

Phylogenetic Systematics of Peccaries (Tayassuidae: Artiodactyla) and a Classification of South American Tayassuids

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Published online: 13 September 2016
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Abstract Tayassuidae is a family of pig-like Artiodactyla restricted to the New World. Despite its rich fossil history, they have received less attention from a taxonomic and phylogenetic perspective when compared to the Old World pigs, Suidae. In this study, we performed a computer assisted phylogenetic analysis using morphological and molecular data including fossil and extant Tayassuidae, using parsimony and Bayesian approaches. We recovered the monophyly of the family Tayassuidae, confirming previous proposals, as well as the monophyly of the subfamilies Hesperhyinae and Tayassuinae, and the genus *Platygonus*, which we placed in a new taxon of tribe level. The three living peccaries and a number of fossil species belong to a new, tribe level, monophyletic group. The genus *Catagonus* comes out as paraphyletic, leading us to propose to restrict the generic name to the type species, *C. metropolitanus*, and a new taxonomic arrangement for the remaining species previously included in

it, revalidating the genera *Brasiliochoerus* and *Parachoerus*, and describing a new genus, *Protherohyus*, gen. nov.

Keywords Tayassuidae · Phylogeny · *Catagonus* · *Protherohyus* gen. nov. · *Brasiliochoerus* · *Parachoerus*

Introduction

The family Tayassuidae is a successful group of pig-like artiodactyls known as peccaries or javelinas (Prothero 2009). Currently, three recent species are recognized, ranging from southern North America to north-central Argentina: *Tayassu pecari*, *Pecari tajacu*, and *Catagonus wagneri*. However, tayassuids were much more diverse in the past, with a history spanning over 37 million years, and with several fossil species described (Wright 1989; Gasparini 2007, 2013; Prothero 2015).

Fossil peccaries are relatively common in paleontological sites all over the American continent (Parisi Dutra et al. 2016), but studies focused on their taxonomy and phylogenetic relationships are relatively scarce. Wright (1998) presented a phylogenetic hypothesis for Tayassuidae using 15 characters, including both extant and extinct species, although the methodology used was not explicitly stated. He found both subfamilies, Hesperhyinae and Tayassuinae, to be monophyletic, and *Catagonus* to be sister group of *Pecari*, while *Tayassu* grouped with other South American fossil genera. Gongora and Moran (2005), using molecular data, made a phylogeny focused only on the three extant peccary species, recovering *C. wagneri* as sister group of *T. pecari*, and both of *P. tajacu*, unlike the proposition of Wright (1998). Two years later, Gasparini (2007), in an unpublished PhD thesis, made a comprehensive morphological phylogeny using 51 craniodental characters. This work remains the most inclusive phylogenetic analysis made for the group until now. Gongora et al. (2011), in an attempt to test the proposal of

Electronic supplementary material The online version of this article (doi:10.1007/s10914-016-9347-8) contains supplementary material, which is available to authorized users.

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Van Roosmalen et al. (2007) of a new extant species of *Pecari*, performed a phylogeographic analysis, confirming his previous results, and refuting the proposition of this new taxon. Prothero (2015) detailed a phylogenetic hypothesis for the subfamily Hesperhyinae, based on Wright's (1998) proposal, but without explaining the methodology used.

As it should be clear, the relationships between the many species of extinct and extant peccaries are not clearly established. Most of the South American genera of Tayassuidae are assumed to be monophyletic (e.g., Rusconi 1930; Wetzel et al. 1975; Menégaz and Ortiz Jaureguizar 1995), but, except for Gasparini (2007), but never have been formally tested in a phylogenetic framework. A comprehensive phylogenetic hypothesis is essential to clarify these and other issues pertaining to the evolutionary history of the family Tayassuidae. The objective of this paper is to perform the first comprehensive phylogenetic analysis using computational methods with both morphological and molecular data of extant and extinct Tayassuidae.

Material and Methods

Institutional abbreviations: MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; TMM: Texas Memorial Museum, Austin, Texas, USA; ZMK: Zoologisk Museum, Copenhagen, Denmark.

Datasets

The morphological dataset comprises two complexes of characters, the first from overall skull morphology, scored after direct observation of specimens or indirectly from the literature (e.g., Wright 1989; Pickford and Moya-Sola 1994; Gasparini 2007; Pickford 2011; Prothero and Pollen 2013; Prothero 2015), resulting in 64 characters for five extant and 23 fossil taxa of Suoidea (Table 1). Most of these characters are new or were revised from the original sources (see [Electronic Supplementary Material](#)). The second morphological complex, containing 30 characters, was added from the study of Orliac (2013) of the petrosal of Suoidea, and was revised with the available material. Hypotheses of primary homology (de Pinna 1991) were established for the binary and multistate characters, with the last being treated as unordered in all analysis. The complete dataset is available as [Electronic Supplementary Material](#).

To increase the amount of data for phylogenetic inferences, molecular sequences from six markers, three mitochondrial and three nuclear, were downloaded from GenBank for the five living taxa included in the present study (Table 2), including complete or partial sequences. Each marker was individually aligned using ClustalW, implemented in MEGA6 (Tamura et al. 2013), using the default settings.

Subsequently, manual adjustments were performed visually on the alignment. The molecular markers were concatenated using FASconCAT (Kück and Meusemann 2010). The combined matrix, including morphological and molecular datasets, was concatenated using Mesquite 2.75 (Maddison and Maddison 2011) and is available as [Electronic Supplementary Material](#).

Outgroup

In previous phylogenetic studies of the family Tayassuidae (e.g., Gongora and Moran 2005; Gasparini 2007), the genus *Sus* was selected as outgroup. However, recent works on early suids (Orliac 2013), and about petrosal anatomy of artiodactyls (O’Leary 2010) suggested that the genus *Perchoerus*, usually considered a tayassuid, has characters that appear to be more primitive in relation to both Tayassuidae and Suidae. For that reason, a non-suiodea taxon, *Cebochoerus* (Cebochoeridae), a basal Suiformes, *Archeotherium* (Entelodontidae), and a Suoidea, *Taucanamo pygmaeum* (Paleochoeridae) were included, along with two extant suids *Sus scrofa* and *Potamochoerus porcus*.

Ingroup

Specimens of both extant and fossil species of peccaries were included as the ingroup. Additional material described by Gazin (1938), Prothero and Pollen (2013), and Prothero (2015) were also included (Table 2). Whenever possible, we included the type material of each taxon. The taxa represented only by very fragmentary materials (e.g., *Platygonus marplatensis*, *Platygonus kraglievichi*, *Cynorca sociale*) were excluded from the analysis, with the exception of *Catagonus metropolitanus*, which is the type species of *Catagonus* (see Discussion below). The type material of *Platygonus cinctus* is missing (besides it consists of isolated teeth), so that we excluded it from our analysis.

Pecari maximus, described by Van Roosmalen (2007), was not included because, as Gongora et al. (2011) demonstrated, it is a synonym of *Pecari tajacu*. Other named species of *Pecari*, such *P. angulatus* and *P. crassus* (Groves and Grubb 2011), are also not widely accepted. The Miocene tayassuids *Sylvochoerus woodburnei* and *Waldochoerus bassleri*, described by Frailey and Campbell (2012), were also not included. The chronological information about the bearing sediments of those remains in the Amazonian region of Peru is not accurate, and the taxonomic allocation of these specimens is questionable (Parisi Dutra et al. in prep.).

Phylogenetic Analyses

A combined morphological and molecular data maximum parsimony analysis was conducted in TNT (Goloboff et al. 2008), using implied weighting (Goloboff 1993) parameters.

