pecari* and *P. tajacu* than in *P. wagneri* (Table 1). However, the size-corrected analysis reveals the strongest resistance to dorsoventral loads in the mandible of *P. tajacu* (Table 1; Fig. 5). *Parachoerus wagneri* presents greater absolute and size-corrected stress under bending than *P. tajacu* and *T. pecari* (Table 1; Fig. 5). Absolute and size-corrected resistance to shear is larger in the mandible of *T. pecari* than *P. wagneri* and *P. tajacu,* while highest shear stress occurs in the mandibular corpus of *P. tajacu* (Table 1; Fig. 5). The mandibular morphology of *T. pecari* is stronger than that of the other two peccaries.

Absolute and size-corrected condyle reaction force is larger in *P. tajacu* and *T. pecari* than in *P. wagneri* (Table 1; Fig. 6). The largest condyle stress, however, occurs in *P. tajacu* (Table 1; Fig. 6). *Tayassu pecari* and *P. tajacu* also showed larger relative symphysis length than *P. wagneri* (Table 1; Fig. 6).

Discussion

Our combined geometric morphometric and biomechanical approach provides meaningful insights on form and function relationships in peccaries. Our results reveal 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*. *P. tajacu* and *T. pecari* are capable of a high biomechanical performance characterized by the larger bite forces as well as greater resistance to loads in the mandibular corpus. These features suggest that *P. tajacu* and *T. pecari* jaws are biomechanically better suited to apply and resist larger bite forces than is *P. wagneri* (Hylander 1979, 1988; Ravosa 1991, 1992; Perez-Barberia and Gordon 1999; Ravosa et al. 2000; Taylor 2006).

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 corroborate 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*. Some mandibular shape features are shared by *P. tajacu* and *T. pecari* which are not shared with *P. wagneri*. *Pecari tajacu* and *T. pecari* have shorter and deeper mandibular corpora with a marked increase in the area of adductor musculature compared to the *P. wagneri* (Fig. 2). The shape traits of both *P. tajacu* and *T. pecari* are generally characteristic of forest mammals engaged in leaf or fruit mastication (Hylander 1979, 1988; Taylor 2006; Meloro et al. 2015). In turn, shape traits seen in *P. wagneri* are common features in browsing ungulates (Perez-Barberia and Gordon 1999; Mendoza et al. 2002; Raia et al. 2010), and even in extinct peccaries of genus *Platygonus* (Wetzel 1977; Gasparini 2013).

As we expected, the craniomandibular shape of peccaries seems to reflect their biomechanical performance (Hylander 1979, 1988; Ross and Iriarte-Diaz 2014). We found larger bite forces, greater resistance to ventral bending loads, and lower stress (except at molars)

emerging from the deeper and proportionally wider shape traits of both *P. tajacu* and *T. pecari*. In contrast, lower bite forces, higher stress, and lower resistance for dorsoventral and torsional loads are associated with the smaller muscle attachment areas and shallower and more elongate mandible of *P. wagneri* (see Hylander 1979, 1988; Ravosa 1991, 1992; Ravosa et al. 2000; Taylor 2006; Maestri et al. 2016). 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 fracture risk from higher biomechanical demands than *P. wagneri*.

Diet is an important selective pressure acting on the craniomandibular morphologies of mammals, including in peccaries (Kiltie 1985; Perez-Barberia and Gordon 1999). Its effects could be even more pronounced on mandible shape given its more precise functional role in feeding (Raia et al. 2010; Ross and Iriarte-Diaz 2014). Mandible shape traits and biomechanical performance documented here for *P. tajacu* and *T. pecari* have been implicated as adaptations for consuming hard foods in others omnivorous mammals (Nogueira et al. 2009; Maestri et al. 2016), especially in primates feeding on fruits or leaves (Hylander 1979, 1988; Ravosa 1991, 1992; Ravosa et al. 2000; Taylor 2006). Tougher foods such as palm fruits, seeds, roots, and nuts comprise the principal diet of *P. tajacu* and *T. pecari* (Taber et al. 2011). Stronger bites are usually explained by the tough diet of these two peccaries (Kiltie 1982; Sicuro and Oliveira 2002). In turn, the shape traits and biomechanical attributes of *P. wagneri* are shared with browsing ungulates, i.e. those eating woody and non-woody dicotyledonous plants (Mendoza et al. 2002; Raia et al. 2010). Fruits, flowers, and roots of dicots, mainly Cactaceae, indeed predominate in its diet (Taber et al. 1994; Taber et al. 2011). Although these foods can be also tough, they are likely less tough than palm fruits, seeds and nuts ingested by *P. tajacu* and *T. pecari* (Perez-Barberia and Gordon 1999). Some estimates suggest that loads ranging between 100 -1260 kg are need to break the nuts and seeds ingested by these two peccaries (Kiltie 1982).

Thus, the mandible shape of *P. wagneri* reflecting a more relaxed biomechanical performance, can be related to a diet that is presumably less tough than that of either *P. tajacu* or *T. pecari*.

Further comparative support emerges from the differences in the feeding behaviour 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 is likely an adaptation to resist large bending moments mainly in the dorsoventral plane (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). Evidences of incisal engagement are evident in these peccaries (Herring 1972). The mandible shape of *P. tajacu* and *T. pecari* may be thus better adapted to resist higher bending moments generated during crushing mastication or even during incisor biting of mechanically tough foods. On the other hand, increases of forces in balancing side resulting from grinding mastication in combination with a smaller condyle area and more slender mandible can result in the lower bite force and decreased vertical bending loads of *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*, during chewing, crests in perpetual contact maintain high occlusal pressure on foods even if occlusal force is reduced (Herring 1985). However, our stress measures do not take dental topography into account as we measured the whole tooth surface area.

Some studies have also highlighted the role of phylogeny in shaping the mandibular traits of ungulates (Perez-Barberia and Gordon 1999; Raia et al. 2010). 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). But this is debateable as their similar morphologies could be the result of convergence, as molecular studies suggest *T. pecari* and *P. wagneri* are more closely related (Theimer and Keim 1998; Gongora and Moran 2005; Perry et al. 2017). Under any scenario, the mandibular traits of *P. wagneri* appear more conservative, retaining a browsing pattern verified in extinct peccaries of the genus *Platygonus*, which were likely well adapted in open, arid environments like those where *P. wagneri* is found (Wetzel 1977; Gasparini 2013). Some authors even argue that *P. tajacu* and *T. pecari* display advanced morphological traits for the family Tayassuidae (Wetzel 1977). Improved feeding performance may have been a key factor in the expansion of dietary niches of these two peccaries enabling them to exploit food items with a wide range of toughness over a variety of habitats, from tropical forest to open arid environments (Wetzel 1997).

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 than *P. wagneri*. Our analysis and corroborative ecological observations support the hypothesis that shape closely reflects the biomechanical performance of species. Although one must be cautious to attribute these outcomes solely to feeding adaptations, at some level the functional implications of this variation must reflect the demands of feeding behaviour in these peccaries.

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Table 1. - Results from the absolute and size-corrected analyses of ANOVA and Tukey´s tests comparing biomechanical performance related variables between peccary species. PW: *Parachoerus wagneri*, Chacoan peccary; PT: *Pecari tajacu*, collared peccary; TP: *Tayassu pecari*, white-lipped peccary

	Absolute analyses					**Size-corrected analyses**				
	ANOVA		Significance level of Tukey´s test			ANOVA		Significance level of Tukey´s test		
	F	P	PW vs. PT	PW vs. TP	PT vs. TP	F	P	PW vs. PT	PW vs. TP	PT vs. 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*

