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The Scelidotheriinae Ameghino, 1904 (Phyllophaga, Xenarthra) from the Ensenadan–Lujanian Stage/Ages (Early Pleistocene to Early-Middle Pleistocene–Early Holocene) of Argentina

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ABSTRACT

Review of the specimens assigned to Scelidotheriinae (Phyllophaga, Xenarthra) from the Ensenadan–Lujanian Stage/Ages of Argentina, showed that two genera are recognized for this territory: *Scelidotherium* (Owen) and *Scelidodon* (Ameghino), with the following species: *Scelidotherium bravardi* (Lydekker), for the Ensenadan Stage/Age (Early Pleistocene to Early-Middle Pleistocene), restricted to Buenos Aires Province, and the Pleistocene of San Luis Province; *Scelidotherium leptocephalum* (Owen), for the Bonaerian–Lujanian Stage/Ages (Middle Pleistocene–Early Holocene), of the Buenos Aires Province, in the Lujanian Stage/Age of Salta and Córdoba Provinces; *Scelidotherium* sp. for the Lujanian Stage/Age of Corrientes Province, Bonaerian-Lujanian Stage/Ages of Chaco Province; *Scelidodon tarijensis* (Gervais and Ameghino), for the Ensenadan–Bonaerian Stage/Ages of Buenos Aires Province, in Pleistocene of Córdoba Province; *Scelidodon chiliense* (Lydekker) for the Lujanian Stage/Age of San Luis Province, and *Scelidodon* sp. for the Lujanian Stage/Age of Corrientes, Buenos Aires and Entre Ríos Provinces, and the Pleistocene of Tucumán Province.

1. Introduction

The Scelidotheriinae Ameghino 1904 (Mylodontidae) are a particular South American group of tardigrades which, in spite of their wide geographic distribution, did not take part in the Great American Biotic Interchange (GABI) (Hoffstetter, 1952; Scillato-Yané et al., 1995; Woodburne et al., 2006). Which were actually their first records is quite difficult to be determined because it depends on which genera are included in this subfamily. According to Cattoi (1962), *Chubutherium fereloi* Cattoi, 1962, from the Late Oligocene of Patagonia (Argentina), could be the first scelidothere. This hypothesis was accepted by different authors, although not in the same way (e.g. Hirschfeld, 1985; McKenna and Bell, 1997). However, Scillato-Yané (1977) did not recognize *Chubuterium* within the scelidotheres, but included it within the Chubuteriinae Scillato-Yané, 1977. More restrictedly, Scillato-Yané and Carlini (1998) proposed that the first records are those of the "Friasian" – Middle Miocene – interval (see Scillato-Yané and Carlini, 1998), represented by the genera *Neonematherium* and *Sibyllotherium*; whereas for McDonald (1987) they could have originated in the Santacrucian Stage/Age (Early Miocene), from such forms as *Nematherium*. According to Scillato-Yané (1977) this latter genus should be included in a different subfamily, the Nematheriinae.

Abbreviations: AMNH, American Museum of Natural History, USA; BMNH, British Museum of Natural History, London, England; CC, Museo Universitario "Florentino y Carlos Ameghino", Universidad Nacional de Rosario, Santa Fe, Argentina; CICYTTP-PV-M, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Entre Ríos, Argentina; CTES-PZ, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; FCS, Facultad de Ciencias Sociales, Universidad Nacional del Centro, Olavarría, Buenos Aires, Argentina; FMNH, Field Museum of Natural History Chicago, USA; GCF, Grupo Conservacionista de Fósiles, San Pedro, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCA, Museo de Ciencias Naturales "Carlos Ameghino", Mercedes, Buenos Aires, Argentina; MD, Museo de Ciencias Naturales Carlos Darwin, Punta Alta, Buenos Aires, Argentina; MDVS-PV, Museo Dalmacio Vélez Sársfield Paleontología Vertebrados, Córdoba, Argentina; MHN-UNSL-GEO V, Universidad Nacional de San Luis, Argentina; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia", Argentina; MMPH, Museo Municipal "Punta Hermengo", Buenos Aires, Argentina; MSP, Museo Paleontológico Municipal "Fray Manuel de Torres", San Pedro, Buenos Aires, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRCH, Museo Regional Municipal del Sudeste Chaqueño, Charata, Chaco, Argentina; UNRC-PV, Universidad Nacional de Río Cuarto-Paleontología Vertebrados, Río Cuarto, Córdoba, Argentina; PVL, Colección Paleontológica Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto "Miguel Lillo", Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina.

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According to McDonald and Perea (2002), the following genera are recognized within the scelidotheres: *Sibyllotherium* Scillato-Yané and Carlini, 1998; *Nematherium* Ameghino, 1887; *Neonematherium* Ameghino, 1904; *Proscelidodon* Bordas, 1935 (=*Elassotherium* Cabrera, 1939); *Scelidotherium* Owen, 1839, and *Catonyx* Ameghino, 1891. The two latter are restricted to the Pliocene–Pleistocene (McDonald and Perea, 2002). However, Pujos (2000) considers *Scelidodon* Ameghino, 1881, as a valid genus, also present in the Pleistocene.

From an anatomical point of view, the specimens of this subfamily are characterized by having a tubular and elongate skull (Pascual et al., 1966; McDonald, 1987; McDonald and Perea, 2002), parallel dental series, laterally compressed molariforms (McDonald, 1987; Pascual et al., 1966), and quadrangular and antero-posteriorly compressed femur, with concave facet of the astragalus for the cuboid (Pascual et al., 1966; McDonald and Perea, 2002).

Many authors have recognized several Scelidotheriinae genera and species for the Pleistocene of Argentina, Bolivia, Brazil, Chile and Ecuador (e.g. Gervais, 1855; Gervais and Ameghino, 1880; Ameghino, 1889; Lydekker, 1894, and Hoffstetter, 1952). However, most of the specimens have no precise geographic and stratigraphic provenance.