Table 1 Taxa included in the present work, their authorship, and geologic age. When the type specimen was analyzed, it is marked in the last column

Taxon	Authorship	Age	Type specimen
<i>Cebochoerus</i>	Gervais, 1852	Middle-Late Eocene	
<i>Archaeotherium</i>	Leidy, 1850	Late Eocene - Late Oligocene	
<i>Tauncanamo pygmaeum</i>	(Depéret, 1892)	Middle Miocene - Late Miocene	
<i>Perchoerus</i>	Leidy, 1869	Late Eocene - Early Oligocene	
<i>Dyseohyus frickii</i>	Stock, 1937	Middle Miocene	x
<i>Sus scrofa</i>	Linnaeus, 1758	Middle Miocene - Recent	
<i>Potamochoerus porcus</i>	Linnaeus, 1758	Late Miocene - Recent	
<i>Hesperhys vagrans</i>	Douglass, 1903	Early Miocene - Late Miocene	x
<i>Desmathyus pinensis</i>	Matthew, 1907	Early Miocene	x
<i>Wrightohyus yatkolay</i>	Prothero, 2015	Early Miocene	x
<i>Lucashyus coombsae</i>	Prothero, 2015	Early Miocene	x
<i>Stuckyhyus siouxensis</i>	(Peterson, 1905)	Early Miocene - Middle Miocene	x
<i>Prosthennops xiphodonticus</i>	Woodburne, 1969	Middle Miocene	x
<i>Pecari tajacu</i>	(Linnaeus, 1758)	Middle Pleistocene - Recent	
<i>Tayassu pecari</i>	(Link, 1795)	Middle Pleistocene - Recent	
<i>Catagonus stenocephalus</i>	(Lund in Reinhardt, 1880)	Middle Pleistocene - Late Pleistocene-Earliest Holocene	x
<i>Catagonus carlesi</i>	(Rusconi, 1930)	Middle Pleistocene	x
<i>Catagonus wagneri</i>	(Rusconi, 1930)	Late Pleistocene - Recent	x
<i>Catagonus brachydontus</i>	(Dalquest and Mooser, 1980)	Middle Miocene	
<i>Skynnerhyus shermerorum</i>	(Prothero and Pollen, 2013)	Late Miocene	x
<i>Macrogenis crassigesis</i>	(Gidley, 1904)	Middle Miocene - Late Miocene	x
<i>Mylohyus elmori</i>	(White, 1942)	Middle Miocene - Early Pliocene	
<i>Mylohyus nassutus</i>	(Leidy, 1869)	Pleistocene	
<i>Platygonus pearcei</i>	Gazin, 1938	Early Pliocene - Early Pleistocene	
<i>Platygonus cumberlandensis</i>	Gidley, 1920	Pleistocene	
<i>Platygonus compressus</i>	Le Conte, 1848	Early Pleistocene - Middle Pleistocene	x
<i>Platygonus scagliai</i>	(Reig, 1952)	Late Pliocene	x
<i>Platygonus chapadmalensis</i>	(Ameghino, 1908)	Late Pliocene	x

Sensitivity analyses were performed for different values of the concavity function (k) using Mirande's script (Mirande 2009). The values were explored using the default configuration, with distortions that varied from 50 % to 90 %, with 11 categories of k values. We performed sensitivity analyses in the morphological and molecular datasets separately, and as it returned different ranges of values of k, we assumed that the two partitions differed in their degree of homoplasy. Besides that, the partitions also differ in the degree of missing data, and

for these reasons we chose to apply to each of them its respective estimated value of k. The analysis was conducted with extended implied weighting (Goloboff 2014), with each dataset having its own k value, being the degree of homoplasy calculated independently for each character and not as an average for the whole partition. For the molecular dataset, we excluded all parsimony uninformative (invariable or autapomorphic) characters of the k's estimation and phylogenetic analysis. We also evaluated the possibility of giving

Table 2 Molecular markers and their respective accession numbers on GenBank for the five living species included in our analysis

Taxa/marker	COI	CytB	D-loop	K-Casein	Thyrotropin	Tyrosinase
<i>Sus scrofa</i>	576,597,389:6611–8155	576,597,389:15,440–16,579	576,597,389:1–1275	55,742,765	14,993,367	9,581,876
<i>Potamochoerus porcus</i>	470,235,492:5339–6883	470,235,492:14,168–15,307	470,235,492:15,440–16,693	-	-	-
<i>Catagonus wagneri</i>	-	1,655,916	47,088,240	47,586,879	47,586,905	51,320,042
<i>Tayassu pecari</i>	327,504,541	1,655,920	19,773,580	47,586,880	47,586,906	51,320,040
<i>Pecari tajacu</i>	223,976,148:5335–6879	223,976,148:14,162–15,301	19,773,580	47,586,881	47,586,904	51,320,038

equal weights only to the molecular partition, as it presents a massive amount of missing data. The most parsimonious tree was searched with Traditional Search (100 RAS + TBR; + TBR). Branch support was assessed with Relative Bremer Support (Goloboff and Farris 2001). Synapomorphies were mapped on the resulting topology, using the unambiguous optimization in the software Winclada (Nixon 1999–2002). To access the stability of taxa in the most parsimonious tree, we used the script “iterpcr” (Pol and Escapa 2009).

The Bayesian combined analysis was conducted on MrBayes 3.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The dataset was partitioned, with each of the six molecular markers and the morphological data having its parameters estimated independently, except for branch lengths. For each marker, a model choice was performed on jModelTest2 (Guindon and Gascuel 2003; Darriba et al. 2012) using Akaike information criterion (AIC) and Bayesian information criteria (BIC), using the default settings. The models suggested for each criterion are presented in Table 2. When faced with different suggestions between AIC and BIC, the model chosen was the parameter richer, adjusting to the options available for implementation in MrBayes 3.2. The Mk(v) model of Lewis (2001) was used for the morphological data, associated with a Gamma distribution to account for the rate heterogeneity between characters. The coding option was set to “=variable,” to avoid the coding bias that is usually present in morphological datasets and can return incorrect branch length estimations (Lewis 2001).

Two runs comprising four chains with gradual increasing temperature were performed, with the temperatures following the default of MrBayes 3.2. The search was performed through five million generations, with the sampling frequency = 100. For the summaries (SUMP and SUMT), a burnin of 25 % of the samples was defined. The convergence of the two independent runs was checked using MrBayes summary and Tracer v1.6 (Rambaut et al. 2014), inspecting the standard deviation of split frequencies, ESS and PSRF (see the outputs in the [Electronic Supplementary Material](#)). We accessed branch support through posterior probabilities (Huelsenbeck et al. 2001).

The graphical editing of the most parsimonious and the majority rule tree were performed with FigTree v1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Results

Maximum Parsimony Analysis

The sensitivity analysis returned very stable values of k for each dataset, showing that, for the explored ranges of distortion, the different values of k change little or do not change the topology obtained. For the molecular dataset (range of k :

0.190–1.710), all trees were identical (SPR diff. = 0) and we set $k = 1$. There was no difference in topology or fit values when using equal weights or $k = 1$ for the molecular dataset. In the case of the morphological dataset, nine of 11 values of k are in a “stability zone” (stable range of k : 0.976–4.448), meaning that any value in this range of k values explored are an equally justified choice because they will result in the same topology. The other two values (5.998, 8.787) defined trees with four SPR steps away from the ones in the stability zone (SPR diff. = 4), and seemed to be idiosyncratic results, obtained only if we assume that a homoplasy carries 85 % or more of the phylogenetic information of a perfectly hierarchical character. Due to these results, we set $k = 3$ in the morphological partition (see the outputs in the [Electronic Supplementary Material](#)).

The Maximum Parsimony analysis (MP) of the combined data returned a single most parsimonious tree with fit = 79.00714 (Fig. 1). The topology of this tree is completely resolved and, although some clades are not well supported, there were some exceptions (see Discussion below).

