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Hoplophorinae) from the middle Pleistocene of the Pampean region, Argentina**

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A new species of *Neosclerocalyptus* Paula Couto, 1957 (Xenarthra, Glyptodontidae, Hoplophorinae) from the middle Pleistocene of the Pampean region, Argentina

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ABSTRACT

A new species of the genus *Neosclerocalyptus* Paula Couto, 1957 (= *Sclerocalyptus* Ameghino, 1891), *N. gouldi* n. sp. (Cingulata, Glyptodontidae, Hoplophorini) is described. This new taxon, comes from the Bonaerian Stage (middle Pleistocene; c. 0.4-0.13 Ma) of San Andrés de Giles, Buenos Aires province, Argentina. The type consists mainly of an associated skull, mandible and cephalic shield in an excellent state of preservation. Morphological characters that distinguish the species include: a) lesser pneumatization and lateral expansion of fronto-nasal sinuses compared to *N. paskoensis*; b) descending processes of maxillaries and zygomatic arches very robust and with marked ridges; c) lower third of descending processes markedly inclined toward the sagittal plane; d) inclination of the parieto-occipital skull region intermediate between those of Ensenadan and Lujanian forms; e) infraorbital foramina larger than in *N. paskoensis*, similar in size to those of *N. ornatus*; and f) occipital area less expanded laterally than in *N. paskoensis*. This new taxon completes the chronological distribution of genus *Neosclerocalyptus* which, until now, included two well-characterized species for the Ensenadan (early Pleistocene: *N. pseudornatus* and *N. ornatus*) and one Lujanian (late Pleistocene-early Holocene: *N. paskoensis*). The Bonaerian species, *N. migoyanus*, recognized by Ameghino, should be considered as a *nomen dubium*, due to the lack of diagnostic characters.

KEY WORDS

Xenarthra,
Glyptodontidae,
Hoplophorini,
Neosclerocalyptus
gouldi n. sp.,
Pleistocene,
Bonaerian Stage,
Pampean region,
Argentina.

RÉSUMÉ

Une nouvelle espèce de *Neosclerocalyptus* Paula Couto, 1957 (*Xenarthra*, *Glyptodontidae*, *Hoplophorinae*) du Pléistocène moyen de la région pampéenne d'Argentine. Une nouvelle espèce du genre *Neosclerocalyptus* Paula Couto, 1957 (= *Sclerocalyptus* Ameghino, 1891), *N. gouldi* n. sp. (*Cingulata*, *Glyptodontidae*, *Hoplophorini*), est décrit. Ce taxon nouveau vient de l'Étage Bonaérien (Pleistocène moyen; *c.* 0.4-0.13 Ma) de San Andrés de Giles, province de Buenos Aires, Argentine. Le spécimen est représenté par un crâne, une mandibule et un bouclier céphalique associés, excellent état de préservation. Les caractéristiques morphologiques qui distinguent l'espèce incluent: a) une pneumatisation et une expansion latérale des sinus fronto-nasaux moindres par rapport à *N. paskoensis*; b) des processus descendants des arches maxillaires et zygomatiques très robustes et avec des dorsales marquées; c) le tiers inférieur des processus descendants incliné de manière marquée vers le plan sagittal; d) une inclinaison de la région crânienne pariéto-occipitale intermédiaire entre celles des formes ensénadéennes et lujanéennes; e) des forams infraorbitaux plus grands que chez *N. paskoensis*, de même longueur que ceux de *N. ornatus*; et f) une région occipitale moins développée latéralement que chez *N. paskoensis*. Ce nouveau taxon complète la distribution chronologique du genre *Neosclerocalyptus*, qui, jusqu'à présent, incluait deux espèces bien caractérisées propres à l'Ensenadéen (Pleistocène inférieur: *N. pseudornatus* et *N. ornatus*) et une autre limitée au Lujanéen (Pleistocène supérieur-Holocène inférieur: *N. paskoensis*). L'espèce bonaérienne, *N. migoyanus*, reconnue par Ameghino doit être considérée comme un *nomen dubium*, par son manque de caractères diagnostiques.

MOTS CLÉS

Xenarthra,
Glyptodontidae,
Hoplophorini,
Neosclerocalyptus
gouldi n. sp.,
Pleistocène,
Étage Bonaérien,
région pampéenne,
Argentine.

