

Short Communication

Morphometry of *Catagonus stenocephalus* (Lund in Reinhardt 1880) (Artiodactyla: Tayassuidae) and taxonomical considerations about *Catagonus Ameghino 1904*

Rafaela Velloso Missagia^{1*}, Rodrigo Parisi-Dutra¹ & Mario Alberto Cozzuol²

1- PGG-Zoologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais – Av. Antônio Carlos, 6627, Pampulha, Belo Horizonte, MG.

2- Laboratório de Paleozoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais

*Corresponding author: rafaelamissagia@hotmail.com

Abstract

Factors such as the discordance on the choice of characters by different authors and the fragmentary condition of the majority of fossils are responsible for many issues on the taxonomy of the South American Tayassuidae. The extinct Tayassuidae species *Catagonus stenocephalus* (Lund in Reinhardt 1880) presents a confuse nomenclatural history and a questionable genus designation. The morphometric analysis performed in this study, based on craniomandibular and dental characters, allowed to distinguished three groups morphologically distant from each other within the *Catagonus* genus. This result highlights the need for more precise phylogenetic analysis for the definition of taxonomic groups in the South American Tayassuidae.

Keywords: *Catagonus stenocephalus*, morphometric analysis, Quaternary, taxonomy.

Introduction

The species *Catagonus stenocephalus* (Lund in Reinhardt 1880) is a medium to large size extinct tayassuid recorded from the middle to late Pleistocene in South American sediments (Gasparini 2013). It is known from several locations of South America: Argentina (Buenos Aires Province; Gasparini 2013), Uruguay (Sopas Formation, northwestern Uruguay; Gasparini et al. 2009b), Brazil (Touro Passo Formation, southeastern Brazil; Gasparini et al. 2009a; karstic caves of Lagoa Santa, Minas Gerais state; Fonseca 1979; Paula Couto 1975, 1981; Gruta dos Moura cave, in Tocantins state; Avilla et al. 2013; Gruta do Vale do Ribeira, Paraná State, southeastern Brazil; Dias da Silva et al. 2010) and Bolívia (Tarija Valley; Gasparini et al. 2010).

The species was originally described as *Dicotyles stenocephalus* by Lund in 1838 from fossil remains found in Brazilian caves and presents a confusing nomenclatural history. In 1930, it was included in the genus *Platygonus* Le Conte 1848 by Rusconi, which created the subgenus *Brasiliochoerus* to designate it. Subsequently, Paula Couto (1981) defines the species as *Brasiliochoerus stenocephalus*, as already proposed by Fonseca (1979). However, some authors pointed out the similarity between *Brasiliochoerus* and *Catagonus* (Wetzel 1977a; Menegáz & Ortiz Jaureguizar 1995). Since then, the species *C. stenocephalus* has been included in the genus *Catagonus* (Mayer & Wetzel 1986; Gasparini 2007, 2013; Gasparini et al. 2009a; Avilla et al. 2013).

Before the last phylogenetic review proposed by Gasparini (2007), only Rusconi (1930) showed concern about the systematics of the Tayassuidae, including both fossil and extant *taxa*. Instead, recent studies have focused on a molecular approach for phylogenetic inferences of extant species (Theimer & Keim 1998; Gongora & Moran 2005; Gongora et al. 2006).

This contribution aims to: (1) present a morphometric analysis of specimens of *Tayassu*,

Pecary and *Catagonus* genus; and (2) comment about the taxonomical validity of the genus *Catagonus*.

Material and Methods

Measurements were taken using digital callipers with 0.01 mm accuracy, and included craniodentary and dental traits (Table 1). They were submitted to a Canonical Variance Analysis (CVA), held at 2.17 PAST software (Hammer et al. 2012).

Table 1. Measurements used on the discriminant analysis.