The MP topology recovered a monophyletic Suoidea (*Perchoerus* + *Taucanamo pygmaeum* + Suidae + Tayassuidae), supported by two unambiguous synapomorphies [72(1), 93(1)] and two ambiguous [32(1), 48(0)] (RBS = 11). Except for the Paleochoeridae *Taucanamo pygmaeum*, the group formed by the genus *Perchoerus*, Suidae, and Tayassuidae is united by a single unambiguous synapomorphy [68(1)] (RBS = 34). Suidae (*Sus scrofa* and *Potamochoerus porcus*) is recovered as sister group of Tayassuidae, with the whole clade being supported by seven unambiguous synapomorphies [6(0), 13(0), 17(1), 21(1), 22(1), 27(1), 91(1)] (RBS = 20). The Tayassuidae clade (*Dyseohyus frickii* + Hesperhyinae + Tayassuinae) is supported by a single unambiguous synapomorphy [93(2)] (RBS = 10). Inside of Tayassuidae, the clade uniting Hesperhyinae and Tayassuinae is supported by two ambiguous synapomorphies [40(1), 72(0)] (RBS = 10). Hesperhyinae is supported by one ambiguous [73(1)] and one unambiguous [74(0)] synapomorphy (RBS = 42). Tayassuinae (*Prosthennops xiphodonticus* (= *Dyseohyus stirtoni*, see Wright 1998) + tribe Tayassuini + tribe Platygonini (for tribes, see discussion below)) is supported by two unambiguous [34(2), 41(1)] (Fig. 2) and two ambiguous [43(1), 54(1)] (RBS = 10) synapomorphies. The group uniting the two tribes is supported by a single unambiguous [55(1)] and one ambiguous [59(2)] synapomorphy (RBS = 30). The tribe Tayassuini (*Pecari tajacu* (*Tayassu pecari* (“*Catagonus*” *stenocephalus* (“*Catagonus*” *wagneri* + “*Catagonus*” *carlesi*))), is supported by a single ambiguous synapomorphy [67(1)] (RBS = 52). With the exception of *P. tajacu*, the remaining taxa are united by three morphological synapomorphies, wherein one unambiguous [60(1)] (Fig. 3), two ambiguous [61(1), 73(0)], and 59 nucleotide substitutions (RBS = 39).

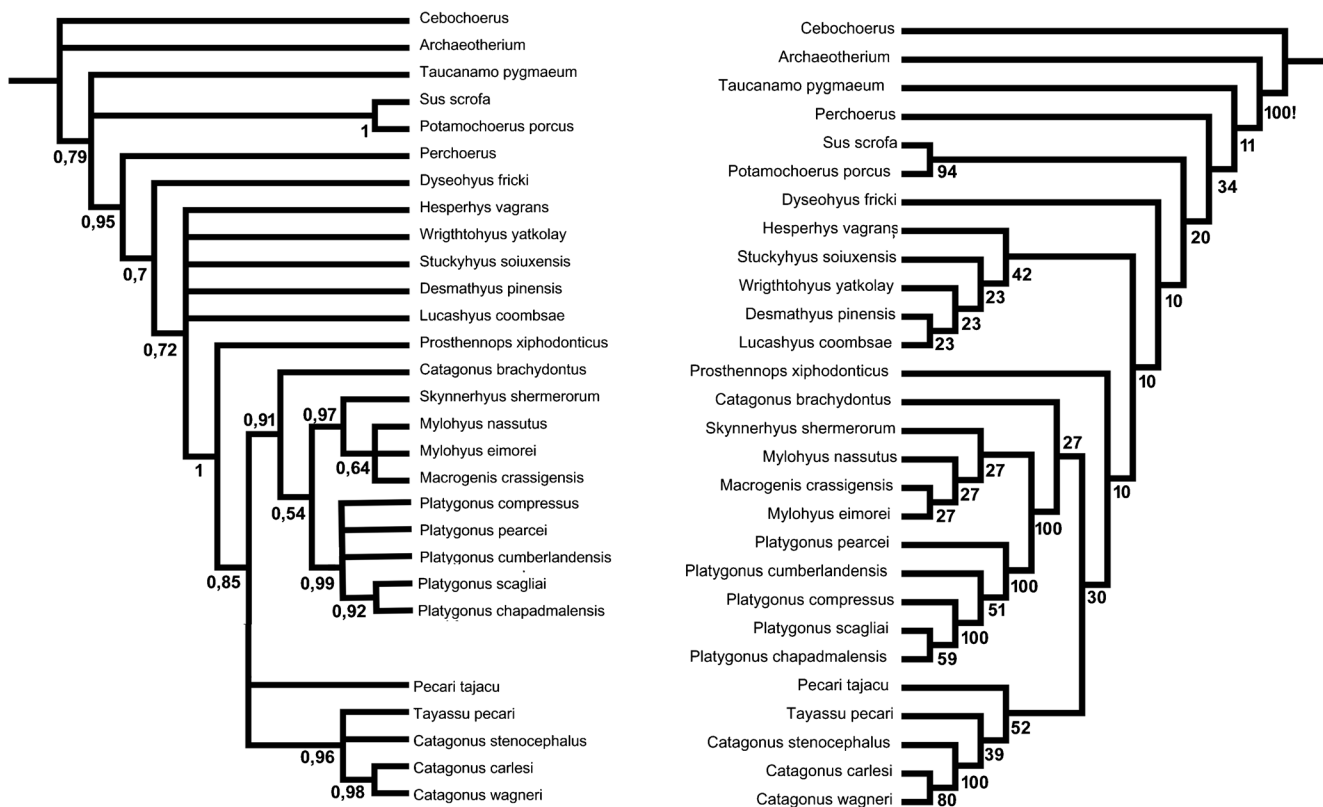


Fig. 1 Single most parsimonious tree from implied weighting analysis with Relative Bremer Supports (RBS) on each node (*Right*) and Bayesian inference with posterior probability on each node (*Left*)