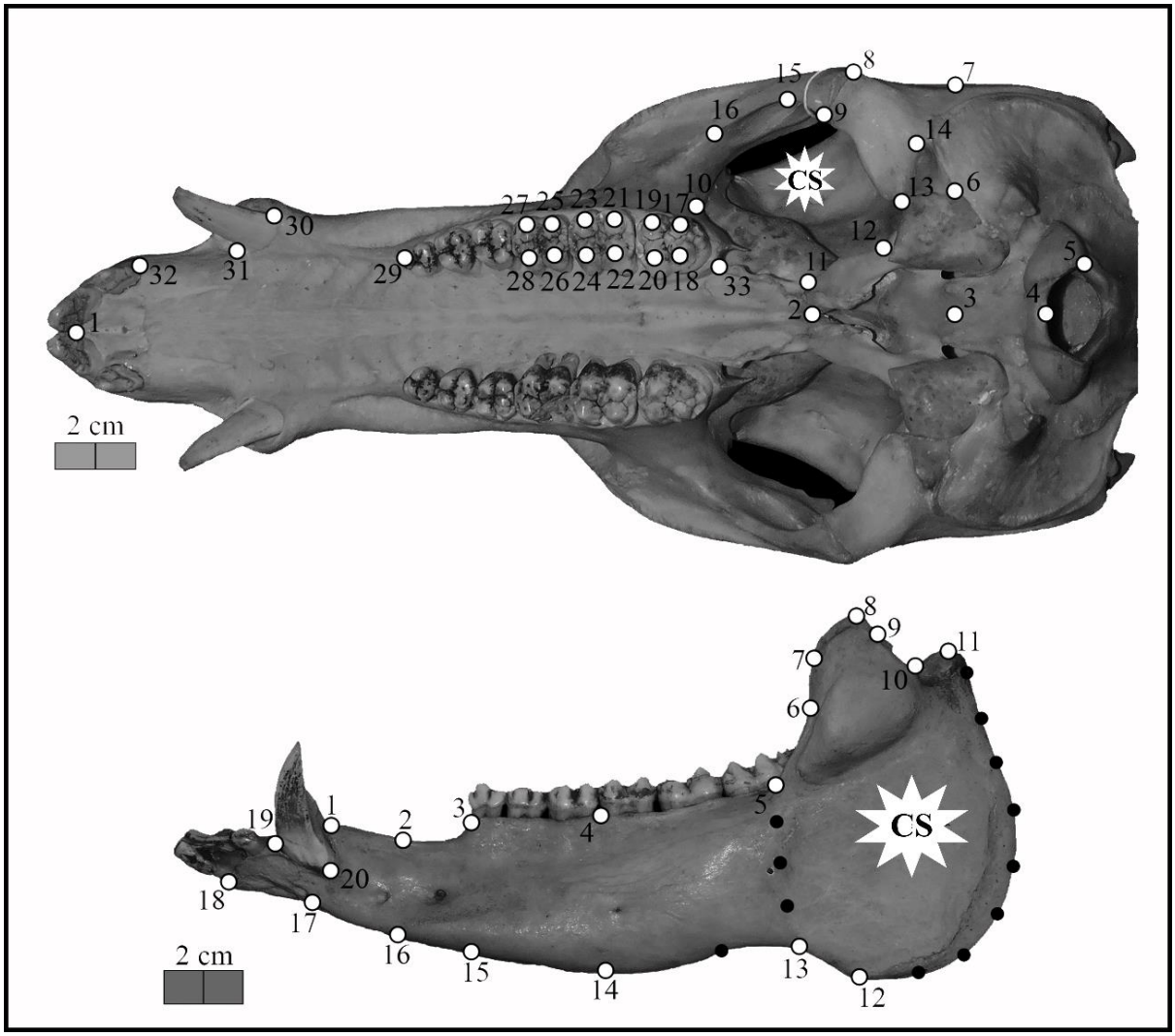


Fig. 1. - Position of the landmarks (white circles) and semilandmarks (black circles) on the ventral view of the cranium and lateral view on the mandible of peccaries. Landmark descriptions are in Supplementary Data S1. CS illustrates the temporalis muscle insertion area in the cranium and of the masseter attachment in the mandible.

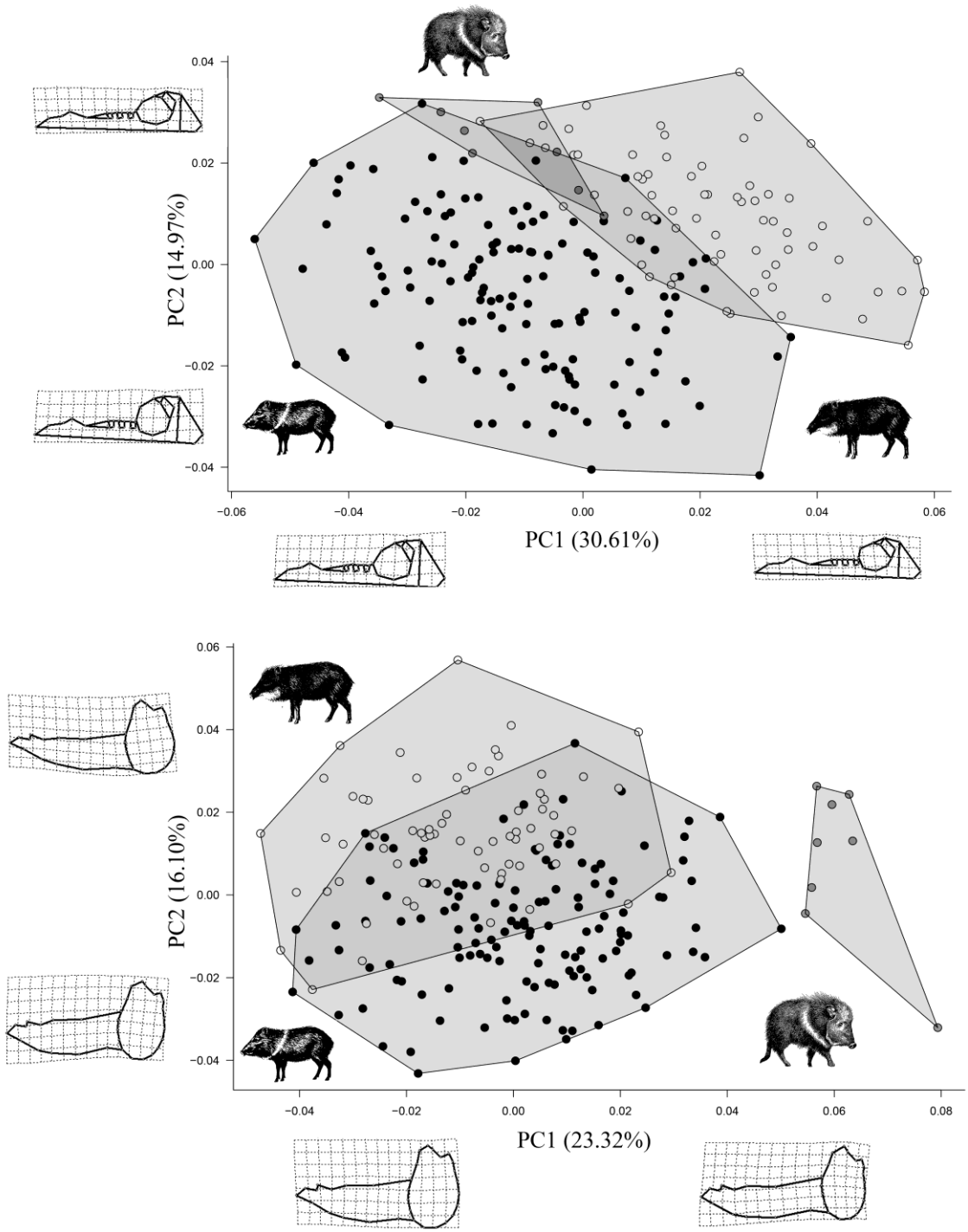


Fig. 2. - Cranial and mandibular morphospace identified for peccaries by the principal component analysis. Transformation grids show the shape deformations relative to the mean at the positive and negative extremes of the first two principal component axes. Solid circles = *Pecari tajacu* (collared peccary); Open circles = *Tayassu pecari* (white-lipped peccary); Gray circles = *Parachoerus wagneri* (Chacoan peccary).

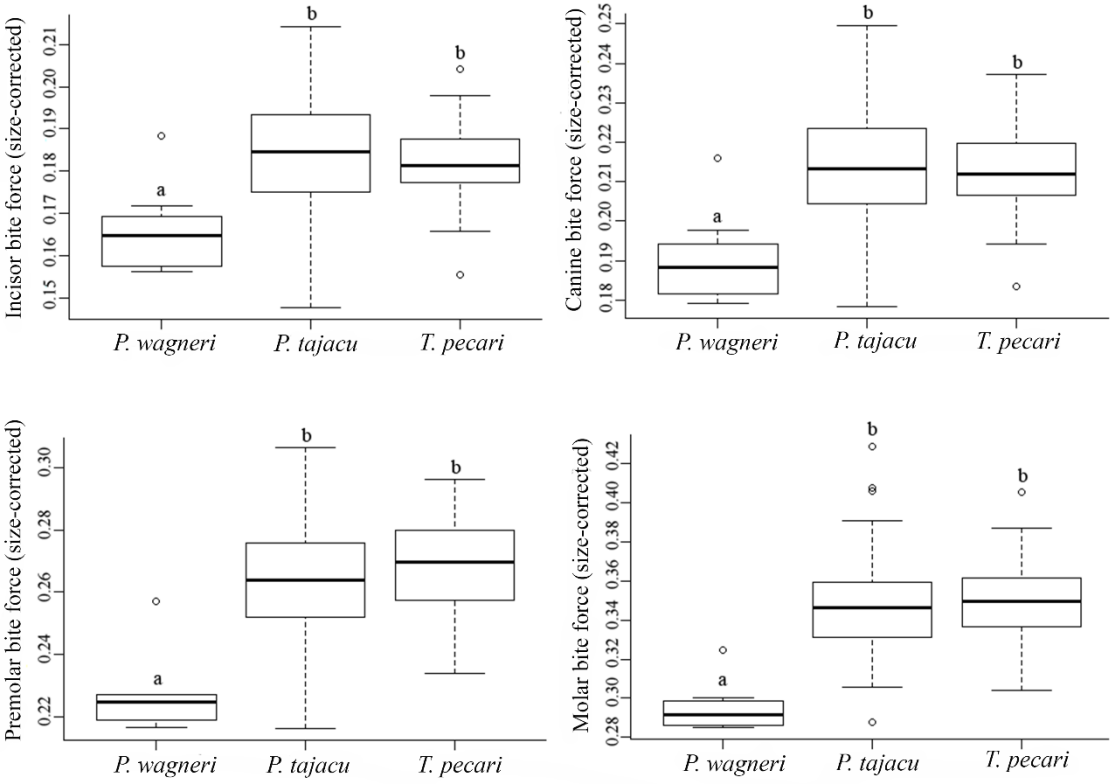


Fig. 3. - Variation in relative bite forces at incisor, canine, premolar and molar among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey pairwise comparisons between species (equal letters mean no significance; different letters mean significance).

