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Paleozoogeographic, biostratigraphic, and systematic aspects of the Genus *Sclerocalyptus* Ameghino, 1891 (Xenarthra, Glyptodontidae) of Argentina

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Abstract

Using species of the genus *Sclerocalyptus* Ameghino, 1891, found in Argentina and considered valid, the authors recognize: (1) four species for the Ensenadan stage (Late Pliocene–Middle Pleistocene): *S. pseudornatus* (Ameghino), restricted to Buenos Aires province; *S. ornatus* (Owen), recorded at Buenos Aires, Córdoba, and Santa Fe provinces; *S. perfectus* (Gervais and Ameghino) in Buenos Aires and Santiago del Estero provinces; and *S. cordubensis* (Ameghino), endemic to west-central Córdoba province; (2) a single species for the Bonaerian stage (Middle–Late Pleistocene), *S.* migoyanus, restricted to the Buenos Aires province; and (3) Lujanian taxa (Late Pleistocene–Early Holocene) represented by *Sclerocalyptus* cf. S. *heusseri* (Ameghino), distributed in Buenos Aires, Córdoba, Tucumán, Corrientes, and Santa Fe provinces, and *S. evidens* (Ameghino) in Salta province. From a paleoenvironmental standpoint, the *Sclerocalyptus* species show adaptations to arid–semiarid and cold environments, such as strong development of the fronto-nasal sinuses, a characteristic that probably appeared during the Sanadresian–Ensenadan. *Sclerocalyptus* is not frequent in those areas in which relatively more humid and warm climates than those inferred for the Pampean region and central northern Argentina (e.g. Mesopotamia, west of Uruguay, south of Brazil) prevailed during the Quaternary.

Keywords: Argentina; Bonaerian; Ensenadan; Lujanian; Paleoecology; Paleoenvironment; Pleistocene; *Sclerocalyptus*

Resumen

A base de las especies del género *Sclerocalyptus* Ameghino, 1891, presentes en Argentina y que nosotros consideramos válidas se observa que, para el Piso Ensenadense (Plioceno tardío–Pleistoceno medio), es posible reconocer cuatro especies: *S. pseudornatus* (Ameghino), limitado a la provincia de Buenos Aires; *S. ornatus* (Owen), con registros en las provincias de Buenos Aires, Córdoba y Santa Fe; *S. perfectus* (Gervais y Ameghino), en las provincias de Buenos Aires y Santiago del Estero; y *S. cordubensis* (Ameghino), endémico del centro-oeste de la provincia de Córdoba. En el Piso Bonaerense (Pleistoceno medio-tardío) es posible reconocer una sola especie (*S. migoyanus*), limitado a la provincia de Buenos Aires. Por último, los taxones de antigüedad Lujanense (Pleistoceno tardío-Holoceno temprano) están representados por *Sclerocalyptus* cf. *S. heusseri* (Ameghino), distribuido en las provincias de Buenos Aires, Córdoba, Tucumán, Corrientes y Santa Fe y *S. evidens* (Ameghino), en la provincia de Salta. Desde una perspectiva paleoambiental, las especies de *Sclerocalyptus* muestran claras adaptaciones a la vida en ambientes áridos o semiáridos y fríos, como el gran desarrollo de los senos fronto-nasales, carácter posiblemente aparecido en el límite Sanadresense–Ensenadense. *Sclerocalyptus* es poco frecuente en zonas en las que han prevalecido, durante el Cuaternario, climas relativamente más húmedos y cálidos que aquéllos inferidos en la región Pampeana y centro-norte de la Argentina (e.g. región Mesopotámica, parte occidental de Uruguay y sur de Brasil).

1. Introduction

From the Late Pliocene–Pleistocene of Argentina, several authors (e.g. Gervais and Ameghino, 1880;

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Ameghino, 1888, 1889, 1895; Castellanos, 1925, 1951) have recognized a large number of species within the genus *Sclerocalyptus* Ameghino, 1891. Most species were based on a few of scutes or fragments from the dorsal carapace and part of the caudal tube, mostly unassociated and without accurate stratigraphic provenance. Consequently, the systematic assignment of this genus included a large number of rarely found species, as a result of a typological classification criterion based on descriptive but not always significant morphological features that ruled the systematics until recently (Giraudo, 1997).

Chronologically, the genus *Sclerocalyptus* is recorded from the Vorohuean? (Late Pliocene) to the Lujanian (Late Pleistocene–Early Holocene) (Scillato-Yané et al., 1995; Carlini and Scillato-Yané, 1999). The species have a wide latitudinal distribution; their southernmost limit is the Chubut province (Scillato-Yané et al., 1995), and their northern limit reaches Las Lajitas locality in Salta province (25°S; Zurita et al., 2002b) and the coast of the Pilcomayo River, Formosa province (25°S, 58°10°O; Tonni and Scillato-Yané, 1997). Outside Argentina, the northernmost records are those of the Bolivian locality Ñuapua (20°52′S, 63°04′O; Hoffstetter, 1968) and Santa Cruz de la Sierra (18°S, 64°O; Ameghino, 1889).

