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Paleobiogeography, biostratigraphy and systematics of the Hoplophorini (Xenarthra, Glyptodontoidea, Hoplophorinae) from the Ensenadan Stage (early Pleistocene to early-middle Pleistocene)

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ABSTRACT

Neosclerocalyptus Paula Couto (=*Hoplophorus* = *Sclerocalyptus*) is a Pleistocene genus of Glyptodontidae Hoplophorini (=Sclerocalyptini) that includes several (ca. twelve) species, many of which have been recognized by typological/morphological taxonomic criteria. Four species have been described for the Ensenadan Stage (early Pleistocene to early-middle Pleistocene) of the Pampean region, Argentina. However, this study shows only two of them to be valid: *Neosclerocalyptus pseudornatus* and *Neosclerocalyptus ornatus*. An evident synapomorphy of *Neosclerocalyptus* is the notable pneumatization and lateral expansion of the fronto-nasal sinuses, which becomes evident in *N. pseudornatus* (ca. 1.07–0.98 Ma) and even more so in *N. ornatus* (ca. 0.98–0.40 Ma). This character, interpreted here as a probable response to the cold and arid/semiarid Pleistocene climate, is maximally manifested in the taxa from the middle Pleistocene (Bonaerian Stage) and late Pleistocene (Lujanian Stage). *Neosclerocalyptus* is very common in the Pampean region and north-central Argentina, but very scarce or absent in the Argentinian Mesopotamia, Uruguay and southern Brazil, areas that were subject to relatively more humid and warmer climates during most of the Pleistocene. From a biogeographical perspective, both Ensenadan species are restricted to the current Pampean region. *N. pseudornatus* is recorded in the "Toscas" (caliche duricrusts) of Río de La Plata (Buenos Aires City and Olivos) and Mar del Plata (Buenos Aires province), while *N. ornatus* is recorded in Mar del Plata and San Pedro (Buenos Aires province), and Granadero Baigorria (Santa Fe province).

1. Introduction

The Glyptodontidae were one of the most conspicuous groups of Xenarthra in South America during most of the Cenozoic. From a taxonomic perspective, this clade experienced significant diversification (ca. 65 genera; see McKenna and Bell, 1997), as well as extensive temporal distribution (late Eocene–early Holocene; Hoffstetter, 1958; Paula Couto, 1979; Politis and Gutierrez, 1998; Carlini and Scillato-Yané, 1999; Cione et al., 2003; Zurita et al., 2005).

Even though Glyptodontidae taxonomy is complex, some consensus exists at present for the recognition of five subfamilies: a) Glyptatelinae (late Eocene – late Miocene – late Pleistocene? Scillato-Yané, 1977, 1986; Downing and White, 1995; Carlini et al., 1997, 2004, 2008a; Vizcaíno et al., 2003; Bostelmann et al., 2008); b) Propalaehoplophorinae (late Oligocene–middle Miocene; Scott, 1903–1904; Scillato-Yané, 1977, 1986; Bondesio et al., 1980); c) Glyptodontinae (middle Miocene–early Holocene; Cabrera, 1944; Castellanos, 1953; Carlini and Scillato-Yané, 1999; Carlini et al., 2008b); d) Doedicurinae (late Miocene–early Holocene; Hoffstetter, 1958; Paula Couto, 1979); e) Hoplophorinae (=Sclerocalyptinae) (middle Miocene–early Holocene; Scillato-Yané and Carlini, 1998a; Scillato-Yané et al., 1995; Carlini and Scillato-Yané, 1999; Zurita et al., 2005; Zurita, 2007).

In this context, the Hoplophorinae are probably the Glyptodontidae subfamily with greatest taxonomic complexity and

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Abbreviations: GABI, Great American Biotic Interchange; M–m, upper and lower molariforms, respectively; CC, Museo Universitario "Florentino y Carlos Ameghino", Universidad Nacional de Rosario (ex Instituto de Fisiografía y Geología "Alfredo Castellanos"), Rosario; MACN, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata; MSP, Museo Paleontológico Municipal "Fray Manuel de Torres", San Pedro; MMP, Museo Municipal de Ciencias Naturales del Mar del Plata "Lorenzo Scaglia; RCS, "Royal College of Surgeons", London, UK.

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morphological heterogeneity. This is due to the remarkable number of taxa included within its seven recognized tribes (Hoplophorini, Neuryurini, Palaeohoplophorini, Plohophorini, Panochthini, Lomaphorini and Neothoracophorini) and the poor morphological characterization of most Hoplophorinae species (Zurita, 2007). Indeed, these have been mostly recognized on the basis of typological criteria characteristic of the 19th and early 20th centuries. In the words of Hoffstetter (1958: 577): *"Il est difficile de donner de l' ensemble une définition précise, car trop de genres, surtout ceux du Mio-Pliocéne, sont connus d'une façon très fragmentaire."*

In addition, recent preliminary phylogenetic analyses have questioned the monophyly of this subfamily (Fernícola et al., 2002; Fernícola, 2005).

The Hoplophorinae Hoplophorini (=Sclerocalyptini) have traditionally presented a similar prospect, with remarkable taxonomic overestimation; about 8 genera and 26 species have been traditionally included in this tribe (see, among others, Ameghino, 1889, 1895, 1919; Rovereto, 1914; Castellanos, 1925, 1948, 1951; Cabrera, 1939, 1944; Scillato-Yané and Carlini, 1998a; Zurita, 2002). Thus, *Neosclerocalyptus* (=*Sclerocalyptus* = *Hoplophorus* = *Isolinia*; see Paula Couto, 1957; Zurita et al., 2007), one of the two Pleistocene genera of Hoplophorini, is the taxon with greatest proposed taxonomic overestimation. About 15 species have been attributed to this taxon (see Mones, 1986), four of which would be Ensenadan in age (see Ameghino, 1889).

However, a recent revision of this tribe has shown that the Hoplophorini from the present Argentinian territory are represented with certainty by 2 genera (*Eosclerocalyptus* and *Neosclerocalyptus*) and 7 species (Zurita, 2007), and probably an additional genus, *Eonaucum*, although little material of the latter is known (see Scillato-Yané and Carlini, 1998a). Furthermore, the stratigraphic distribution of these genera agrees with the pattern of morphological changes observed in relation to inferred climatic changes. The present contribution discusses the species of *Neosclerocalyptus* (Ensenadan–Lujanian; early Pleistocene–early Holocene) of Ensenadan age (early Pleistocene to early-middle Pleistocene) considered as valid, and assesses their significance as biostratigraphic, paleobiogeographic and paleoenvironmental indicators.

The nomenclatural and taxonomical schemes used here agree with the proposals of Paula Couto (1957, 1965) and Zurita et al. (2007). The chronological and biostratigraphic schemes used here follow those of Cione and Tonni (2005).