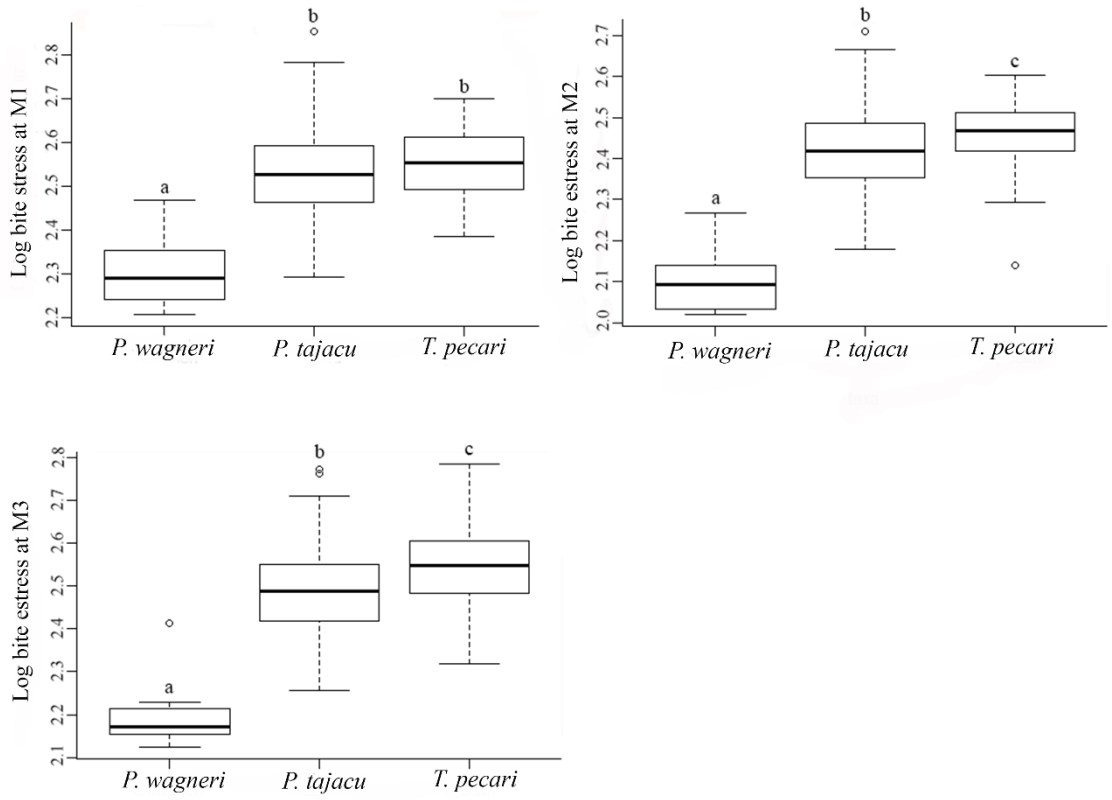


Fig. 4. - Variation in bite stress at first molar (M1), second molar (M2) and third molar (M3) among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey pairwise comparisons between species (equal letters mean no significance; different letters mean significance).

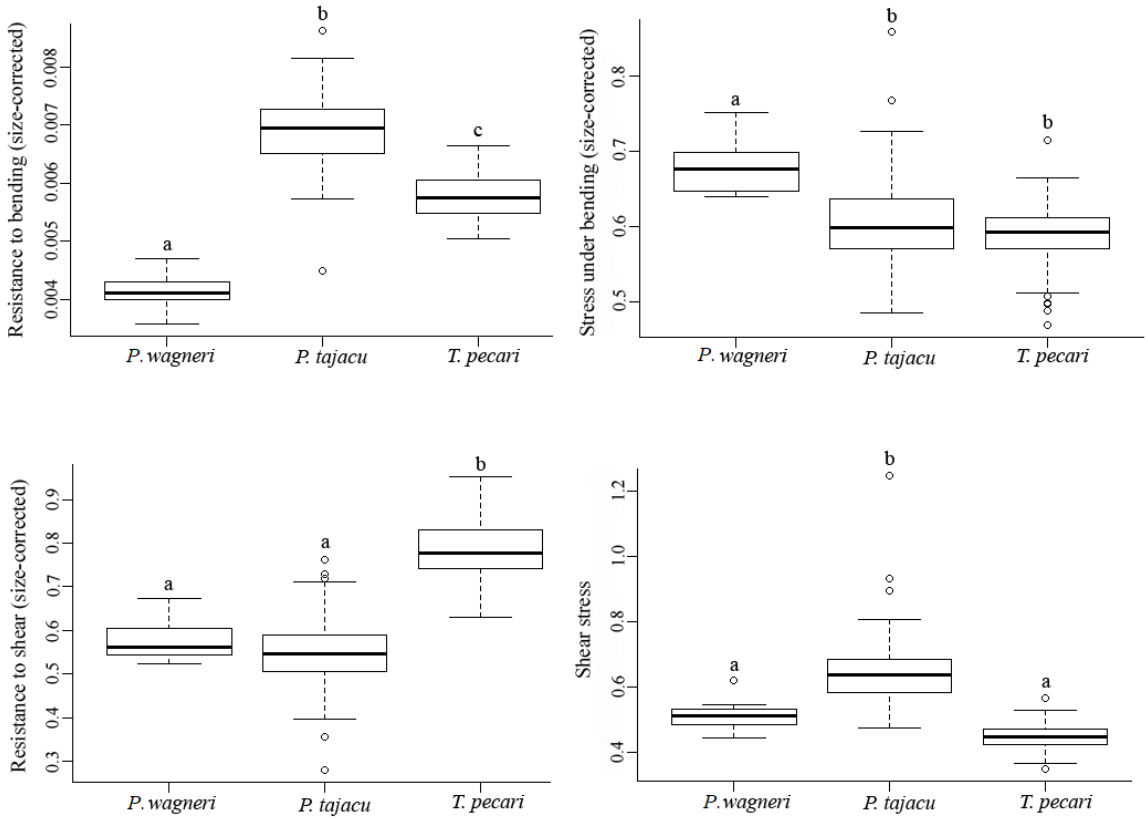


Fig. 5. - Variation in bending and shear stress on the mandibular corpus among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey pairwise comparisons between species (equal letters mean no significance; different letters mean significance).