INTRODUCTION

The Pleistocene (*c.* 1.8-0.008 Ma) Glyptodontidae of South America achieved high taxonomic diversity (*c.* 11 genera; see Ameghino 1889; Mones 1986a; McKenna & Bell 1997, among others) and wide latitudinal distributional range, from Patagonia in Santa Cruz Province, Argentina (Tonni & Carlini 2008) to Venezuela (Carlini *et al.* 2008). Their remains, particularly those from the late Pleistocene, are encountered frequently. The extensive geographical distribution attained by the Glyptodontidae could have been promoted by the rise of extensive open areas occupied by steppes and grasslands (Scillato-Yané *et al.* 1995; Carlini & Scillato-Yané 1999), resulting from the progressive cooling and aridization trend of the uppermost Sanandresian (late Pliocene; *c.* 2.5-1.8 Ma) (Shackleton 1995). This progressive environmental-climatic deterioration, which persisted during the Pleistocene and early

Holocene (see Tonni & Fidalgo 1979; Williams *et al.* 1988; Clapperton 1993; Tonni & Cione 1994; Cione & Tonni 1995, 1999, 2001; Tonni *et al.* 1999a; Tonni *et al.* 2003; Bobe Quinteros *et al.* 2004; Verzi & Quintana 2005) would have promoted development of the typical open homogeneous Pleistocene grassland environments that were widely distributed latitudinally, and this, in turn, permitted the extensive distribution of numerous megamammal taxa, including the Glyptodontidae (Tonni & Scillato-Yané 1997), whose anatomy suggests that they were active grazers (Pérez *et al.* 2000; Fariña & Vizcaíno 2001; Vizcaíno *et al.* 2006).

During the Pleistocene, the Glyptodontidae attained their maximum size, even greater than those of Oligocene forms (see Scillato-Yané 1977), with body masses close to 2000 kg (e.g., *Doedicurus clavicaudatus* Owen, 1847; *Panochthus intermedius* Lydekker, 1894; *Glyptodon elongatus* Burmeister,

1866; see Scillato-Yané & Carlini 1998; Fariña & Vizcaíno 1999).

The genus *Neosclerocalyptus* Paula Couto, 1957 (early Pleistocene-early Holocene) is one of the smallest taxa among the Pleistocene Glyptodontidae, with an estimated body mass no greater than 300 kg (Fariña 1995) and a length of approximately 2.5 m (Carlini & Tonni 2000; Zurita 2007). Morphologically, this genus is characterized by a low, elongated and subcylindrical dorsal carapace, with anterolateral margins directed outward and wing-like. The skull is characterized by progressive pneumatization of the fronto-nasal sinuses, which become extremely evident in the Lujanian species, *N. paskoensis* (Zurita, 2002). The dorsal carapace maintains the primitive “rosette” ornamentation pattern, similar to that of the Propalaeohoplophorinae Ameghino, 1891, with sulci between the central figure and peripherals, and between adjacent peripherals, parabolic in transversal section (see Scott 1903, 1904; Zurita 2007).

The Glyptodontidae taxa recognized as specific to the Bonaerian Stage (middle Pleistocene; *c.* 0.40–0.130 Ma; see Cione & Tonni 1999, 2005) include two species of Hoplophorinae Lomaphorini Hoffstetter, 1958 (*Lomaphorus elegans* (Burmeister, 1871) and *L. elevatus* Nodot, 1857), one Doedicurinae Ameghino, 1889 (*Doedicurus pouchetii* Gervais & Ameghino, 1880) and one Hoplophorinae Hoplophorini (*N. migoyanus* Ameghino, 1889) (see Cione & Tonni 1999, 2005). However, the latter Hoplophorini species (recognized by Ameghino 1889), should be considered as *nomen dubium* (see Richter 1943; Mones 1986b, among others), because the combination of diagnostic characters provided by Ameghino (1889: 818; 1895: 535) based on the holotype (MACN 14035) (e.g., length and degree of curvature of the caudal sheath, number of lateral figures, shape of distal limb, etc.) do not allow confirmation of the validity of this taxon.

In this context, a recent systematic review of the Hoplophorinae Hoplophorini has shown that many species of the genus *Neosclerocalyptus*, are invalid and that currently only four species can be adequately characterized and should be recognized (Zurita 2007).

In this work we describe a new species of this genus, with a stratigraphic distribution restricted to the Bonaerian Stage (middle Pleistocene) of the Pampean

region in Argentina, along with an analysis of its stratigraphic and paleoclimatic-environmental context.

Our nomenclature and taxonomy follow those proposed by Paula Couto (1957, 1965), Zurita *et al.* (2007) and Zurita (2007). Chronology and biostratigraphy follow those proposed by Cione & Tonni (1995, 1999, 2001, 2005).

ABBREVIATIONS

CC	Museo Universitario “Florentino y Carlos Ameghino”, Universidad Nacional de Rosario (ex Instituto de Fisiografía y Geología “Alfredo Castellanos”), Rosario;
Ctes-PZ	Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes;
MCA	Museo de Ciencias Naturales “Carlos Ameghino”, Mercedes, Buenos Aires;
MACN	Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”;
MLP	División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata;
LE	total skull length;
MDFN	maximum transversal diameter of fronto-nasal sinuses;
MDZA	maximum bizygomatic diameter.

