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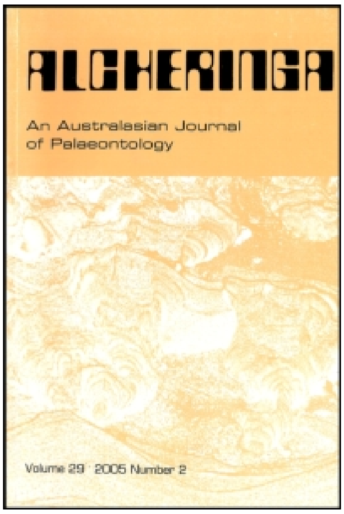

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A review of the Quaternary Tayassuidae (Mammalia, Artiodactyla) from the Tarija Valley, Bolivia

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Three genera of Tayassuidae are recognized in South America: *Platygonus* Le Conte, 1848, *Catagonus* Ameghino, 1904 and *Tayassu* Fischer, 1814. This study provides the first systematic review of the Pleistocene tayassuids yet reported from Bolivia. The richest records of the family in South America derived from central-eastern Argentina and southern Brazil. *Catagonus stenocephalus* (Lund in Reinhardt, 1880) is documented for the first time in Bolivia, significantly extending the geographic distribution of this species in South America. We cannot confirm the validity of *Platygonus tarijensis* (Ameghino, 1904), but accept its generic allocation. Both taxa show adaptations to arid or semi-arid and relatively open environments, which is consistent with the palaeoenvironmental conditions previously proposed for the Tarija Valley. The veracity of other records of the family from Bolivia cannot be confirmed.

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Key words: Tayassuids, peccaries, biogeography, *Catagonus stenocephalus*, *Platygonus*, Palaeoecology, Pleistocene.

ALTHOUGH it is acknowledged that a taxon's centre of origin cannot be empirically determined from the fossil record, some authors have suggested that the Tayassuidae and Suidae (Mammalia, Artiodactyla) may have differentiated from their common ancestor during the late Eocene in Eurasia based on the distribution of their oldest fossil records (Romer 1966, Wright 1998, Hulbert 2001). Younger records suggest that the Tayassuidae may have expanded their range to North America, where they reached their greatest diversity (see Savage & Russell 1983, Wright 1998, Gasparini 2007). From there they appear to have extended their distribution to South America during the 'Great American Biotic Interchange' (GABI). They represent one of the first North American mammalian immigrants, after procyonids (Carnivora) and cricetid rodents (Prevosti *et al.* 2006, Woodburne *et al.* 2006, Gasparini 2007, and bibliographies cited therein). The oldest fossil tayassuid in South America dates to the beginning of the late Chapadmalalan (middle Pliocene, *ca* 3.3–4 Ma; Prevosti *et al.* 2006).

In the modern fauna, Tayassuidae (commonly known as peccaries) are distributed in the American continent from the southwestern USA to north-central Argentina (Mayer & Brandt 1982, Redford & Eisenberg 1992, Nowak 1999, Gasparini 2002, 2007, Gasparini *et al.* 2005, 2006), and they are represented by at least two genera and three species (Gasparini 2007 and bibliographies cited therein). However, the taxonomic diversity and geographic distribution

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of the tayassuids were greater in the past. There are records of tayassuids in Asia (late Eocene to late Miocene), Europe (early Oligocene to late Miocene), Africa (middle Miocene to early Pliocene), North America (late Eocene to Holocene), Central America (late Miocene to Holocene) and South America (middle Pliocene to Holocene) based on the studies of McKenna & Bell (1997), Gasparini (2007) and works cited therein.

The greatest generic and specific diversity of Tayassuidae in South America derives from sediments exposed in Argentina (especially in Buenos Aires Province). The family has also been found in Brazil, Uruguay, Bolivia and Colombia, together with doubtful records from Peru (Rusconi 1930, 1952, Stirton 1947, Paula Couto 1975, 1981, Menegaz & Ortiz Jaureguizar 1995, Rancy 1999, Campbell *et al.* 2000a, 2000b, 2001, Martins & Oliveira 2003, Ubilla 2004, Ubilla *et al.* 2004, Gasparini 2007).