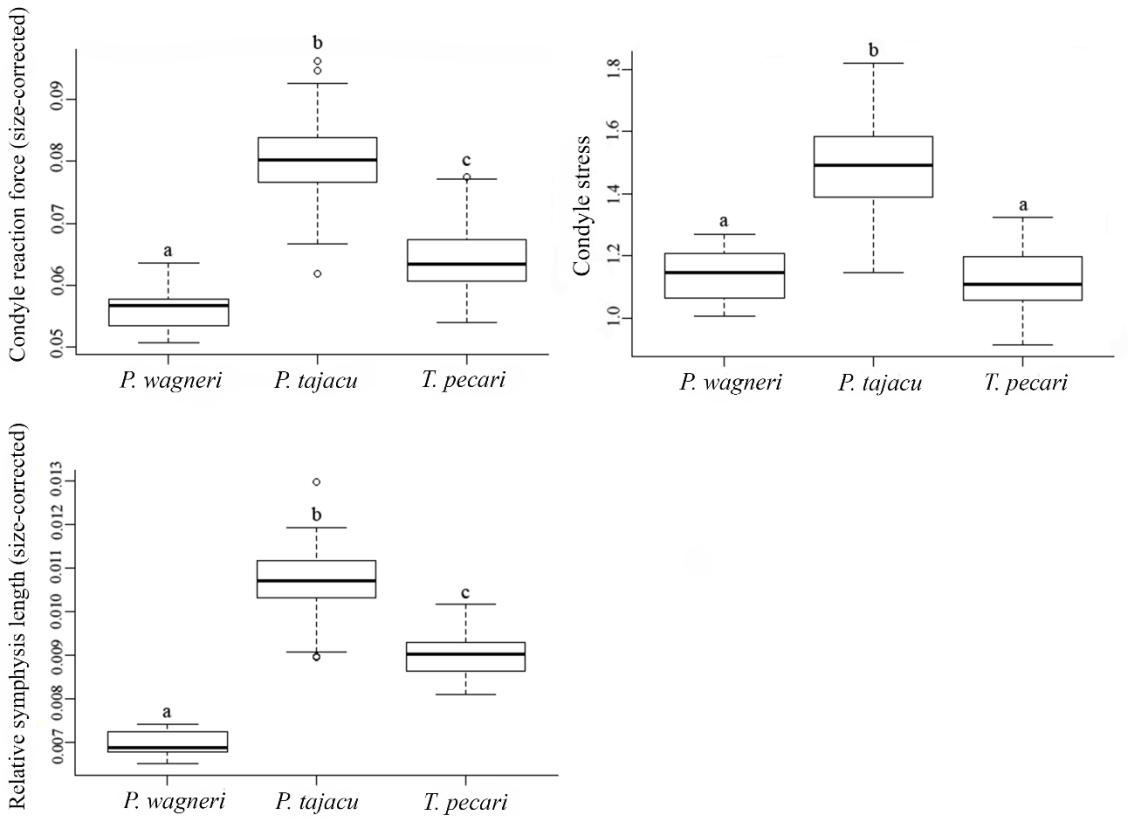


Fig. 6. - Variation in condylar stress among peccary species. Boxes represent the third and first quartiles, plus the median (bold line), and upper and lower limits. Extreme values are shown as open circles. Letters above plots indicate statistical significance (at α = 0.05) in Tukey pairwise comparisons between species (equal letters mean no significance; different letters mean significance).

Supplementary Data S1. - Definition of landmarks placed on the cranium and mandible views and caliper measurements taken on the mandible of each peccary specimen.

Ventral view of the cranium:

L1 = midpoint of central incisors; **L2** = posteriormost point of interpalatine suture; **L3** = vertical projections of landmark 6 and 7 in an angle of 90 degrees; **L4** = anteriormost point of the foramen magnum along the midline; **L5** = posteriormost margin of the occipital condyle; **L6** = anteriormost external border of the auditory bulla; **L7** = lateral point of the skull at the region of post-glenoid process; **L8** = suture between jugal and squamosal in the zygomatic arch; **L9, 11, 12, 13, 15, 16, 33** = temporal muscle insertion area; **L10** = curvature between the maxilla and the ***zygomatic arch*; L14** = extremity of the post-glenoid process; **L17, 18, 19, 20** = third molar area; **L21, 22, 23, 24** = second molar area; **L25, 26, 27, 28** = first molar area; **L29** = anteriormost tip of the first premolar; **L30** = posteriormost point of the lateral canine; **L31** = anteriormost point of the lateral canine; **L32** = posteriormost point of the lateral incisor.

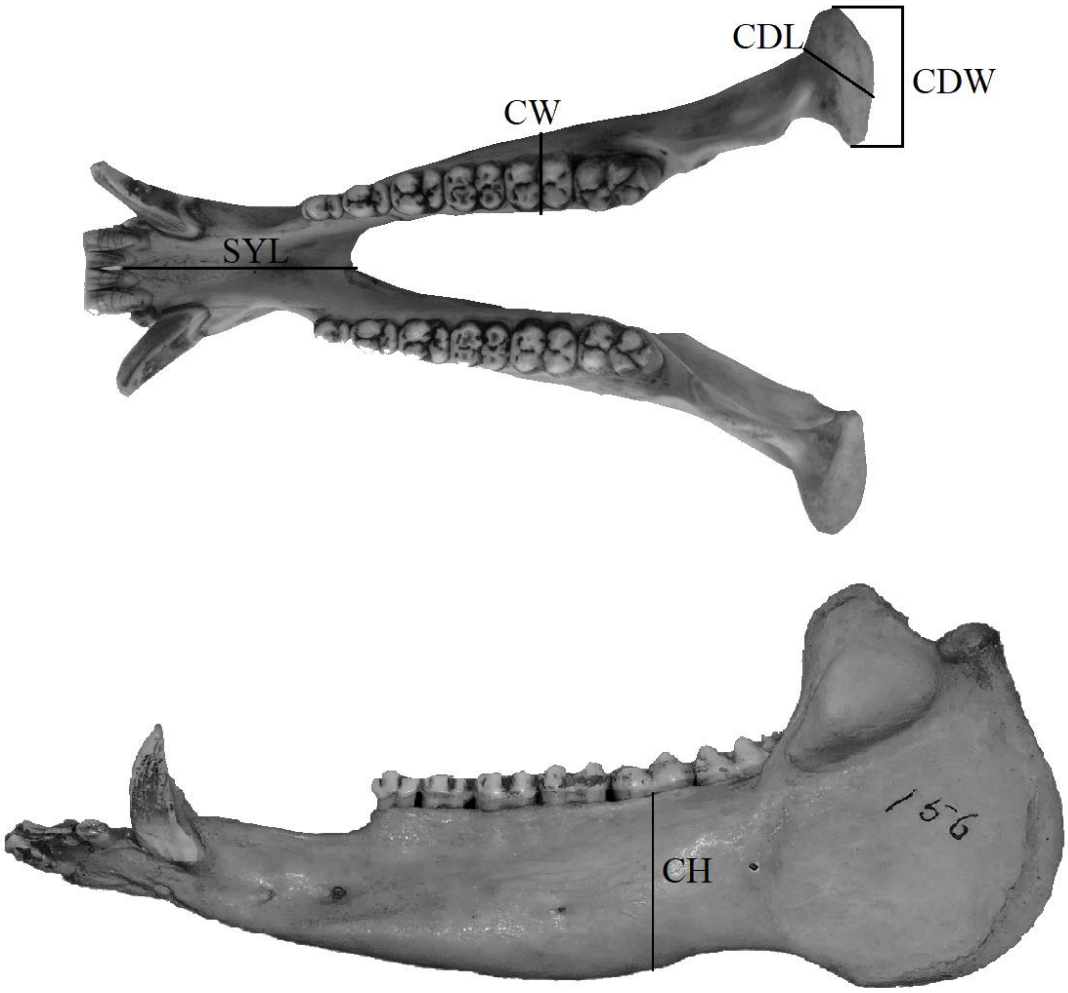
Lateral view of the mandible:

L1 = posteriormost point of the canine alveolus; **L2** = midpoint of the diastema **L3** = anteriormost point of the first premolar alveolus; **L4** = anteriormost point of the first molar alveolus; **L5** = junction between ramus and mandibular corpora at third molar; **L6** = anteriormost point of the coronoid process; **L7** = midpoint of the coronoid process; **L8 =** tip of the coronoid process; **L9** = posteriormost point of the coronoid process; **L10** = point of maximum curvature between the coronoid and condylar process; **L11** = tip of the condylar process as seen in the lateral view; **L12** = end of the lateral border of the angular process; **L13** = junction between mandibular corpora and masseteric crest; **L14, 15, 16** = vertical projections of landmark 4, 3 and 2 (respectively) in an angle of 90 degrees; **L17**: lateral cavity in mandibular

corpora at the region of canine as seen in the lateral view, **L18** = anteriormost point of the incisor alveolus; **L19** = anteriomost point of the canine alveolus; **L20** = midpoint of the canine alveolus.