Abbreviation	Measurement
HZA	Hight of the zygomatic arches
BZD	Bizygomatic diameter
WR	Width of the rostrum
MWR	Maximum width of the rostrum
WP	Widht of the palate
LDPREC	Length of the pre-canine diastema
LDPOSC	Length of the post-canine diastema
LM1-M3	Length of the upper molar series (from M1 to M3)
LPM2-PM4	Length of the upper premolar series (from PM2 to PM4)
LPM2	Length of second upper premolar
WPM2	Width of second upper premolar
LPM3	Length of third upper premolar
WPM3	Width of third upper premolar
LPM4	Length of fourth upper premolar
WPM4	Width of fourth upper premolar
LM1	Length of first upper molar
WM1	Width of first upper molar
LM2	Length of second upper molar
WM2	Width of second upper molar
LM3	Length of third upper molar
WM3	Width of third upper molar
Lm1-m3	Length of the lower molar series (from m1 to m3)
Lpm2	Length of second lower premolar
Wpm2	Width of second lower premolar
Lpm3	Length of third lower premolar
Wpm3	Width of third lower premolar
Lpm4	Length of fourth lower premolar
Wpm4	Width of fourth lower premolar
Lm1	Length of first lower molar
Wm1	Width of first lower molar
Lm2	Length of second lower molar
Wm2	Width of second lower molar
Lm3	Length of third lower molar
Wm3	Width of third lower molar
Hrmhpm2	Height of the mandibular ramus on the second lower premolar
Hrmhm1	Height of the mandibular ramus on the first lower molar
Hrmhm2	Height of the mandibular ramus on the second lower molar
Hrmhm3	Height of the mandibular ramus on the third lower molar
Hm2	Height of the second lower molar
Hm3	Height of the third lower molar

For the discriminant analysis, were included 21 *Catagonus* specimens, belonging to the South American species *C. stenocephalus*, *C. metropolitanus* Ameghino, 1904, *C. bonaerensis* (Ameghino, 1904), *C. wagneri* (Rusconi, 1930), *C. carlesi* (Rusconi, 1930) e *Catagonus* sp. Except for a *C. stenocephalus* skull housed at the scientific collection of Museu de História Natural e Jardim Botânico da Universidade Federal de Minas Gerais, the measurements of the specimens were taken from a unpublished PhD thesis (Gasparini 2007) and papers (Gasparini et al. 2009a; Gasparini et al. 2010; Avilla et al. 2013). Besides that, 88 specimens of *Tayassu pecari* and 60 specimens of *Peari tajacu* (Hall & Kelson 1959, Menegáz & Ortiz Jaureguizar 1995, Keuroghlian et al. 2004, Gasparini 2007, 2013) were included. These specimens of extant Tayassuidae are housed at the following scientific institutions: Museu de História Natural e Jardim Botânico da Universidade Federal de Minas Gerais, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Departamento de Zoologia da Universidade Federal de Minas Gerais. *Catagonus metropolitanus*, *C. bonaerensis*, *C. carlesi* and *Catagonus* sp. were grouped into a single category in CVA analysis due to the small number of specimens, which did not interfere on the graphic distribution of the specimens.

Results and Discussion

The first two canonical axis comprise 89% of the variance. The CVA indicated that the differences of means among groups were significant (Wilk's $\lambda = 0.00367$). The width of the second upper premolar (WPM2=-0.95) and the length of the third lower premolar (Lpm3=0.97) were the most discriminant characters for the first and second canonical axis, respectively.

The discriminant analysis shows three distinct groups within the *Catagonus* genus (Figure 1). The first (colored in green), comprising specimens of *C. stenocephalus*, is close to *Tayassu pecari*, taken into account their morphometric characters. The second group (colored in gray) comprises other four South American species of the genus (*C. bonaerensis*, *C.*

carlesi, *C. metropolitanus* and *Catagonus* sp.) and the third (colored in yellow) is represented by the five specimens of *C. wagneri*.