2. Paleontological systematics

Order **Cingulata** Illiger, 1811
Superfamily **Glyptodontoidea** Gray, 1869
Family **Glyptodontidae** Gray, 1869
Subfamily **Hoplophorinae** Huxley, 1864
Tribe **Hoplophorini** Huxley, 1864
Genus *Neosclerocalyptus* Paula Couto, 1957
Synonymy. *Sclerocalyptus* Ameghino, 1891; *Isolinia* Castellanos, 1951 [*partim*] n. sin; *Chacus* Zurita, 2002 n. sin.
Type species. *Glyptodon ornatus* Owen, 1845

Stratigraphic and geographic distribution. Early Pleistocene–early Holocene (Ensenadan–Lujanian) of the Argentinian provinces Buenos Aires, La Pampa, Córdoba, Mendoza, San Luis, Santa Fe, Entre Ríos, Corrientes, Chaco, Santiago del Estero, Tucumán, Formosa and Salta (Zurita et al., 2005). Pleistocene of Uruguay, Paraguay (Villa Hayes and Boquerón Departments) (Zurita, 2007) and Bolivia (Ñuapua and Santa Cruz de la Sierra; see Ameghino, 1889; Hoffstetter, 1968; Zurita et al., 2009).

Diagnosis. Small-sized compared with other Pleistocene Glyptodontidae. Cephalic shield wide (especially at naso-frontal level), with subquadrangular outline and formed by numerous osteoderms (approximately 80) with ornamentation similar to that of the dorsal carapace. Dorsal carapace low and elongated, subcylindrical, dorsal outline almost straight, formed by approximately 50–55 transversal rows of osteoderms at the sides of the carapace; in some cases carapace with slight middle constriction separating cephalic and caudal halves; antero-lateral margins flaring outwards as "wings" and formed by very small pentagonal or hexagonal osteoderms; these osteoderms with thick perforations at each intersection of the sulcus surrounding the central figure with the sulci that separate peripheral figures, in the area adjacent to the cephalic notch. Osteoderms with primitive ornamentation similar to that of Propalaehoplophorinae, relatively thin and large, formed by a flat or somewhat concave central figure surrounded by a row of smaller polygonal figures, 7–10 in the anterior and middle regions of the carapace, and 10–12 (exceptionally 13 or 14) in the posterior region (occasionally with an accessory row of peripherals in this area), with shallow sulci separating the figures from each other. Lateral carapace osteoderms rectangular and anteroposteriorly elongated, with a large central figure, and arranged in transversal rows; this arrangement disappearing toward the dorsum where the osteoderms become pentagonal or hexagonal with more developed peripheral figures. Caudal shield formed by four or five rings (each with two osteoderm rows) and a cylindrical–conical caudal tube somewhat flattened dorsoventrally and tapering distally, with two large terminal dorsolateral figures. Laterally with 5–7 oval figures, increasingly larger toward the apex; the last four lateral figures occupying more than half of the tube length. Each central figure may be surrounded by one or two rows of peripherals, contrasting with the single peripheral row of *Eosclerocalyptus*. Skull with highly developed and pneumatized fronto-nasal sinuses (maximally developed in Lujanian species), directed ventrally, although not as much as in *Panochthus*, and separated from the rest of the skull by an evident V-shaped notch; orbit closed posteriorly by a postorbital apophysis. Area anterior to orbital (nasal and frontal) notches semicircular, a condition associated with increased pneumatization of the sinuses. Infraorbital foramen projected in a plane passing at M3 level, differing from *Eosclerocalyptus* in which this plane passes through the M3–M4 boundary. Predental region of palate narrower and more extended anteroposteriorly than in *Eosclerocalyptus* and *Propalaehoplophorinae*, with dental series ending posteriorly to zygomatic process of squamosal. Paroccipital processes more developed and more laterally projecting than in *Eosclerocalyptus*. Supraoccipital is placed at an angle of 40–50° with respect to basilar plane. First molariform simple and elongated anteroposteriorly; second molariform with incipient lobation; other molariforms clearly trilobed. Molariforms M6–M8 have bilaterally symmetrical lobes and anterior wall of first lobe is flat or slightly convex. Humerus similar to that of *Hoplophorus euphractus*, somewhat shorter and more robust, with posterior margin of deltoid 'V' more developed and entepicondylar foramen more proximal, as in *Panochthus*. Scapula has sinuous acromion. Pes and manus tetradactyl due to loss of digit I; digit V is highly reduced.

2.1. Neosclerocalyptus pseudornatus *(Ameghino, 1889)* *(Fig. 1 A–H)*

Synonymy. *Hoplophorus pseudornatus* Ameghino, 1889; *Sclerocalyptus pseudornatus* (Ameghino, 1889).

Lectotype. MACN 1233, fragment of dorsal carapace with 13 osteoderms.

Paralectotype. **MACN 13084**, distal half of caudal tube.