SYSTEMATIC PALEONTOLOGY

- Superorder XENARTHRA Cope, 1889
- 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

Neosclerocalyptus Paula Couto, 1957: 7.

Chacus Zurita, 2002 n. syn.: 175–182.

Hoplophoridae Huxley 1864 has priority over Glyptodontidae Gray 1869, but this latter has been used by most of the authors since 1899 (e.g., among others, Scott, 1903, 1904; Richter 1911; Pascual *et al.* 1966; Mones 1986a; Carlini *et al.* 2008a, b) that it must be retained as a *nomen protectum*

TABLE 1. — Comparative measurements (in mm) among *Neosclerocalyptus* species. *, Approximate measurement.

	<i>N. pseudornatus</i> (MACN 8579)	<i>N. ornatus</i> (MLP 16-28)	<i>N. gouldi</i> n. sp. (MCA 2010)	<i>N. paskoensis</i> (MACN 18107)
Skull				
Length (LE)	295	320	310	289
Maximum diameter of fronto-nasal sinuses (MDFN)	161	180	190	197
MDFN/LE	0.54	0.56	0.61	0.68
Maximum diameter between zygomatic arches (MDZA)	213	230	205	233
MDZA/LE	0.72	0.72	0.66	0.80
Maximum diameter of postorbital narrow	103	96	—	110
Height of skull at level of:				
M1	141	145	—	165
M4-M5	160	170	—	190
M8	173	185	—	185
Length of palate	—	216	195	210
Length of tooth rows	160	179	175	183
Mandible (MACN 5858)				
Length	265	270	275	265
Length of tooth rows	164	165	173	178
Anteroposterior diameter of ascending ramus at alveolar level	105	106	106	104
Height of ascending ramus	—	195	210	207
Cephalic shield (MACN 8773) (CC 656) (AGM 002)				
Length	315	305*	305	350
Maximum transverse diameter	222	220	220	235
Carapace (PZ-Ctes 5879)				
Length (dorsal circumference)	1100	1240*	—	1300
Caudal tube (CC 21)				
Length	445	430	—	450

(ICZN 1999: Art. 23.9; see McKenna & Bell 1997; Zurita *et al.* 2007). In this sense, the name Hoplophorinae Huxley 1864 (*nom. transl.* Weber & Abel, 1928) has priority over Sclerocalyptinae Ameghino, 1895 (*nom. transl.* Trouessart, 1898) (ICNZ 1999: Art. 23.2) (see Paula Couto 1957).

Neosclerocalyptus gouldi n. sp.
(Fig. 1)

HOLOTYPE. — MCA 2010, skull and cephalic shield, right humerus and fragmentary dorsal carapace.

ETYMOLOGY. — Named in honour of Stephen Jay Gould (1941-2002), outstanding paleontologist and popular science writer, who was also a fierce critic of all forms

of oppression and of the social use of science as an ideological foundation for power.

TYPE LOCALITY. — Intersection of Route no. 41 and earth road to the town of San Andrés de Giles, Buenos Aires, Argentina (34°26'57"S, 59°26'56"W) (Fig. 2).

CHRONOLOGICAL AND GEOGRAPHICAL DISTRIBUTION. — Buenos Aires Formation. Middle Pleistocene (Bonaerian Stage; *c.* 0.40-0.13 Ma). San Andrés de Giles, Buenos Aires Province, Argentina.

DIAGNOSIS. — A Hoplophorini similar to *N. paskoensis* (Zurita, 2002) but more robust, with a narrower skull and more extended anteroposteriorly (MDZA/LE: 0.66) (Table 1). The dorsal profile of skull is convex, with the parieto-occipital region directed downwards as in *N. paskoensis* and *Eosclerocalyptus tapinocephalus* (Cabrera, 1939), although less markedly so than in these