Despite the restrictions of a reconstruction based completely on extinct clades (Fidalgo and Tonni, 1978; Prieto, 1996), the Plio–Pleistocene Glyptodontidae have been regarded as taxa clearly adapted to open arid–semiarid environments (Scillato-Yané et al., 1995; Carlini and Scillato-Yané, 1999), and their herbivorous grazer ecological role has been inferred by several authors (e.g. Fidalgo and Tonni, 1978; Pérez et al., 2000). Within this context, some morphological features of the genus *Panochthus* Burmeister and *Sclerocalyptus* Ameghino, mainly of the skull (e.g. development of the fronto-nasal sinuses), have been interpreted as adaptations to a cold, semiarid climate, in that these strongly pneumatized structures may have played a major role in thermoregulation.

A preliminary systematic review of the species of the genus *Sclerocalyptus* suggests that valid species are represented by *S. pseudornatus* (Ameghino, 1889) from the Late Pliocene–Middle Pleistocene of Buenos Aires province; *S. cordubensis* (Ameghino, 1888) from the Late Pliocene–Middle Pleistocene of Córdoba province; *S. perfectus* (Gervais and Ameghino, 1880) from the Late Pliocene–Middle Pleistocene of the provinces of Buenos Aires and Santiago del Estero; *S. ornatus* (Owen, 1845) from the Middle Pleistocene of Buenos Aires, Córdoba, and Santa Fe provinces; *S. migoyanus* from the Middle–Late Pleistocene of Buenos Aires province; *Sclerocalyptus* cf. *S. heusseri* (Ameghino, 1889) from Late Pleistocene–Early Holocene sediments of Buenos Aires, Córdoba, Santa Fe, Tucumán, and Corrientes provinces; and *S. evidens* (Ameghino, 1889) from the Late Pleistocene of Salta province.

This article discusses some paleozoogeographic, paleoenvironmental, and biostratigraphic aspects of the species of *Sclerocalyptus* that we regard as valid and analyzes their correlation with information provided by other disciplines. We follow the biostratigraphic and chronostratigraphic schemes of Cione and Tonni (1995a,b, 1999, 2001). For the systematic schemes, we follow mainly Ameghino (1891) and Hoffstetter (1958, 1969, 1982) rather than Paula Couto (1965).

2. Abbreviations

The materials analyzed herein belong to the following Argentine collections: (1) PZ-Ctes, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes); (2) MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (La Plata); (3) MACN, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires); (4) CC, Museo Universitario 'Florentino y Carlos Ameghino,' Universidad Nacional de Rosario (Rosario, Santa Fe); (5) MCNL, Museo de Ciencias Naturales de Lobería (Lobería, Buenos Aires); (6) MMP, Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia' (Mar del Plata, Buenos Aires); (7) PVL, Paleontología Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto 'Miguel Lillo' (Tucumán); (8) MCA, Museo de Ciencias Naturales 'Carlos Ameghino' (Mercedes, Buenos Aires); and (9) MBM, Museo Provincial de Ciencias Naturales 'Bartolomé Mitre' (Córdoba City).

3. Systematic considerations

Historically, many species of the genus *Sclerocalyptus* have been nominated (Paula Couto, 1979). The following taxa were described for the Ensenadan–Lujanian of eastern Buenos Aires province: *S. ornatus*, *S. pseudornatus*, *S. perfectus*, *S. scrobiculatus* (recognized by Ameghino, 1889, on the basis of a dorsal carapace belonging to the genus *Lomaphorus* Ameghino; see Ameghino, 1895), *S. migoyanus*, and *S. heusseri* (Ameghino, 1889). From out the Pampean region, the nominated taxa were *S. evidens* for the Pleistocene of Santa Cruz de la Sierra, Bolivia; *S. matthewi* Castellanos, 1925, *S. cordubensis* (=*Isolinia cordubensis* Castellanos, 1951), and *I. reartensis* Castellanos for the Marplatan?—Ensenadan of the central-west Córdoba province; and *S. bergi* (Ameghino, 1889) from the Pleistocene of this latter province (Ameghino, 1888; Castellanos, 1925, 1951). In this sense, it is important to note that previously, no diagnostic characteristics of this taxa could be identified (Zurita, pers. obs.).

In the following, we summarize the species we consider valid, along with a thorough comparison of the type specimens and the referred materials.

Subfamily Sclerocalyptinae Ameghino, 1895.

Tribe Sclerocalyptini Ameghino, 1895.

Genus *Sclerocalyptus* Ameghino, 1891.