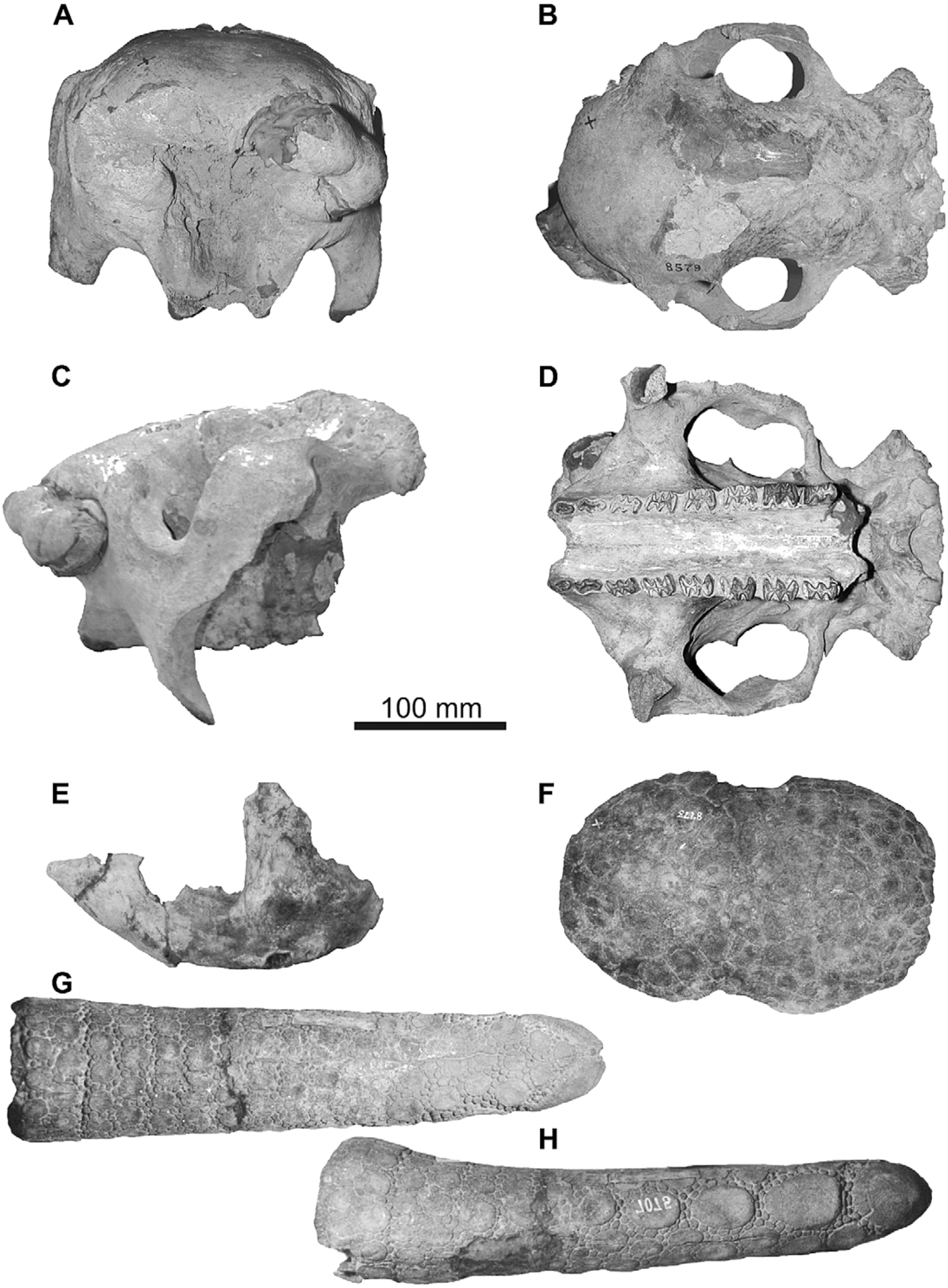

Fig. 1. *Neosclerocalyptus pseudornatus*. (A) Skull in frontal view, (B) In dorsal view, (C) Lateral view, (D) Ventral view (**MACN 8579**), (E) Left hemimandible in lateral view (**MACN 5858**), (F) Cephalic shield in dorsal view (**MACN 8773**), (G) Caudal tube in dorsal view, (H) Caudal tube in lateral view (**MACN 7075**).

Type locality. "Toscas del Río de La Plata", (caliche duricrusts outcropping at the margins and bed of the river), Buenos Aires City, Argentina (34°38′ S, 58°28′ W).

Referred materials. **CC 20**, caudal tube; **CC 107**, complete skull; **CC 21** caudal tube; **CC 167**, lateral right portion of dorsal carapace; **MMP 234**, right half of skull; **MACN 8579**, complete skull; **MACN 8773**, complete skull; **MACN 2936**, left femur; **MACN 8676**, right femur; **MACN 5858**, right hemimandible; **MACN 2262**, right hemimandible; **MACN 5007**, caudal tube; **MACN 13084**, caudal tube (figured by Ameghino, 1889: pl., LXLII, Figs. 1–3); **MACN 1798**, caudal tube; **MACN 5028**, caudal tube; **MACN 7075**, caudal tube; **MACN 12543**, carapace fragment; **MACN 1930**, large fragment of right humerus; **MACN 1966**, right mandibular ramus; **MACN 1989**, left humerus; **MACN 2209**, left radius; **MACN 2014**, left radius; **MACN 2018**, left radius; **MACN 2262**, left mandibular ramus; **MACN 2332**, distal half of left femur; **MACN 2315**, atlas; **MACN 2273**, right tibiofibula; **MACN 2276**, distal half of caudal tube; **MACN 1793**, proximal portion of left ulna; **MACN 2019**, distal half of left humerus; **MACN 2316**, proximal portion of right ulna; **MACN 2272**, right tibiofibula; **MACN 1836**, caudal tube; **MACN 2232**, distal half of left femur; **MACN 2076**, distal half of left femur; **MLP 16–144**, distal half of caudal tube.

Diagnosis. Skull with parietoccipital region directed dorsally, but not as much as in *Neosclerocalyptus ornatus*, with sagittal crest similar to that of *Eosclerocalyptus proximus*. Fronto-nasal sinuses little pneumatized and laterally expanded, with external bony lamina recurved in helicoidal fashion (Fig. 1A,C). Anteriormost portion of nasals is not preserved in any of the specimens. Area between fronto-nasal sinuses and postorbital processes of frontal bone more developed transversally and anteroposteriorly than in *N. ornatus*, *Neosclerocalyptus gouldi* Zurita et al. (2008) and *Neosclerocalyptus paskoensis*, due to lesser pneumatization of the sinuses (Fig. 1B,C). Zygomatic arches high and straight, similar to those of *E. proximus* and *N. ornatus* and clearly different from those of *E. tapinocephalus* (whose zygomatic arches become shorter toward the orbital notches) (Fig. 1C). Descendent processes of maxillae very developed at jugal level. Infraorbital foramen is small, but with extremely thick lower bony margin (Fig. 1D). Foramen *magnum* is larger transversally than dorsoventrally, oval in shape. First upper molariform is elliptical in cross section, with greater axis parallel to the sagittal plane; M2 with incipient lobation; M3–M8 clearly trilobed (Fig. 1D). Cephalic shield wide (especially at naso-frontal level) and formed by numerous osteoderms (approximately 80) with ornamentation similar to that of dorsal carapace (Fig. 1F). Mandible and caudal tube are morphologically similar to those of *N. ornatus* (Fig. 1E,G,H). Dorsal carapace very similar in shape to that of *N. ornatus*, that is, low, subcylindrical, elongated and with almost straight dorsal outline, different from more globose carapace of *E. proximus*; in one specimen (**CC 167**), plate rows adjacent to caudal notch with accessory rows of peripheral osteoderms at proximal and distal margins.

Chronological and geographical distribution. Early-middle Ensenadan (1.07–0.98 Ma) (early Pleistocene) (Fig. 3). ‘‘Toscas del Río de La Plata’’ (see above; Buenos Aires City and Olivos) and Mar del Plata, Buenos Aires province, Argentina (Fig. 4).

Historical and taxonomic aspects. This species was originally recognized by Ameghino (1889) as *H. pseudornatus* on the basis of fragmentary dorsal carapace osteoderms and a proximally broken caudal tube collected from the sediments of the ‘‘Toscas’’ of Río de La Plata (Buenos Aires). These materials had been figured earlier by Lydekker (1887) as *Hoplophorus* sp. a?; some time afterwards, however, this same author (Lydekker, 1894) classified these remains as *Lomaphorus ornatus*. In his published response, Ameghino (1895) again asserted the validity of this species and summarized its main distinctive characters. Since Ameghino (1889: 808–809) did not choose a holotype from the type serie (MACN 1233 and MACN 13084), we select (in the context of this taxonomic revision) the MACN 1233 as the lectotype of this species (see ICZN, 1999, art. 74).

2.2. N. ornatus *(Owen, 1845) (Fig. 2A–F)*

Synonymy. *G. ornatus* Owen, 1845; *Hoplophorus ornatus* (Owen, 1845); *Sclerocalyptus ornatus* (Owen, 1845).

Holotype. RCS 3606 (ex **RCS 554**), four dorsal carapace osteoderms (Owen, 1845: 119).

Type locality. Near Matanzas river, approximately 32 km south of Buenos Aires City, Argentina.

Neotype. (**MACN**?; missing), complete dorsal carapace, caudal rings and caudal tube (figured by Burmeister, 1871, pl. XVII) (Lydekker, 1887: 128) (see discussion below)

Type locality: Buenos Aires province, Argentina.

Referred materials. **MLP 16–28**, complete skeleton and dorsal carapace (figured by Lydekker, 1894; plates XI, XII and XIII); **MMP 4300**, complete dorsal carapace and caudal tube; **MACN 8091**, dorsoventrally compressed skull; **CC 656**, skull, mandible and cephalic shield; **MACN 11948**, mandibular ramus; **MSP 12**, almost complete dorsal carapace, complete caudal rings and caudal tube, and very fragmentary posterior skull with matching portion of cephalic shield.