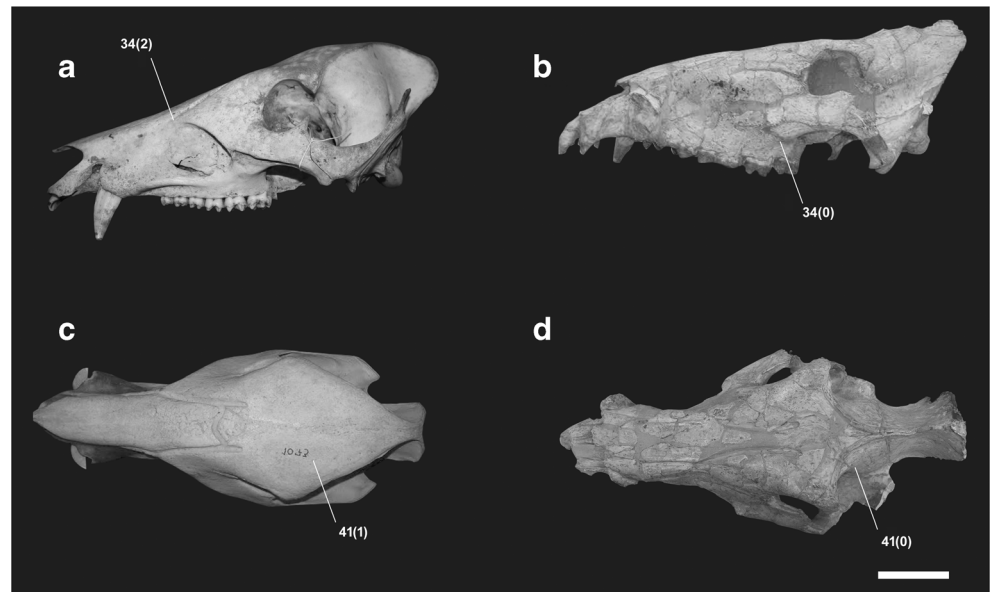
When *Catagonus metropolitanus*, the type species of the genus *Catagonus*, was included in the analyses, the consensus of each analysis (MP and BI) recovered it inside Tayassuini in a polytomy with the other taxa. In the analysis using “iterpcr” script, it became evident that *Catagonus metropolitanus* is an unstable taxon due the lack of scoring for several characters (see the output in the [Electronic Supplementary Material](#)). The Platygonini tribe (“*Catagonus*” *brachydontus* ((*Skynnerhyus shermerorum* (*Mylohyus nasutus* (*Mylohyus elmorei* + *Macrogenis crassigenis*))) (*Platygonus pearcei* (*Platygonus cumberlandensis* (*Platygonus compressus* (*Platygonus chapadmalensis* + *Platygonus scaglii*)))))) is supported by three unambiguous [36(0), 54(2), 64(1)] (Figs. 3 and 4), and a single ambiguous [42(0)] (RBS = 27) synapomorphy. With the exception of *Catagonus brachydontus*, the remaining taxa are grouped by one unambiguous [30(1)] and an ambiguous synapomorphy [43(0)] (RBS = 100). A clade composed exclusively by Miocene taxa (*Skynnerhyus shermerorum* (*Mylohyus nasutus* (*Mylohyus elmorei* + “*Macrogenis*” *crassigenis*))) is supported by three unambiguous synapomorphies [36(3), 60(2), 61(2)] (RBS = 27). The group of flat-headed peccaries (*Platygonus pearcei* (*Platygonus cumberlandensis* (*Platygonus compressus* (*Platygonus chapadmalensis* + *Platygonus scaglii*)))) is supported by one unambiguous [56(2)] and four ambiguous [50(2), 57(1), 63(1)] (RBS = 100) synapomorphies.

Bayesian Inference

The topology recovered by the Bayesian inference (BI), through the majority rule tree (50 %), showed great similarity with the MP analysis (see the [Electronic Supplementary Material](#)), also presenting some major clades retrieved with parsimony, with minor differences. The values of posterior probability were low (<0.95) for the majority of the recovered clades (see Discussion below), with some important exceptions.

As in the MP analysis, Suoidea was recovered as monophyletic (PP = 0.79), composed of *Taucanamo pygmaeum*, Suidae (*Sus scrofa* + *Potamochoerus porcus*; PP = 1.00), and Tayassuidae (PP = 0.95). Different from the MP analysis, *Taucanamo pygmaeum* emerged in a polytomy with the other two clades. In contrast with what we recovered in MP, BI placed the taxon *Perchoerus* among the Tayassuidae. In Tayassuidae, *Perchoerus* diverged first, followed by *Dyseohyus fricki* + remaining taxa (PP = 0.70). The next clade was recovered in a polytomy with the five taxa that were recovered in MP as Hesperhyinae, plus Tayassuinae (PP = 0.72). The next clade to diverge is Tayassuinae, and it is maximally supported in the BI (PP = 1.00) and, as in MP tree, is composed of *Prosthenops xiphodonticus* and the remaining Tayassuinae (PP = 0.85). Inside Tayassuinae, BI also recovered the two tribes, each relatively well supported. The

Fig. 2 Synapomorphies supporting Tayassuinae. **a, c**, *Tayassu pecari* (MLPzool 1073), lateral and dorsal view; **b, d**, *Desmathyus pinensis* (AMNH 12936), lateral and dorsal view. Character 34 - Position of the facial crest: (0) Horizontal; (2) reaching the naso-maxillary suture; Character 41 - Cranium enlargement: (0) Absent; (1) Present



major difference here is the position of *Pecari tajacu*, which falls outside Tayassuini, in a polytomy with the two tribes. Moreover, the remainder of the tribe Tayassuini (PP = 0.96) showed a different internal resolution when compared to what was observed using parsimony criterion. The tribe Platygonini (PP = 0.91) included the two clades present in MP analysis, plus “*Catagonus*” *brachyodontus*, which diverges before the split between the tribes. The clade with exclusive Miocene taxa received strong support (PP = 0.97) but, different from the parsimony tree, the relation between *Mylohyus* and “*Macrogenis*” was not resolved. The flat-headed peccaries were also well supported as a monophyletic group (PP = 0.99), with the internal relations less resolved than in

MP, although the two South American flat-headed peccaries, *Platygonus scagliai* and *Platygonus chapadmalensis*, were recovered as sister groups in both analyses.

Discussion

Phylogeny of the Family Tayassuidae

The MP and BI analyses recovered mostly similar topologies, supporting some of the major clades, but differing in the position of a few taxa, most notably the position of *Perchoerus* and *Pecari tajacu*, the existence of the subfamily

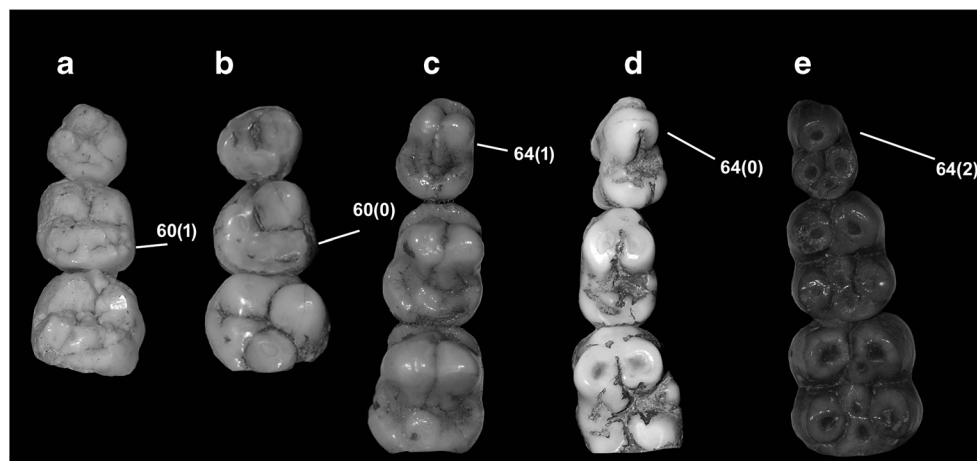
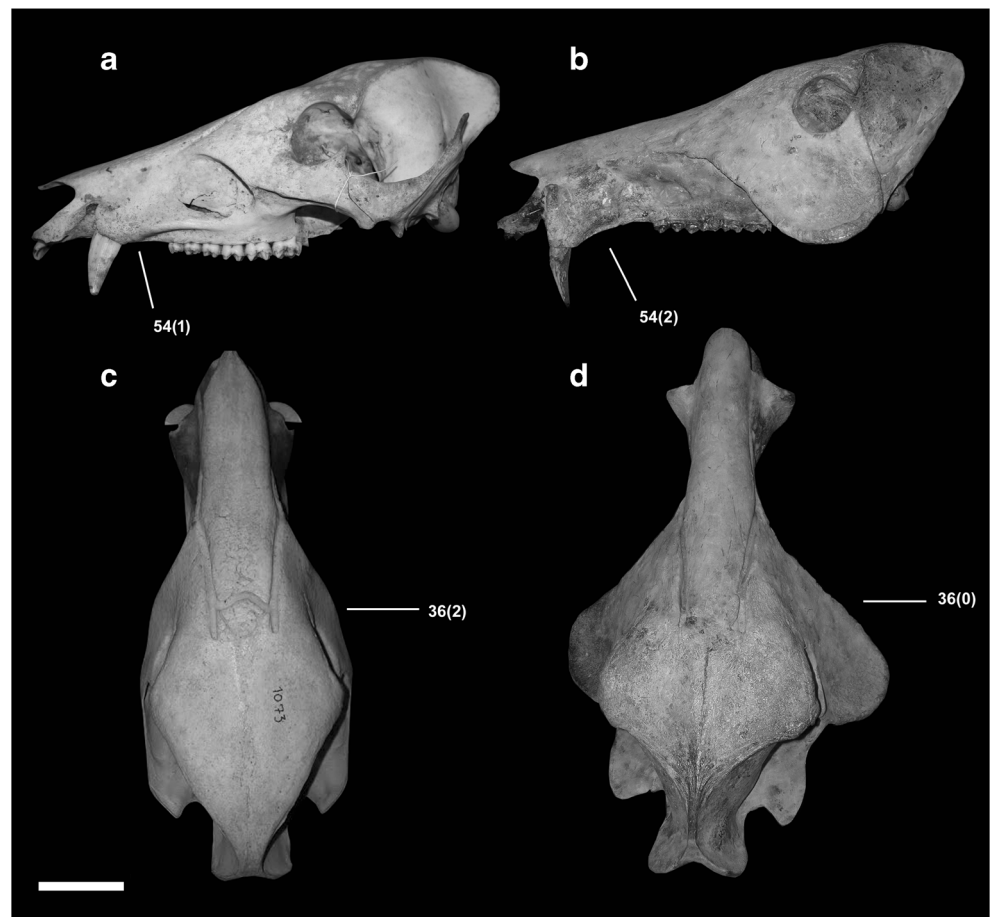