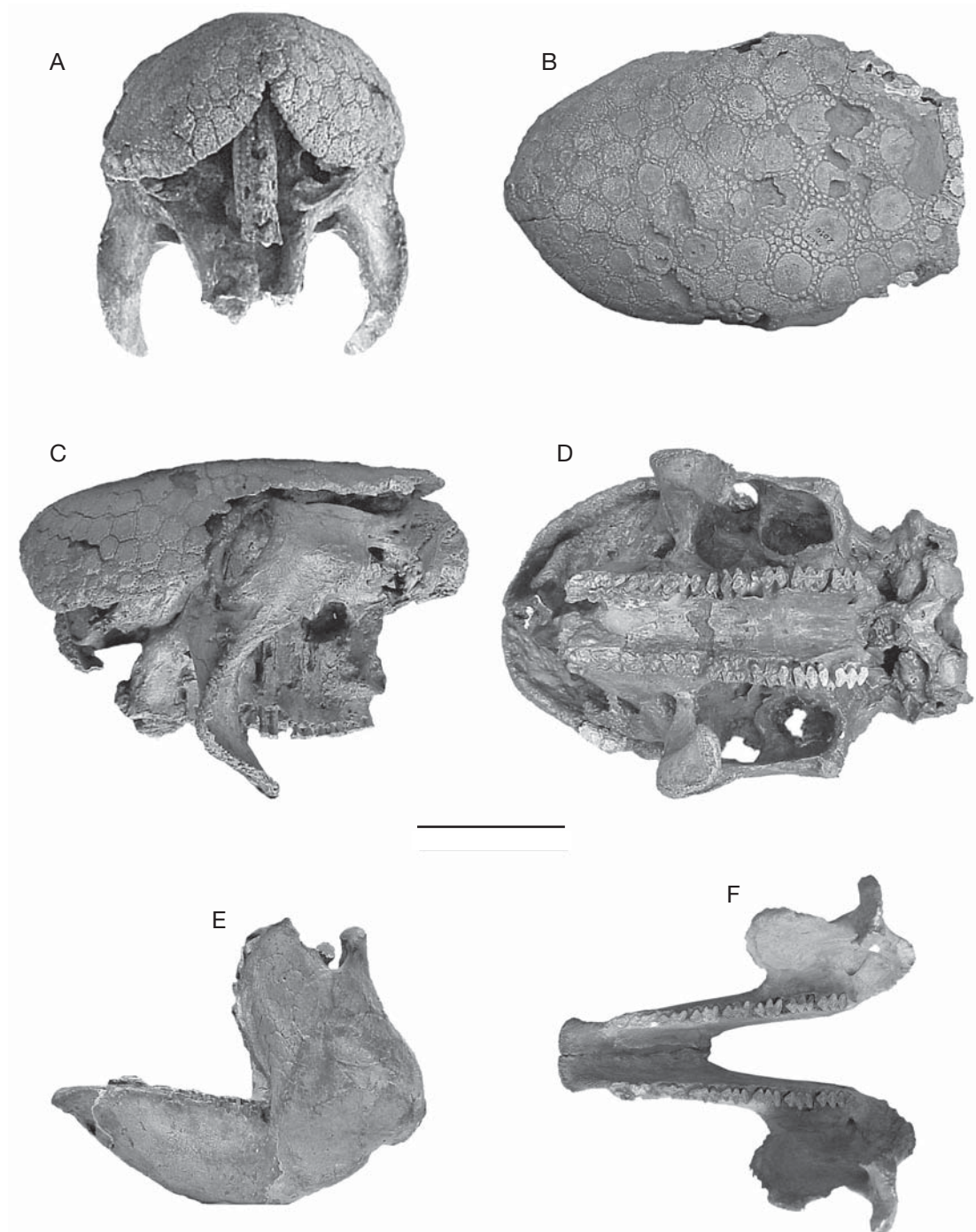


FIG. 1. — *Neosclerocalyptus gouldi* n. sp. (MCA 2010): **A-D**, skull; **E, F**, mandible; **A**, frontal view; **B**, dorsal view; **C, E**, lateral views; **D**, ventral view; **F**, occlusal view. Scale bar: 1 cm.

species. The fronto-nasal sinuses are similar to those of *N. paskoensis*, but less expanded laterally (MDFE/LE: 0.61) (Table 1) and less pneumatized. They are separated from the maxillaries and frontals, and from each other by a V-shaped notch. An extremely well-developed septum divides the nasal cavity into two chambers. The orbital notch has a distinct subelliptical outline, with the lower half directed distally. The sagittal crest is replaced by a medial concavity extending from the confluence of both nuchal crests to approximately the posterior third of the frontals. The zygomatic arches and descending processes of the maxillaries are much more developed than in other *Neosclerocalyptus* species, with the external margin of these structures with prominent ridges and rugosities extending to the ventralmost region of descending processes, at which point they are notably inclined towards the sagittal plane. The squamosal portions of zygomatic arches are subparallel to each other, differing from the condition of *N. ornatus* (Owen, 1845) and *N. paskoensis*, in which they diverge distally. The infraorbital foramina are larger than those of *N. paskoensis* and *N. pseudornatus* (Ameghino, 1889), and similar in size to those of *N. ornatus*, but more medially positioned. The occipital area is less expanded laterally than in *N. paskoensis*, but with greatly developed supraoccipital and paroccipital processes. The upper molariforms are almost undistinguishable from those of *N. paskoensis*. The mandible is robust, especially because of the greater anteroposterior width of the ascending rami, as in *N. ornatus*. The first lower molariform is simple and elongated longitudinally and the second molariform has incipient lobation, while the remaining molariforms are distinctly trilobed.

