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Neosclerocalyptus spp. (Cingulata: Glyptodontidae: Hoplophorini): cranial morphology and palaeoenvironments along the changing Quaternary

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We propose that the particular high latitudinal distribution of *Neosclerocalyptus* (Glyptodontidae) and the cyclic nature of the Pleistocene glacial–interglacial events were factors that probably stimulated morphological evolution of its fronto-nasal sinuses, a feature unique among glyptodonts. The distributions of the species, and the majority of its records, are associated with sediments related to arid and semi-arid environments. Four species are recognized during the last million years in southern South America. The first record of *Neosclerocalyptus* (*N. pseudornatus*) coincides with the "Great Patagonian Glaciation" and shows the lowest grade of pneumatization on its skull. *Neosclerocalyptus paskoensis* (the most derived species), limited to Oxygen Isotopic Stage 2, shows the greatest development of fronto-nasal pneumatization. The restricted geographic range of *Neosclerocalyptus*, the possible absence of geographic barriers during the Pleistocene, and the absence of cases of sympatry, allow us to speculate the existence of a single continuous lineage of successive species, showing an anagenetic process.

Keywords: *Neosclerocalyptus* Paula Couto; Pleistocene; Palaeoenvironments; cranial morphology; fronto-nasal sinuses

Introduction

In the Pleistocene [c. 2.6–0.011 million years ago (Ma)] ensemble of Cingulata Glyptodontidae, *Neosclerocalyptus* Paula Couto 1957 (= *Sclerocalyptus* Ameghino 1891) is one of the genera with the highest frequency of records in southern South America (Zurita et al. 2005). The biogeographical evolution of this genus is quite unique compared with that of other Pleistocene genera (e.g. *Glyptodon* Owen, *Panochthus* Burmeister, *Neuryurus* Ameghino). Its geographical distribution, limited to southern South America, ranges from Santa Cruz de la Sierra, Bolivia (17°47′ S, 63°11′ W) to the localities Lobería (38°10′ S, 58°46′ W) and Bahía Blanca (38°43′ S, 62°16′ W), Buenos Aires province, Argentina (Zurita et al. 2009).

The first certain records of this taxon correspond to the Ensenadan Stage (early to middle Pleistocene; c. 1.8–0.4 Ma; Soibelzon et al. 2008), when *Neosclerocalyptus pseudornatus* (Ameghino 1889) and *Neosclerocalyptus ornatus* (Owen 1845) are recorded

(see Zurita 2007). The species *Neosclerocalyptus gouldi* has been recently recognized from the Bonaerian Stage (middle Pleistocene; c. 0.40–0.130 Ma) (Zurita et al. 2008), while the Lujanian Stage [late Pleistocene to early Holocene; c. 130–8 thousand years ago (ka)] is characterized by the species *Neosclerocalyptus paskoensis* (Zurita 2002), widely distributed in the loessic sediments of present-day Argentina.

One of the most remarkable synapomorphies of *Neosclerocalyptus* is the development and pneumatization of the rostral area (Figure 1), especially the fronto-nasal sinuses (unique among the Cingulata Glyptodontidae). The increasing size and pneumatization becomes progressively evident in succeeding species, reaching its maximum expression in *N. paskoensis* (Zurita 2007; Zurita et al. 2009) (Figure 2). This trait has been interpreted by diverse authors from an adaptive perspective (see Tonni and Fidalgo 1979; Carlini and Scillato-Yané 1999; Zurita et al. 2005) as a response to the predominantly cold and arid/semiarid Pleistocene environments (Tonni, Cione et al. 1999; Tonni, Nabel et al. 1999; Lambeck et al. 2002), but no further evidence has been provided to support this hypothesis.

At present the species of the genus show a clear pattern of successive stratigraphic distribution, with no cases of sympatry. This could be interpreted as a series of "replacement" events (anagenetic evolution) in which each species replaced the previous one within the last million years; rapid morphological evolution, especially in the fronto-nasal sinuses, is evident during this period.

The goals of this work are to contribute new evidence and a synthesis of previous findings about the palaeoclimatic–environmental context that constituted the setting for the morphological evolution of the fronto-nasal sinuses, and the possible correlation between climate–environment and sinus morphology. Our discussion is mainly focused on *N. paskoensis*, the species with a rich fossil record and resolved stratigraphy.

Materials and methods

The chronological and biostratigraphical schemes used in this work correspond to those proposed by Cione and Tonni (2001, 2005) and Soibelzon et al. (2008).

All the values included in tables are expressed in millimetres, with an error range of 0.5 mm (Table 1). Measurements < 150 mm were taken with Vernier callipers; measurements > 150 mm were taken using anthropometric spreading callipers. Osteological terminology is based mainly on the contributions of Ameghino (1889), Paula Couto (1957) and Gillette and Ray (1981).