Diagnosis. Hoplophorini slightly larger than *N. pseudornatus*, similar in size to *N. gouldi*. Skull with convex profile, parietoccipital region elevated, even more so than in *N. pseudornatus*, and marked sagittal crest (Fig. 2A–C). Fronto-nasal sinuses more defined than in *N. pseudornatus*, ‘funnel’-shaped, inclined ventrally, clearly pneumatized and laterally expanded (more so than in *N. pseudornatus* and *H. euphractus*, but not as much as in *N. gouldi* and *N. paskoensis*), separated from each other and from the frontal and maxillary bones by evident V-shaped cleft; free margins of nasals curved inward, especially at their middle and lower portion (Fig. 2A–C). Region between fronto-nasal sinuses and postorbital processes of frontal less developed transversally and anteroposteriorly than in *N. pseudornatus*, due to greater pneumatization of sinuses. Zygomatic arches high and straight, very similar to those of *N. pseudornatus* and *E. proximus* (Fig. 2C). Infraorbital foramen larger than that of *N. pseudornatus*, with thinner lower bony margin very similar to that of *N. gouldi* (Fig. 2D). Foramen *magnum* similar to that of *N. pseudornatus*, i.e., with oval outline. First molariform simple, elongated anteroposteriorly; second molariform with incipient lobation, as in *N. pseudornatus*; remaining molariforms trilobed and similar to those of other species of *Neosclerocalyptus* (Fig. 2D). Mandible similar to that of *N. pseudornatus* and *N. gouldi*, with ascending rami extended anteroposteriorly, although not as much as in *E. proximus*, and inclined forward. Dorsal carapace elongated, low, subcylindrical, and with dorsal outline almost completely straight, with slight narrowing at the middle separating two parts: anterior low narrow portion, and posterior somewhat higher and broader portion (Fig. 2E). Some specimens have accessory rows of peripheral figures at distal and proximal margins of osteoderm rows adjacent to caudal notch, as in *N. pseudornatus*.

Chronological and geographic distribution. Middle-late Ensenadan (0.98–0.40 Ma) (early-middle Pleistocene) (Fig. 3). Mar del Plata and San Pedro (Buenos Aires province), Granadero Baigorria (Santa Fe province) (Fig. 4).

Historical and taxonomic aspects. This species was recognized and figured by Owen (1845: Fig. 5) based on a series of four or five associated osteoderms from a dorsal carapace collected from Pleistocene sediments in the vicinity of Matanzas river, some 32 km southwest from Buenos Aires City (Owen, 1845; see Rusconi, 1930). Originally, Owen (1845) assigned these remains to genus *Glyptodon* Owen, 1839 and recognized the species ‘‘*G. ornatus*’’, whose type was deposited in the collections of the ‘‘Royal College of Surgeons’’ (**RCS**) (Londres), where Owen worked as curator. Although the precise stratigraphic provenance of the material collected by Owen (1845) (**RCS 3606**) cannot be established, diverse authors have recognized Ensenadan outcroppings at several sectors of Matanzas river (see Rusconi, 1930, 1936). Added to these considerations is the fact that the **RCS** collection was greatly damaged during a series of bombing raids that affected London in 1941. As a consequence, only 175 of the original 5200 catalogued specimens could be rescued (Currant, pers. comm.). Cave’s (1942) list of the materials that were not destroyed does not include the type of *N. ornatus*, and consequently it should be considered lost.

Given that the type material of this Hoplophorini species did not present relevant diagnostic characters, Lydekker (1887: 128 *“Since there may be possibly be a doubt as to the identity of the complete*

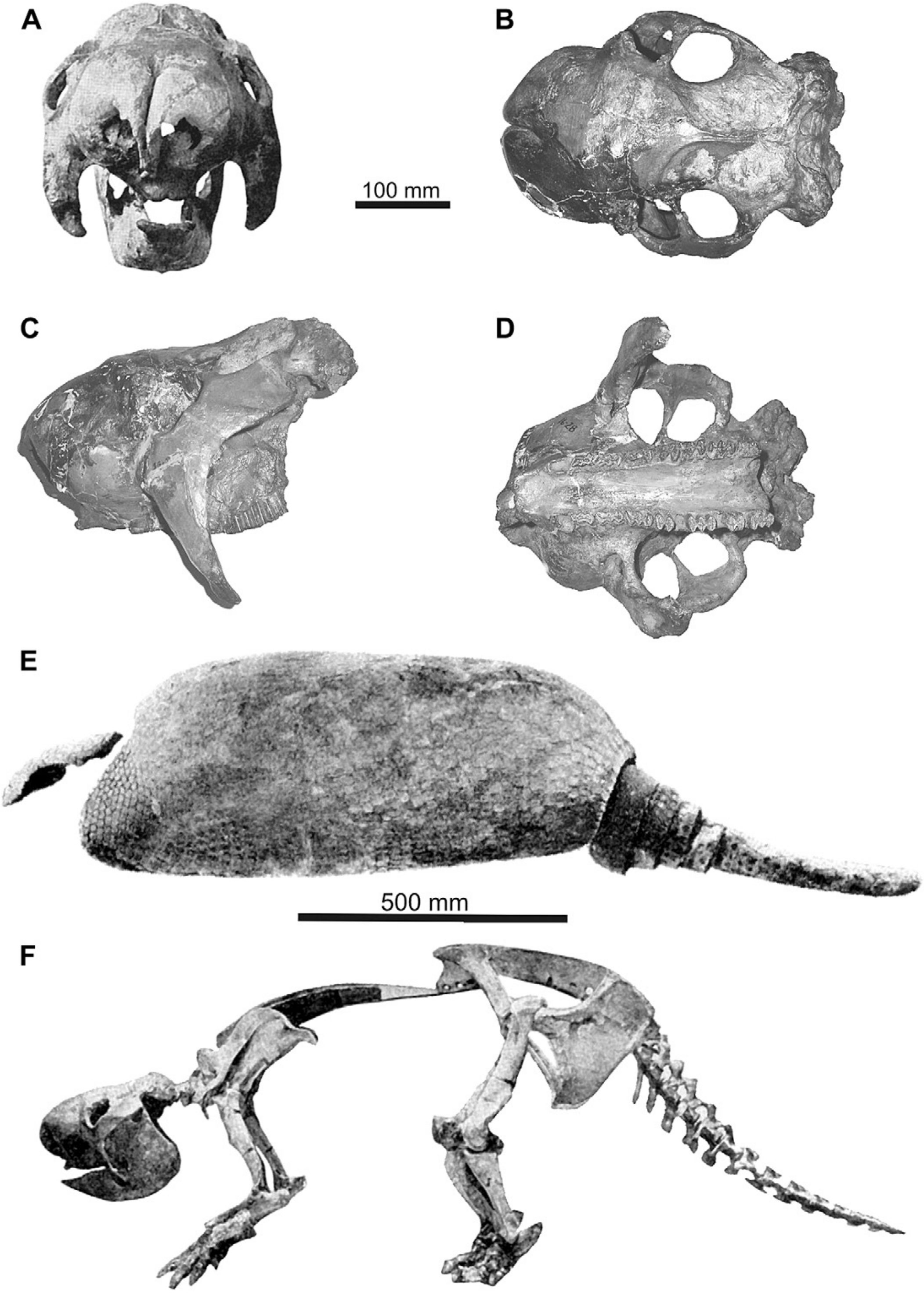

Fig. 2. *Neosclerocalyptus ornatus* (**MLP 16–28**). (A) Skull in frontal view, (B) In dorsal view, (C) In lateral view, (D) In ventral view, (E) Cephalic shield, dorsal carapace, caudal rings and caudal tube in lateral view, (F) Complete skeleton in lateral view.

carapace figured by Burmeister in the "An. Mus. Buenos Aires" under the present name with the fragment to which the name "G" ornatus was applied, it will be advisable to regard the former as the type") designated as neotype a very well preserved dorsal carapace with associated caudal rings and caudal tube that had been figured by Burmeister (1871; plate XVII). Unfortunately, this material has not been found in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", and is thus considered as missing.