DESCRIPTION

Skull

The skull is similar in general morphology to that of *N. paskoensis*, with its convex dorsal profile, but it is more elongated anteroposteriorly (Table 1); and less expanded laterally. There is less pneumatized of the fronto-nasal sinuses (Fig. 1A, B, D).

In lateral view (Fig. 1C), the parieto-occipital region is directed downwards as in *N. paskoensis* and *E. tapinocephalus*, although less markedly so than in these taxa. The zygomatic arches are much more robust than in the other species of *Neosclerocalyptus* (although proportionately shorter), with a rugose surface and a large tuberosity at its postero-inferior end. The zygomatic arches tend to be subparallel at the level of the squamosal portion, similar to the condition in *Eosclerocalyptus proximus* (Moreno & Mercerat, 1891), and differing from the condition in the other *Neosclerocalyptus*

species in which these structures diverge distally. The orbital notches are clearly elliptical, with a notable dorsoventral development and the lower half markedly inclined distally. The descending process of maxillary is very robust and marked by a series of well-defined rugosities and ridges on its latero-external margin that have not been observed in any other Hoplophorinae Hoplophorini. The fronto-nasal sinuses are morphologically similar to those of *N. paskoensis*, with free margins straight, and differing from *N. pseudornatus* and *N. ornatus* in which these structures are recurved forming “loops”. These sinuses are separated from the maxillaries and frontals by a V-shaped notch, which is less evident than in *N. ornatus*.

In dorsal view, it was not possible to separate the cephalic shield from the skull. The parietals and frontals have a greater transverse diameter than in Ensenadan species. The sagittal crest present in *N. pseudornatus* and *N. ornatus* is replaced in this new species by a medial concavity extending approximately to the posterior third of the frontals, it then bifurcates to contact the origins of postorbital apophyses of frontals. Anteriorly, there is a notch separating the nasals from the rest of the skull, but it is not as deep as in *N. ornatus*.

In ventral view (Fig. 1D), the infraorbital foramina are remarkably large, and located more medially than in *N. paskoensis* and *N. ornatus*; so they are more similar to those of *N. ornatus* and clearly different from those of *E. tapinocephalus*, *N. pseudornatus* and *N. paskoensis*. In these latter species, the infraorbital foramina are smaller and with a thicker lower margin. These foramina are located on a plane passing through M3, as in *N. paskoensis*. The lower third of the descending processes of the maxillary is inclined medially, more so than in *N. ornatus* and *N. paskoensis*. Both the upper and lower dental series tend to diverge anteriorly. The occipital area is not as expanded laterally as in *N. paskoensis* and *N. pseudornatus*, although it has a greater antero-posterior diameter. The palatal region anterior to M1 is not preserved, but the inferred morphology is very similar to that of the other species of *Neosclerocalyptus*. The M1 is simple, but slightly more elongated than in *N. pseudornatus* and *N. ornatus*. The M2 is already trilobate, and the rest of molariforms (M3-M8) are

not appreciably different from those of *N. pseudornatus*, *N. ornatus* and *N. paskoensis*.

In occipital view, the most prominent trait is the great development of supraoccipital and paraoccipital processes, which are the largest among the Hoplophorinae Hoplophorini. The *foramen magnum* has a more circular outline than in Ensenadan species, as in *N. paskoensis*. This character is probably related to the greater skull depth. As in *N. ornatus*, the choanae have a subrectangular outline and are taller dorsoventrally than the transverse width.

In frontal view (Fig. 1A), the nasal openings are large, and similar in outline to those of *N. ornatus*, but the free margins of nasals lack any curvature. The *septum* between both cavities is very well developed, more so than in *N. ornatus* and *N. paskoensis*, and homogeneously thick along nearly its entire dorso-ventral extension. The sinuses are morphologically similar to those of *N. paskoensis*, but less expanded transversally (Table 1). Internally, the development of the trabecular tissue filling the sinuses is similar to that of *N. ornatus*, and not as dense as in *N. paskoensis*.

Mandible (Fig. 1E, F; Table 1)

The mandible is morphologically very similar to that of *N. ornatus* and *N. pseudornatus*, and more robust than that of *N. paskoensis*. The only remarkable characteristics are the greater lobation of M2 and the morphology of the coronoid apophysis, which is slightly higher than the condyle. In addition, the anterior margin of the ascending ramus has a series of ridges on its upper third, immediately below the coronoid apophysis. Lastly, sigmoid notch is slightly deeper than in *N. ornatus*, and more similar in this aspect to that of *N. paskoensis*.