Fig. 3 Synapomorphies supporting the grouping of (*Tayassu pecari* (“*Catagonus*” *stenocephalus* (“*Catagonus*” *wagneri* + “*Catagonus*” *carlesi*))) **a**, *Pecari tajacu* (MACNzool 8.x.97.4) left upper molar series; **b**, *Tayassu pecari* (MLPzool 1073) left upper molar series; **c**, *Platygonus*

compressus (FM 45724) left lower premolar series; **d**, *Pecari tajacu* (MACNzool 8.x.97.4) left lower premolar series; **e**, *Mylohyus* sp. (FM 23504) right lower premolar series. Character 60 - (0) Absent; (1) Reduced; Character 64 - (0) One cusp; (1) Two cusps; (2) Three to four cusps

Fig. 4 Synapomorphies supporting Platygonini. **a, c**, *Tayassu pecari* (MLPzool 1073), lateral and dorsal view; **b, d**, *Platygonus cumberlandensis* (AMNH FM 27871) lateral and dorsal view. Character 36 - Zygomatic process: (0) Enlarged jugal bone, with the ventral margin strong to moderate expanded; (2) Flat jugal bone without enlargement. Character 54 - Upper postcanine diastema: (0) Absent; (2) Long (greater length than the molar series)



Hesperhyinae, and the internal resolution of a few groups. The Mk(v) model and its implementation on MrBayes allows modelling rate heterogeneity between characters, rate asymmetry between character-state changes, and can deal with coding bias in morphological datasets (Lewis 2001; Ronquist et al. 2011; Wright and Hillis 2014; contra Spencer and Wilberg 2013). To date, only a few have explored how the change in those parameters affects the accuracy of topology inference (Wagner 2012; Harrison and Larsson 2015; Wright et al. 2015), demanding further attention. For this reason, although the BI topology is similar to the tree recovery by the MP, the phylogenetic and taxonomic discussion of this work is based primarily on the MP. The BI results are discussed when it differs from parsimony analysis to the point of having different taxonomic implications.

Although many clades are not well supported, as much of the material are represented by fragmentary fossils and do not have molecular data available, this was expected. We think that the lack of phylogenetic studies with the family Tayassuidae using an explicit phylogenetic methodology hampers our knowledge of the evolution and classification of this group, and compels us to accept the results presented here, even if not so well supported.

Despite not being the main scope of our work, the basal position of *Taucanamo*, recovered in both topologies, must be noted. This European genus is frequently placed inside the Tayassuidae (McKenna and Bell 1997), while some studies included it in Suidae (Harris and Liu 2007) or in the family Palaeochoeridae (Van der Made 1997). Liu (2003), Orliac et al. (2010), and Orliac (2013), using a multiple source character approach, also recovered *Taucanamo* in a basal position in relation to Tayassuidae, thus rejecting the idea that it represents an “Old World” Tayassuidae.

The topologies resulting from the MP and BI analyses recovered the genus *Perchoerus* in different positions. In the MP analysis, *Perchoerus* was recovered as sister group of the Suidae + Tayassuidae clade, as in Orliac (2013) using petrosal bone characters. However, BI retrieved *Perchoerus* as the first divergence of the Tayassuidae. Gasparini (2007) also recovered it in a basal position of the Tayassuidae clade, sharing with *Dyseohyus frickii* some primitive characters, such as the low complexity of the molar morphology. The taxonomic history of the Eocene tayassuids is still controversial, and only a few studies have been conducted about it (Prothero 2009).

The family Tayassuidae consists of two lineages, one composed by the stem Tayassuidae *Dyseohyus frickii*, and a clade

including the remaining taxa in the analysis. The genus *Dyseohyus* was described from North American Miocene material, and includes a single species (*D. frickii*). It shares a more posterior position of choana with all others Tayassuidae. The position of the external auditory meatus at the same level of the glenoid fossa is here considered a plesiomorphy that reappeared in this taxon, after being lost after *Perchoerus*.

The subfamily Hesperhyinae was recovered as monophyletic in our MP analysis, corroborating Prothero (2015), who diagnosed it based on a shared presence of a palatine structure called by him “plesiochoanal chamber” or “plesiochoanal fossa.” This character is a synapomorphy in our analysis that supports this clade along with the sagittal crest restricted to the parietal bone. The internal relationships in the subfamily are completely resolved, but with little support for the relationships found. As the BI analyses does not offer support for a monophyletic Hesperhyinae, we think that more studies are needed to elucidate their phylogenetic relationships.

The other clade, which includes the remaining Tayassuidae, constitutes the subfamily Tayassuinae, whose content is here revised and its diagnosis emended (see below). This clade is composed of a basal Tayassuinae, *Prosthennops xiphodonticus*, and a clade including two tribes, one of which is named and described here. The position of the facial crest and an enlargement of the crania are the main synapomorphies of this subfamily. In the BI tree, *P. tajacu* emerges in a polytomy along with the two other clades of crown Tayassuinae. In the MP analysis, *P. tajacu* groups with the Tayassuini (see taxonomic discussion for the definition of the tribe), a position supported by a single ambiguous synapomorphy (presence of accessories cusps in the lower premolar series). As the available biostratigraphic evidence points out that the collared peccary is not older than middle Pleistocene (Gasparini 2013), it seems plausible to consider its position in MP tree as more accurate. This implies that the extant peccaries are closely related to each other, although not forming an exclusive monophyletic group. Gasparini (2007) found a closer relation between *Tayassu pecari* and *Pecari tajacu* than with *Catagonus wagneri*, which nested within what was considered by him, members of the genus *Catagonus*. This led Gasparini to consider *Pecari tajacu* congeneric with *Tayassu pecari* in the genus *Tayassu*, but, as our analysis shows, *Pecari tajacu* is more likely the first offshoot member of its tribe, and, then, supports a generic separation of it from others members of the tribe, which is in agreement with recent molecular phylogenies (Gongora and Moran 2005; Gongora et al. 2011) and taxonomic practice (Grubb 2005).