Lastly, in a taxonomic revision, Lydekker (1894: 20–24) described and illustrated an excellent specimen of this species (**MLP 16–28**; Fig. 2A–F), from the Ensenadan of Mar del Plata, Buenos Aires province, which is morphologically almost identical to the specimen that he had earlier designated as the neotype.

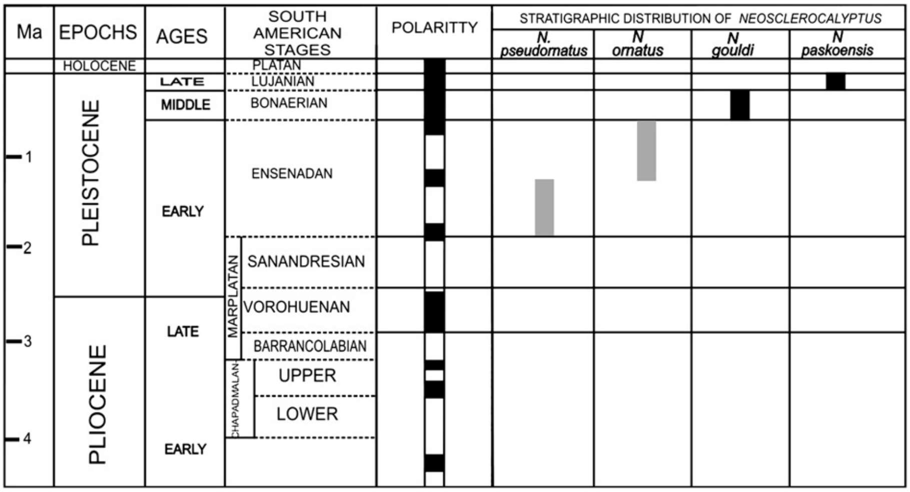

Fig. 3. Chronological distribution of the species of *Neosclerocalyptus*.

Since then, and until now, for a period of 113 years, all the specialists have directly or indirectly associated this specimen (**MLP 16–28**) with the name *N. ornatus* (=*H. ornatus* = *S. ornatus*) (see, among others, Ameghino, 1895; Richter, 1911; Vinacci, 1939; Hoffstetter, 1958; Pascual et al., 1966; Paula Couto, 1979; Zurita et al., 2005).

To paraphrase Ameghino (1895: 845) *"Es un soberbio ejemplar de un individuo completamente adulto (…) y deberá ser consultada preferentemente por los paleontólogos porque representa aproximadamente la forma exacta del animal"* ("It is a superb sample of a fully grown adult (…) and it should be preferably consulted by paleontologists because it represents approximately the actual shape of the animal").

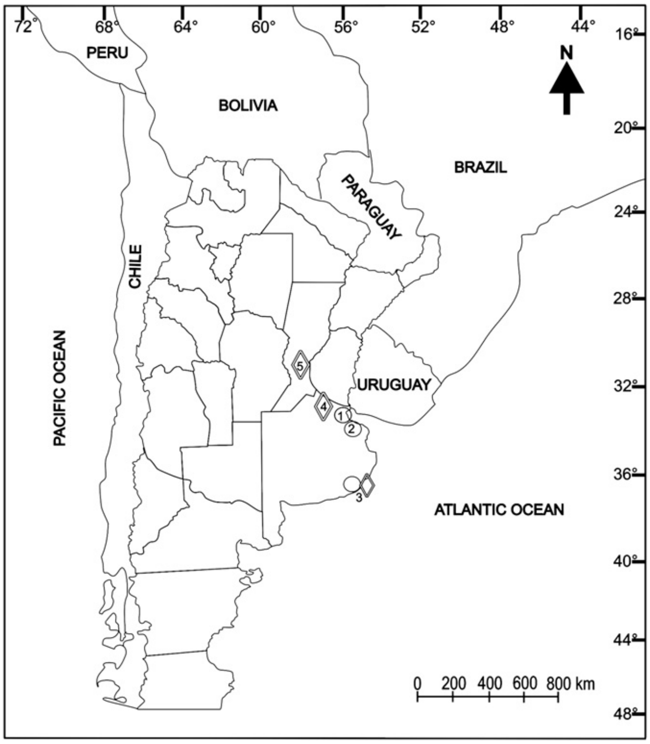

Fig. 4. Geographic distribution of *Neosclerocalyptus pseudornatus* (circle) and *N. ornatus* (triangle). 1 Ciudad de Buenos Aires, 2 Olivos, 3 Mar del Plata, 4, San Pedro, 5 Granadero Baigorria.

3. Other Ensenadan Hoplophorini? problematic issues

As previously mentioned, *Neosclerocalyptus* is a genus with remarkable taxonomic overestimation, since most of the species were recognized based on fundamentally typological taxonomic criteria (see Giraudo, 1997; Hevia and Romero, 1999). Consequently, many of the characters used for recognition of new species (e.g. osteoderm thickness and number of peripheral figures in dorsal carapace osteoderms; shape, length, degree of flattening and number of lateral figures in the caudal tube) are currently insufficient, as their intraspecific variability has not been adequately evaluated, as demonstrated for other Glyptodontidae Hoplophorinae (Perea, 2005).

In this taxonomic context, *"Hoplophorus" perfectus* Gervais and Ameghino is a species created in 1880 whose type is a small dorsal carapace fragment collected from the "Toscas del río de La Plata", Buenos Aires City (**MACN 1232**). Later on, Ameghino figured the type material (1889, pl. LXIV, Fig. 1) while he also associated new materials to this taxon without adequate justification, particularly a caudal tube (**MACN 7079**) possibly from the Bonaerian deposits, or even the Lujanian beds, of Luján river at Colonia Salazar (*unpublished.*) (Ameghino, 1889, pl. XC, Figs. 1–3). The characters used by Gervais and Ameghino (1880), for the original identification of the species, are insufficient, because the only diagnostic features mentioned by these authors are larger size of osteoderms and central figures, and greater number of peripheral figures (11–13). However, the materials that correspond to the lectotype (three dorsal carapace osteoderms; **MACN 1232**) do not display clear diagnostic characters that could link them to the Pleistocene genus *Neosclerocalyptus* (Zurita et al., 2005; Zurita, 2007). A thorough analysis of these osteoderms indicates that their morphology does not correspond to the known variability for dorsal carapaces of Glyptodontidae Hoplophorini. They probably correspond to the tribe Panochthini (cf. *Panochthus intermedius*) given the size proportion between central and peripheral figures (see Lydekker, 1894).