Cephalic shield (Fig. 1B)

As in other species of *Neosclerocalyptus*, the cephalic shield is rectangular in outline and formed by approximately 80 plates firmly sutured to each other. The central plates in the proximal half of the shield are the largest, with the rest decreasing in size laterally and posteriorly. Each plate bears a large circular or subcircular central figure with a smooth flat surface, although the largest ones have a small central concavity. Each central figure

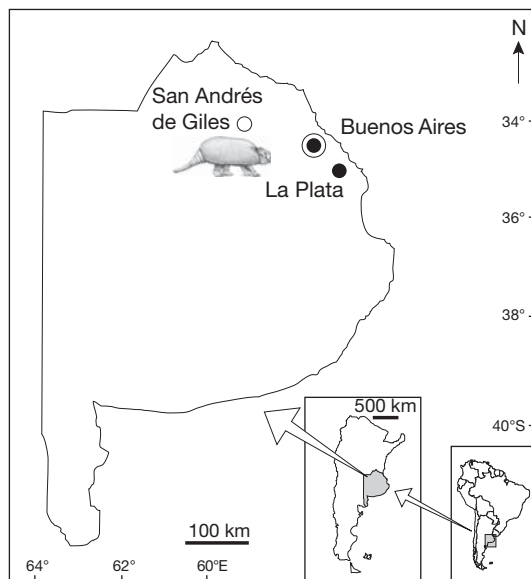


FIG. 2. — Location map of San Andrés de Giles (Buenos Aires province, Argentina).

is encircled by a row of figures, smaller but slightly more defined (especially those corresponding to the largest plates) than those of *N. pseudornatus* and *N. ornatus*. They are more rudimentary in shield area over the fronto-nasal sinuses, and almost disappear in ventralmost plates. The cephalic shield is not significantly different from other *Neosclerocalyptus* species in other aspects.

Humerus

The humerus is well preserved, showing the same basic morphology observed in the other species of *Neosclerocalyptus* (for more details see Zurita 2007).

GEOLOGICAL AND STRATIGRAPHICAL CONTEXT

Ameghino (1889: 32-36) used the term Bonaerian as a synonym of “upper Pampean”. According to the views of this author (Ameghino 1889: 32), the Bonaerian was characterized sedimentologically “by having in general lower proportion of lime and greater amount of sand, although at some points there are also large deposits of calcretes (‘toscas’); however, it might be said to be less compact and

coherent than the lower pampean, and formed by a mass of pulverulent elements". Another detailed mineralogical description of the "Bonaerian" was provided by Frenguelli (1957: 35): "Its grain is fine and homogeneous, its mass traversed by countless minute channels left by extremely fine roots, it is porous, non stratified, slightly calciferous, and its coloration is uniform light brown, generally with reddish hues."

From a paleontological perspective, some authors (see Pascual *et al.* 1965, 1966; Marshall *et al.* 1984, among others) have not recognized the existence of the "Bonaerian", arguing that its faunal composition was undistinguishable from that of the Lujanian *s.s.*, and the use of this term was dropped as a result. Scillato-Yané (1979) and Reig (1981) were among the first authors to defend a differentiation within the Lujanian Mammal Age (*sensu* Pascual *et al.* 1965) and, following Ameghino, proposed its subdivision into two subages: Bonaerian and Lujanian. More recently, the Bonaerian Stage has been reincorporated into the chrono-biostratigraphic schemes, given that, although it is not clearly different from the Lujanian *s.s.* (*sensu* Ameghino 1889) from a lithological perspective, it is clearly differentiable based on its biostratigraphy (see Cione & Tonni 1995, 1999; Tonni *et al.* 1999b). Currently, the Bonaerian is characterized biostratigraphically by the *Megatherium americanum* Cuvier, 1796 (Tardigrada Megatheriinae Owen, 1842) biozone (Cione & Tonni 1999, 2005).

Most of the geological units recognized for the Bonaerian are located within the modern limits of Buenos Aires province, and represented by the Buenos Aires Formation (see Parodi & Parodi 1952), and include the "Bonaerian Stage" and the "Belgranian Stage" (*sensu* Ameghino 1889) (Cione & Tonni 1999). Although with some uncertainty, the Bonaerian Stage could range chronologically from 0.40 to 0.13 Ma (Cione & Tonni 1999). MacFadden (2000) places the boundary between the Ensenadan and Bonaerian as slightly older, at approximately 0.6 Ma.

As we have already commented, the holotype of *Neosclerocalyptus gouldi* n. sp. (MCA 2010) consists of the complete skull, mandible, cephalic shield and a right humerus of a specimen from

Bonaerian sediments collected in the vicinity of San Andrés de Giles, Buenos Aires Province, and most likely corresponds to the Buenos Aires Formation. Paleomagnetic and chronostratigraphic studies performed near the Zárate locality indicate that the fossil bearing sediments could be correlatable with the Buenos Aires Formation (see Parodi & Parodi 1952), whose base is situated within the Matuyama Chron (reverse polarity), although most of it is included in the Brunhes Chron (normal polarity) (Bobbio *et al.* 1986; Nabel 1993; Nabel *et al.* 1993, 2000).