Three genera of Tayassuidae are recognized in South America: *Platygonus* Le Conte, 1848 (middle Pliocene to early Pleistocene); *Catagonus* Ameghino, 1904 (late Pliocene? to Holocene); and *Tayassu* Fischer, 1814 (middle Pleistocene to Holocene); see Gasparini (2007). From a palaeonvironmental point of view, several authors (Guilday *et al.* 1971, Wetzel 1977, Menegaz & Ortiz Jaureguizar 1995, Gasparini 2007) have suggested that *Platygonus* and *Catagonus* represent taxa adapted to dry and relatively open environments, whereas *Tayassu* represents a taxon adapted mainly to humid climates and woodland and forest environments. However, the presence of *Tayassu* alone is insufficient to infer environmental conditions, because of its extensive geographic range and ecological tolerances (Menegaz & Ortiz Jaureguizar 1995, Gasparini & Zurita 2005, Gasparini 2007).

In Bolivia, tayassuids have been recorded in the Tarija Valley (Ameghino 1904, Boule & Thévenin 1920, Rusconi 1930, Hoffstetter 1963, Takai *et al.* 1982) between Mojotorillo and Khoña Paya localities, Potosí Department (Daza & Shockey 1999), and in the Ñuapua Formation (Ñuapua 1 member: basal portion of the formation) between Carandaití and Capiranda (Marshall & Sempere 1991). No modern reviews have been undertaken of the Bolivian fossil mammals, except that of Zurita *et al.* (2009b), which documents the diversity of Xenarthra, Glyptodontidae.

This paper aims to: (1) review and revise the record of Tayassuidae in Bolivia and discuss the taxonomic implications of the fossils; and (2) assess the ecological context and geographic and biostratigraphic distribution in South America of those taxa present in Bolivia (Fig. 1).

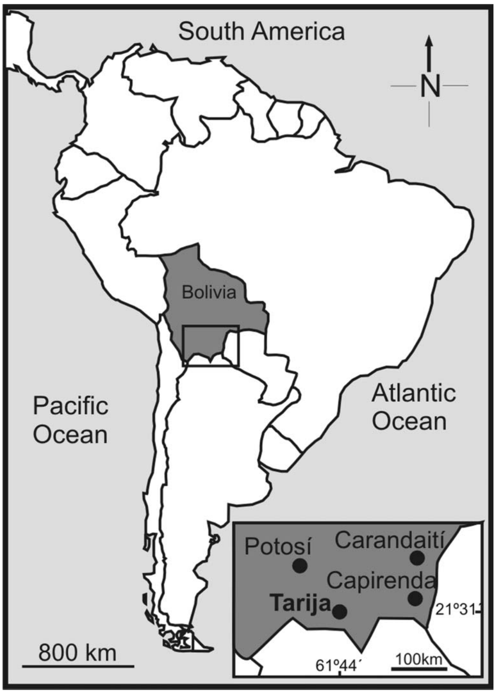

Fig. 1. Location map of the palaeontological sites.

Previous studies of the Tayassuidae

There has been little consensus in either fossil or extant South American Tayassuidae systematics owing to: differing significance assigned to certain characters by previous authors; the episodic nature of investigations of this group; and the discovery of new taxa, both fossil and extant (Menegaz & Ortiz Jaureguizar 1995, Gasparini 2007, and literature cited therein).

Following a systematic review of Argentinean, Brazilian and Bolivian tayassuids by Rusconi (1930), opinions diverged about the taxonomic composition of the family and phylogenetic relationships of its members (e.g. Pascual *et al.* 1966, Woodburne 1968, Wetzel 1977, Reig 1981, Marshall *et al.* 1984, Ortiz Jaureguizar & López Armengol 1984, Ortiz Jaureguizar & Prado 1986, Menegaz & Ortiz Jaureguizar 1995). The various classificatory proposals covered only a fraction of Tayassuidae diversity and many are intuitive schemes rather than being based on rigorous analysis of shared derived characters (e.g. Reig 1981, p. 41; Reig in Marshall *et al.* 1984, p. 21). This paper adopts the system proposed by Gasparini (2007), since this is the most recent integral review of the South American Tayassuidae.

Abbreviations

Institutions. MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; MNPA-V: Museo Nacional de Paleontología y Antropología, Tarija, Bolivia; ZMK: Zoologisk Museum, Copenhagen, Denmark.

Measurements. *Skull*: AH: Maximum width of 'snout': measured across the outer borders of the alveoli of C; AMH: Maximum width 'snout': measured from the outer borders of the paracanine's process to that on the other side of the jaw; AP: Palatal width: measured between PM4 and M1; LDPOSTC: Length of the diastema—from the front border of the alveolus of PM2 to the back border of the alveolus of C.