Caliper measurements

CH = corpus height, **CW** = corpus width, **CDL** = condyle length, **CDW** = condyle width, **SYL** = Symphysis length



Suplementary Data S2. - List of specimens of the peccary species *Pecari tajacu*, *Tayassu pecari* and *Parachoerus wagneri* examined and morphometric measurements. CH = corpus height, CW = corpus width, CDL = condyle length, CDW = condyle width, SYL = Symphysis length

Species	**Museum Number**	**Sex**	**CH**	**CW**	**CDL**	**CDW**	**SYL**
Pecari tajacu	AMNH 29442	unknown	3.04	1.51	1.35	2.15	4.81
Pecari tajacu	AMNH 28954	male	3.21	1.58	1.24	2.14	4.74
Pecari tajacu	AMNH 29443	male	2.79	1.54	1.09	2.09	4.68
Pecari tajacu	AMNH 37613	female	3.15	1.64	1.1	1.91	4.93
Pecari tajacu	AMNH 36701	male	3.05	1.74	1.22	2.34	4.56
Pecari tajacu	AMNH 17266	male	2.9	1.6	1.23	2.11	4.72
Pecari tajacu	AMNH 17267	male	3.22	0.82	1.16	2.34	5.34
Pecari tajacu	AMNH 17268	female	3.13	1.55	1.2	2.26	4.86
Pecari tajacu	AMNH 24587	male	3.52	1.91	1.2	2.27	5.56
Pecari tajacu	AMNH 24593	male	2.65	1.64	1.52	2.2	4.27
Pecari tajacu	AMNH 24586	unknown	3.45	1.75	1.36	2.4	5.11
Pecari tajacu	AMNH 23874	female	3.36	1.75	1.28	2.31	5.15
Pecari tajacu	AMNH 24592	female	3.12	1.81	1.26	2.29	5.14
Pecari tajacu	AMNH 24584	male	3.21	1.69	1.09	2.23	5.19
Pecari tajacu	AMNH 399	unknown	3.36	1.8	1.25	2.6	4.98
Pecari tajacu	AMNH 174311	unknown	3.54	1.84	1.27	2.09	4.85
Pecari tajacu	AMNH 184218	female	3.23	1.61	1.28	2.33	4.73
Pecari tajacu	AMNH 184220	male	3.33	1.68	1.22	2.49	4.62
Pecari tajacu	AMNH 184219	unknown	3.33	1.67	1.32	2.25	4.91
Pecari tajacu	AMNH 184217	unknown	3.36	1.71	1.31	2.29	4.86
Pecari tajacu	AMNH M-173556	unknown	2.98	1.43	1.28	2.15	5.1
Pecari tajacu	AMNH 397	unknown	3.05	1.51	1.11	2.32	5.25
Pecari tajacu	AMNH 22674	female	3.13	1.58	1.1	2.29	4.77
Pecari tajacu	AMNH 396	unknown	2.97	1.53	1.2	2.15	4.66
Pecari tajacu	AMNH 37789	male	2.98	1.58	1.07	1.97	4.83
Pecari tajacu	AMNH 145963	female	2.82	1.64	1.15	2	4.66
Pecari tajacu	AMNH 206835	unknown	3.35	1.71	1.23	2.12	5.29
Pecari tajacu	AMNH 25782	female	2.78	1.4	1.13	2.1	4.73
Pecari tajacu	AMNH 26004	male	3.33	1.43	1.23	2.33	5.23
Pecari tajacu	AMNH 25951	male	2.97	1.24	1.17	2.4	4.58
Pecari tajacu	AMNH 67723	male	3.11	1.73	0.99	2.07	4.58
Pecari tajacu	AMNH 67722	female	2.92	1.7	1.44	2.36	4.67
Pecari tajacu	AMNH 64001	female	3.32	2.03	1.34	2.23	4.56
Pecari tajacu	AMNH 66749	male	2.82	1.79	1.02	2.15	5.12
Pecari tajacu	AMNH 69420	unknown	2.88	1.35	0.97	2.3	4.81
Pecari tajacu	AMNH 41937	unknown	3.18	1.44	1.1	2.27	4.57
Pecari tajacu	AMNH48145	unknown	3.05	1.46	1.04	2.11	5.21
Pecari tajacu	AMNH 48223	unknown	3.14	1.49	1.26	2.12	4.65
Pecari tajacu	AMNH 80300	unknown	3.14	1.66	1.11	2.07	4.61
Pecari tajacu	AMNH 130458	male	3.14	1.74	1.24	2.11	5.41

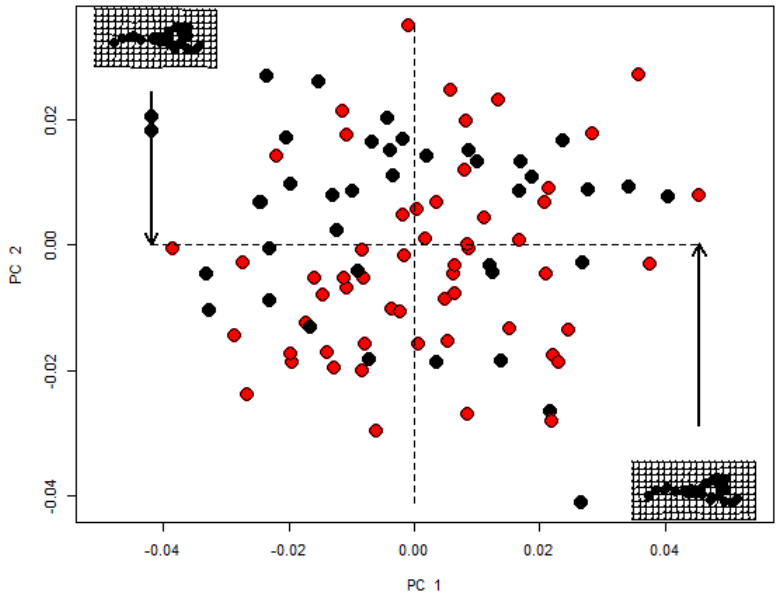
Pecari tajacu	AMNH 76903	female	2.71	1.59	1.06	2.02	4.15
Pecari tajacu	AMNH 69600	female	2.78	1.67	1.08	2.02	4.51
Pecari tajacu	AMNH 95822	female	3.11	1.64	1.05	2.04	4.81
Pecari tajacu	AMNH 95823	female	3.38	1.57	1.13	2.08	4.82
Pecari tajacu	AMNH 157	unknown	3.22	1.88	1.21	2.31	4.9
Pecari tajacu	AMNH 214749	unknown	3.19	1.84	1.16	2.11	4.41
Pecari tajacu	AMNH 263363	unknown	3.06	1.66	1.04	2.19	3.81
Pecari tajacu	AMNH 215157	male	2.77	1.72	1.09	2.15	3.91
Pecari tajacu	AMNH 215154	male	3.06	1.72	1.14	2.09	4.67
Pecari tajacu	AMNH 61796	male	2.95	1.55	0.97	2.11	4.21
Pecari tajacu	AMNH 92843	male	3.42	1.75	1.23	1.97	5.4
Pecari tajacu	AMNH 91721	female	3.12	1.73	1.19	2.1	4.57
Pecari tajacu	AMNH 93100	male	3.15	1.74	1.11	2.31	5.17
Pecari tajacu	AMNH 79523	female	3.11	1.78	1.23	2.09	4.72
Pecari tajacu	AMNH 324	unknown	3.1	1.62	1.12	2.16	4.52
Pecari tajacu	AMNH 323	unknown	2.82	1.55	1.12	2.15	4.19
Pecari tajacu	AMNH 95828	male	3.11	1.76	1.06	2.19	4.36
Pecari tajacu	AMNH 96142	female	2.64	1.62	1.08	1.96	4.43
Pecari tajacu	FMNH 22400	unknown	3.17	1.57	1.19	2.04	5.12
Pecari tajacu	FMNH 63922	Male	3.21	1.54	1.19	1.98	4.93
Pecari tajacu	FMNH 63923	Female	2.92	1.74	1.04	2.15	5.06
Pecari tajacu	FMNH 34332	Male	3.07	1.65	1.12	1.94	4.21
Pecari tajacu	FMNH 21384	Male	3.18	1.84	0.86	2.21	4.91
Pecari tajacu	FMNH 51088	Female	3.02	1.76	1.17	2.04	5.4
Pecari tajacu	FMNH 28314	Male	2.81	1.64	1.04	2.11	5.16
Pecari tajacu	FMNH 28315	Male	2.81	1.77	1.03	2.1	4.31
Pecari tajacu	FMNH 28316	Male	2.59	1.69	1.04	2.02	4.46
Pecari tajacu	FMNH 28317	Female	3.13	1.71	1.06	2.18	4.5
Pecari tajacu	FMNH 50889	Male	3.12	1.62	1.04	2.23	4.36
Pecari tajacu	FMNH 51087	Female	3.05	1.61	1.08	2.27	4.82
Pecari tajacu	FMNH 20024	unknown	3.02	1.71	1.04	2.21	4.85
Pecari tajacu	FMNH 52330	Male	2.71	1.56	1.01	2.1	4.32
Pecari tajacu	FMNH 90028	Male	2.7	1.61	1.1	2.04	4.5
Pecari tajacu	FMNH 90032	Female	3.11	1.83	1.21	2.05	4.78
Pecari tajacu	FMNH 69638	Female	2.86	1.63	1.15	2.14	4.61
Pecari tajacu	FMNH 69639	Female	3.14	1.7	1.18	1.97	4.73
Pecari tajacu	FMNH 69640	Male	3.44	1.54	1.14	2.1	4.83
Pecari tajacu	FMNH 69641	Male	3.04	1.75	1.23	2.19	4.78
Pecari tajacu	FMNH 69642	Female	2.75	1.79	1.25	2.03	4.5
Pecari tajacu	FMNH 69643	Male	2.97	1.52	1.25	2.25	4.58
Pecari tajacu	FMNH 69644	Male	3.21	1.57	1.28	2.06	4.46
Pecari tajacu	FMNH 68802	Male	2.96	1.61	0.97	2.05	4.83
Pecari tajacu	FMNH 87874	Female	3.38	1.65	1.1	2.26	4.9
Pecari tajacu	FMNH 87875	Male	3.06	1.7	1.04	2.32	4.68