The first nominated and figured genus is *Scelidotherium* (see Scillato-Yané et al., 1995), which according to Pascual et al. (1966) is very similar to *Scelidodon*. As a consequence of this apparent "similarity", many mistakes have been made in the assignment of different materials (e.g. Gervais, 1855; Gervais and Ameghino, 1880; Lydekker 1886; Ameghino, 1889; Hoffstetter, 1952; among others). Pascual and Odreman Rivas (1973: 32, and literature therein), stated that from a morphologic point of view, the Scelidotheriinae are very homogeneous. In the last revision of the group, McDonald and Perea (2002) mentioned that scelidotheriines retain the conservative morphology which makes difficult the recognition of species, especially among the Pleistocene taxa. However, and as it will be explained below, Pleistocene genera can be determined precisely, as well as several of the species previously nominated.

There are a few hypotheses about phylogenetic relationships among genera and species of the subfamily. According to Paula-Couto (1979) and Kraglievich (1923) *Scelidodon* is less "specialized" than *Scelidotherium*, on the basis of some cranial, dental and post-cranial features, such as the presence of short pre-maxillaries in the first genus. More recently, Cuenca Anaya (1995) disagreed with this opinion and discussed the arguments of Kraglievich (1923) and Paula-Couto (1979), although not taking into account the latitudinal distribution of each genus. Likely, as in other group of xenarthrans (e.g. Megatheriinae – Carlini et al., 2006a, Mylodontoidea – Carlini et al., 2006b, Glyptodontinae – Carlini et al., 2008a and b) or other mammals (Carlini et al., 2006c, and literature therein), distributions in low latitudes match with some kind of retention of primitive characters.

More recent contributions propose new species of Scelidotheriinae, although not formally nominated, for Late Pleistocene sediments of Argentina (Carlini et al., 2005), Brazil (Pereira and Oliveira, 2003) and Uruguay (Perea et al., 2006); those of the Middle–Late Pleistocene have not been revised.

Neither comprehensive systematic revisions nor modern biostratigraphic and/or paleozoogeographic interpretations of Ensenadan and Lujanian genera (Early Pleistocene to Early-Middle Pleistocene–Early Holocene) have recently been accomplished. However, the contributions of McDonald (1987) and Pujos (2000) must be underlined. One of the main goals of this paper is the revision of the materials assigned to Scelidotheriinae or those found in the Ensenadan–Lujanian of Argentina and their potential correlation with those of other countries of southern South America.

Although the main purpose of this contribution is to analyze the records of scelidotheres of the Early Pleistocene to Early-Middle Pleistocene (Ensenadan Stage/Age), this analysis cannot be done without a revision of the valid taxa. For this reason, a synthesis of the diversity of species, in which only those best defined are included, is presented below.

For biostratigraphic and chronostratigraphic matters, the scheme of Cione and Tonni (2005) is followed. Systematics follow tentatively, and at the generic level, the work of Kraglievich (1923), Pascual et al. (1966), Hoffstetter (1982) and Pujos (2000) for Pleistocene scelidotheres.

2. Systematic paleontology

The validity of some Pleistocene genera of scelidotheres is controversial (McDonald, 1987; Pujos, 2000). As mentioned above, McDonald (1987) and McDonald and Perea (2002) do not recognize the validity of *Scelidodon*, which would be a junior synonym of *Scelidotherium*. For this reason they replaced *Scelidodon* for *Catonyx* Ameghino 1891, to include the Pleistocene scelidotheres of Brazil, since *Platyonyx* Lund was pre-occupied as a coleopteran genus. However, Pujos (2000) stated that *Scelidodon*, *Scelidotherium* and *Catonyx* are three different genera, on the basis of cranial-dental and post-cranial features.

Consequently, at the genus level, this paper follow Kraglievich (1923), Pascual et al. (1966), Hoffstetter (1982) and Pujos (2000), as they recognize three different genera: *Scelidodon*, *Scelidotherium* and *Catonyx*.

Order **Tardigrada** Latham and Davis, 1795
Family **Mylodontidae** Gill, 1872
Subfamily **Scelidotheriinae** Ameghino, 1904
Genus *Scelidotherium* Owen, 1839
Type species. *Scelidotherium leptocephalum* Owen, 1839
Diagnosis of the genus. Skull elongate, low and narrow, the dorsal profile of braincase flat; the fronto-nasal region is narrow. In anterior view, the outline of the nasal opening is sub-triangular with vertex toward the palate region; maxillaries are almost vertical. Nasal processes extend beyond the anterior margin of the maxillary. Pre-maxillaries are very developed. The predented region is longer than the dental series of the maxillary. The M 1–5 are simple-crowned, subcylindrical, obliquely implanted and rather elongate antero-posteriorly. The mandible is more graceful, the horizontal ramus is low with the ventral margin almost straight. The mandibular symphysis extends on a very long predentary region, quadrangular in oclusal view. Mandibular keel is less evident. Humerus with graceful diaphysis. Anterior foot with finger I atrophied and without ungueal phalange. Femur with distal epiphysis wider than proximal; in posterior view and with distal condyles horizontal, the head is more medially placed than the medial condyle; medial epicondyle more conspicuous than the lateral.

2.1. Chronologic, geographic and systematic considerations of the genus Scelidotherium

The major problem of the Pleistocene Scelidotheriinae in the fossil record is the poor information about the stratigraphic and geographic provenance of the specimens (McDonald, 1987).

Scillato-Yané et al. (1995) and Carlini and Scillato-Yané (1999) reported the following taxa for the Ensenadan-Lujanian lapse of Argentina, in the current territory of Buenos Aires Province: *Scelidotherium* sp. *Scelidotherium floweri* Ameghino, 1881, *S. leptocephalum* and *Scelidotherium* nov. sp.

S. floweri was recognized by Ameghino (1881) on the basis of a posterior fragment of a left hemimandible (type MLP 3-761) with the m3-m4, found in the "Piso Belgranense" Ameghino (1889), of Villa Luján, Buenos Aires Province. Probably, this species is not valid, although Scillato-Yané et al. (1995) and Carlini and Scillato-Yané (1999) mentioned this taxon for the Lujanian *s.l.* of the Pampean Region, based on literature data, and without referred materials.