Upper tooth series: LPM-M: Length of the premolar-molar row, measured near the biting surface; LPM2-PM4: Length of the premolar row, measured near the biting surface; LM1-M3: Length of the molar row, measured near the biting surface; LPM2: maximum length of premolar 2 in a parallel line to the sagittal plane; APM2: maximum width of premolar 2 in a perpendicular line to the sagittal plane; LPM3: maximum length of premolar 3 in a parallel line to the sagittal plane; APM3: maximum width of premolar 3 in a perpendicular line to the sagittal plane; LPM4: maximum length of premolar 4 in a parallel line to the sagittal plane; APM4: maximum width of premolar 4 in a perpendicular line to the sagittal plane; LM1: maximum length of molar 1 in a parallel line to the sagittal plane; AM1: maximum width of premolar 2 in a perpendicular line to the sagittal plane; LM2: maximum length of molar 1 in a parallel line to the sagittal plane; AM2: maximum width of molar 2 in a perpendicular line to the sagittal plane; LM3: maximum length of molar 3 in a parallel line to the sagittal plane; AM3: maximum width of molar 3 in a perpendicular line to the sagittal plane.

Lower tooth series: Lm2: maximum length of molar 2 in a parallel line to the sagittal plane; Am2: maximum width of molar 2 in a perpendicular line to the sagittal plane.

Materials and methods

The studied specimens are labelled as being derived from the Tarija Valley in southern Bolivia (Fig. 1) but little other locality information is available. Measurements were taken using digital callipers, with 0.01 mm precision; data have been expressed in millimetres. In the descriptions of the main cusps of maxillary premolars, the names 'paracone,' 'metacone,' 'protocone' and 'hypocone' in quotations are used to indicate topological position, and do not infer serial homologies with the cusps of the molars, since there is no general agreement on this matter (Rusconi 1929, Mones 1979, Wetzel 1977, Gasparini 2001). Biostratigraphic zones (Fig. 2) correspond to those of Cione & Tonni (2005) and Soibelzon *et al.* (2008a).

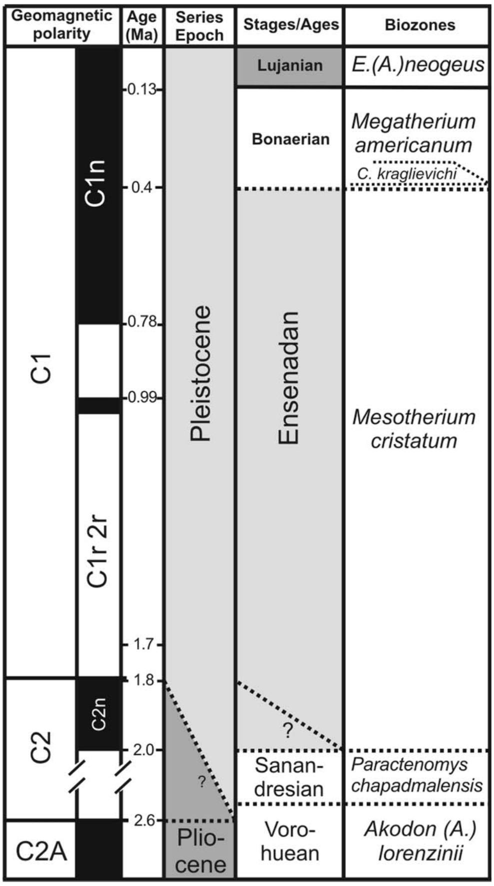

Fig. 2. Pliocene to Pleistocene chronostratigraphic scale of the Pampean Region (Argentina) in comparison with Geomagnetic Polarity Scale (Cande & Kent 1992) and the International Stratigraphic Chart (ICS 2008). Pampean mammal biostratigraphy according to Cione &Tonni (2005) and Soibelzon *et al.* (2008a).

Systematic palaeontology

Order ARTIODACTYLA Owen, 1848
Suborder SUIFORMES Jaeckel, 1911
Infraorder SUOIDEA Gray, 1821
Family TAYASSUIDAE Palmer, 1897

Catagonus Ameghino, 1904

Type species. Catagonus metropolitanus Ameghino, 1904

Catagonus stenocephalus (Lund in Reinhardt, 1880) (Fig. 3A, B).

Synonymy

1838–1841 *Dicotyles stenocephalus* Lund, p. 1–56 [nomen nudum: appears in an unpublished catalogue; see Article 50.1.1 of the Zoological Nomenclature Code: the authorship of Lund is explicit].