"Hoplophorus" scrobiculatus, a taxon described by Ameghino (1889), is another recognized Ensenadan species. The story of this species is quite singular, as Ameghino designated as type material a dorsal carapace and caudal tube that were deposited in the

collections of the then Museo Nacional de Buenos Aires (today the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"), and which he presented as associated materials. At the time, Ameghino noted that the small size of the specimen, as well as the particular morphology of the osteoderms, indicated a supposed transition to genus *Lomaphorus*. Thus, the diagnostic characters supplied by Ameghino (1889: 817) (e.g. number of peripheral figures surrounding each central figure, slight concavity on dorsal surface of osteoderms, large penultimate lateral figure of caudal tube, etc.) are common to the Hoplophorinae Hoplophorini. Furthermore, he only illustrated three associated osteoderms (Ameghino, 1889; pl. LXXXV, Fig. 4).

However, six years later, Ameghino (1895: 543–544) stated that this species should disappear because it had been described based on a dorsal carapace that was referable to the Lomaphorini "*Lomaphorus compressus*" and a caudal tube probably assignable to *Neosclerocalyptus*, although, as stated above, these materials had never figured. Unfortunately, the materials on which Ameghino based his description have not been found in the collections of Museo Argentino de Ciencias Naturales, and consequently this taxon should be considered *in querenda*.

4. Paleobiogeography and biostratigraphy of *Neosclerocalyptus*, with emphasis on Ensenadan species

The biogeographical history of the Glyptodontidae Hoplophorini (late Miocene–early Holocene) is apparently restricted to the southern cone of South America, where their range extends with certainty from about 20° S to 38° S latitudinally and from 43° W to 66° W longitudinally. This contrasts with the case of the Glyptodontidae Glyptodontinae, the other characteristic and frequent taxon for the late Neogene, whose first records date from the late Miocene of Colombia (Carlini et al., 2008b); the distribution of glyptodontines during the Pleistocene included South America from Argentina to Venezuela, Central America, and North America up to ca. 35° N (Marshall et al., 1984; Tonni and Scillato-Yané, 1997; Rincón, 2006; Carlini et al., 2008a). In addition, this is probably the only Glyptodontidae subfamily that participated in the Great American Biotic Interchange (GABI) and underwent cladogenesis, which is reflected in five described species (Gilette and Ray, 1981; Flynn et al., 2005; Morgan and White, 2005; White and Morgan, 2005; Carlini et al., 2008a).

Neosclerocalyptus is a typical Pampean genus of Hoplophorinae Hoplophorini, geographically restricted to the present territories of Argentina, Bolivia, Paraguay and Uruguay (Zurita et al., 2005; Zurita, 2007). It was probably well adapted to progressively colder and more arid environments (Tonni and Fidalgo, 1979; Fidalgo and Tonni, 1983), as the records of this genus are very scarce in areas that were relatively humid and warm during most of the Pleistocene (Argentinian Mesopotamia, western Uruguay and southern Brazil) (Kraglievich, 1932; Scillato-Yané et al., 1998; Carlini et al., 2004; Noriega et al., 2004), but are very abundant in the area that currently comprises the Pampean region and central-northern Argentina (Zurita et al., 2004), and they are the only well represented Hoplophorini in Paraguay. Accordingly, *Neosclerocalyptus* is characterized by an evident and progressive increase of pneumatization and lateral expansion of the fronto-nasal sinuses, a feature that becomes even more evident in the middle and late Pleistocene species. This increasing pneumatization of the fronto-nasal sinuses is a probable response to the cold arid or semiarid Pleistocene environments (see Clapperton, 1993; Tonni et al., 1999a,b; Cione and Tonni, 2001; Prado et al., 2001; Cione et al., 2003; Tonni et al., 2003; Zurita et al., 2005).

Latitudinally, the northernmost record of the genus in Argentina corresponds to Las Lajitas, in Salta province (24°42′ S) (see Zurita et al., 2002); in Argentina, the distribution of species of this genus ranges from 26°41′ S (Avia Terai, Chaco province) to 38°44′ S (Bahía Blanca, Buenos Aires province), and longitudinally from 57°33′ W (Mar del Plata, Buenos Aires province) to 65°02′ W (Merlo, San Luis province; see Chiesa et al., 2000, 2005). Outside Argentina, the northernmost records correspond to the localities of Ñuapua (20° 52′ S; 63° 04′ W; see Hoffstetter, 1968) and Santa Cruz de la Sierra (17° 47′ S, 63° 11′ W; see Zurita et al., 2009), in Bolivia.

Taxonomically, four *Neosclerocalyptus* species can be recognized with certainty. As we have mentioned, *N. pseudornatus* and *N. ornatus* are recorded in the Ensenadan Stage (early Pleistocene to early-middle Pleistocene), while a single species (*N. goudi*) is recognized for the Bonaerian Stage (middle Pleistocene). Lastly, *N. paskoensis* is an exclusively Lujanian (late Pleistocene–early Holocene) species (Fig. 3), widely distributed in the present Argentinian territory between 26°41′ S (Avia Terai, Chaco province) and 38°44′ S (Bahía Blanca, Buenos Aires province) (Zurita, 2007).

Chronologically, the Ensenadan Stage (early Pleistocene to early-middle Pleistocene; 1.8–0.4 Ma) spans a wide interval of more than 1 million years, during which numerous climatic–environmental changes that drastically affected faunal composition and diversity (Cione and Tonni, 1999, 2001; Rabassa et al., 2005; Soibelzon, 2005) took place within a general climate cooling trend. In this context, the paleoenvironmental evidence suggests that the Ensenadan Stage of southern South America was characterized by the defined predominance of cold arid or semiarid climates interspersed with brief warmer and more humid pulses (Tonni and Cione, 1994, 1995; Tonni et al., 1999b; Cione and Tonni, 2001; Soibelzon et al., 2006a). Specific pulses have been detected at approximately 1.0 Ma (Nabel et al., 2000) and 0.4 Ma (Soibelzon et al., 2006a). Considering the entire Pleistocene (ca. 2.6 Ma to 10 ka B.P.), the Ensenadan Stage seems to have been the period with the highest proportion of mammals adapted to open arid environments (Bobe Quinteros et al., 2004). In the current Pampean region, these climatic–environmental processes favored the expansion of characteristic elements from the Central and Patagonian Domains (e.g. *Microcavia australis*, *Lestodelphys halli*, *Tolypeutes matacus*). One distinctive feature of this period is the large size attained by some taxa, greater than that observed during the middle Pleistocene–early Holocene (e.g. *P. intermedius*, *Glyptodon munizi*, *Toxodon ensenadensis*) (Scillato-Yané and Carlini, 1998b; Cione et al., 2003; Soibelzon et al., 2006b), as well as the marked proliferation of herbivorous megamammals belonging to several orders (e.g. Notoungulata, Xenarthra Phyllophaga, Litopterna; Tonni and Cione, 1994).