Diagnosis. Small-sized glyptodonts, with low and elongate dorsal carapace, subcylindrical in shape, in some cases with a small middle constriction that divides the anterior from the posterior half. The lateral-anterior end opens outward like wings and is composed of very small penta- or hexagonal scutes. Scutes with ornamentation similar to those of Propalaehoplophorinae, relatively thin and large, formed by a central figure of flat or somewhat concave surface surrounded by an array of 7–10 small polygonal figures in the middle and anterior area of the carapace and 10–12 (exceptionally, 13 or 14) on the posterior area, with furrows separating inconspicuous figures from one another. Lateral scutes rectangular and elongate distal proximally, with a large central figure in dorsolateral arrays; dorsally, this disposition vanishes, and the scutes acquire penta- or hexagonal shape with more developed peripheral figures. Caudal tube with four or five rings, cylindrical–conic somewhat depressed dorsoventrally and decreasing in diameter distally, with two large dorsolateral terminal figures. Laterally, there are 5–7 oval figures that increase in size distally. The tube has a similar ornamentation to that observed in the carapace. Feet and hands with four digits (because of the loss of digit I), the fifth is very reduced. Skull with very developed and pneumatized fronto-nasal sinuses (the strongest development in Lujanian species) downward inclined, though not as much as in *Panochthus*; the orbit is closed posteriorly.

Chronological distribution. Late Pliocene (Vorohuean?)–Late Pleistocene–Early Holocene (Lujanian) (Scillato-Yané et al., 1995; Carlini and Scillato-Yané, 1999).

Geographical distribution. In Argentina, provinces of Chubut, Buenos Aires, La Pampa, Córdoba, Mendoza, Santa Fe, Entre Ríos, Corrientes, Chaco, Santiago del Estero, Tucumán, Formosa, and Salta. Also Uruguay, Paraguay, and Bolivia.

4. Biostratigraphy and paleozoogeography

Historically, the first record of the genus is *Sclerocalyptus ornatus* (='*Glyptodon*' *ornatus* Owen) (Fig. 1A) found near the Matanza River, 32 km south of Buenos Aires, according to Owen (1845), in 'Tertiary' sediments. Today, the bearing sediments cannot be considered older than Early Pleistocene. This species is characterized by an intermediate size between *S. pseudornatus* and *S. heusseri*; the fronto-nasal sinuses are funnel shaped, separated from each other and from the frontals by a neat cleft and inclined downward. The anterior margins are slightly curved inward, and the base of the nasal partition wall is very developed.

Regarding the geographic (Fig. 2) and stratigraphic (Fig. 3) distribution, reliable records include two specimens