For the Pleistocene of Catamarca Province, *Scelidotherium laevidens* Moreno and Mercerat 1891 (type MLP 3-440), was described on a left hemimandible with m1–m2. This species is not well characterized, is only represented by the type, and lacks diagnostic features; hence, it is tentatively considered as not valid. No new specimens of Pleistocene scelidotheres have been so far reported for this province.

McDonald (1987) and McDonald and Perea (2002) mentioned only two species for *Scelidotherium*: a) *S. parodii* Kraglievich, 1923, from the Chapadmalalan (Upper Pliocene). Kraglievich (1934) arose the genus *Scelidotheridium* and included *S. parodii* (these authors discarded the validity of the genus *Scelidotheridium* Kraglievich 1934, which they included within *Scelidotherium*); b) *S. leptocephalum*, as the single species for the Ensenadan–Lujanian (ca. 0.78 Ma–8.5 ka BP; see Cione and Tonni, 2005) of the Pampean Region, Argentina, and for the Lujanian Stage/Age of Brazil and Uruguay.

Scillato-Yané et al. (1995) and Carlini and Scillato-Yané (1999), recognized *Scelidotherium* nov. sp. for the Ensenadan Stage/Age (Early Pleistocene to Early-Middle Pleistocene). This putative new species (represented by an astragalus, although it could not be found to date in the repository) is characterized by its small size. This is in accordance with what McDonald (1987), and McDonald and Perea (2002) stated, that Ensenadan scelidotherines are small compared to those of the Late Pleistocene, but, as mentioned above, they only recognized *S. leptocephalum* as the single member of the genus in the Pleistocene. It must be noted that McDonald (1987: 190) stated that the specimens of *S. leptocephalum* lack of precise data about stratigraphic and geographic provenance.

S. bravardi (Lydekker, 1886) was only mentioned by Rusconi (1936: 14) for the Ensenadan Stage/Age (ca. 0.78 Ma–0.5 Ma BP; see Cione and Tonni, 2005) and it was not considered in later papers (Scillato-Yané et al., 1995; Cione et al., 1999; Carlini and Scillato-Yané, 1999; Cione and Tonni, 2005, among others). Based on our systematic review, this species must be validated; the holotype (BMNH 37626, 37630-31-32-33-34-35, 37644-49) comes from the "Toscas del Río de la Plata", Buenos Aires Province (ca. 1.07–0.98 Ma; Soibelzon et al., 2008). Noteworthy, Ameghino (1889) mentioned that the materials assigned to *Scelidotherium* similar to the type of *S. bravardi* (Fig. 1A) are frequent in the "Toscas del Río de la Plata" (Fig. 2) and in excavations of the La Plata harbour, both localities which yielded Ensenadan faunas (Ameghino, 1889, Soibelzon, 2005). Lydekker (1894) doubted the validity of *S. bravardi*, and synonymyzed it with *S. leptocephalum*, since he interpreted the morphological variations as caused by sexual variations. However, the recognition of morphological variations related to sex is

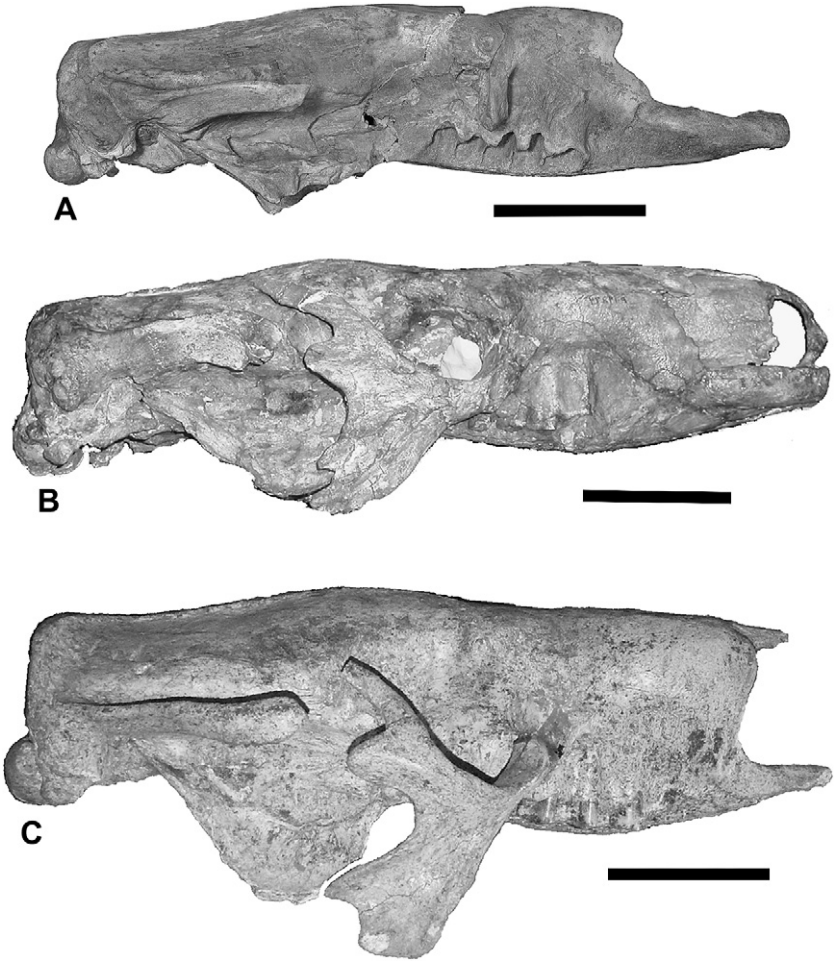

Fig. 1. Skulls in lateral view right. (A) *S. bravardi* (Holotype BMNH 37626), (B) *S. leptocephalum* (FMNH P 14274) and (C) *Sc. tarijensis* (MMP 1267-M). Scale: 10 cm.