Tayassu pecari appears as the sister group of other three species usually included in the genus *Catagonus*: “*Catagonus*” *stenocephalus*, “*Catagonus*” *carlesi*, and “*Catagonus*” *wagneri*. They share the presence of a reduced hypocone in the upper premolar series and a parietal sagittal

crest as morphological synapomorphies. It is noteworthy that the other reputed *Catagonus* species (“*Catagonus*” *brachydontus*) included in our analysis are not part of this clade. Gasparini (2007) recovered a monophyletic *Catagonus*, but with the support being achieved only via ambiguous synapomorphies. Gasparini (2007) included the type species, *Catagonus metropolitanus*, in his phylogenetic analysis. We explored the inclusion of this fragmentary taxon (see taxonomic discussion below) in both analyses, but we decided to exclude it from the final analysis because of the lack of many important sources of character information. In the analyses with maximum parsimony, we verified that the taxon was completely unstable inside the tribe, emerging as sister group of any other taxa in the MPTs. Moreover, we think that there are good reasons to revise the taxonomy of *Catagonus* (see more in the taxonomic discussion below). In the BI, *Tayassu pecari* is not the first to emerge, but appears in a polytomy with “*Catagonus*” *stenocephalus* and the strongly supported clade of “*Catagonus*” *carlesi* and “*Catagonus*” *wagneri*.

In the other tribe, the Platygonini (see taxonomic discussion below for the definition of the tribe), the position of “*Catagonus*” *brachydontus* was recovered as the sister group of the remaining taxa. A long, superior postcanine diastema, the expansion of the jugal, a PM2 with two cusps, and an acuminate nasal fossae are the morphological traits shared by the Platygonini clade. With the exclusion of “*Catagonus*” *brachydontus*, the remaining Platygonini share an accentuated postorbital depression. The presence of two well-supported clades (*Skynnerhyus*-*Mylohyus*-*Macrogenis* clade and the genus *Platygonus*) is common to both analyses, despite differences in the internal resolution. It is important to note that the two South American flat-headed peccaries included in our analysis comprise a well-supported monophyletic group, in agreement with their South American distribution. The *Skynnerhyus*-*Mylohyus*-*Macrogenis* clade shares a lateral expansion of the jugal forming a “wing” in the zygomatic arch, and a developed hypocone in the PM3–4, while the genus *Platygonus* shares a unique bunolophodont crown morphology on the molars. Gasparini (2007) also recovered a monophyletic *Platygonus*, although not closely related with *Skynnerhyus*, *Mylohyus*, or *Macrogenis*, and as sister group of the genus *Catagonus*. The close relationship between *Mylohyus* and *Macrogenis* was also retrieved by Gasparini (2007). In our analysis, *Skynnerhyus* is also part of this group. It is important to note that the genus *Mylohyus* was recovered as paraphyletic in our analysis, requiring more morphological and taxonomic studies.

Taxonomic Arrangements

The topology resultant of our phylogenetic analysis shows significant differences in taxa relationships when compared to others works (Wright 1989; Gongora and Moran 2005;

Gasparini 2007). Some groups in our analyses are para-polyphyletic, and suggest the necessity of expressive changes in tayassuid classification. For these reasons, a new taxonomic arrangement is proposed below. The characters of the emended diagnosis are the synapomorphies of the resultant topology.

Systematics

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1838

Suborder Suiformes Jaekel, 1911

Infraorder Suoidea Gray, 1821

Family Tayassuidae Palmer, 1897

Subfamily Tayassuinae Palmer, 1897

Synonyms:

Dicotylinae Leidy, 1869

Tayassuidae Palmer, 1897

Tayassuinae Hay, 1902

Emended Diagnosis: The most anterior part of the facial crest reaches the naso-maxillary suture, differing from the Hesperhyinae, in which the facial crest reaches only above the infraorbital foramen. The angle formed by the anterior portion of the facial crest and the molar series is about 45°. The origin of the naso-labial elevator, superior labial, and canine muscles are well developed, forming a hollow surface. An enlargement of the crania is also a diagnostic character among the Tayassuinae.

Revised content: *Prosthennops xiphodonticus* Woodburne, 1969; *Pecari tajacu* (Linnaeus, 1758); *Tayassu pecari* (Link, 1795); *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880); *Parachoerus wagneri* (Rusconi, 1930); *Parachoerus carlesi* (Rusconi, 1930); *Protherohyus* gen. nov. *brachydontus* (Dalquest and Mooser, 1980); *Skynerhyus shermerorum* (Prothero and Pollen, 2013); *Mylohyus nasutus* (Leidy, 1869); *Mylohyus eimorei* (White, 1942); *Macrogenis crassigenis* (Gidley, 1904); *Platygonus pearcei* Gazin, 1938; *Platygonus cumberlandensis* Gidley, 1920; *Platygonus compressus* Le Conte, 1848; *Platygonus chapadmalensis* (Ameghino, 1908); *Platygonus scagliai* (Reig, 1952); *Catagonus metropolitanus* Ameghino, 1904; ?*Catagonus bonaerensis* (Ameghino, 1904); ?*Platygonus marplatensis* Reig, 1952; ?*Platygonus kraglievichi* Rusconi, 1930; ?*Platygonus cinctus* (Ameghino, 1886).

Remarks: Gasparini (2007) considered the species “*marplatensis*,” “*kraglievichi*,” and “*cinctus*” as members of the genus *Platygonus*. All these three species share bunolophodont mesodont molars and bicuspid premolars with *Platygonus*. This also seems to be the case of *Catagonus bonaerensis*, which has similar tooth morphology to the genus “*Catagonus*” (sensu Gasparini 2007). For this reason, we decided to include these species in the subfamily Tayassuinae with doubt, and suggest that more morphological analyses are needed.

Tribe Tayassuini Palmer, 1897

Diagnosis: Tayassuinae with a short postcanine upper diastema and presence of accessories cusps in the inferior premolar series.

Revised content: *Pecari tajacu* (Linnaeus, 1758); *Tayassu pecari* (Link, 1795); *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880); *Parachoerus wagneri* (Rusconi, 1930); *Parachoerus carlesi* (Rusconi, 1930); *Catagonus metropolitanus* Ameghino, 1904; ?*Catagonus bonaerensis* (Ameghino, 1904).

Remarks: The tribe Tayassuini is composed of a Pleistocene/Recent South American lineage of pig-like peccaries. Currently, the species *P. tajacu* and *T. pecari* are widely distributed in the American Continent. *Pecari tajacu* has the largest geographic distribution of any Tayassuini, being recorded from north-central Argentina to southwestern USA, while *T. pecari* is distributed from northern Argentina to southern Mexico (Gasparini 2013; Gasparini et al. 2014). *Parachoerus wagneri* has a restricted geographical distribution, being endemic to the dry Chaco in western Paraguay, southeastern Bolivia, and northern Argentina (Gasparini et al. 2006). All three extant species belong to this tribe. Bunodont teeth, brachydont crown morphology, and a cranium with no postorbital depression, are shared characters of the tribe.

Genus *Catagonus* Ameghino, 1904

Type species: *Catagonus metropolitanus* Ameghino, 1904

Emended diagnosis: Tayassuini with a laterally expanded rostrum, well-developed upper canines, and developed hypocone in the PM3–4.