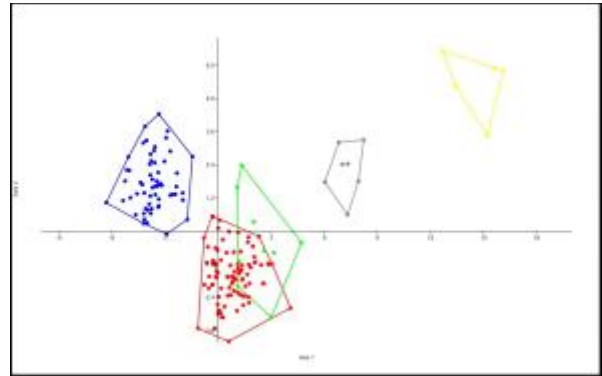


Figure 1. Projection of the scores of the first two canonical axis based on 40 craniomandibular and dental measurements, for *Tayassu*, *Pecary* and *Catagonus* genera. *T. pecari* (red), *P. tajacu* (blue), *C. stenocephalus* (green), *C. wagneri* (yellow) and *C. metropolitanus*, *C. bonaerensis*, *C. carlesi* and *Catagonus* sp. (gray).

Based on craniodentary and dental morphometric characters, it can be clearly seen on the graph that the *C. stenocephalus* specimens are closer to *T. pecari* than to the other species of the genus. Furthermore, the three *Catagonus* groups are more distant of each other than the extant Tayassuidae species.

The discriminant analysis by itself is taxonomically inconclusive, but it may allow certain considerations about the validity of the group as a genus. Menegáz and Ortiz Jaureguizar (1995) suggested that the diversity of *Platygonus* was increased artificially and that a further review should be performed to confirm the validity of some species of the genus, which was made by Gasparini (2007). The same authors questioned, based on the fragmentary condition of its remains, the allocation of *C. metropolitanus* and *C. bonaerensis* to the same genus of *C. wagneri*, an issue already mentioned by Reig (1981). Most South American *Catagonus* and *Platygonus* specimens are fragmentary, which can make it difficult to determine its taxonomic position. We can attribute this difficulty to two factors: (1) the amount of characters shared by *Catagonus* with *Platygonus* and *Tayassu* (Wetzel 1977a; Menegáz & Ortiz Jaureguizar 1995; Gasparini 2007); (2) the phylogenetic proximity

between *Platygonus* and *Catagonus*, which form a monophyletic group supported by two synapomorphies (mesodont dental growth and a cingulum developed on the labial side of the molar series) and a homoplasy (development of labial cingulum in the premolar series) shared with the extinct North American species *Mylohyus elmorei* Wright & Webb 1984 (Gasparini 2007). According to Wetzel (1977a), *Catagonus* evolved in the early Pleistocene from primitive *Platygonus* descendants which migrated to South America during the “Great American Biotic Interchange” (Woodburne 2010). Among the features common to both genera that indicates an adaptation to dry and open environments, we can cite: teeth with mesodont crown as adaptation to their browser diet, in contrast to the braquiodont crowns of the omnivorous genus *Tayassu*; distinct basicranial flexure with the long axis of the orbits located at a more oblique angle to the longitudinal axis of the skull; orbits set in a posterior position on the skull as result of the elongation of the snout; development of the olfactory and sinus chambers, as adaptations to environments subject to dust and wind, essential for the maintenance of the developed olfactory sense (Wetzel 1977a, 1977b; Menegáz & Ortíz Jaureguizar 1995; Gasparini 2007; Gasparini et al. 2009a; Avilla et al. 2013).

The last phylogenetic analysis performed for the group (Gasparini 2007) highlights the fact that, despite sharing many characteristics with *Platygonus*, *Catagonus* is defined only by homoplasies, all shared with at least one species of extant Tayassuidae, without any apomorphy that can distinguish this taxon.

Even considering the fragmentary state of most specimens of the genus, we suggest a reevaluation of morphological and morphometric characters of Tayassuidae to be compared with previous phylogenies (Wright 1989, 1998; Gasparini 2007). Besides that, we suggest to include postcranial characters, which has not received much attention on previous studies. A study comprising all the extant and extinct species is necessary to elucidate the phylogenetic relationships of the family

Tayassuidae, an important part of the New World Artiodactyla.

Acknowledgements

We would like to thank Germán M. Gasparini for providing the data acquired during his thesis, for his help with the taxonomical issues of the group and for the valuable comments on the early version of the manuscript; and FAPEMIG for financial support.