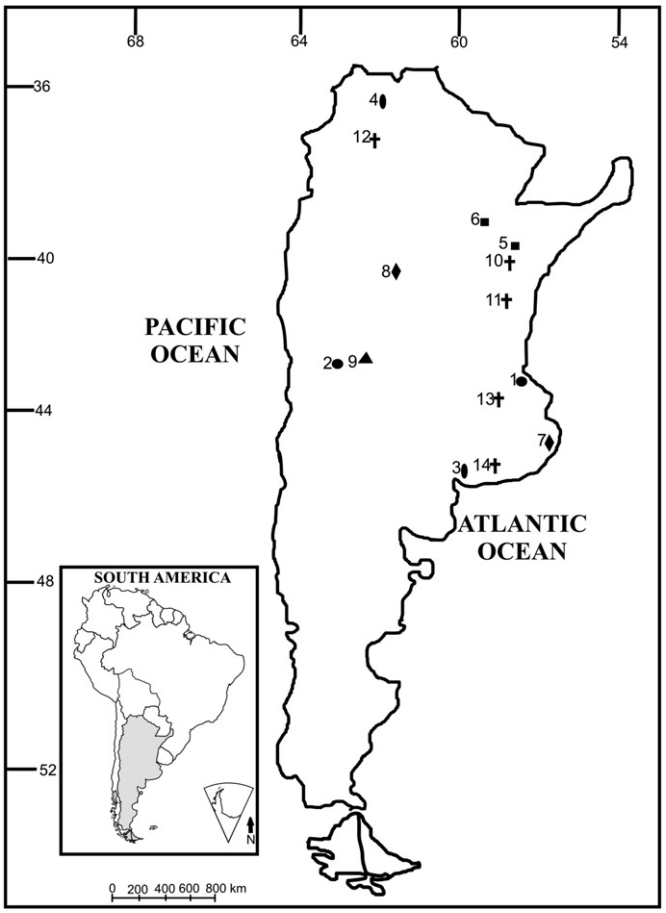

Fig. 2. Distribution of the genus *Scelidotherium* and genus *Scelidodon* in Argentina. Circle, *S. bravardi*; ellipse, *S. leptocephalum*; square, *Scelidotherium* sp.; rhombus, *Sc. tarijensis*; triangle, *Sc. chiliense*; cross, *Scelidodon* sp. (1) Toscas del Río de La Plata, (2) San Luis, (3) Punta Alta, (4) Salta, (5) Arroyo Toropí, (6) Chaco, (7) Mar del Plata, (8) Río Tercero, (9) San Luis, (10) Arroyo Toropí, (11) Entre Ríos, (12) Tafí Viejo, (13) Luján, (14) Quequén Salado.

difficult, even more in fossil species of lineages without living representatives, as stated by McDonald (2006). Hence, provisionally we do not agree with Lydekker (1894) since, as we will further underline, the remains assigned to this taxon have diagnostic features.

S. leptocephalum is the best studied species. The materials were found in the late Pleistocene of Punta Alta, Buenos Aires Province (Fig. 2), Argentina (Owen, 1857; Ameghino, 1889; Scillato-Yané et al., 1995). According to Scillato-Yané et al. (1995) and Carlini and Scillato-Yané (1999), this is an exclusive species of the Lujanian *s.l.*, since in these papers the Lujanian *s.l.* Stage was interpreted as including the Bonaerian + Lujanian *s.st.* (ca. 0.4 Ma–8.5 ka BP; see Cione and Tonni, 2005). So far, the most modern record of this species was dated in 7760 ± 120 years ^{14}C (early Holocene), on fragments of post-cranium found in the San Luis Province (Chiesa et al., 1999).

S. leptocephalum (although the specimen is currently lost) (Esteban et al., 1992), and cf. *S. leptocephalum* (MLP 89-XII-6-4) (Carlini et al., 1999) have been reported for Pleistocene sediments of the Salta Province (Fig. 2).

Zurita et al. (2004) reported *Scelidotherium* cf. *S. leptocephalum* (MRCH 109) for the Bonaerian–Lujanian Stage/Ages of Chaco Province (Fig. 2). In fact, the specimen is represented by a single m1 (MRCH 109) and must be assigned to *Scelidotherium* sp., until further evidence justifies its specific assignment.

Recently, in Lujanian sediments of the Toropí Formation, Corrientes Province (Fig. 2), a left hemimandible (CTES-PZ 7444) was found, assigned to *Scelidotherium* based on the following characters: a) horizontal ramus low and b) ventral margin almost straight. This specimen is the first record of the genus for the Pleistocene of Corrientes Province. This lithostratigraphic unit has an interesting mix of typically Pampean and Brazilian faunas (Carlini et al., 2004).

Tonni (2004: 32) mentioned *Scelidotherium* sp. in aeolian sediments overlying the conglomerates of the El Palmar Formation (Late Pleistocene) near the Colón and San José, Entre Ríos Province. Ferrero et al. (2007) revisited the Pleistocene mammals of the El Palmar Formation near Concordia, but *Scelidotherium* was not identified. Noriega et al. (2004) cited this taxon in the late Pleistocene of the Feliciano creek basin, near Diamante, but without referring materials.

The anatomical differences between *S. bravardi* (*S. b.*) and *S. leptocephalum* (*S. l.*) (Fig. 1B) are the following: the skull of *S. b.* is relatively narrower, with narrower fronto-parietal crest, and in posterior view, the occipital outline is less arched that that of *S. l.*; mandible, in *S. b.*, the symphysis is longer, narrower and strongly upward directed than that of *S. l.* Size: *S. bravardi* is smaller than *S. leptocephalum*.

In the MACN vertebrate paleontology collections there are several specimens found in "Toscas del Río de la Plata" (Fig. 2), Buenos Aires (Argentina), tentatively assigned to *Scelidotherium* (see Soibelzon, 2008). Noteworthy, most of these specimens are isolated elements of the post-cranium (e.g. astragali, calcanei, metacarpians). In fact, large part of these specimens must be referred to Scelidotheriinae until more evidence is available.

As a result of this revision, in the Ensenadan and Lujanian Stage/Ages of Argentina, *Scelidotherium* is represented by *S. bravardi*, Lydekker, 1886, recorded in the Ensenadan Stage/Age, and *S. leptocephalum* Owen, 1839, in the Bonaerian-Lujanian Stage/Ages.

Outside the Argentine territory, Pascual and Odreman Rivas (1973) mentioned *Scelidotherium* in the upper Pleistocene of Peru, although a recent synthesis of the Xenarthra from this country does not mention the presence of this genus (Pujos and Salas, 2004).