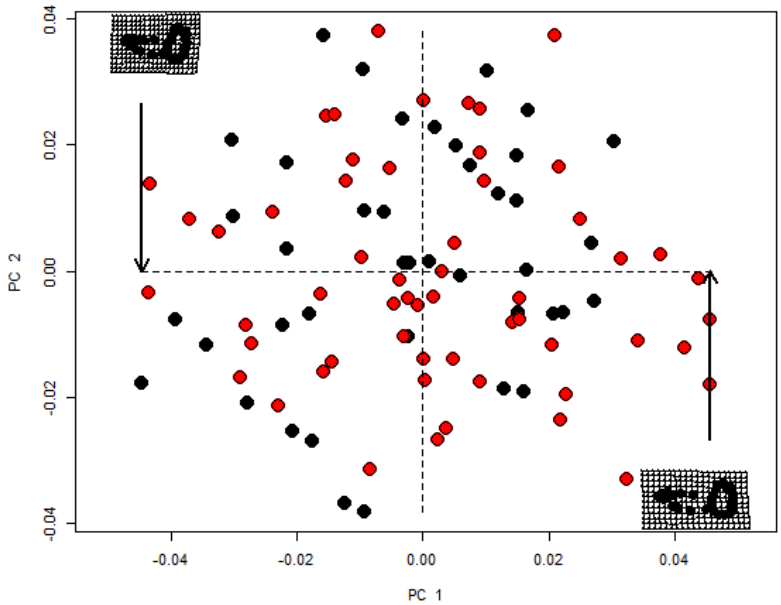
Pecari tajacu	FMNH 87876	Female	3.52	1.77	1.35	2.31	5.07
Pecari tajacu	FMNH 70565	Male	3.15	1.67	1.04	2.12	5.12
Pecari tajacu	FMNH 86744	Male	2.76	1.68	1.2	2.04	4.7
Pecari tajacu	FMNH 125121	unknown	3.38	1.97	1.45	2.78	-
Pecari tajacu	FMNH 41622	unknown	3.09	1.69	1.54	2.25	4.91
Pecari tajacu	FMNH 15932	unknown	3.22	1.56	1.31	2.15	5.24
Pecari tajacu	FMNH 15996	Male	3.1	1.77	1.28	2.2	5.14
Pecari tajacu	FMNH 15997	Female	2.91	1.82	1.31	2.12	4.74
Pecari tajacu	FMNH 14038	Female	3.28	1.51	1.25	2.5	4.91
Pecari tajacu	FMNH 14039	Female	3.11	1.7	1.31	1.98	4.78
Pecari tajacu	FMNH 16011	Male	3.07	1.73	1.29	2.37	4.51
Pecari tajacu	FMNH 16012	Male	3.13	1.49	1.14	2.2	4.41
Pecari tajacu	FMNH 14028	Male	3.55	1.56	1.14	2.28	5.06
Pecari tajacu	FMNH 14032	Male	3.32	1.48	1.32	2.3	5.05
Pecari tajacu	FMNH 14033	Male	3.2	1.61	1.13	2.44	4.72
Pecari tajacu	FMNH 14034	Female	3.47	1.51	1.21	2.32	5
Pecari tajacu	FMNH 14035	Male	3.25	1.87	0.98	2.27	5.04
Pecari tajacu	FMNH 14037	Male	3.51	1.6	1.38	2.45	4.71
Pecari tajacu	FMNH 14029	Male	3.66	1.53	1.11	2.41	5.23
Pecari tajacu	FMNH 15992	Male	2.97	1.71	1	2.3	5.18
Pecari tajacu	FMNH 95534	Male	3.48	1.46	0.98	2.28	5.4
Pecari tajacu	FMNH 95800	Male	3.01	1.56	1.05	2.23	4.56
Pecari tajacu	FMNH 95801	Male	2.96	1.71	0.99	2.3	5.03
Pecari tajacu	FMNH 95802	Female	2.9	1.69	1.06	2.28	4.51
Pecari tajacu	FMNH 26645	Female	2.94	1.64	1.09	2.02	3.88
Pecari tajacu	FMNH 26646	Female	3.02	1.5	1.13	2.24	4.47
Pecari tajacu	FMNH 34298	unknown	3.21	1.74	1.14	2.1	4.31
Pecari tajacu	FMNH 34299	unknown	3.48	1.68	1.07	2.26	4.62
Pecari tajacu	FMNH 89175	Male	2.85	1.68	1.14	2.12	5.24
Pecari tajacu	FMNH 86897	Female	3.57	1.91	1.05	2.23	4.95
Pecari tajacu	FMNH 88799	Female	3.21	1.81	1.13	2.2	4.79
Pecari tajacu	FMNH 88800	Female	3.28	2.04	1.33	2.41	5.18
Pecari tajacu	FMNH 88802	Female	3.62	1.84	1.35	2.37	5.29
Pecari tajacu	FMNH 89176	Male	3.51	2.1	1.14	2.42	5.25
Pecari tajacu	FMNH 89177	Male	3.43	1.92	1.22	2.34	4.42
Pecari tajacu	FMNH 88803	Male	3.67	2.04	1.31	2.64	5.28
Pecari tajacu	FMNH 34305	Male	3.53	1.9	1.13	2.54	5.37
Pecari tajacu	FMNH 79926	Female	2.81	1.81	1.27	2.05	4.22
Pecari tajacu	FMNH 79929	Female	3.44	1.93	1.16	2.17	5
Pecari tajacu	FMNH 52861	unknown	2.97	1.75	1.15	2.26	4.74
Pecari tajacu	FMNH 134434	unknown	3.21	1.67	1.4	2.64	4.93
Pecari tajacu	FMNH 53022	unknown	2.97	1.43	1.06	2.17	4.65
Pecari tajacu	FMNH 53023	unknown	2.87	1.49	1.1	2.2	4.82
Pecari tajacu	FMNH 53024	unknown	2.73	1.45	1.14	2.11	5.22

Pecari tajacu	FMNH 53028	unknown	2.79	1.55	1.2	2.11	5.18
Pecari tajacu	FMNH 53030	unknown	2.01	1.63	1.26	2.32	5.16
Pecari tajacu	FMNH 53032	unknown	2.91	1.69	1.05	2.19	5.09
Pecari tajacu	FMNH 53033	unknown	3	1.53	1.13	2.19	5.36
Pecari tajacu	FMNH 22434	unknown	2.95	1.65	1.11	2.08	4.04
Pecari tajacu	FMNH 69645	unknown	2.87	1.61	1.11	2.15	4.89
Pecari tajacu	FMNH 34314	unknown	3	1.57	1.07	2.22	4.44
Pecari tajacu	FMNH 34312	unknown	2.83	1.5	0.92	2.08	4.31
Tayassu pecari	AMNH 207423	unknown	3.33	2.06	1.63	2.64	5.64
Tayassu pecari	AMNH 32675	Female	3.62	2.12	1.73	2.49	5.56
Tayassu pecari	AMNH 32673	Male	3.25	2.16	1.55	2.53	5.15
Tayassu pecari	AMNH 32674	Female	3.71	2.23	1.5	2.75	5.21
Tayassu pecari	AMNH 15464	Female	3.51	2.24	1.75	2.68	5.55
Tayassu pecari	AMNH M-209143	unknown	3.78	2.15	1.51	2.62	6.81
Tayassu pecari	AMNH M-260332	unknown	3.81	2.29	1.8	2.63	5.82
Tayassu pecari	AMNH M-247728	unknown	4.63	2.31	1.44	2.76	7.18
Tayassu pecari	AMNH M-66750	Male	3.85	2.42	1.84	2.85	6.29
Tayassu pecari	AMNH M-67731	unknown	4.42	2.28	1.79	2.24	7.18
Tayassu pecari	AMNH M-46549	unknown	4.22	2.4	1.77	2.95	6.43
Tayassu pecari	AMNH M-64097	Male	4.45	2.2	1.55	3	5.97
Tayassu pecari	AMNH M-42876	unknown	3.71	2.23	1.43	2.65	5.73
Tayassu pecari	AMNH M-64098	Male	4.12	2.17	1.63	2.63	5.98
Tayassu pecari	AMNH M-42410	Male	3.82	2.37	1.64	2.69	5.93
Tayassu pecari	AMNH M-130451	Male	4.14	2.27	1.83	2.05	6.33
Tayassu pecari	AMNH M-130455	Male	3.91	2.12	1.56	2.66	6.28
Tayassu pecari	AMNH M-130456	Female	3.55	2.19	1.48	2.47	5.66
Tayassu pecari	AMNH M-130457	Female	3.98	2.15	1.6	2.64	6.46
Tayassu pecari	AMNH MO-156	unknown	3.76	2.16	1.55	2.68	5.78
Tayassu pecari	AMNH M-36656	Female	3.71	2.41	1.4	2.51	5.8
Tayassu pecari	AMNH M-94172	Female	3.98	2.16	1.64	2.59	6.59
Tayassu pecari	AMNH 93727	Female	3.88	2.27	1.52	2.72	6.13
Tayassu pecari	AMNH 93728	Female	4.04	2.23	1.55	2.44	6.44
Tayassu pecari	AMNH M-96134	Female	3.97	2.25	1.62	2.59	6.51
Tayassu pecari	AMNH M-96132	Male	4.56	2.52	1.69	2.93	6.22
Tayassu pecari	AMNH M-96140	Female	3.83	2.3	1.47	2.46	6.13
Tayassu pecari	AMNH M-96151	Male	3.82	2.35	1.49	2.71	5.61
Tayassu pecari	AMNH M-96154	Male	4.17	2.43	1.66	2.81	6.22
Tayassu pecari	AMNH M-78551	Male	4.41	2.44	1.54	2.94	6.23
Tayassu pecari	AMNH M-78553	Female	4	2.26	1.3	2.48	6.21
Tayassu pecari	AMNH M-61537	Female	3.89	2.21	1.69	2.91	6.64
Tayassu pecari	AMNH M-61538	Female	3.82	2.01	1.39	2.68	6.11
Tayassu pecari	FMNH 121193	unknown	3.5	2.25	1.56	2.51	5.86
Tayassu pecari	FMNH 51086	unknown	3.97	2.18	1.57	2.8	5.95
Tayassu pecari	FMNH 20025	unknown	3.75	2.37	1.6	2.57	6.39