1869 *Dicotyles stenocephalus* Lund; Gervais, p. 252 [nomen nudum].

1880 *Dicotyles stenocephalus* Lund; Reinhardt, pp. 271–301, pl. VII, figs 1–2.

1889 *Dicotyles stenocephalus* Lund; Ameghino, p. 575.

1906 *Dicotyles stenocephalus* Lund; Winge, p. 55, pl. VI, figs 1–4.

1920 *Dicotyles* sp. cf. *D. major* Lund; Boule & Thevenin, pp. 140–142.

1930 *Platygonus (Brasiliochoerus) stenocephalus* (Lund); Rusconi, pp. 160, 162.

1930 *Prosthennops* sp. cf. *P. doello-juradoi* Rusconi, pp. 188–190, pl. XIII, figs 1–2.

1950 *Platygonus stenocephalus* (Lund); Paula Couto, pp. 1–88.

1963 *Platygonus stenocephalus* (Lund); Hoffstetter, p. 200.

1979 *Brasiliochoerus stenocephalus* (Lund); Fonseca, p. 88.

1981 *Brasiliochoerus stenocephalus* (Lund); Paula Couto, pp. 75–78.

1982 *Platygonus stenocephalus* (Lund); Takai *et al.,* p. 11, pl. 9, fig. 24.