In Brazil, *S. leptocephalum* (Bombín, 1976) is also cited but without referred material. However, according to Oliveira (personal communication to Miño-Boilini, 2007), the specimens studied by Bombín (1976) have been lost, and in addition, they had no precise stratigraphic and geographic data.

In Uruguay, Ubilla et al. (2004) cited cf. *Scelidotherium*. In Paraguay, Hoffstetter (1978) mentioned *Scelidotherium*, but this author considered *Scelidodon* within *Scelidotherium* in that moment. In summary, all the records of *Scelidotherium* outside the present Argentine territory are at least debatable; consequently, the genus would be restricted to the present territory of Argentina, and particularly to the Pampean Region, where the frequency of records is very high.

Genus *Scelidodon* Ameghino, 1881

Type species. *Scelidodon copei* Ameghino, 1881

Diagnosis of the genus. Skull elongate, slightly higher. The fronto-nasal region transversely vaulted, with the nasal chamber bulging. In anterior view, the nasal opening is circular or sub-circular. Pre-maxillaries are less developed, acute in their sagittal joint. Upper pre-dented region is as long as or shorter than the maxillary dental series. M2–4 more triangular in section than those of *Scelidotherium*, and with well defined lingual furrow. Robust mandible, the horizontal ramus is high, the ventral margin markedly convex. Mandibular symphysis strongly upward inclined. Mandibular keel is very evident. Humerus with more robust diaphysis and deltoid tubercle more evident than in *Scelidotherium*. Anterior foot with finger I

developed with ungueal phalange sheathed. Femur, in posterior view and with distal condyles horizontally, with the head in vertical line over the medial condyle, distal epiphysis narrower.

2.1.1. Chronological, geographic and systematic considerations of the genus Scelidodon

Scillato-Yané et al. (1995), Cione et al. (1999) and Carlini and Scillato-Yané (1999) restrict the biochron of *Scelidodon*, in the Pampean Region, to the Ensenadan. However, Kraglievich (1934: 290) and Aramayo (1984) cited this genus in late Pleistocene sediments of Tandil and Luján respectively (Buenos Aires Province), although, only Aramayo (1984) figured the specimen MLP 3-576 (two complete feet; unfortunately, only part of this specimen could be found).

An isolated left astragalus (MACN 5110) from the late Pleistocene of Tandil belongs to a large specimen. This is mentioned by Aramayo (1984: 591), and assigned to *Scelidodon*. According to this revision, the specimens MLP 3-576 and MACN 5110 are assigned to cf. *Scelidodon*, both of them belonging to large individuals.

The type species is *Scelidodon copei*, Ameghino 1881, based on a left maxillary (MACN A-1158) from the Pleistocene of Mercedes, Buenos Aires Province (Argentina) (Bonaerian Stage/Age, Middle Pleistocene, ca. 0.4–0.130 Ma AP; see Cione and Tonni, 2005). Later, Ameghino (1889) cited this species for Ensenadan sediments but without referring materials.

McDonald (1987) and McDonald and Perea (2002) considered *Scelidodon* as a junior synonym of *Scelidotherium* and replaced the generic name for *Catonyx* Ameghino 1891, to include the scelidotherines from the late Pleistocene of Brazil, which were included in the genus *Platyonyx* Lund 1840. However, Pujos (2000) considered *Scelidodon* as a valid genus, different from *Catonyx*, which he also recognized as valid, and gave characters to define them. *Catonyx* is restricted to the late Pleistocene of Brazil, represented by *Catonyx cuvieri* (McDonald and Perea, 2002). This *Catonyx* is characterized by: a) humerus lacks entepiconylar foramen, b) tibia presents is the presence of a bar of bone over this muscle scar for the insertion of the muscle *semimembranosus* (see McDonald, 1987; Pujos, 2000).

The type of *Scelidodon tarijensis* (=*Catonyx tarijensis*) (Gervais and Ameghino 1880) is a skull and mandible of a single individual from the Tarija Valley, Bolivia, that was first figured by Gervais (1855: 50, plate XI, Fig. 2). On this material, Gervais and Ameghino (1880: 148) founded the species *Scelidotherium tarijensis*, erroneously included in *Scelidotherium*. These authors reported mainly the diagnostic features pointed out by Gervais (1855) who also included originally these materials in the genus *Scelidotherium*. Finally, Ameghino himself (1889) transferred the species to the genus *Scelidodon*. This species is characterized by: a) it is the largest species of the genus; b) in the skull, the sagittal and temporal crests are very evident; c) in the mandible, the m1 has one labial lobe, and the m4 has an accessory lobe (McDonald and Perea, 2002).

The type of *Sc. tarijensis* (MNHN TAR 1260) has no precise geographic and stratigraphic data, as well as other materials of this species found in the Valle de Tarija (Miño-Boilini and Carlini, 2007). However, McDonald (1987) reported it for the Ensenadan of Tarija. Although MacFadden (2000) dated recently the lower unit, which would be approximately 1Ma old, and thus coeval with part of the Ensenadan from the Pampean Region (Argentina), these are not the most fossiliferous levels of the area of the Valle de Tarija. They are quite sterile or the fossils found in them are fragmentary. Instead, the upper levels of the different sequences of the Valle de Tarija are the ones that provide the rich Pleistocene fauna of the area (Takai et al., 1984). Numerous specimens very well preserved and quite complete have been recovered from these upper levels. Finally, studies carried on by Coltorti et al. (2007) in several localities of the Valle de Tarija suggest that they would likely correspond to the upper units (see also Tonni et al., 2009). Despite that, as mentioned above, there are no precise stratigraphic data of the holotype of *Sc. tarijensis* and having in mind the type of material and its preservation, the hypothesis that they come from the upper levels, tentatively correlated to the Bonaerian and Lujanian, would be quite probable.