Tayassu pecari	FMNH 52331	Male	3.81	2.25	1.5	2.71	6.32
Tayassu pecari	FMNH 92370	Female	3.91	2.21	1.47	2.57	5.45
Tayassu pecari	FMNH 92368	Male	3.98	2.26	1.55	2.64	6.1
Tayassu pecari	FMNH 92369	Male	3.42	2.16	1.52	2.57	5.82
Tayassu pecari	FMNH 13167	unknown	4.04	2.09	1.5	2.1	5.91
Tayassu pecari	FMNH 87878	Male	4.07	2.36	1.5	2.78	6.57
Tayassu pecari	FMNH 87879	Female	4.27	2.35	1.62	2.96	7.06
Tayassu pecari	FMNH 18286	unknown	3.75	2.41	1.55	2.73	5.7
Tayassu pecari	FMNH 125120	unknown	4.35	2.32	1.65	2.89	6.96
Tayassu pecari	FMNH 15971	Female	3.52	2.39	1.61	2.73	6
Tayassu pecari	FMNH 15972	Female	3.68	2.36	1.58	2.65	5.94
Tayassu pecari	FMNH 15973	Female	3.76	2.33	1.7	2.82	6.05
Tayassu pecari	FMNH 15974	Male	3.81	2.37	1.68	2.78	6.28
Tayassu pecari	FMNH 95536	Female	3.62	2.3	1.59	2.66	5.73
Tayassu pecari	FMNH 95803	Male	4	2.4	1.75	2.7	6.03
Tayassu pecari	FMNH 19549	Female	4.17	2.39	1.92	2.66	6.05
Tayassu pecari	FMNH 123027	male	4.1	2.52	1.55	2.83	6.31
Tayassu pecari	FMNH 88795	Female	4.07	2.67	1.7	2.73	6.49
Tayassu pecari	FMNH 88796	Female	3.84	2.49	1.6	2.84	6.36
Tayassu pecari	FMNH 88797	Male	4	2.32	1.68	2.73	5.99
Tayassu pecari	FMNH 88798	Male	4.35	2.44	1.52	3.01	7.15
Tayassu pecari	FMNH 34300	unknown	3.8	2.42	1.83	2.66	5.87
Tayassu pecari	FMNH 34301	unknown	4.19	2.21	1.56	2.75	6.41
Tayassu pecari	FMNH 52498	Female	4.07	2.28	1.48	2.62	5.88
Tayassu pecari	FMNH 79927	Male	3.97	2.44	1.67	2.74	6.34
Tayassu pecari	FMNH 79928	Female	4.27	2.34	1.69	2.79	6.37
Tayassu pecari	FMNH 79930	Male	3.92	2.5	1.74	2.79	6.55
Tayassu pecari	FMNH 62081	Male	3.96	2.15	1.48	2.81	6.1
Tayassu pecari	FMNH 36102	unknown	4.28	2.19	1.57	2.61	5.83
Tayassu pecari	FMNH 21924	Female	3.7	2.14	1.41	2.46	5.43
Tayassu pecari	FMNH 145320	unknown	3.85	2.42	1.5	2.6	6.23
Tayassu pecari	FMNH 34309	unknown	4.55	2.41	1.61	2.68	6.85
Tayassu pecari	FMNH 34310	unknown	4	2.3	1.55	2.52	6.64
Parachoerus wagneri	AMNH M-237508	unknown	3.06	2.41	1.56	2.49	5.57
Parachoerus wagneri	AMNH M-248471	unknown	2.93	2.25	1.45	2.44	5.61
Parachoerus wagneri	FMNH 157397	Female	3.23	2.34	1.45	2.82	5.28
Parachoerus wagneri	FMNH 157398	Female	3.05	2.21	1.25	2.49	5.04
Parachoerus wagneri	FMNH 157399	Male	3.38	2.37	1.33	2.57	5.17
Parachoerus wagneri	FMNH 157396	Male	3.11	2.24	1.19	2.5	5.13
Parachoerus wagneri	FMNH 157401	Female	3.04	2.14	1.38	2.7	5
Parachoerus wagneri	FMNH 58646	unknown	3.04	2.06	1.51	2.45	5.02

Supplementary Data S3. - Principal Component projections of cranium and mandible for males and females of *Pecari tajacu.* Red circles = males, Black circles = females.





Discussão geral

Os padrões de variação na forma do crânio de *Pecari tajacu* e *Tayassu pecari* diferem ao longo de suas distribuições geográficas na América do Sul. Em ambientes mais sazonais e menos produtivos *P. tajacu* exibe características de forma relacionadas com um focinho proporcionalmente mais longo, molares maiores, com a área de inserção do musculo temporal posicionada mais próxima da série molar. Características interpretadas como adaptações para o consumo de uma variedade de alimentos em outros mamíferos, ao sul da Bacia Amazônica (CÁCERES et al., 2014; MELORO et al., 2014). De fato, a dieta de *P. tajacu* é composta por uma ampla gama de itens alimentares, sobretudo em condições de menor abundância e disponibilidade de frutos (TABER et al., 2011). Em ambientes úmidos e mais produtivos, o focinho proporcionalmente mais curto e os molares mais estreitos podem refletir o consumo de alimentos mais suaves e mais seletivos, tais como a polpa de frutos (FRAGOSO, 1999).

Um crânio proporcionalmente mais largo e com maior área para fixação do músculo temporal sinaliza uma maior força mastigatória para *T. pecari* em ambientes sazonais. No entanto, pouca ou nenhuma variação geográfica foi observada nos molares. Considerando a função principal dos dentes no processamento de alimentos (SOUTO-LIMA & MILLIEN, 2014), essa característica sugere um comportamento alimentar mais seletivo para *T. pecari* em comparação com *P. tajacu*. Embora, frutos são predominantes na dieta destes dois tayassuídeos, eles são ainda mais abundantes na dieta de *T. pecari* (BECK, 2006). Em ambientes sazonais, frutos duros, como os de palmeira, são largamente consumidos por *T. pecari* (KEUROGLIAN & EATON, 2008). Tais alimentos poderiam mesmo exigir uma poderosa força mastigatória.

Variáveis ambientais (precipitação e temperatura) explicaram a maior parte da variação da forma do crânio destes dois tayassuídeos, sugerindo que os padrões encontrados podem ser adaptativos. Embora, possíveis efeitos da plasticidade fenotípica não podem ser descartados, dado o efeito mais pronunciado do ambiente na espécie ecologicamente mais plástica, *P. tajacu* (SOUTO-LIMA & MILLIEN, 2014). Uma pequena parte da variação da forma em *P. tajacu* foi também explicada por processos espacialmente estruturados como o fluxo gênico entre as populações. O pequeno ou ausente efeito da alometria na forma do crânio destes dois tayassuídeos parece ser prevalente em morfologias de ungulados (RAIA et al., 2010).