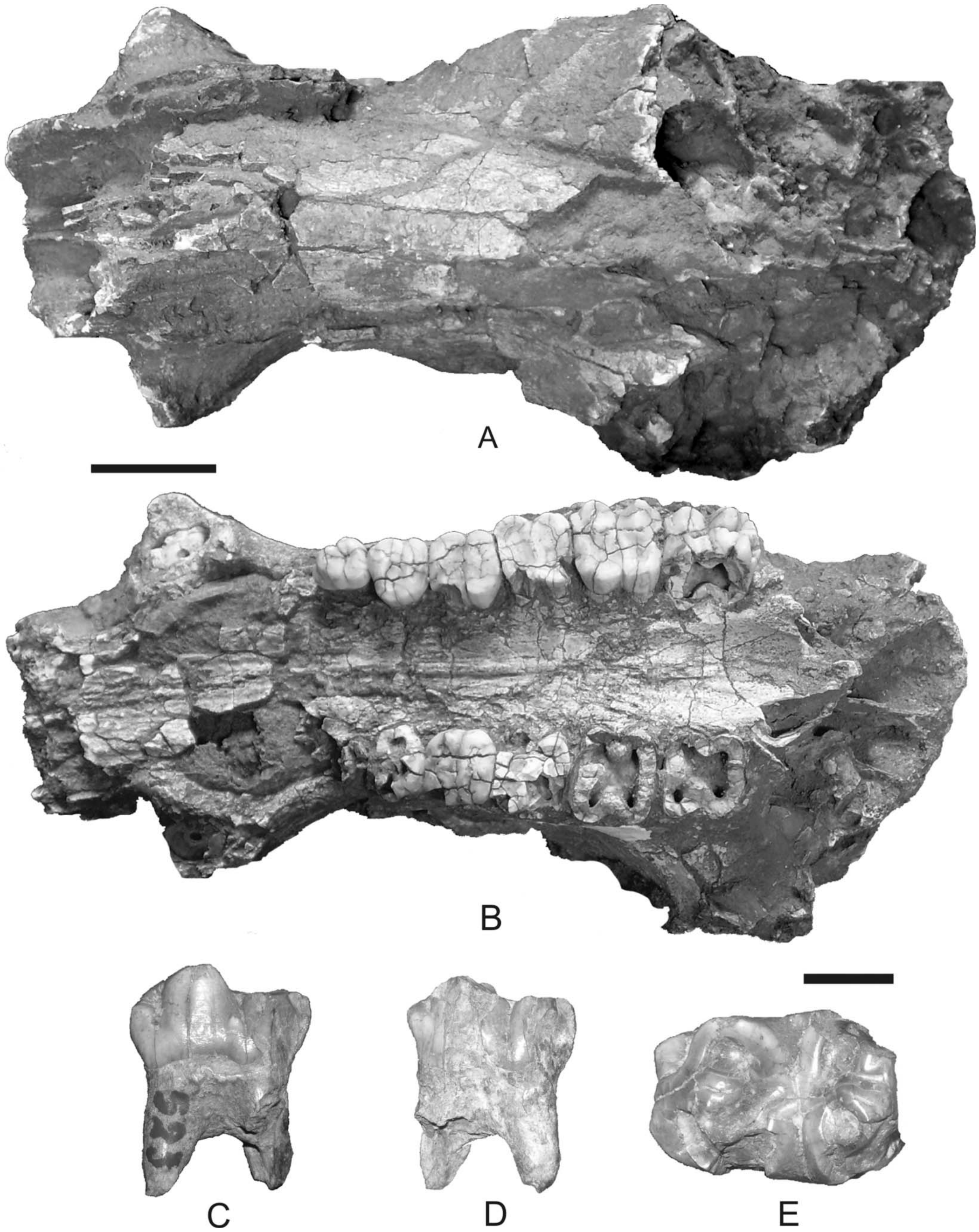

Fig. 3. Catagonus stenocephalus (Lund in Reinhardt, 1880); MNPA-V 1450. Skull in: **A**, dorsal view; **B**, occlusal view. *Platygonus* sp.; MACN 525. m2 in: **C**, labial view; **D**, lingual view; **E**, occlusal view. Scale bars = 10 mm.

2007 *Catagonus stenocephalus* (Lund); Gasparini, pp. 213–214, fig. 50. [=*Prosthennops* sp. cf. *P. doello-juradoi* Rusconi, 1930].

Type material. ZMK 8617 and 8638, skull and partial left mandible, respectively.

Type locality and age. 'Gruta Lapa da Escrivaninha, N° 11,' Lagoa Santa, Minas Gerais, Brazil; late Pleistocene.

Studied material. MNPA-V 1450, Tarija Valley, Bolivia; Pleistocene (Fig. 1). A partial skull that preserves the nasal, maxillary and palate (from the most anterior part of the precanine diastema up to the posterior portion of M3); right cheek teeth series complete and basal portion of canine; the PM4 is the only complete tooth on the left side.

Description

Skull (Fig. 3A, B). Despite its incomplete preservation, the anterior edge of the orbit clearly lies behind the posterior margin of M3 at a distance less than the length of the molar series. The articular fossa on the anterior side of the zygomatic arch is absent. A pair of supraorbital canals on the skull's dorsal surface extends from the frontals, becoming lateral in the nasals, and then passing anteriorly to the nasal aperture. The rostrum has a convex lateral profile. The dorsal surface of the nasals is transversely convex. Despite incomplete preservation of the Bolivian specimen, it clearly has a short postcanine diastema.

Upper tooth series. The premolar-molar series is strongly worn. Consequently, the crown is expressed as two wide transverse lobes, typical of a bunodont tooth. The crown height of the tooth is mesodont.

PM1. The PM1 is absent in this specimen.

PM2. This tooth is triangular in outline. The crown has a complex configuration due to the presence of several cusps of various sizes. The largest cusp is located anteriorly on the longitudinal axis of the tooth. Behind this, and on the lingual side, there is a less-developed cusp and further along the lingual side is a pair of very small cusps. The cingulum is basal and continuous.

PM3. This tooth is subquadrangular and readily differentiated from the typical quadrangular outline of the molars, since the lingual side is slightly convex rather than planar. Despite significant wear and fragmentation, the PM3 reveals four well-developed cusps ('paracone,' 'protocone,' 'metacone' and 'hypocone'). The cingulum is well defined on the anterior, lingual and posterior sides.

PM4. This tooth is quadrangular and larger than the PM3. It has four main well-defined cusps ('paracone,' 'protocone,' 'metacone' and 'hypocone'). The cingulum is developed on the anterior, labial and posterior sides.

M1. This molar is quadrangular in outline, with two pairs of cusps (paracone-protocone anterior and metacone-hypocone posterior, respectively) separated by a valley. The morphology of the valley is difficult to determine due to the high wear suffered. However, it is clearly narrow.

M2. This tooth is quadrangular and much wider and longer than the M1. It is wider than M3.

M3. The M3 is quadrangular in outline with two anterior cusps having a greater width and separation than the posterior pair. In its posterior portion there is a cingulum almost as wide as the tooth, where several small accessory cusps can be recognized. The basal cingulum surrounds the anterior, labial and posterior margins of the tooth.