Another species mentioned for the Ensenadan of Buenos Aires, Argentina, is *Scelidodon capellini* (Gervais and Ameghino, 1880), founded on a left hemimandible (MNHN PAM 231) that lacks precise geographic and stratigraphic data and was first figured by McDonald (1987: 245, Fig. 53). In turn, Ameghino (1889, plate LXIII, Fig. 1) reproduced the drawings of Burmeister (1886) of a skull and hemimandible (probably MACN 994 and MACN 1041, according to Kraglievich (1923: 338) and assigned it to *Sc. capellini*. According to Ameghino (1889) these specimens would have been previously referred by Burmeister (1886) to *Scelidotherium magnum* (invalid taxon, since it was only mentioned in a taxonomic list of Bravard, 1857).

These materials were found in the "Toscas del Río de la Plata"; the skull (MACN 994) is restored and the fronto-nasal area is transversally vaulted, with bulging nasal chamber. In anterior view the nasal opening is circular in shape, typical of *Scelidodon*. The horizontal ramus of the right hemimandible (MACN 1041) is high, and the ventral margin convex. The mandibular symphysis is strongly upward directed, the mandibular keel very conspicuous. So far, these materials show characters of the genus *Scelidodon*.

Ameghino (1889, plate XLVIII, Fig. 3) figured a second specimen also assigned to *Sc. capellini*, represented by a partial skull. Unfortunately, to date, this specimen has not been found in the Argentine collections where it should be deposited.

In summary, some specimens referred to *Sc. capellini* are dubious, and the holotype has no precise geographic and stratigraphic data.

Finally, Scillato-Yané et al. (1995), Cione et al. (1999), Carlini and Scillato-Yané (1999) and Cione and Tonni (2005) mentioned *Sc. capellini* as exclusive for the Ensenadan, but without referring materials.

Kraglievich (1923), Hoffstetter (1978), McDonald (1987) and McDonald and Perea (2002) synonymyzed *Sc. capellini* with *Sc. tarijensis* (=*C. tarijensis*). However, Kraglievich (1923) and Hoffstetter (1952, 1963) supplied no evidence to support the synonymy of these taxa, neither mentioned characters to support this hypothesis.

McDonald and Perea (2002) recognized *Sc. tarijensis* (MMP 1266 M, Fig. 1C) for the Ensenadan of Argentina, in the Miramar Formation. However, noteworthy, the correct number of the specimen is MMP 1267 M (not MMP 1266, as they cited) and it was found in an excavation made in the northern side of the city of Mar del Plata (Fig. 2). Although we agree in the specific assignment of the authors, this specimen has slight differences in the upper dental series (e.g. the labial furrow of the M2–3 less marked) in relation to those specimens found in the Valle de Tarija. In addition, the precise stratigraphic provenance of this material (MMP 1267 M) is difficult to evaluate, since it may come from sediments referable to the overlying Bonaerian, having in mind that it was found at a depth of 6 m (in schedule) and that according to Federico Isla (personal communication, 2008) certain Ensenadan sediments are located below a depth of 10 m.

Voglino and Pardiñas (2005) report *Scelidodon* sp. for sector C of the Paraná River cliffs at the city of Ramallo, Buenos Aires (US 8 see Voglino and Pardiñas, 2005: 147) and restricted the age of this unit

to the uppermost Ensenadan ("Ensenadense cuspidal"). This level also yielded *Theriodictis platensis*, whose biochron is restricted in the Pampean Region to the Ensenadan (Prevosti et al., 2004). However, noteworthy, these materials do not belong to *Scelidodon* but to *Scelidotherium* sp. in view of the skull and dental morphology (e.g. the fronto-nasal region not transversally bulging, molariforms subcylindrical).

Both the type of *Sc. tarijensis* (MNHN TAR 1260), from the Valle de Tarija, and the specimens assigned to this species (MMP 1267 M, MACN 18223, FCS 96.I15/1/2) from Buenos Aires, have no precise stratigraphic data, but the specimens MACN 1041, MACN 10159 and MLP 3-479 do have it. These latter are assigned to *Scelidodon* sp., particularly MACN 1041 which was found in the "Toscas del Río de la Plata". MMP 8989, referred to *Sc. tarijensis*, was found in the Ensenadan of the city of Mar del Plata, in the same levels as a specimen of *Glyptodon munizi* (MMP 3985) which according to Soibelzon et al. (2006) is restricted to Ensenadan levels. In summary, this species was undoubtedly present in the Pampean Region during the Ensenadan and, probably, at least in part of the Bonaerian.

In the Pleistocene of Córdoba Province is recorded *Sc. tarijensis* (MDVS-PV 0025), near Río Tercero (Fig. 2). Recently, Tauber et al. (2007) mentioned *Sc. tarijensis* in excavations of the city of Córdoba.

This genus is also cited for younger geological units and outside the Pampean Region, but the specific assignment is less precise. Sayago et al. (1987) reported one Scelidotheriinae for the Province of Tucumán, in Pleistocene deposits at Tafi del Valle; it is a very damaged fragment of right hemimandible, with part of m3 and m4, with according to our current revision must be assigned to *Scelidodon* sp. (PVL 4637). Esteban et al. (1988) reported *Scelidodon* (although the specimen was not found in the repository PVL) for the locality of Tafí Viejo (Fig. 2), in sediments of the Tucumán Formation, a lithostratigraphic unit that would encompass the Ensenadan/Lujanian lapse; however, Powell (1998) recently restricted the age of this unit to the Lujanian.

In the present territory of Buenos Aires Province, the specimen MACN 9653, assigned to *Scelidodon* sp., was collected in the Quequén Salado River (Fig. 2) (near Paso del Médano), but no stratigraphic details are known. Pardiñas et al. (1996) studied the fossil fauna from the Quequén Salado River and, according to these authors, the fossil mammal association suggests a Lujanian Age (Late Pleistocene-Early Holocene); consequently, the specimen of *Scelidodon* (MACN 9653) would probably have this age. In addition, another specimen (FMNH P 14301) would have been found in the Quequén River (unfortunately it is not stated whether it is the Quequén Grande or Quequén Salado), Buenos Aires Province. This specimen has only post-cranial elements and we have assigned it to *Scelidodon* in view of the following characters: a) the humerus has a robust diaphysis, with very conspicuous deltoid tuberosity and b) the femur has a narrow distal epiphysis.