This unit is sedimentologically very similar to the underlying formation (Ensenada Formation), but with less consolidated sediments (Tonni *et al.* 1999b), and the predominance of smectites could be linked to greater water content at the time of sedimentation (Nabel *et al.* 1993).

PALEOENVIRONMENTAL AND PALEOCLIMATIC CONTEXT

Sedimentological analyses of the Buenos Aires Formation show that, like the Ensenada Formation, is composed of alternating loess (deposited under cold arid conditions) and paleosols (indicators of warmer and more humid climatic-environmental conditions), but with sediments less consolidated than in the underlying unit (Ensenada Formation) (Orgeira *et al.* 1998; Tonni *et al.* 1999b; Nabel *et al.* 2000). In this sense, the Bonaerian seems to represent a predominantly cold arid or semiarid phase (Cione & Tonni 2001), with brief interspersed warmer and more humid periods (Tonni & Cione 1994). This interpretation is supported by both sedimentological and paleofaunal evidence; the predominant loess-type sedimentation of the uppermost Ensenada Formation indicates a shift toward colder and more arid conditions (Tonni *et al.* 1999b; Nabel *et al.* 2000), also suggested by the presence of taxa clearly adapted to this type of environments (e.g., *Lestodelphis halli* (Thomas, 1921), *Microcavia* Gervais & Ameghino, 1889, *Ctenomys* Blainville, 1826 and *Zaedyus* Ameghino, 1889; Nabel *et al.* 2000); thus, an important faunal turnover occurred between the Ensenadan and the Bonaerian (Ameghino 1889; Tonni *et al.* 1999b; Cione & Tonni 2001).

In this context, Fidalgo & Tonni (1983) described a micromammal association referable to the early-late Pleistocene from Punta Hermengo, Buenos Aires Province. These authors concluded that the entire sequence was deposited under predominantly cold arid conditions, and this hypothesis is supported by the presence of *Zaedyus* cf. *Z. pichiy* (Desmarest, 1806), *Tolypeutes* cf. *T. matacus* (Desmarest, 1804) and *Lagostomus* Brookes, 1828, among other taxa (Tonni & Fidalgo 1982). However, more humid conditions, represented by limolitic sediments and lenses of calcrete clasts, have also been detected. Pardiñas & Lezcano (1995), in their analysis of a faunal association from northeastern Buenos Aires Province assigned to the Bonaerian, found an interesting group of taxa with warm humid ecological requirements (e.g. *Lundomys* Voss & Carleton, 1993 and *Oxymycterus* Waterhouse, 1837) along with others clearly adapted to dry or arid environments (e.g., *Tolypeutes* Illiger, 1811 and *Microcavia*). Assuming that this entire fauna is synchronic, this co-occurrence could indicate the existence of mosaic-like environments, resulting from alternating dry cold phases and brief warm humid pulses. The presence of the latter is also supported by the presence of a chernozem-like paleosoil within the Pascua Formation (Tonni & Fidalgo 1978).

DISCUSSION

Taxonomically speaking, *Neosclerocalyptus* Paula Couto, 1957 (= *Sclerocalyptus* Ameghino, 1891 = *Chacus* Zurita, 2002) was, along with *Glyptodon* Owen, 1839, one of the Pleistocene genera of Glyptodontidae with the highest number of described species. Diverse authors (Gervais & Ameghino 1880; Ameghino 1889, 1895; Castellanos 1925; Richter 1911) recognized approximately 15 species (see Zurita *et al.* 2005; Zurita 2007). Of this set of species, only one, *N. migoyanus*, was assigned to a chronological provenance “from the bonaerian stage [...] of diverse points in Buenos Aires province” (Ameghino 1889: 818). However, analysis of the type material (MACN 14035, a caudal sheath broken at the left half of its proximal end) clearly indicates that the characterization of

this species, *N. migoyanus*, was performed within a strictly typological/morphological taxonomic framework (see Giraudó 1997; Hevia & Romero 1999) without using valid diagnostic characters, and with only a vague geographical provenance. According to Mones (1986b: 233), the term *nomen dubium* is to be used for those nominal taxa with doubtful application according to currently available evidence, but whose status might eventually be elucidated by future findings; consequently, this species should be considered as *nomen dubium*. In agreement with this, the *International Code of Zoological Nomenclature* (1999) defines *nomen dubium* as: “A descriptive term meaning a name of unknown or doubtful application.”