Measurements. AH, 59.12 mm; AMH, 68.46 mm; AP, 28.73 mm; LDPOSTC, 17.63 mm; LPM-M, 73.65 mm; LPM2-PM4, 30.73 mm; LM1-M3, 42.92 mm; LPM2, 8.81 mm; APM2, 8.45 mm; LPM3, 10.17 mm; APM3, 10.89 mm; LPM4, 11.93 mm; APM4, 12.55 mm; LM1, 12.03 mm; AM1, 13.59 mm; LM2, 14.87 mm; AM2, 15.87 mm; LM3, 16.59 mm; AM3, 14.71 mm.

Comparisons and interpretation

In this material, the orbits are set well posterior in the skull, behind the last molars at a distance less than the length of the molar series. The same feature is also found in species of *Catagonus* Ameghino, 1904, *Platygonus* Le Conte, 1848, *Prosthennops* Gidley, 1904, *Dyseohyus* Stock, 1937 and *Perchoerus rostratus* (Cope, 1888) In contrast, *Tayassu* Fischer, 1814, *Hesperhys* Douglass, 1903 and the North American *Perchoerus pristinus* (Cope, 1888), have the anterior margins of their orbits above the M2 or M3 (Gasparini 2007).

The convex lateral profile of the rostrum in this species is shared with *Catagonus wagneri* (Rusconi, 1930) among the South American tayassuids, and with *Platygonus compressus* Le Conte, 1848 and *Perchoerus pristinus* (Cope, 1888), among North American representatives.

Platygonus and *Catagonus* species from North and South America have a transversely convex rostrum. This feature is also developed in the exclusively North American *Prosthennops* species, *Perchoerus pristinus* (Cope, 1888), and in the extant *Tayassu tajacu* (Linnaeus, 1758); see Gasparini (2007). Among extant South American peccaries, the only one with a flat rostrum in transverse section is *Tayassu pecari* (Link, 1795). The remaining taxa possessing this character are from North America: *Perchoerus* Leidy, 1869 (e.g. *P. rostratus*), *Mylohyus* (Cope, 1889), *Dyseohyus* and *Hesperhys* (e.g. *H. pinensis*); see Gasparini (2007).

Despite incomplete preservation of the Bolivian specimen, it clearly has a short postcanine diastema similar to that of *Tayassu tajacu* (Linnaeus, 1758).

Within the upper tooth series of this specimen, the PM1 is absent. This tooth is typically lost in North and South American tayassuids, except in certain very ancient genera (e.g. *Perchoerus* Leidy, 1869 and *Hesperhys* Douglass, 1903).

A molariform PM3 is found in *Mylohyus*, *Prosthennops* and *Catagonus brachydontus* (Dalquest & Mooser, 1980) among the North American taxa, and *Catagonus metropolitanus* Ameghino, 1904 and *Catagonus stenocephalus* among South American species. This morphology is also present in the extant species *Catagonus wagneri* and *Tayassu pecari*. The main difference in the degree of the molarization in these taxa, is the differential development of the 'hypocone' in the PM3.

The molarization evident in premolars of this species is equivalent to that in *Catagonus metropolitanus* (among South American forms) and in North American *Prosthennops* and *Mylohyus* species. In contrast, taxa in which the 'hypocone' is less developed on PM4 than the rest of the principal cusps include *Tayassu pecari* and *Catagonus wagneri*, among living species, and the remaining fossil species of *Catagonus* [*C. bonaerensis* (Ameghino, 1904), *C. carlesi* (Rusconi, 1930) and *C. brachydontus*].

Comments. Boule & Thevenin (1920, pp. 140–142) assigned this material to *Dicotyles* sp. cf. *D. major* Lund, 1841. Later, this specimen was transferred to *Platygonus stenocephalus* (Lund in Gervais, 1869) by Hoffstetter (1963), without appropriate justification. The features described herein favour its reassignment to *Catagonus stenocephalus* (Lund in Reinhardt, 1880).

Platygonus Le Conte, 1848

Type species. Platygonus compressus Le Conte, 1848.

Platygonus sp. (Fig. 3C–E)

Studied material. MACN 525, m2; Tarija Valley (21°33'S, 64°46′E), Bolivia (Fig. 1). Ensenadan Age? (*sensu* Ameghino 1904).

Description. The crown surface of the specimen is worn. The following morphological and morphometrical features clearly indicate that it belongs to *Platygonus*, but its features are insufficient for more specific determination: the enamel of the anterior and posterior crests form a transversely orientated diamond shape; the anterior crest is taller and larger than the posterior crest, these being separated by a valley; a well-developed anterior cingulum occupies the entire width of the tooth, whereas the posterior cingulum is less developed; the tooth has four roots.