In the current Pampean region, the sediments of Ensenadan age correspond to the Miramar and Ensenada formations (including Ameghino's 'Preensenadan' stage) and the outcroppings of Vorohué and San Andrés formations located north of Mar del Plata (Soibelzon, 2005).

In this context, *N. pseudornatus* (ca. 1.07–0.98 Ma) is the oldest species of the genus, and already begins to show a tendency toward increased pneumatization and development of the fronto-nasal sinuses, possibly as a response to climatic–environmental conditions (Zurita et al., 2005; Zurita, 2007). To date, the geographical distribution of this species is restricted from 34° 31′ S ("Toscas del Río de La Plata", Buenos Aires City) to 38° S (Mar del Plata), i.e., central-eastern Argentina (Fig. 4).

From a stratigraphic perspective, the sediments that correspond to "Toscas del Río de la Plata" were initially correlated by Ameghino (1889) with the uppermost ('cuspidal') Ensenadan beds. Unfortunately, as already noted by Ameghino and Kraglievich (1921: 136) "*…los típicos yacimientos del Ensenadense con su rica y variada fauna están destinados a desaparecer totalmente en un futuro no lejano a consecuencia de las modificaciones que experimenta… la antigua ribera de Buenos Aires, a lo largo de la cual… la bajante del río ponía al* *descubierto las clásicas toscas*" (the typical Ensenadan fossil beds with their rich and varied fauna are doomed to complete disappearance in the near future due to the modifications suffered by… the old coastline of Buenos Aires, along which… low levels of the river have uncovered the typical 'tosca' [*caliche duricrusts*] rocks).

These sediments are currently considered to represent a period between the Jaramillo and Olduvai events, corresponding to Chron 1 (reversed magnetic polarity). In this sense, the presence of the Notoungulata *Mesotherium cristatum*, considered as a guide fossil for the upper Ensenadan Stage, supports this temporal assignation (Tonni and Cione, 1994), and so does the presence of the bird *Pseudoseisura* sp. *nov.* (Tonni et al., 1999b). Chronologically, this implies that these sediments could be dated between 1.07 Ma and 0.98 Ma (early-middle Ensenadan Stage) (see Soibelzon et al., 2008).

From a paleoenvironmental viewpoint, the micromammals of this age (1.0 Ma; middle Ensenadan Stage) indicate clear predominance of cold arid climatic conditions, interspersed with some brief humid periods (Tonni et al., 1999b). In an independent study, Bonadonna and Alberdi (1987) detected an important cold arid pulse (ca. 1.0 Ma) that implied some faunal changes. Thus, the temporal distribution of this Hoplophorini species coincides partially with the "Great Patagonian Glaciation", which took place between 1.168 and 1.016 Ma (Rabassa et al., 2005). The same fossil beds from which the remains of *N. pseudornatus* were collected ("Toscas del Río de La Plata"), have also yielded remains of *Lama guanicoe* (Muller) (Menegaz and Ortiz Jaureguizar, 1995; Menegaz, 2000), a clear indicator of dry–cold climates, along with *M. cristatum* Serres, 1867, and probably also 'Brasilic' fauna such as *Tapirus* Brisson (the southernmost record of this genus), *Calomys* Waterhouse, and Procyonidae, which indicate more tropical and humid climates (Bond et al., 1995; Tonni and Cione, 1995; Bond, 1999; Soibelzon et al., 2005). The possible coexistence of taxa with different ecological requirements and current allopatric distribution could be interpreted as an indicator of the occurrence of heterogeneous environments (Tonni et al., 1998). However, given the lack of high resolution biostratigraphic studies, the possibility that the taxa indicative of warmer climates and those suggestive of colder drier climates were not actually coeval, but the result of time-averaging sediments, cannot be dismissed.

Lastly, the specimen from Mar del Plata (**MMP 234**) was collected from Miramar Formation (see Isla and Dondas, 2001), which was assigned by Cione and Tonni (1995, 1999) to the Ensenadan Stage *sensu lato* (*s.l.*). The paleomagnetic studies made by Orgeira (1987) suggest a Matuyama *s.l.* paleomagnetic age, greater than 0.7 Ma and less than 2.41 Ma.

N. ornatus is a species restricted to the final Ensenadan Stage (0.98–0.40 Ma) (Fig. 3). Its geographical distribution is wider than that of *N. pseudornatus*, encompassing central and central-eastern Argentina (Buenos Aires and Santa Fe provinces), from 32° 53′ S (Granadero Baigorria, Santa Fe province) to 38° S (Mar del Plata, Buenos Aires province) (Fig. 4). Stratigraphically, the unquestionable records of *N. ornatus* in Buenos Aires province correspond to two specimens (**MLP 16–28 and MACN 8091**) collected from the cliffs situated north of Mar del Plata, and possibly from the Miramar Formation (see Kraglievich, 1952). These sedimentary sequences have been little studied compared to those located south of Mar del Plata, which have been the subject of intense paleontological, paleomagnetic and sedimentological studies (Bidegain et al., 2003).

Magnetostratigraphic (Bidegain et al., 1998, 2003) and biostratigraphic (Tonni et al., 1998) studies of Ensenadan levels indicate that these sediments are somewhat more recent than those from the "Toscas del Río de La Plata", and even though no absolute datings have been made, their age could range between 0.98 and 0.40 Ma (middle-late Ensenadan Stage; Tonni et al., 1998; Bidegain et al., 2003). Another record, represented by a complete dorsal carapace associated with a caudal tube (**MMP 4300**), has been unquestionably collected from the Miramar Formation in Mar del Plata (see Isla and Dondas, 2001). The sediments from this unit were originally nominated by Ameghino (1908) as the Ensenada Formation, and by Frenguelli (1928) as part of the Ensenadan Stage. It was formally recognized by Kraglievich (1952), who designated it as the Miramar Formation. This formation, which underlies the San Andrés Formation and overlies the Arroyo Seco Formation (Bidegain et al., 1998), is 1–3 m thick and primarily composed of fluvio-lacustrine sediments, including several lithological types: "*…conglomerados de fenoclastos de limo endurecido cementados por limo arcilloso verdoso o pardo grisáceo. Lentes de limo muy arcilloso verde o azul y camadas lenticulares de acarreo fluvial compuestas por pequeños fragmentos rodados de rocas…en su sección superior comprende bancos loésicos pardos cubiertos por una costra calcárea…*" ("…conglomerates of hardened silt phenoclasts cemented by greenish or grayish brown clayey silt. Blue or green highly clayey silt lenses and fluvial-transported lenticular bedding formed by small rock pebbles… at its upper section includes brown loessic banks covered by a calcareous crust…") (Kraglievich, 1952: 18; see also Isla and Dondas, 2001). Early on, Orgeira (1987) and Tonni et al. (1992) correlated this unit with the Matuyama Chron (2.48–0.73 Ma). Later, Cione and Tonni (1995, 1999) assigned this formation to the Ensenadan Stage *s.l.* (ca. 1.8–0.4 Ma).