Remarks: The genus *Catagonus* was described by Ameghino in 1904, based on a fragmentary maxillary remain found in Buenos Aires Province, Argentina. This fossil fragment was found in early-middle Pleistocene sediments (Ensenadan stage; see Cione et al. 2015). It consists of a premaxilla and a fragment of maxilla with right PM2 and left PM2–3. Since its description, no additional material has been assigned to the species. Ameghino stated that the genotype (*Catagonus metropolitanus*) has bunodont crown morphology, which is also shared by all Tayassuini. Gasparini (2007) diagnosed the taxon as having a wide rostrum, a large and wide canine, and a well-developed hypocone in PM3–4. These characters are not shared by the others species of *Catagonus* (sensu Gasparini 2007). When *C. metropolitanus* was included in our phylogenetic analysis, it was positioned inside Tayassuini in a basal polytomy, causing instability in the position of the other taxa inside the clade, due the lack of many important sources of character information. For these reasons, we suggest that the genus *Catagonus* should be

restricted only to *C. metropolitanus*. One possible exception is the species *Catagonus bonaerensis*, which was described by Ameghino as part of the suid genus *Listriodon*, based on isolated teeth. Rusconi (1930), based on tooth morphology, placed “*bonaerensis*” in the genus *Catagonus*. The characters used by Rusconi are also widespread among all Tayassuini taxa. We decided to provisionally maintain “*bonaerensis*” in the genus *Catagonus*, due to lack of more information.

Genus *Parachoerus* Rusconi, 1930

Synonyms:

Platygonus partim. Rusconi 1930

Parachoerus Kraglievich and Rusconi, 1931

Platygonus partim. Rusconi 1948

Catagonus partim. Wetzel et al. 1975

Type species: *Parachoerus carlesi* (Rusconi, 1930)

Included taxa: *Parachoerus carlesi* (Rusconi, 1930) and *Parachoerus wagneri* (Rusconi, 1930).

Emended diagnosis: Tayassuini with a long rostrum (with the anterior part of the orbits just behind the vertical plane of the posterior part of the M3), with the anterior portion of the zygomatic arch’s facial crest reaching the level just above the infraorbital foramen, and the origin of the facial muscles on the zygomatic arch with a hollow surface.

Remarks: Rusconi (1930) described the two species “*carlesi*” and “*wagneri*,” including them in the subgenus *Parachoerus* of the genus *Platygonus*. Rusconi (1930) stated that high-crowned teeth and inflated sinuses were traits shared by all *Platygonus* species. Wetzel et al. (1975) suggested that these characters are not present in all *Platygonus*, and that a molarized condition of the upper premolars distinguishes the “South American peccaries” from the “North American *Platygonus*.” For this reason, Wetzel et al. (1975) included “*carlesi*” and “*wagneri*” in the genus *Catagonus*. As stated above, we consider the genus *Catagonus* monotypic, and a new genus is needed to place those species. Rusconi (1930) established *Parachoerus* as a subgenus, and therefore we elevate it to generic level.

Parachoerus carlesi (Rusconi, 1930)

Synonyms:

Platygonus (*Parachoerus*) *carlesi* Rusconi, 1930

Catagonus carlesi (Rusconi, 1930)

Holotype: MACN 1308, an almost complete skull, without mandible, from Río Dulce, Las Termas, Santiago del Estero province, Argentina; middle Pleistocene sic Rusconi (1930).

Emended Diagnosis: *Parachoerus carlesi* differs from *Parachoerus wagneri* by having bunodont brachydont molars, a canine fossa that extends to almost the naso-maxillary suture, and absence of a sagittal crest.

Remarks: Since Rusconi (1930) described the species, no other material has been assigned to *P. carlesi*. The collection number MACN 7013, used by Rusconi (1930), is an erroneous attribution. The correct number is MACN 1308 (Gasparini 2007).

Parachoerus wagneri (Rusconi, 1930)

Synonyms:

Platygonus (*Parachoerus*) *carlesi wagneri* Rusconi, 1930

Parachoerus carlesi wagneri Kraglievich and Rusconi, 1931

Platygonus (*Parachoerus*) *wagneri* Rusconi, 1948

Catagonus wagneri Wetzel et al., 1975

Holotype: MACN 14670, an almost complete skull from Llajta Maüca, Santiago del Estero province, Argentina. Pre-Hispanic deposits.

Emended Diagnosis: *Parachoerus wagneri* differs from *Parachoerus carlesi* by having high crowned bunodont teeth [referred as “zygodont” by some authors (Gasparini 2007; Gasparini et al. 2009, 2013; Prothero and Grenader 2012)], a mesodont crown height, a small upper canine fossa, and a sagittal crest extending to the frontals.

Remarks: The type specimen, recovered from Holocene sediments from Argentina, was originally placed in the extinct genus *Platygonus*. Wetzel et al. (1975) found a living population of peccaries, which they considered to be conspecific with *Platygonus wagneri*. However, based on cranial morphology, those authors placed the species in the genus *Catagonus*. With the arrangement proposed here, these living populations should be assigned as *Parachoerus wagneri*.

Genus *Brasiliochoerus* Rusconi, 1930

Type species: *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880)

Included taxon: Monotypic genus.

Emended diagnosis: Tayassuini with long rostrum (with the anterior part of the orbits just behind the vertical plane of the posterior part of the M3), with 90° angle of the anterior portion of the zygomatic arch’s facial crest in relation to the molar series, bunodont and brachydont teeth, and absence of a sagittal crest.

Remarks: The genus *Brasiliochoerus* was described by Rusconi (1930) as a subgenus of *Platygonus*. Rusconi (1930), as in the genus *Parachoerus*, stated that the high-crowned teeth and inflated sinuses were traits shared by all *Platygonus* species. Wetzel et al. (1975) also suggested that the species “*stenocephalus*” should be included in the genus *Catagonus* for the same reasons as the species of the genus *Parachoerus*. In our analysis, *Brasiliochoerus* does not have a close relation with *Platygonus*, being, in fact, from a different tribe. As we consider *Catagonus* a monotypic genus, as stated above, *Brasiliochoerus* is the first valid genus and a more adequate one to place “*stenocephalus*.”

Brasiliochoerus stenocephalus (Lund in Reinhardt, 1880)

Synonyms:

Dicotyles stenocephalus Lund, 1838–1841 [name unavailable, appears in an unpublished catalogue; Article 50.1.1 of the Zoological Nomenclature Code: the authorship of LUND is explicit]

Dicotyles stenocephalus Gervais, 1867 [nomen nudum]

Dicotyles stenocephalus Lund in Reinhardt, 1880

Platygonus (Brasiliochoerus) stenocephalus Rusconi, 1930

Platygonus stenocephalus Paula Couto, 1950

Brasiliochoerus stenocephalus Paula Couto, 1981

Catagonus stenocephalus Gasparini et al., 2009

Holotype: ZMK 8638 and 8617, a skull and a partial left mandible, respectively. Peter W. Lund Collection. “Gruta Lapa da Escrivania, N °11,” Lagoa Santa, Minas Gerais, Brazil; late Pleistocene.

Emended diagnosis: The same of the genus *Brasiliochoerus*, by monotypy.

Tribe Platygonini, new

Diagnosis: A long postcanine upper diastema (longer than the molar series) and a pm2 with two principal cusps are morphological traits shared by all Platygonini.

Included taxa: *Protherohyus* gen. nov. *brachydontus* (Dalquest and Mooser, 1980); *Skynnerhyus shermerorum* Prothero and Pollen, 2013; *Mylohyus nasutus* (Leidy, 1869); *Mylohyus eimorei* (White, 1942); *Macrogenis crassigenis* Gidley, 1904; *Platygonus pearcei* Gazin, 1938; *Platygonus cumberlandensis* Gidley, 1920; *Platygonus compressus* Le Conte, 1848; *Platygonus chapadmalensis* (Ameghino, 1908); *Platygonus scagliai* (Reig, 1952); ?*Platygonus marplatensis* Reig, 1952; ?*Platygonus kraglievichi* Rusconi, 1930; ?*Platygonus cinctus* (Ameghino, 1886).