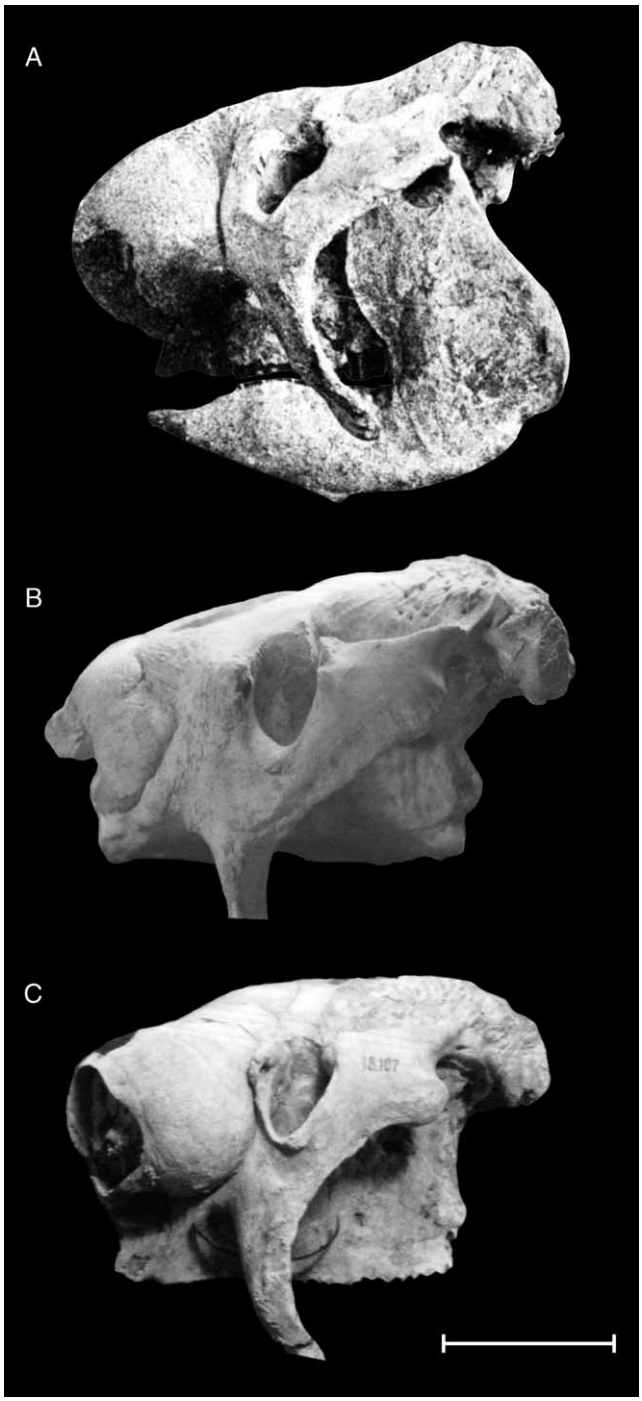

Fig. 1. Skulls in lateral view. (A) *Sclerocalyptus ornatus* (MLP 16–28; modified from Lydekker, 1894). (B) *Sclerocalyptus pseudornatus* (IFG 107). (C) *Sclerocalyptus* cf. *S. heusseri* (MACN 18107). Scale bar: 10 cm.

from the cliffs of north of Mar del Plata (Fig. 2). The sedimentary sequences have been studied since Ameghino (1908) recognized Ensenadan at the base, overlain by Bonaerian. Studies of the magnetostratigraphy (Bidegain et al., 1998) and biostratigraphy (Tonni et al., 1998) of the Ensenadan sector suggest a somewhat younger age than that of the 'Toscas del Río de La Plata,' and though reliable dating has not been accomplished yet, they may be