Measurements. Lm2, 19 mm; Am2, 13 mm.

Comments. The material, an m2, was designated the holotype of *Listriodon tarijensis* by Ameghino (1904, pp. 187–188) but reanalysis of this specimen (above) indicates that it must be assigned to *Platygonus*. Its segregation as a distinct species appears to be unwarranted until additional material becomes available.

Discussion

Taxonomic, biogeographic and biostratigraphic aspects

Boule & Thevenin (1920, pp. 140–142) documented the presence of the tayassuid *Dicotyles* sp. cf. *D. major* in the Tarija Valley from a partially preserved skull (MNPA-V 1450). They based their identification on the following features: gross dimensions, lateral profile of the rostrum, orientation of the upper canines, shape of the incisors, and dental formula. They compared the material with specimens found in the caves of Brazil (see Lund 1841) and concluded, based mainly on the large size of the Bolivian material, that this specimen should be assigned to *Dicotyles* sp. cf. *D. major*. Later, Hoffstetter (1963) synonymized *Dicotyles* sp. cf. *D. major* with *Platygonus stenocephalus* (Lund), without providing any justification. This taxonomic allocation was also followed by Takai *et al.* (1982, pl. 9, fig. 24), who first illustrated the material.

We have shown in the description above that this partial skull is referable to *Catagonus stenocephalus* (Lund in Reinhardt, 1880) based on the: (a) form of the nasals in cross-section (they are convex); (b) development of the articular fossa on the anterior side of the zygomatic arch (it is absent); and (c) development of the 'hypocone' (a well-developed cusp in the PM3-4).

Catagonus stenocephalus is recorded from the end of the early Pleistocene to the earliest Holocene (Ensenadan–Bonaerian and Lujanian Stages *sensu* Cione & Tonni 2005, Soibelzon *et al.* 2008a). This species has been recorded at various localities in the northeast, east and southeast regions of Buenos Aires province, Argentina; in Lagoa Santa, Minas Gerais, Brazil (Gasparini 2007) and in the Touro Passo Formation, southern Brazil (Gasparini *et al.* in press). This study extends the range of this species to Bolivia.

Listriodon tarijensis was reported by Ameghino (1904) based on an m2 (MACN 525), originally interpreted as a PM4. He described this specimen in detail but did not illustrate it. Subsequently, Rusconi (1930, pp. 137–139, figs 3a, 3b and 3c) re-examined the specimen, re-interpreted it as an m2 and concluded that it should be assigned to *Platygonus tarijensis*. Based on the new systematic scheme of South American Tayassuidae (Gasparini 2007), morphological and morphometrical features evident in this fossil, indicate that it is referable to *Platygonus,* but it has no diagnostic characters permitting assignment at the species level.

One specimen deserving attention is the partial skeleton studied by Daza & Shockey (1999) from Pleistocene beds near kilometre 101 of Route 5, between Mojotorillo and Khoña Paya localities, Potosí Department, Bolivia. The skeleton was found in association with Xenarthra, Perissodactyla, Carnivora and Artiodactyla fossils. Daza & Shockey (1999) tentatively assigned the specimen to *Catagonus metropolitanus*, arguing that the only reason for this assignment was its larger size compared with the living species *Catagonus wagneri*. Considering the estimated body mass for fossil species of South American Tayassuidae (Gasparini 2007, and literature cited therein), it appears that *Catagonus* species, and especially *C. bonaerensis* represent tayassuids of higher body mass. The fossil species of *Catagonus*, with the exception of Argentinean representatives of *C. stenocephalus* are larger than the only living species of the genus, *C. wagneri* (see Gasparini 2007). Therefore, we suggest that the evidence provided by Daza & Shockey (1999) is insufficient for specific determination of the material in question.

Similarly, the presence of this family in the Ñuapua Formation is limited to only a few fossils assigned to Tayassuidae indet. within a palaeofaunal list and without reference material or repository (Marshall & Sempere 1991, p. 643). The identification cannot be confirmed.

The stratigraphic and geographic ranges of South American tayassuids are: *Platygonus* (middle Pliocene to middle Pleistocene) in Argentina, Colombia and Bolivia; *Catagonus* (late Pliocene? to Holocene) in Argentina, Bolivia, Uruguay and Brazil; and *Tayassu* (middle Pleistocene to Holocene) in Argentina, Uruguay and Brazil (Gasparini 2007).