Thus, the same levels that yielded these three *N. ornatus* specimens (**MMP 4300**, **MLP 16–28** and **MACN 8091**), contain an assemblage of vertebrates (*Lestodelphys halli*, *Tympanoctomys barrerae*, Thinocoridae) that suggests persistence of the cold arid climate that existed during the Sanandresian–Ensenadan stages (Tonni et al., 1998). This could be correlated with a global cooling event that took place in the 0.80–0.50 Ma lapse (Tonni et al., 1998). Along these lines, Verzi et al. (2002) have noted the presence of the octodontid *Tympanoctomys cordubensis* (Ameghino, 1889) in what is currently the territory of Córdoba province (near the city capital) as well as in Buenos Aires province, in sediments dated at 0.90–0.78 Ma. *Tympanoctomys* is currently considered as the South American rodent most adapted to xeric conditions (Ojeda et al., 1996), and its presence demonstrates the existence of cold arid climate during that lapse. Similarly, the sediments that are close to the transition between the Matuyama and Brunhes Chrons (ca. 0.78 Ma) indicate a shift toward colder and more arid conditions (Soibelzon et al., 2006a).

Another specimen comes from the Ensenadan beds at San Pedro, Buenos Aires province (**MSP 12**). Diverse paleomagnetic and magnetostratigraphic studies (Bobbio et al., 1986; Nabel et al., 1993; Nabel, 1993) have indicated that these sequences correspond to the upper section of the Ensenada Formation (late Ensenadan Stage) and the Buenos Aires Formation (Bonaerian Stage), and noted that the Brunhes–Matuyama boundary (0.73 Ma) was found at the uppermost part of the Ensenada Formation. The lithological characterization includes silty clayey sediments in its basal sector (unit I) and silty-sandy sediments with light brown or yellowish gray coloration near the top of the formation (units II–V). The entire sequence is characterized by high content of volcanic glass, possibly of Eolian origin, that becomes especially evident within the levels closer to the Brunhes–Matuyama boundary (Nabel et al., 1993).

From a sedimentological standpoint, a series of studies of the uppermost section of the Ensenada and Buenos Aires formations at the city of La Plata, Buenos Aires province, have shown alternance of loess and paleosols throughout the sequence, indicating cyclic climatic changes from cold and arid or semiarid (loess) to warmer and more humid (paleosols) (Tonni et al., 1999b).

A series of paleomagnetic studies performed on sediments from the vicinity of Baradero, Buenos Aires province (see Nabel et al., 1993, 1993), show a significant increase in amounts of volcanic glass toward the upper part of the Ensenada Formation, near the Brunhes–Matuyama boundary (0.78 Ma). On the other hand, the base of the Brunhes polarity zone shows predominantly loessic sedimentation (Nabel et al., 2000). Primarily, both phenomena would be correlated with increased aridity and cold, in accordance with available paleontological evidence (Tonni et al., 1999b). The taxa characteristic of warm humid environments (e.g. Tapiridae, Procyonidae and Echimyidae) which are recorded during the early and middle Ensenadan Stage (Nabel et al., 2000), disappear from the fossil record later on, as taxa adapted to more arid environments (*Microcavia*, *Reithrodon*, *Zaedyus* and *Tolypeutes*; Tonni and Cione, 1994) are recorded. However, the paleosol located at the Brunhes–Matuyama boundary might basically indicate some climatic stability and the presence of a conspicuous plant cover (Nabel et al., 2000; Voglino and Pardiñas, 2005). The study of a sequence attributable to the uppermost Ensenadan Stage (ca. 0.78 Ma), at Ramallo, in northern Buenos Aires province, agrees with this model, as it shows a transition from warm humid to cold arid conditions (e.g. *Lestodelphys* and *Microcavia*), immediately above the Brunhes–Matuyama boundary (ca. 0.73 Ma) (Voglino and Pardiñas, 2005).

Coincidentally, at lower latitudes (Tarija, Bolivia), MacFadden (2000) has noted that the uppermost section of the Tolomosa Formation (ca. 1.1–0.70 Ma) shows a change of faunal composition in the transition from arid to warmer and more humid environmental conditions (but see Coltorti et al., 2007).

Outside Buenos Aires province, a fourth record (**CC 656**) was exhumed from the coastal cliffs of the Paraná River at Granadero Baigorria, Santa Fe province. In the 1960s decade, this material was assigned by Castellanos (*unpublished*) to the "Lower Pleistocene" (="Belgranense", "Belgranian" Stage). Currently, the "Belgranian" Stage in the sense of Ameghino (1889) and Castellanos correspond to the lapse between the end of the Ensenadan and the beginning of the Bonaerian stages (middle Pleistocene) (Cione and Tonni, 1995). The provenance of this specimen possibly corresponds to sediments from the Rosario Formation, of Ensenadan age, which makes up much of the coastal cliffs of Paraná River from Rosario to Puerto San Martín. The sediments from this formation are characterized by predominance of hard silts, reddish brown and green in color, with scarce calcium carbonate concretions and manganese nodules (Iriondo, 1987; Parent et al., 2002).

5. Conclusions

a) Four species of genus *Neosclerocalyptus* have been recognized and described for the Ensenadan Stage: *Neosclerocalyptus scrobiculatus*, *Neosclerocalyptus perfectus*, *N. pseudornatus* and *N. ornatus*; however, this work demonstrates that only two of them can be considered valid. Both of these species are biostratigraphically significant because their biochrons are clearly identified and confined. *N. pseudornatus* holds the earliest record, with a biochron restricted to the early-middle Ensenadan Stage, between 1.07 and 0.98 Ma. The other Ensenadan species, *N. ornatus*, is more recent, with a stratigraphic range restricted to the late Ensenadan Stage, around 0.98–0.40 Ma.

b) Anatomically speaking, the major differences between the two taxa are located in the skull. In *N. pseudornatus*, the fronto-nasal sinuses are less pneumatized and less laterally expanded than in *N. ornatus*, and their external wall exhibits evident "scrolled" shape due to the strong curvature of the free margins of the nasal bones toward the sagittal plane. In addition, the parieto-occipital region is not inclined upwards as markedly as in *N. ornatus*. On the other hand, the fronto-nasal sinuses of *N. ornatus* are better defined and clearly more pneumatized and laterally expanded, with a characteristic "funnel" shape; the infraorbital foramina of all specimens are larger than those of *N. pseudornatus*.

c) From a paleobiogeographical perspective, the range of both species is restricted to the current Pampean region. Thus far, *N. pseudornatus* has been recorded in the "Toscas del Río de La Plata" (Olivos and Buenos Aires City) and in Mar del Plata. Likewise, *N. ornatus* is recorded in San Pedro and Mar del Plata (Buenos Aires province) and Granadero Baigorria (Santa Fe province).

d) The climatic–environmental evidence provided by diverse indicators suggests that these species lived under the arid/semiarid and cold conditions characteristic of most of the Pleistocene, and that they were probably well adapted to such environments. In this context, the increased pneumatization and lateral expansion of the fronto-nasal sinuses is interpreted here as a probable response to this type of environments. In agreement with this interpretation, the records of *Neosclerocalyptus* from the middle and late Pleistocene are very abundant in Eolian sediments of the Pampean region and central-northern Argentina, where cold arid or semiarid climatic–environmental conditions occurred during most of the Pleistocene; in contrast, its records are very scarce in areas that experienced warmer and more humid conditions during the same lapse (e.g. Argentinian Mesopotamia, Uruguay and Brazil).

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