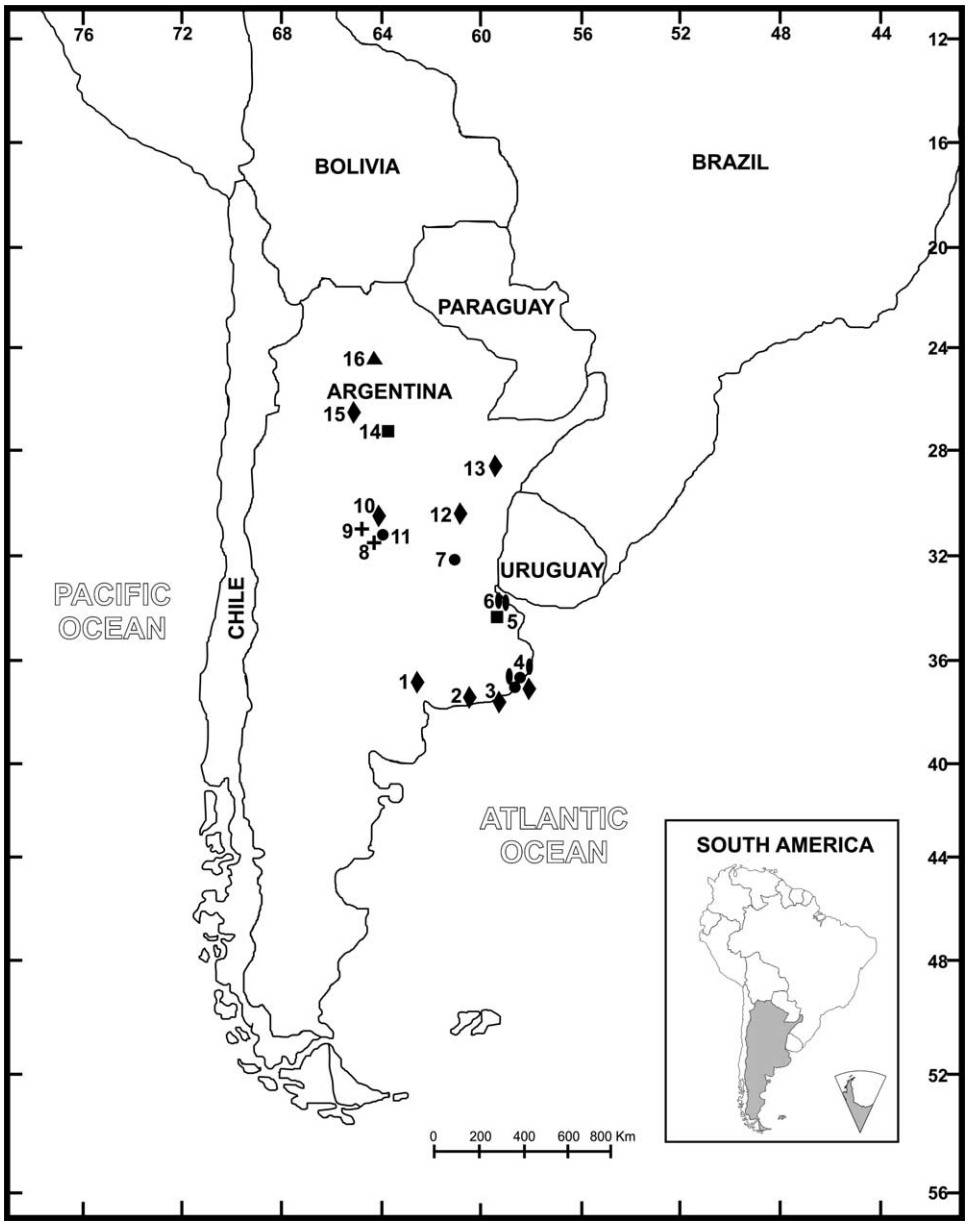

Fig. 2. Distribution of the genus *Sclerocalyptus* in Argentina. Circle, *S. ornatus*; ellipse, *S. pseudornatus*; square, *S. perfectus*; cross, *S. cordubensis*; rhombus, *Sclerocalyptus* cf. *S. heusseri*; triangle, *S. evidens*. (1) Carhué, (2) Lobería, (3) Centinela del Mar, (4) Mar del Plata, (5) Olivos, (6) Buenos Aires, (7) Granadero Baigorria, (8) Los Reartes, (9) Cura Brochero, (10) Córdoba, (11) Río Tercero, (12) Puerto San Martín, (13) Arroyo Toropí, (14) Santiago del Estero, (15) Tafí Viejo, (16) Las Lajitas.

between 0.98 and 0.5 Ma. (late Ensenadan; Tonni et al., 1998). Another record represented by a complete dorsal carapace has been found in the Miramar Formation, Mar del Plata (Isla and Dondas, 2001). Cione and Tonni (1995a, 1999) refer this formation to the Ensenadan s.l. (~2.0–0.5 Ma.). From of Buenos Aires province, a fourth record was found at the cliffs of the Paraná River near Granadero Baigorria, Santa Fe province. In the 1960 s, Castellanos assigned this material to the 'lower Pleistocene' (='Belgranian') (Zurita, pers. obs.). Currently, the Belgranian *sensu* Ameghino (1889) and Castellanos (passim) belongs to the Middle Pleistocene (Late Ensenadan–Early Bonaerian). Finally, a fifth record from the Ensenadan appears in the locality of Río Tercero, Córdoba province (Castellanos, 1944).

Sclerocalyptus pseudornatus (Fig. 1B) is the smallest species of the genus *Sclerocalyptus* and perhaps the least derived (Zurita, pers. obs.). The margins of the nasals are completely curved inward, with scarce development and pneumatization of the fronto-nasal sinuses, which are however strongly walled up. (Unfortunately, the anterior part of the nasal sinuses is not known.)

All specimens that may be assigned with certainty to this species were found at the Toscas del Río de La Plata