Pecari tajacu e *T. pecari* também variam substancialmente em tamanho ao longo de suas distribuições geográficas ao Norte e ao Sul do Equador, mas essa variação é complexa e não possui um único determinante. O gradiente latitudinal no tamanho do crânio e, por

extensão, no tamanho do corpo, não suporta a Regra de Bergmann. O tamanho aumenta em latitudes mais baixas e em áreas menos sazonais próximas ao Equador, para ambas as espécies e em ambos os hemisférios.

Tayassuideos podem usar uma variedade de estratégias para lidar com temperaturas ambientais extremas. Grupos de *P. tajacau* são geralmente observados descansando em tocas, cavernas ou cavidades escavadas nas bases de grandes árvores durante as horas mais quentes do dia (TABER et al., 2011). Alguns registros também indicam que indivíduos dessa espécie podem amontoar-se para dormir em noites frias (BISSONETTE, 1978). Grupos de *T. pecari* são também frequentemente registrados próximos a fontes de água, como rios, lagos e áreas alagadas (FRAGOSO, 1999; CARRILLO et al. 2002). Ambas as espécies também tendem a alterar seus períodos de atividade, passando de mais diurnos no inverno para mais crepusculares ou noturnos na estação seca (TABER et al., 2011; HOFMANN et al., 2015). Estes comportamentos individuais e sociais podem contribuir para a termorregulação, compensando o menor tamanho corporal destes tayassuideos em áreas mais frias (desvantajoso para a conservação do calor) e o maior tamanho em áreas mais quentes (desvantajoso para a perda de calor). Modos de vida espécie-específicos são explicações aos desvios dos padrões de Bergmann também em outros mamíferos (ASHTON et al., 2000; MEDINA et al., 2007).

A precipitação, como um *proxy* para a disponibilidade de recursos, foi positivamente associada à variação do tamanho do crânio no Hemisfério Sul, embora essa relação seja significante somente para *T. pecari* quando a autocorrelação espacial é levada em consideração. Esses resultados enfatizam o papel da disponibilidade de recursos determinando aumentos no tamanho corporal (MCNAB, 2010; SCHIAFFINI, 2016). Um padrão também verificado em outros mamíferos sul americanos (MEDINA et al., 2007; SCHIAFFINI, 2016). Os efeitos da produtividade também são pronunciados no tamanho corporal de vários mamíferos omnívoros (YOM-TOV & GEFFEN 2006), inclusive em mamíferos que vivem em grupos, como estes dois tayassuídeos (primatas: CARDINI et al., 2007). Servindo para determinar clinas em tamanho para *T. pecari*, as correlações de tamanho com a produtividade representam desvios à Regra de Bergmann. A disponibilidade de recursos, especialmente de frutos, e de água podem, assim, exercer fortes pressões seletivas sobre o tamanho corporal dessas espécies, até mesmo maiores do que a temperatura. Evidências de que o ancestral comum mais recente destes tayassuídeos modernos se diversificou em florestas tropicais sugerem a adequabilidade desses ambientes produtivos e úmidos para eles (WETZEL 1977; GASPARINI 2013; PERRY et al., 2017).

A influência humana afeta a variação do tamanho de ambos *P. tajacu* e *T. pecari* e seu efeito é negativo, mas isto é significante apenas no hemisfério sul. Para tayassuídeos, a maior influência humana é geralmente sinônimo de perda de habitat e caça (TABER et al., 2011). Neste contexto, fragmentos perturbados podem não oferecer os requisitos energéticos (principalmente frutos) necessários para eles alcançarem o tamanho máximo de seu corpo. Indivíduos maiores também parecem ser preferencialmente caçados (GABOR & HELLGREN, 2000). Menores tamanhos corporais em áreas com maior influência humana podem ser assim uma consequência da menor disponibilidade de recursos e intensas pressões de caça.

Tayassu pecari é consistentemente maior do que *P. tajacu* em ambos os hemisférios. Entretanto, *P. tajacu* não apresenta mudanças significativas nas relações de tamanho ou tamanho-latitude entre áreas alopátricas e simpátricas. Isso sugere que a competição exploratória interespecífica por recursos alimentares não determina deslocamento do caráter no tamanho corporal de *P. tajacu* (BROWN & WILSON, 1956; ADAMS, 2004). Mesmo assim, a distribuição não sobreposta dos tamanhos corporais entre essas duas espécies ao longo de sua ampla área de simpatria sugere que o tamanho poderia contribuir para a coexistência estável dessas espécies.

Finalmente, nossas análises de forma e biomecânica integradas revelam que a forma craniomandibular de tayassuídeos reflete seus atributos biomecânicos (ROSS & IRIARTE-DIAZ, 2014). *Pecari tajacu* e *T. pecari* têm corpos mandibulares mais curtos e mais profundos com um aumento acentuado na área de inserção da musculatura adutora em comparação com o *P. wagneri*. Estes traços de forma refletem maiores forças de mordida, maior resistência dorsoventral e menores estresses (exceto nos molares) para *P. tajacu* e *T. pecari*, contrastando com os menores índices associados com a mandíbula mais longa e mais baixa de *P. wagneri* (HYLANDER 1979, 1988; TAYLOR, 2006). Em um sentido amplo, esses resultados sugerem que a forma da mandíbula de *P. tajacu* e *T. pecari* lhes permite aplicar forças mais fortes e resistir ao risco de fratura de maiores demandas biomecânicas do que a forma de *P. wagneri*. Embora é necessário ter cautela ao atribuir estes resultados unicamente como adaptações para alimentação, ao menos, em algum grau estes atributos funcionais devem refletir essas demandas. Frutos, flores e raízes de cactos (plantas suculentas) predominam na dieta de *P. wagneri* (TABER et al., 2011). Ainda que esses alimentos também possam ser mecanicamente difíceis, eles são provavelmente menos resistentes do que frutos de palmeiras, sementes e nozes predominantemente ingeridos por *P. tajacu* e *T. pecari* (PEREZ-BARBERIA & GORDON, 1999). Assim, a forma da mandíbula de *P. wagneri*, refletindo um desempenho biomecânico

comparativamente mais baixo, pode estar relacionada a uma dieta que presumivelmente é menos resistente que a de *P. tajacu* ou *T. pecari*

Conclusões gerais

Os resultados do capítulo 1 demonstram um padrão de variação latitudinal na forma do crânio de *Pecari tajacu* e *Tayassu pecari* ao longo de suas distribuições geográficas na América do Sul. A maior parte dessa variação foi explicada pelo ambiente, enquanto um fraco efeito alométrico e de outros processos espacialmente estruturados foi encontrado apenas em *P. tajacu.* Em ambientes sazonais, as formas de crânio sugerem adaptações para o consumo de uma variedade de itens alimentares para *P. tajacu*, e, de alimentos mecanicamente resistentes para *T. pecari*. Este resultado enfatiza o papel da variação ambiental dirigindo clinas na forma do crânio, sobretudo em espécies de ampla distribuição.

Os resultados do capítulo 2 mostram um padrão latitudinal no tamanho do crânio de *P. tajacu* e *T. pecari* inverso a Regra de Bergmann. Este padrão foi positivamente associado à precipitação, um *proxy* para disponibilidades de recursos, e negativamente com a influência humana. Este resultado ressalta que nos trópicos, a disponibilidade de recursos alimentares pode ser um melhor preditor de clinas em tamanho do que a temperatura para mamíferos como estes tayassuídeos, bem como outros animais sociais cujos padrões de utilização de recursos são moldados pela vida em grupo. Apesar de não manifestadas como deslocamento de caráter, as distribuições de tamanho corporal, em grande parte não sobrepostas, também indicam que as diferenças de tamanho podem ser necessárias para a sobreposição simpátrica dessas espécies.

No capítulo 3, os resultados mostram que *P. tajacu* e *T. pecari* compartilham traços de forma craniomandibular (corpo mandibular mais curto e profundo e áreas de inserção muscular mais amplas) que lhes permite aplicar forças mais fortes e resistir ao risco de fraturas de maiores demandas biomecânicas do que a forma de *Parachoerus wagneri* (corpo mandibular mais longo, raso e com menor de inserção da musculatura). Nossas análises corroboraram a hipótese de que a forma reflete de perto o desempenho biomecânico das espécies.

De modo geral, os resultados dessa tese fornecem importantes contribuições para a compreensão de padrões ecogeográficos intraespecíficos e relacionamentos de forma e função em mamíferos. Para a família Tayassuidae, trazem contribuições inéditas sobre a variação morfológica ao longo de toda a sua extensão geográfica e sobre os atributos biomecânicos relacionados às suas formas craniomandibulares. Essa tese, no entanto, não esgota as possibilidades de estudos, e outras questões ainda podem ser exploradas, como por exemplo: (i) a evolução da forma cranial nas espécies atuais e extintas e os papéis da filogenia e do ambiente; (ii) o papel da adequabilidade ambiental moldando a forma e o tamanho do crânio; e, (iii) as trajetórias fenotípicas de ambientes desérticos para florestais.

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