The Tezanos Pinto Formation (Late Pleistocene–Early Holocene) of Entre Ríos Province (Fig. 2) yielded a fragment of hemimandible assigned to *Scelidodon* (CICYTTP-PV-M-1-112), because the m1 has a conspicuous lingual curve, such as the m1 of MACN 9653, from the Lujanian of Buenos Aires.

Recently, Carlini et al. (2005) proposed a new species for this genus from the Toropí Formation, Corrientes Province. These sediments belong to the Lujanian (Cione and Tonni, 2005; Tonni et al., 2005) and particularly to the last ca. 50 ka (Tonni et al., 2005).

Outside Argentina, *Sc. chiliense* (Lydekker, 1886) was nominated and figured based on materials from the late Pleistocene of Chile. This species is also recorded in Peru, Ecuador and Bolivia (Pujos, 2000; McDonald and Perea, 2002) and there is also a single record (MHN-UNSL-GEO V 199) in late Pleistocene sediments of San Luis Province (Fig. 2) (Argentina; Miño-Boilini et al., in press). This taxon is characterized by: a) smooth sagittal crest; b) temporal crests slightly developed; c) suture separating squamosal from parietal and frontal, horizontal; d) smooth constriction at the middle of the frontal. Characters a, b and c are diagnostic of the species and were previously reported by McDonald (1987), Pujos (2000) and McDonald and Perea (2002) to define and differentiate *Sc. chiliense* from *Sc. tarijensis*.

As stated above, the specimens of *Sc. tarijensis* from the Pleistocene of the Tarija Valley (Bolivia) – in most cases skulls and associated mandibles, e.g. MNPA 005769, 32, 298, see Appendix 1 – have no precise stratigraphic and geographic data, preventing a detailed study.

3. Paleobiogeographic considerations of the Pleistocene Scelidotheriinae

From a paleobiogeographic point of view, the records of Scelidotheriinae Mylodontidae are restricted to South America. As mentioned above, identification of the first records of Scelidotheriinae is controversial, although it seems to be in the Miocene (see Scillato-Yané, 1977; McDonald, 1987; Scillato-Yané and Carlini, 1998).

During the Ensenadan and Lujanian Stage/Ages the records of *Scelidotherium* are frequent in the Pampean Region, more precisely in the present territory of Buenos Aires Province. Outside Buenos Aires Province, although the records are scarce compared to those of the Pampean Region and would correspond to the late Pleistocene, *Scelidotheriun* is recorded in Catamarca, Salta, San Luis, Chaco and Corrientes Provinces. Firstly, *Scelidotherium* would have been related preferably to cold and arid environments and, coincidentally, the record of this taxon is poor in the Mesopotamian Region (Corrientes and Entre Ríos Provinces, the region in between the Paraná and Uruguay rivers), so far represented by a single specimen (CTES-PZ 7444).

On the contrary, according to several authors (Scillato-Yané et al., 1995; Cione et al., 1999; Carlini and Scillato-Yané, 1999; Cione and Tonni, 2005), the record of *Scelidodon* would be restricted to the Ensenadan Stage/Age of the Pampean Region. However, on the basis of this revision, the materials referred undoubtedly to *Scelidodon* from the Pampean Region are not so frequent. Outside the Argentine territory, the northernmost records of *Scelidodon* are those mentioned by McDonald and Perea (2002) for the late Pleistocene of Ecuador, in addition to those mentioned in Peru (Pujos, 2000), Chile, Bolivia and Uruguay (McDonald and Perea, 2002).

In summary, *Scelidotherium* was distributed through the East, in southern South America, whereas *Scelidodon*, instead, was distributed through the West, reaching Ecuador. To date, *Catonyx* is restricted to the late Pleistocene of Brazil, represented by a single species, *C. cuvieri* (McDonald and Perea, 2002).

4. Conclusions

a) The Scelidotehriinae from the Ensenadan and Lujanian Stage/Ages (Early Pleistocene to Early-Middle Pleistocene–Early Holocene) of Argentina are represented by two genera: *Scelidotherium* and *Scelidodon*, which are differentiated by cranial, dental and post-cranial characters.
b) The following species are recognized for the genus *Scelidotherium* (see Appendix 1):

S. bravardi Lydekker, 1886, recorded in Buenos Aires Province during the Ensenadan Stage/Age, and in the Pleistocene of San Luis Province.

S. leptocephalum Owen, 1839, recorded in the Lujanian Stage/Age of Córdoba Province, and in the Bonaerian–Lujanian Stage/Ages interval in Buenos Aires Province.

Scelidotherium cf. *S. leptocephalum*, in the Lujanian Stage/Age of Salta Province.

Scelidotherium sp. in the Lujanian Stage/Age of Corrientes Province, probably Entre Ríos Province, and in the Bonaerian-Lujanian Stage/Ages of Chaco Province.

c) The following species are recognized for the genus *Scelidodon* (see Appendix 1):

Sc. tarijensis (Gervais and Ameghino, 1880), in the Ensenadan–Bonaerian Stage/Ages of Buenos Aires Province, in the Pleistocene of Córdoba Province Argentina, and in the Pleistocene of the Valle de Tarija, Bolivia.

Sc. chiliense (Lydekker, 1886), in the Lujanian Stage/Age of San Luis Province, Argentina, and in the late Pleistocene of Bolivia, Chile, Peru and Ecuador.

Scelidodon sp., in the Lujanian Stage/Ages of Buenos Aires Province. This genus is also recorded in the Lujanian Stage/Age of Corrientes, Entre Ríos and Tucumán Provinces.

d) Geographic distribution of *Scelidotherium* and *Scelidodon*:

Scelidotherium is recorded in Argentina and probably in Uruguay and Brazil.

Scelidodon is recorded in Argentina, Bolivia, Chile, Ecuador, Peru and Uruguay.

In summary, *Scelidodon* is geographically more widely distributed than *Scelidotherium*, since this latter has been well represented only in the Bonaerian-Lujanian Stage/Ages sediments of Argentina, especially in the Pampean Region.

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Appendix 1. Acronyms and list of specimens of *Scelidotherium* (*S.*) and *Scelidodon* (*Sc.*) mentioned in the text.