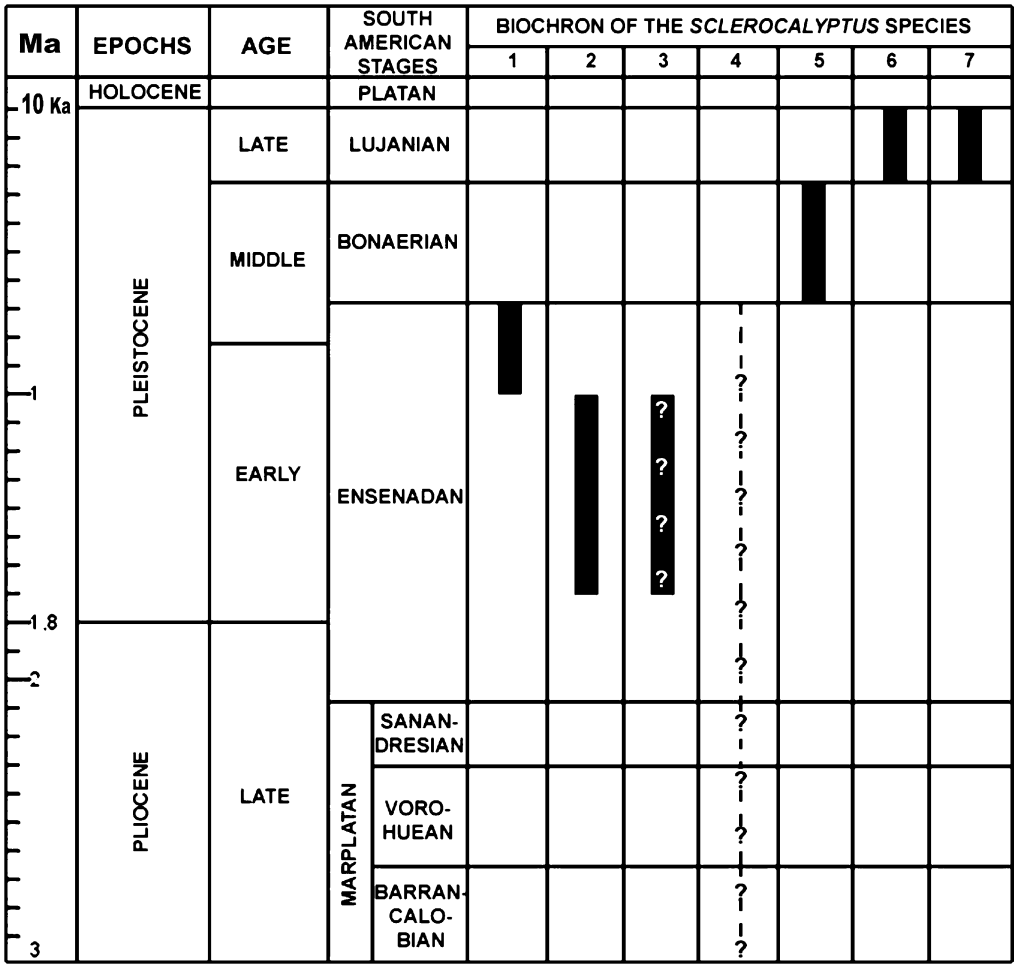

Fig. 3. Chronological distribution of the species of *Sclerocalyptus*. (1) *S. ornatus*, (2) *S. pseudornatus*, (3) *S. perfectus*, (4) *S. cordubensis*, (5) *S. migoyanus*, (6) *Sclerocalyptus* cf. *S. heusseri*, (7) *S. evidens*.

(Olivos and Buenos Aires) and Mar del Plata, Buenos Aires province (Fig. 2). The Toscas del Río de la Plata are placed between Jaramillo and Olduvai, meaning they are more than 0.98 and less than 1.7 Ma. (Middle–Late Ensenadan) (Tonni, pers. comm.). The material from Mar del Plata was found at the Miramar Formation (Isla and Dondas, 2001), referred by Cione and Tonni (1995a, 1999) to the Ensenadan s.l. (Fig. 3).

The species *S. perfectus* is not well characterized, because it includes two records (Fig. 2) represented by only a few scutes of the dorsal carapace. The main diagnostic character of these scutes is the large central figure and high number of small figures surrounding it (Gervais and Ameghino, 1880; Ameghino, 1889, 1895). The only record in Buenos Aires province probably was found in the Toscas del Río de La Plata. The other record was found at Santiago del Estero province, but its probable age is unknown.

Sclerocalyptus cordubensis (=*Isolinia cordubensis*, Castellanos, 1951=*I. reartensis* Castellanos, 1951=*S. matthewi* Castellanos, 1925) is another species that requires more complete materials, because it is known only by a caudal tube, remains of scutes, and a single mandible. In addition, the single diagnostic feature is the rugosity of the scutes of the dorsal carapace, which may result from taphonomic processes because it appears in certain carapaces of *Sclerocalyptus* from Buenos Aires province (Zurita, pers. obs.). The records of this species are restricted to the central western Córdoba province (Cura Brochero and both margins of Los Reartes River, at the homonymous locality) (Fig. 2), where Castellanos (1942, 1944) assigned the 'Horizonte Brocherense' overlain by his 'Ensenadan.' More recent biostratigraphic studies demonstrate that this horizon includes a mix of fauna that, in the Pampean region, has a Marplatan–Ensenadan biochron (Marshall et al., 1984; Cione and Tonni, 1995a) (Fig. 3).

The species *S. migoyanus* was recognized by Ameghino (1889) on a distal half of a caudal tube from the Bonaerian (Middle–Late Pleistocene) of Buenos Aires province. The materials likely to be assigned to this taxon show transitional characteristics between the species of Ensenadan and Lujanian age (Zurita, pers. obs.).

Sclerocalyptus cf. *S. heusseri* (Fig. 1C), together with *S. ornatus*, is the best characterized species because of the many partially complete records. In addition, it is larger than the previous species, and with regard to the fronto-nasal sinuses, it is the most derived species because they are greatly developed. Within the genus, this species has the widest latitudinal distribution (Fig. 2), from approximately 38 to 27°S. In Buenos Aires province, there are three certain records, all from the locality of Carhué. The material was found, according to Scaglia (in schedule), at the Lujanian (Fig. 3). Another record of this species is an almost complete carapace from the La Postrera Formation at the homonymous locality. Cione and Tonni (1999) refer this unit to the Lujanian stage (0.13–0.008 Ma.) because it is completely within the Brunhes chron (Zancheta et al., 1995). Radiocarbon dating on remains of *Glossotherium* (*P.*) *myloides* yields 10.710±50 years B.P. for this geological unit (Figini et al., 1987). The record of Centinela del Mar also was found in Lujanian sediments. At Mar del Plata (Fig. 3), a complete dorsal carapace recently has been exhumed from sediments that may be assigned to the Late Pleistocene (Isla and Dondas, 2001). Furthermore, Lydekker (1894) figured a complete skull of this species that, according to Ameghino (1895), was found at the latter locality, though this material unfortunately was lost. In Corrientes province (Fig. 2), there is a record from the Yupoí Formation (Herbst, 1999). Recent biostratigraphic studies (Scillato-Yané et al., 1998; Cione and Tonni, 1999) suggest that this formation may be assigned to the Lujanian stage. In Tafí Viejo (Fig. 2), Tucumán, two records occur in eolian sediments of the Tucumán Formation (Bonaparte and Bobovnikov, 1974). Esteban et al. (1988) assigned an Ensenadan–Lujanian age to this formation; however, according to the biochron of this species within the Pampean region, the material could be assigned to the Lujanian (0.13–0.008 Ma). There are two more records at Córdoba City from Lujanian sediments, represented by a complete dorsal carapace associated with a skull and caudal tube and another dorsal carapace that is fairly fragmented. Finally, at Puerto San Martín, Santa Fe, Santa Fe province (Fig. 2), a badly preserved skull was found in sediments of Lujanian age.