Anatomical and ecological specializations

One of the most interesting characteristics of the Pleistocene (*ca* 2.6–0.008 Ma, *sensu* ISC 2008) is the regular alternation of glacial and interglacial cycles, with a noteworthy predominance of the glacial phases (90%) in comparison with interglacial events (10%: Lambeck *et al.* 2002). Certainly, these remarkable climatic-environmental cycles had great influences on the evolutionary and palaeobiogeografic history of the different South American mammal communities (Rabassa *et al.* 2005, Soibelzon *et al.* 2009, Zurita *et al.* 2009a). The pronounced conditions of aridity and cold temperatures during the long glacial phases particularly stimulated the development of open and homogenous environments in South America (Clapperton 1993, Iriondo & García 1993).

Platygonus and *Catagonus* have a series of features that allow some interpretation of their locomotion: (a) great development of the sinuses and nasal chambers (they extend posteriorly below the orbits and dorsolaterally up the pterygoid processes); (b) postorbital process of the frontal bones lies behind the preglenoid process; (c) orbits are in an upper-posterior position and behind the M3 due to elongation of the rostrum; (d) the infraorbital foramen is located well to the anterior of the zygomatic arch; (e) possession of a distinct basicranial flexure; and (f) reduction in the lateral digits on the limbs. This set of characters allows us to infer that these animals were ‘runners,’ and lived in dry and relatively open environments (Guilday *et al.* 1971, Wetzel 1977, Menegaz & Ortiz Jaureguizar 1995, Gasparini 2007).

The development of mesodont and bunolophodont cheek teeth and the lateral expansion of the angular process of the jaw (providing greater surface for insertion of the lateral deep masseter muzzle; Wetzel 1977, Menegaz & Ortiz Jaureguizar 1995) in *Platygonus* species suggests a herbivorous diet and probably a foraging habit, but does not discount the possibility of a graminoid component in the diet (Menegaz & Ortiz Jaureguizar 1995).

The development of bunodont and/or 'zygodont' cheek teeth (with higher and sharper cusps than in typical bunodont forms with faint crests) and with a mesodont crown height in *Catagonus* species, supports the interpretation of a herbivorous and foraging diet (Mayer & Brandt 1982, Menegaz & Ortiz Jaureguizar 1995, Gasparini 2007).

Inferences about the ecology of tayassuids in the Tarija Valley are consistent with the palaeoenvironmental reconstruction proposed by Coltorti *et al.* (2007), in which the sediments were deposited under cold and arid conditions. In this sense, the presence of fossils from some key plant families (e.g. Chenopodiaceae, Poaceae, Asteraceae) shows the predominance of an arid/semi-arid environment in the region (Takai *et al.* 1982). In addition, the presence of some specialist grazers such as *Glyptodon*, *Equus* and *Lama* are congruent with this palaeoclimatic scenario. Also, the high frequency of Hydrochoeriidae and Tapiridae, which are representatives of warm and humid climates, suggests the presence of at least, one warm event. According to Tonni *et al.* (2009), the Tarija sequence has taxa shared with the lower to middle Pleistocene (Ensenadan) and the upper Pleistocene–lower Holocene (Lujanian) of the Pampean area.

Conclusions

(a) *Catagonus stenocephalus* is confirmed in Bolivia, extending its known range from central-eastern Argentina and southern Brazil.

(b) On available evidence (a single molar), we can not confirm that *Platygonus tarijensis* represents a distinct species, but its generic allocation is appropriate.

(c) The record of *Platygonus* in the Tarija valley suggests the possible coexistence of *Platygonus* and *Catagonus* during the Pleistocene in Bolivia, similar to that recorded from the Ensenadan in the Pampean Region (Gasparini 2007, Soibelzon *et al.* 2008b).

(d) The mammalian assemblage of Tarija has marked palaeofaunal differences from that of the Pampean Region in Argentina. Known diversity and abundance of Tayassuidae and Glyptodontidae in the Pleistocene of Bolivia are low compared with Argentina. On the other hand, Gomphotheriidae, Equidae, Hydrochoeriidae and Tapiridae are more abundantly represented in Bolivia compared with the Pampean Region (Tonni *et al.* 2009, Zurita *et al.* 2009b).

(e) Both tayassuid taxa from Bolivia have anatomical adaptations to arid or semi-arid and relatively open environments, which is consistent with the palaeoenvironmental conditions previously proposed for the Tarija Valley.

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