Remarks: Most of Platygonini genera have an exclusive North American distribution, with the exception of *Platygonus*, which has five South American species. The Platygonini includes peccaries with several distinct morphological traits. A group formed by the Miocene genera *Skinnerhyus*, *Mylohyus*, and *Macrogenis* shares a laterally projected jugal, called “wings” by some authors (Prothero and Pollen 2013), and a very elongated rostrum, which are characters that occur only in this group. In the same way, a postorbital depression and a keel in the mandibular symphysis are characters shared by the genus *Platygonus*. This tribe possesses several types of tooth morphology, varying from bunodont brachydont in *Mylohyus*, to bunolophodont mesodont in *Platygonus*. The taxa ?*P. marplatensis*, ?*P. kraglievichi*, and ?*P. cinctus* share bunolophodont and mesodont teeth with others *Platygonus* species. Therefore, considering these features (and their fragmentary conditions) we decided to provisionally include these taxa in the Platygonini tribe.

Genus *Protherohyus*, gen. nov.

Synonyms.

Desmathyus partim. Dalquest and Mooser 1980

Catagonus partim. Wright 1989

Type species: *Protherohyus brachydontus* (Dalquest and Mooser, 1980)

Etymology: The genus name is dedicated to Dr. Donald Prothero, an American paleontologist who made significant contributions to the systematics of peccaries.

Diagnosis: The genus *Protherohyus* differs from *Platygonus* by having a straight temporal crest, brachydont crown morphology, and by not having a postorbital depression. Differs from the other genera of Platygonini by having non-molariform premolars and a short rostrum.

Protherohyus brachydontus (Dalquest and Mooser, 1980)

Holotype: TMM 41685–13, lower third molar.

Emended diagnosis: Genus *Protherohyus* by monotypy.

Remarks: This species was described based on isolated teeth found in Mexico by Dalquest and Mooser (1980), and later was allocated to the genus *Catagonus* by Wright (1983). Besides that, this last author, assigned several more complete materials to this species. Despite the fact that the genus *Catagonus* (sensu Wright 1998 and Gasparini 2007) is polyphyletic in our analysis, the taxon “*brachydontus*” shares bunolophodont teeth and a lateral expansion of the jugal with the Platygonini. The taxon “*brachydontus*” was first placed in the genus *Desmathyus*, a monotypic Hesperhyinae genus (Prothero 2015), which does not share diagnostic characters with “*brachydontus*.” Besides that, if “*brachydontus*” was placed in the genus *Desmathyus*, a paraphyletic group would be formed. Considering the situation, we suggest a creation of a new genus to place “*brachydontus*.”

Conclusion

In the present contribution, the family Tayassuidae was recovered as monophyletic and sister group of the family Suidae, with the three extant species closely related to each other. The genus *Catagonus* is polyphyletic, which led us to revalidate two genera (*Brasiliochoerus* and *Parachoerus*) and describe a new one (*Protherohyus*). Inside the family, two clades were recovered: the subfamilies Tayassuinae and Hesperhyinae, with the subfamily Tayassuinae comprising two clades: Tayassuini and Platygonini. The genus *Platygonus* was retrieved as monophyletic and sister group of the Miocene clade, which includes the remaining species of the Platygonini tribe (*S. shermerorum*, *M. crassigenis*, *M. elmorei*, and *M. nasutus*). These new phylogenetic proposals (Fig. 5) shed some light in some questions associated with South American tayassuid relationships that

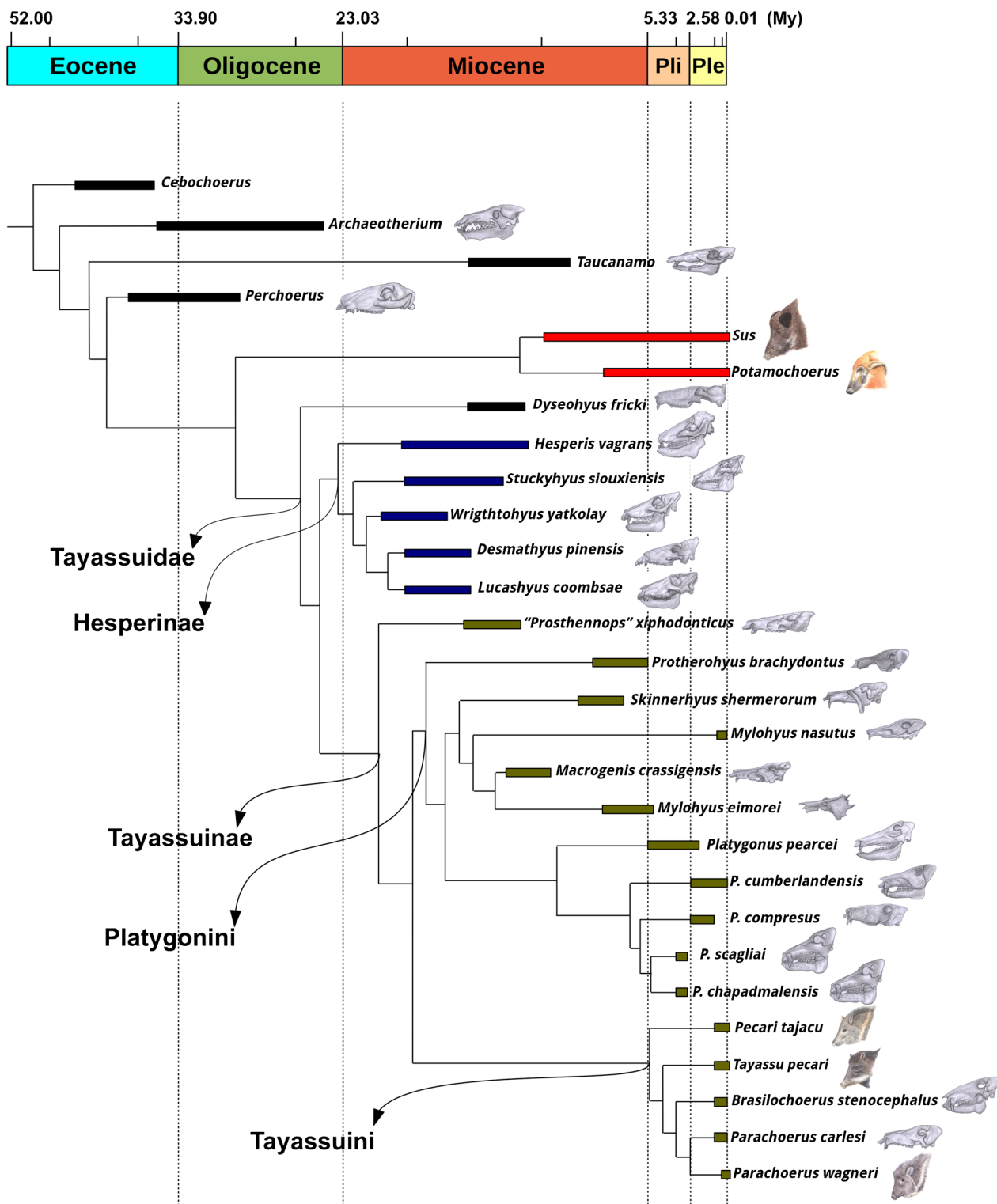


Fig. 5 Single most parsimonious tree from implied weighting analysis with temporal distribution of the taxa. Drawings by Barbara Rossi

remained unaddressed in previous works. However, some phylogenetic issues remain, such as the relation of the genus *Perchoerus*, a traditionally Tayassuidae, but recovered in our

results both inside and outside the clade. A more detailed analysis of the North American Suoidea is necessary to elucidate and clarify the evolutionary history of the New World peccaries.

Acknowledgments The authors thank to the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), CAPES and FAPEMIG for financial support; and the authorities of palaeontological collections for providing material for analysis. We also want to thank Barbara Rossi (UFMG) for the drawings of skulls and living taxa on the phylogeny.

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