S. evidens was recognized by Ameghino (1889) from several scutes of the posterior region of the dorsal carapace found at Santa Cruz de la Sierra, Bolivia, which he assigned to his 'Formación Pampeana' (=Pleistocene). The main diagnostic feature is the central figure of the scutes of the caudal notch, which have the major axis transversely oriented, whereas the main axis of following scutes is longitudinally oriented.

In addition, the great thickness of these scutes is outstanding. The caudal tube is cylindrical. The single record of this species was reported by Zurita et al. (2002a). The material was exhumed at the locality of Las Lajitas, Salta province (25°S) (Fig. 2) from sediments referable to the Late Pleistocene (Lujanian) (Fig. 3).

5. Paleoenvironmental features

From a paleoenvironmental standpoint, the period between the Late Pliocene and Early Holocene (Ensenadan–Lujanian) from the southern tip of South America was characterized by the predominance of cold and arid–semiarid climates with short, alternating, more humid periods (Tricart, 1973; Tonni and Fidalgo, 1979, 1982; Tonni and Scillato-Yané, 1997; Cione and Tonni, 2001), a pattern especially applicable to the Pampean region. Preliminary studies suggest that this climatic environmental process may have extended to central and central northern Argentina (Tonni and Scillato-Yané, 1997; Zurita et al., 2001, 2002), Paraguay (Hoffstetter, 1978; Carlini and Tonni, 2000), and part of Bolivia (Hoffstetter, 1968). In spite of this, the Mesopotamian region, together with southern Brazil and western Uruguay, may have developed—especially during the Lujanian s.l. (0.5–0.008 Ma.)—climatic environmental processes more humid than those observed for the Pampean region (Tonni, 1992), as suggested by paleofaunal (Oliveira, 1996; Tonni, 1992; Ubilla, 1985, 1996) and sedimentological (Iriondo and García, 1993) evidence.

Within this paleoclimatic environmental context, the Sclerocalyptini from the Ensenadan, Bonaerian, and Lujanian have been traditionally related to arid and cold environments, because they are very common in eolian sediments (Fidalgo and Tonni, 1983). In this sense, one of the most outstanding evolutionary trends is the gradual increase in the pneumatization and the development of the fronto-nasal sinuses, probably as an adaptive response to the progressive cooling and aridization observed in the uppermost Sanandresian (Late Pliocene), which continued during part of the Ensenadan (Cione and Tonni, 1995a, 1999, 2001; Tonni et al., 1999a,b). Thus, this trend becomes perceivable through the species *S. pseudornatus*. In support of this hypothesis, the micromastofauna of this age (1.0 Ma.; Late Ensenadan) suggests the clear predominance of cold and arid climatic conditions, alternating with some short humid periods (Tonni et al., 1999b). The same sites in which *S. pseudornatus* was found also yield remains of *Lama guanicoe* (Muller) (Menégaz, 1995), an indicator of dry and cold climates; *Mesotherium* Serrés, 1867; and Brazilian fauna such as *Tapirus* Brisson and *Calomys* Waterhouse, which are typical of more humid and tropical climates (Vucetich et al., 1997; Bond and Cerdeño, 1995; Bond, 1999). Recently, Verzi et al. (2002) reported that the presence of the octodontid *Tympanoctomys* Ameghino, 1889, in central Argentina and Buenos Aires province in sediments dated 0.9–0.78 Ma demonstrates arid, cold climate during that time.

The trend related to the increase of the fronto-nasal sinuses is emphasized in *S. ornatus*. The records of this species, from north of Mar del Plata (Late Ensenadan; 0.98–0.5 Ma.), probably younger than those of the Toscas del Río de La Plata, suggest the continuation of the climatic

conditions established at the beginning of the Ensenadan, namely, cold and arid ones (Tonni et al., 1998, 1999b; Cione and Tonni, 2001).

The Bonaerian–Lujanian, which ends with the extinction of the megafauna and the end of loessic sedimentation (~0.5 Ma–8.5 ka; Cione and Tonni, 1999), would have been characterized by the predominance of arid–semiarid and cold climates, alternating with short humid, relatively warm periods (Iriondo and García, 1993; Krohling and Iriondo, 1999; Iriondo, 1999; Tonni et al., 1999a). Thus, *Sclerocalyptus* cf. *S. heusseri* shows the culmination of the evolutionary trend toward the development and pneumatization of the fronto-nasal sinuses. This phenomenon would have been partly stimulated by the cold, strongly arid periods observed by several authors during the last glacial cycle in the uppermost part of the Pleistocene (<0.13 Ma.) (Iriondo and García, 1993; Zancheta et al., 1995; Tonni and Scillato-Yané, 1997; Tonni et al., 1999a), in which the mean temperatures were markedly lower than the present ones in the Pampean region (Prado et al., 1987).