References

- Avilla, L.S.; Muller, L.; Gasparini, G.M.; Soibelzon, L.; Absolon, B.; Pêgo, F.B.; Silva, R.C.; Kinoshita, A.; Figueiredo, A.M.G. & Baffa, O. 2013. The northernmost record of *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Cetartiodactyla) and its palaeoenvironmental and palaeobiogeographical significance. *Journal of South American Earth Sciences* 42: 39-46.
- Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* 58: 1-291.
- Dias da Silva, D.; Sedor, F.A. & Oliveira, E.V. 2010. A presença de *Catagonus* e *Tayassu* (Artiodactyla, Tayassuidae) no Pleistoceno do Estado do Paraná, Brasil. In: 7º Simpósio Brasileiro de Paleontologia de Vertebrados, Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, pp. 112.
- Fonseca, J.S. 1979. Taiassuídeos do Pleistoceno de cavernas calcárias de Minas Gerais. Universidade Federal do Rio Grande do Sul, Master Thesis.
- Gasparini, G.M. 2007. Sistemática, biogeografía, ecología y bioestratigrafía de los Tayassuidae (Mammalia, Artiodactyla) fósiles y actuales de América del Sur, con especial énfasis en las especies fósiles de la provincia de Buenos Aires. Universidad Nacional de La Plata, Argentina, Ph.D. Thesis, 508 p.
- Gasparini, G.M. 2013. Records and stratigraphical ranges of South American Tayassuidae (Mammalian, Artiodactyla). *Journal of Mammalian Evolution* 20:57-68.

- Gasparini, G.M.; Kerber, L. & Oliveira, E. 2009a. *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Tayassuidae) in the Touro Passo Formation (late Pleistocene), Rio Grande do Sul, Brazil. Taxonomic and palaeoenvironmental comments. Neues Jahrb Geol Paläontol Abhandl 254 (3): 261-273.
- Gasparini, G.M.; Ubilla, M. & Tonni, E.P. 2009b. Tres especies de tayasuidos (*Catagonus wagneri*, *C. stenocephalus* y *Tayassu pecari*) en el Pleistoceno tardío del norte de Uruguay (Fm. Sopas). Ameghiniana 46 (4): 80.
- Gasparini, G.M.; Soibelzon, E.; Zurita, A.E. & Miño-Boilini, A.R. 2010. A review of the Quaternary Tayassuidae (Mammalia, Artiodactyla) from the Tarija Valley, Bolivia. Alcheringa. An Australasian Journal of Palaeontology 1: 7-20.
- Gasparini, G.M.; Ubilla, M. & Tonni, E.P. 2012. The Chacoan peccary, *Catagonus wagneri* (Mammalia, Tayassuidae), in the late Pleistocene (northern Uruguay, South America): paleoecological and paleobiogeographic considerations. Historical Biology 25 (5-6): 679-690.
- Gasparini, G.M.; Rodriguez, S.; Soibelzon, L.H.; Beilinson, E.; Soibelzon, E. & Missagia, R.V. 2014. *Tayassu pecari* (Link, 1795) (Mammalia, Cetartiodactyla): comments on its South American fossil record, taxonomy and paleobiogeography. Historical Biology 26 (6): 785-800.
- Gongora, J. & Moran, C. 2005. Nuclear and mitochondrial evolutionary analyses of Collared, White-lipped, and Chacoan peccaries (Tayassuidae). Molecular Phylogenetics and Evolution 34: 181-189.
- Gongora, J.; Morales, S.; Bernal J.E. & Moran, C. 2006. Phylogenetic divisions among Collared peccaries (*Pecari tajacu*) detected using mitochondrial and nuclear sequences. Molecular phylogenetics and evolution 41 (1): 1-11.
- Grubb, P. & Groves, C.P. 1993. The Neotropical Tayassuids *Tayassu* and *Catagonus*. In: Oliver, W.L.R. (Ed.) Pigs, Peccaries and Hippos Action Plan, IUCN, The World Conservation Union, pp. 5-7.
- Guilday, J. E. 1967. Differential extinction during Late-Pleistocene and Recent Times. In: Martin, P.S. & Wright, H.E. (Eds.) Pleistocene extinctions: the search for a cause. New Haven, Yale University Press, pp. 121-140.
- Hall, E.R. & Kelson, K.R. 1959. The mammals of North America. New York, The Ronald Press Co, 1083 p.
- Hammer, Ø.; Harper, D.A.T. & Ryan, P. 2012. PAST. Palaeontological Statistics, Version 2.17.
- Keuroghlian, A., Eaton D.P. & Longland W.S. 2004. Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biological Conservation 120: 411-425.
- Kraglievich, J.L. 1959. Rectificación acerca de los supuestos molares humanos fósiles de Miramar. Revista Instituto Antropología 1: 223-236.
- Le Conte, J.L. 1848. On *Platygonus compressus*: a new fossil pachyderm. Memoirs of the American Academy of Arts and Science, pp. 257-274.
- Marshall, L.G.; Berta, A.; Hoffstetter, R.; Pascual, R.; Reig, O.A.; Bombin, M. & Mones, A. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing quaternary of South America. Palaeovertebrata, Mémoires Extraordinaire, pp. 1-76.
- Mayer, J.J. & Wetzel, R.M. 1986. *Catagonus wagneri*. Mammalian Species 259: 1-5.
- Menégaz, A.N. & Ortiz Jaureguizar, E. 1995. Los artiodáctilos. In: Alberdi, M.T.; Leone, G. & Tonni, E.P. (Eds.) Evolución biológica y climática de la región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental. Madrid, Monografías CSIC, pp. 311-335.
- Paula Couto, C. de. 1975. Mamíferos fósseis do Quaternário do sudeste brasileiro. Boletim Paranaense de Geociências 33: 89-132.
- Paula Couto, C. de. 1981. On an extinct peccary from the Pleistocene of Minas Gerais. Iheringia Série Geologia, Porto Alegre 6: 75-78.