In this context, the finding of an associated skull, mandible, cephalic shield and a right humerus in exceptional state of preservation and showing clear diagnostic characters, collected from the Bonaerian Stage in the vicinity of San Andrés de Giles (34°26'57"S, 59°26'56"W), in central-north Buenos Aires province, has allowed the recognition of a new species of Bonaerian (middle Pleistocene) age. Likewise, the stratigraphic distribution of genus *Neosclerocalyptus* is partially completed with the inclusion of four species that can be clearly differentiated morphologically, representing different stratigraphic intervals. These are: *N. pseudornatus* (early Pleistocene; *c.* 1.07-0.98 Ma; see Soibelzon *et al.* 2008); *N. ornatus* (early-middle Pleistocene; *c.* 0.98-0.40 Ma); *N. gouldi* n. sp. (middle Pleistocene; *c.* 0.40-0.13 Ma); *N. paskoensis* (late Pleistocene-early Holocene; *c.* 0.13-0.008 Ma).

The sedimentological and associated paleofaunal evidence indicates that this new member of the Hoplophorinae would have lived under cold arid climatic-environmental conditions. Thus, the Bonaerian seems to have been a cold and predominantly arid or semiarid interval (Cione & Tonni 2001), with brief warmer and more humid periods (Tonni & Cione 1994). In this sense the uppermost levels of the Ensenada Formation (Ensenadan) show a clear predominance of loess-type sedimentation that indicates a shift toward colder and more arid conditions (Tonni *et al.* 1999b; Nabel *et al.* 2000); likewise, these levels include taxa clearly adapted to these type of environments (e.g., *Lestodelphis halli*,

Microcavia, *Ctenomys*, *Tolypeutes* and *Zaedyus*; see Nabel *et al.* 2000; Voglino & Pardiñas 2005).

One of the most remarkable morphological traits of the genus is the progressive increase of pneumatization and lateral expansion of the fronto-nasal sinuses, which probably represent a response to the cold arid or semiarid environments of the Pleistocene (Zurita *et al.* 2005; Zurita 2007). Accordingly, *Neosclerocalyptus gouldi* n. sp. exhibits a degree of pneumatization and lateral expansion of these structures intermediate between the conditions of the older *N. ornatus* (middle-late Ensenadan) and the younger *N. paskoensis* (late Pleistocene-early Holocene).

At the present, the geographical distribution of this new taxon is restricted to the type locality in the vicinity of San Andrés de Giles, in central-northern Buenos Aires Province, Argentina. Later, during the late Pleistocene, *Neosclerocalyptus paskoensis* is one of the most frequently recorded glyptodonts of the Pampean region and central-northern Argentina, along with *Glyptodon* Owen, 1839 and *Panochthus* Burmeister, 1866. Its geographical distribution includes the southernmost areas of South America, ranging from 26°41'S (Avia Terai, Chaco) to 38°44'S (Bahía Blanca, Buenos Aires), and from 57°33'W (Mar del Plata, Buenos Aires) to 65°16'W (Tafi Viejo, Tucumán) (Zurita *et al.* 2005; Zurita 2007).

CONCLUSIONS

As mentioned above, until the present contribution only one species of Hoplophorinae Hoplophorini assignable to the Bonaerian Stage was recognized, namely *Neosclerocalyptus migoyanus*; however, the validity of this species is doubtful, and it should be considered as *nomen dubium* given the almost complete lack of diagnostic characters. In this context, *Neosclerocalyptus gouldi* n. sp. presents well-defined diagnostic characters, including: a) fronto-nasal sinuses similar to those of *N. paskoensis*, but slightly less expanded laterally and less pneumatized; b) parieto-occipital region of skull inclined downward in lateral view, but not as much so as in *N. paskoensis*, and differing from the condition in *N. ornatus* and *N. pseudornatus* in which this area is inclined upward;

c) zygomatic arches and descending processes of maxillary greatly developed and very robust, with marked ridges and rugosities on its outer margin that extend onto the ventralmost region of the descending processes; d) sagittal crest replaced by a medial concavity, as in *N. paskoensis*; e) infraorbital foramina larger than those of *N. paskoensis*, similar to *N. ornatus*; f) in ventral view, lower third of descending processes of maxillary inclined toward sagittal plane; g) occipital area less expanded laterally than in *N. paskoensis*; h) great development of supraoccipital and paraoccipital processes; and i) mandible robust, similar to those of *N. ornatus* and *N. pseudornatus*.

The new taxon appears to be restricted stratigraphically to the middle-late Pleistocene (Bonaerian Stage), and thus far, it is geographically limited to central-northern Buenos Aires Province. The scarcity of records may be due partially to the existence of few outcroppings from that age, relative to those referable to the latest Pleistocene. Lastly, this new species completes the stratigraphic distribution of genus *Neosclerocalyptus*, which ranges from the early Pleistocene of the calcretes ("Toscas") of La Plata river (*c.* 1.07-0.98 Ma), to the late Pleistocene-early Holocene (*c.* 0.13-0.008 Ma) of the Pampean region and central-north Argentina.

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