Although the knowledge of the Pleistocene megafauna of central northern Argentina is almost of no account compared with that of the Pampean region, some preliminary works carried out in the provinces of Formosa (Tonni and Scillato-Yané, 1997), Chaco (Zurita et al., 2001), and Santa Fe (Zurita et al., 2002b) seem to show a striking faunal homogeneity with that of the Pampean region; consequently, similar climatic-environmental conditions are inferred. Sedimentological works (Iriondo, 1994, 1999) show similar evidence to results obtained through the paleofaunistic study. This hypothesis is supported by the record of *Sclerocalyptus* in the Bonaerian–Lujanian of this region.

The last certain record of the genus in Argentina is a specimen from the La Postrera Formation, which was dated as approximately 10,710 years BP (Figini et al., 1987), in line with a cold and dry period (Iriondo and García, 1993).

As already stated, this paleoclimatic pattern, which is valid for the Pampean region, central northern Argentina, Paraguay (Hoffstetter, 1978; Carlini and Tonni, 2000), and part of Bolivia (Hoffstetter, 1968), is not completely valid for the Mesopotamian region. There, as in southern Brazil and western Uruguay, climatic environmental processes more humid than those recorded for the Pampean region may have developed, mostly during the Lujanian s.l. (Tonni, 1992), in contrast to the faunal and climatic uniformity proposed by Bombin (1976). The former hypothesis is supported by paleofaunal (Oliveira, 1996; Tonni, 1992; Ubilla, 1985, 1996) and sedimentologic (Iriondo and García, 1993) evidence. This paleoenvironmental differentiation also agrees with the scarceness of the record of Sclerocalyptini reported for Argentinean Mesopotamia (Tonni, 1992; Noriega et al., 2001), southern Brazil, and part of Uruguay (Kraglievich, 1932). Accordingly, the single species of Sclerocalyptini recognized for Brazil is *Hoplophorus euphractus* Lund, 1839, from the Bonaerian? (Cione et al., 1999), which shows much less development and neumatization of the fronto-nasal sinuses than do the Argentine species (Paula Couto, 1957). Finally, there is the noteworthy finding of *Sclerocalyptus* sp. at the Paraguayan Chaco, probably of 7070 years BP (Early Platan; Carlini and Scillato-Yané, 1999). Whether this record is confirmed, it may contradict, at least partially, the hypothesis of Iriondo and García (1993) of a humid and subtropical climate for this lapse.

6. Conclusions

The systematic review results in the following conclusions regarding the biostratigraphic and paleoecological meaning of the species of the genus *Sclerocalyptus*.

First, *Sclerocalyptus* has biostratigraphic value, because the temporal distribution of its species has precise limits. The first record of the genus (*Sclerocalyptus* sp.) could be dates from the Vorohuean substage (Middle–Late Pliocene). *Sclerocalyptus pseudornatus*, *S. perfectus*, and *S. ornatus* would have lived during the Ensenadan stage (~2.0–0.5 Ma). In this sense, the records of *S. perfectus* and *S. pseudornatus* (1.7–0.98 Ma) differ from those of *S. ornatus* (0.98–0.5 Ma). *Sclerocalyptus cordubensis* eventually could be extended to part of the Marplatan (Middle–Late Pliocene). The biochron of *S. migoyanus* would have been restricted to the Middle–Late Pleistocene (0.5–0.13 Ma.; Bonaerian), whereas *Sclerocalyptus* cf. *S. heusseri* and *S. evidens* lived between 0.13 and 0.008 Ma (Lujanian).

Second, the species of *Sclerocalyptus*, in addition to having biostratigraphic significance, are good paleoecological indicators because their distribution and anatomical adaptations show that they must have been a clade that became progressively better adapted to semiarid (or arid) and cold environments. In this sense, they left a minimal record during the Lujanian s.l. in more humid and/or warm environments, as in Argentinean Mesopotamia, Uruguay, and part of Brazil.

Third, from a paleozoogeographic perspective, *S. pseudornatus* seems restricted to the Toscas del Río de La Plata and Mar del Plata, whereas *S. ornatus* was recorded at Mar del Plata, Córdoba, and Granadero Baigorria, Santa Fe. In contrast, *S. cordubensis* is restricted to the central western Córdoba province, and *S. migoyanus* appears within Buenos Aires province. *Sclerocalyptus* cf. *S. heusseri* has the widest latitudinal distribution, from Buenos Aires province to Tucumán. *Sclerocalyptus evidens* seems restricted to the north of Argentina and central Bolivia.

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