- Reig, O.A. 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Monographiae Naturae, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", pp. 1-162.
- Reinhardt, J. 1880. De I de brasilianske knoglehuler fundne Navlesvin – Arter. Videnskabelige Meddelelser fra den Naturhistoriske Forening I Kjobenhavn, Copenhagen, pp. 271- 301.
- Rusconi, C. 1930. Las especies fósiles argentinas de pecaríes y sus relaciones con las del Brasil y Norteamérica. Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia" 36: 121-241.
- Theimer, T.C. & Keim, K. 1998. Phylogenetic relationships of peccaries based on mitochondrial cytochrome *b* DNA sequences. Journal of Mammalogy 79: 566-572.
- Wetzel, R.M. 1977a. The extinction of peccaries and a new case of survival. Annals of the New York Academy of Sciences 288 (1): 538-544.
- Wetzel, R.M. 1977b. The Chacoan peccary, *Catagonus wagneri* (Rusconi). Bulletin of the Carnegie Museum of Natural History 3: 1-36.
- Wetzel, R.M.; Dubos R.E.; Martin R.L. & Myers P. 1975. *Catagonus*, an "extinct" peccary, alive in Paraguay. Science 189: 379-381.
- Woodburne, M.O. 1968. The cranial myology and osteology of *Dicotyles tajacu*, The Collared peccary, and its bearing on classification. Memoirs of the Southern California Academy of Science 7: 1-8.
- Woodburne, M.O. 2010. The great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution 17 (4): 245-264.
- Wright, D.B. & Webb, S.D. 1984. Primitive *Mylohyus* (Artiodactyla: Tayassuidae) from the late Hemphillian Bone Valley of Florida. Journal of Vertebrate Paleontology 3(3): 152-159.
- Wright, D.B. 1989. Phylogenetic relationships of *Catagonus wagneri*: sister taxa from the Tertiary of North America. In: Eisenberg J.F. & Redford K.H. (Eds.) Advances in Neotropical Mammalogy, Gainesville, Sandhill Crane Press, pp. 281-308.
- Wright, D.B. 1998. Tayassuidae. In: Janis, C.M.; Scott, K.M. & Jacobs, L.L. (Eds.) Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulate like Mammals, Cambridge, Cambridge University Press, pp. 389-400.