Material	Taxa	Stratigraphic and geographic procedence
BMNH 37626, 37630/31/32/33/34/35, 37644/49 Type	*S. bravardi*	Ensenadan, Toscas del Río de La Plata, Buenos Aires.
MMP 157-S	*S. bravardi*	Pleistocene, Mar del Plata, Buenos Aires.
MHN-UNSL-V 372	*S. bravardi*	Pleistocene, Villa Larca, San Luis.
MLP 92-VIII-1-2	cf. *S. bravardi*	Ensenadan, La Plata, Buenos Aires.
MLP s/n	cf. *S. bravardi*	Ensenadan, La Plata, Buenos Aires.

Appendix (*continued*)

Material	Taxa	Stratigraphic and geographic procedence
BMNH M 16579, 167781-82-83-84, Type	*S. leptocephalum*	Lujanian; Punta Alta, Buenos Aires.
MLP 3-402	*S. leptocephalum*	Pleistocene.
MLP 3-407-8, 3-420, 3-456	*S. leptocephalum*	Pleistocene.
MLP 3-671	*S. leptocephalum*	Pleistocene, Olavarría, Buenos Aires.
MMP 4220-M	*S. leptocephalum*	Lujanian, Centinela del Mar, Buenos Aires.
FMNH P 14274	*S. leptocephalum*	Pleistocene, Río Quequén, Buenos Aires.
MLP 52-X-5-41	*S. leptocephalum*	Lujanian, Río Quequén Salado, Buenos Aires.
MPS 43	cf. *S. leptocephalum*	Lujanian, San Pedro, Buenos Aires.
GCF 11	cf. *S. leptocephalum*	Lujanian, San Pedro, Buenos Aires.
MLP 89-XII-6-4	cf. *S. leptocephalum*	Lujanian, Salta.
MCA s/n	*S. leptocephalum*	Lujanian, Luján, Buenos Aires.
UNRC-PV 001	*S. leptocephalum*	Fm. La Invernada, Lujanian, Córdoba.
AMNH 11292	*Scelidotherium* sp.	Pleistocene, Olivera, Buenos Aires.
MLP 92-VIII-1-2	*Scelidotherium* sp.	Ensenadan, La Plata.
MLP 92-VIII-1-3	*Scelidotherium* sp.	Ensenadense, La Plata.
MLP 96-III-11-2	*Scelidotherium* sp.	Ensenadan, La Plata.
MACN 2289	*Scelidotherium* sp.	Ensenadan, "Toscas del Río de la Plata".
CC 98 y 174	*Scelidotherium* sp.	Ensenadan, Olivos, Buenos Aires.
CTES-PZ 7444	*Scelidotherium*	Lujanian, Bella Vista, Corrientes.
MRCH 109	*Scelidotherium* sp.	Bonarian-Lujanian, Charata, Chaco.
MLP 99-VIII-1-1	cf. *Scelidotherium*	Ensenadan, La Plata.
MNHN PAM 231 Type	*Sc. capellini*	Pleistocene, Buenos Aires.
MNHN TAR 1260 Type	*Sc. tarijensis*	Pleistocene, Valle de Tarija, Bolivia.
MMP 1267-M	*Sc. tarijensis*	Bonaerian?, Northern Mar del Plata City, Buenos Aires.
MMP 3989-M	*Sc. tarijensis*	Ensenadense, Mar del Plata, Buenos Aires.
FCS 96.I15/1/2	*Sc. tarijensis*	Pleistocene, Olavarría, Buenos Aires.
MACN 18223	cf. *Sc. tarijensis*	Pleistocene, San Nicolás, Buenos Aires.
MDVS-PV 0025	*Sc. tarijensis*	Pleistocene, Río Tercero, Córdoba.
MD 97-23	cf. *Sc. tarijensis*	Pleistocene, Punta Alta, Buenos Aires.
FMNH P 14243	*Sc. tarijensis*	Pleistocene, Tarija, Bolivia.
MNPA 005769	*Sc. tarijensis*	Pleistocene, Tarija, Bolivia.
MNPA 32	*Sc. tarijensis*	Pleistocene, Tarija, Bolivia.
MNPA 368	*Sc. tarijensis*	Pleistocene, Tarija, Bolivia.
MNPA 298	cf. *Sc. tarijensis*	Pleistocene, Tarija, Bolivia.
MHN-UNSL-V 199	*Sc. chiliense*	Lujanian, Pasos Merlo, San Luis.
FMNH P14238	*Sc. chiliense*	Pleistocene, Cuenca Padcaya-Tarija, Bolivia.
MACN 1041	*Scelidodon* sp.	Ensenadan, Toscas del Río de la Plata, Buenos Aires.
MACN 994 y 995	*Scelidodon* sp.	Ensenadan, Toscas del Río de la Plata, Buenos Aires.
MACN 10159	*Scelidodon* sp.	Ensenadan, Buenos Aires.
MACN 9653	*Scelidodon* sp.	Lujanian, Río Quequén Salado, Buenos Aires.
MLP 3-427	*Scelidodon* sp.	Pampean Upper
MMPH 090	*Scelidodon* sp.	Ensenadan?, Miramar, Buenos Aires.
MMPH 091	*Scelidodon* sp.	Ensenadan?, Miramar, Buenos Aires.
CTES-PZ 7151	*Scelidodon* nov. sp	Lujanian, Lavalle, Corrientes.
CTES-PZ 1690	*Scelidodon* sp.	Lujanian, Bella Vista, Corrientes.
FMNH P 14301	*Scelidodon* sp.	Pleistocene, Río Quequén, Buenos Aires.

(*continued on next page*)

Appendix (*continued*)

Material	Taxa	Stratigraphic and geographic procedence
PVL 1508	*Scelidodon* sp.	Ensenadan, Anchorena, Buenos Aires.
PVL 4637	cf. *Scelidodon*	Pleistocene, Tafi del Valle, Tucumán.
CICYTTP-PV-M-1-112	cf. *Scelidodon*	Fm. Tezanos Pinto, Lujanian, Diamante, Entre Ríos.
MLP 96-III-10-3	Scelidotheriinae	Ensenadan, La Plata.

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