Multivariate visualization techniques (Jolliffe 2002; Venables and Ripley 2002) such as principal components analysis (PCA) were used to elucidate the structure and possible relationships of the variables and observations.

Table 1 shows the data matrix that was used in this work (see also Figure 3).

All variables are linear measurements of similar magnitude taken in the same scale; therefore the PCA was performed using these data and the respective eigenvalues and eigenvectors were obtained from singular value decomposition of the variance–covariance matrix. All the analyses were made using the software R version 2.8.1 on Linux (R Development Core Team 2010).
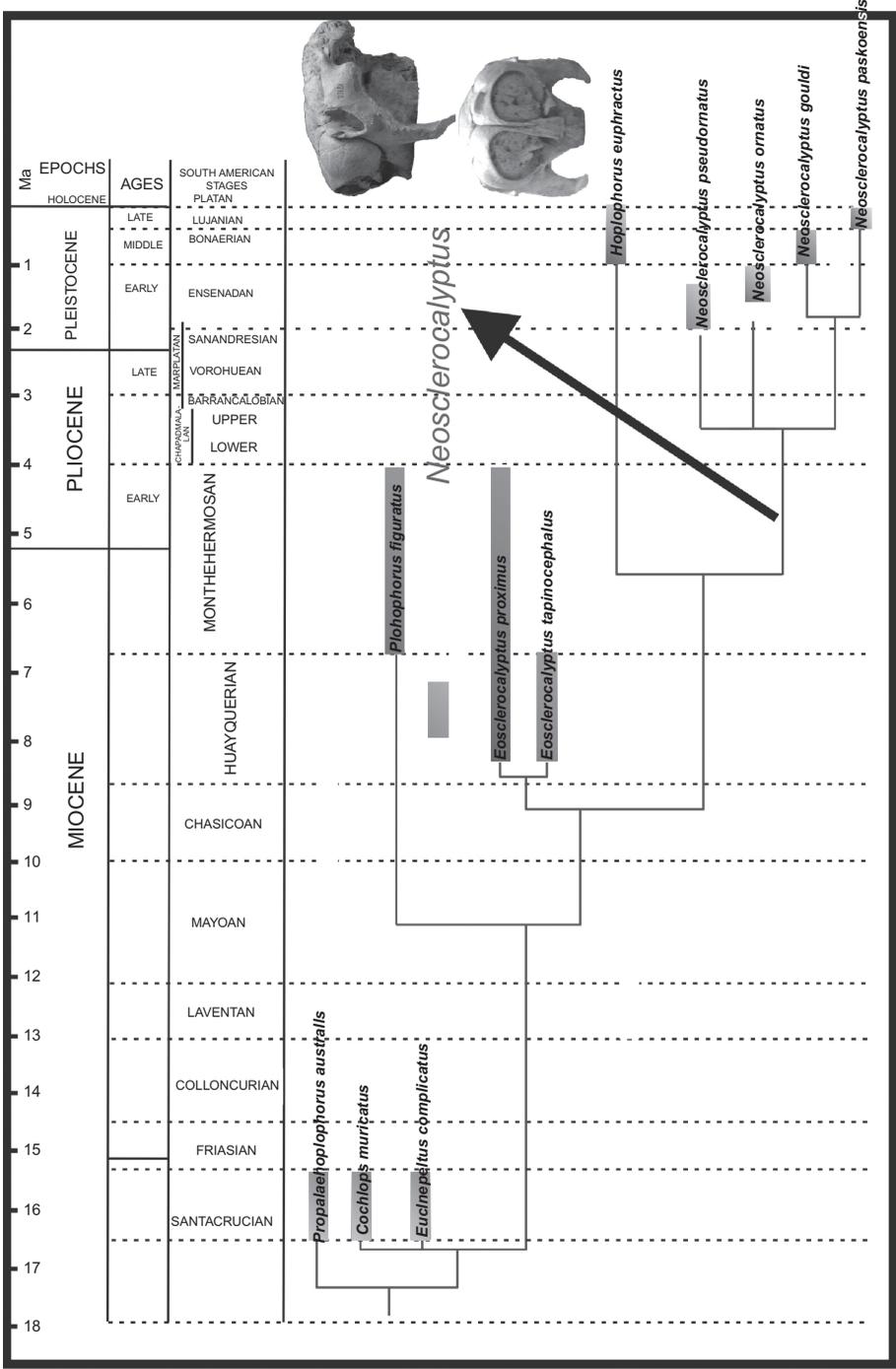
Figure 1.   Phylogenetic relationships and stratigraphic records of the *Neosclerocalyptus* species (modified from Zurita 2007).
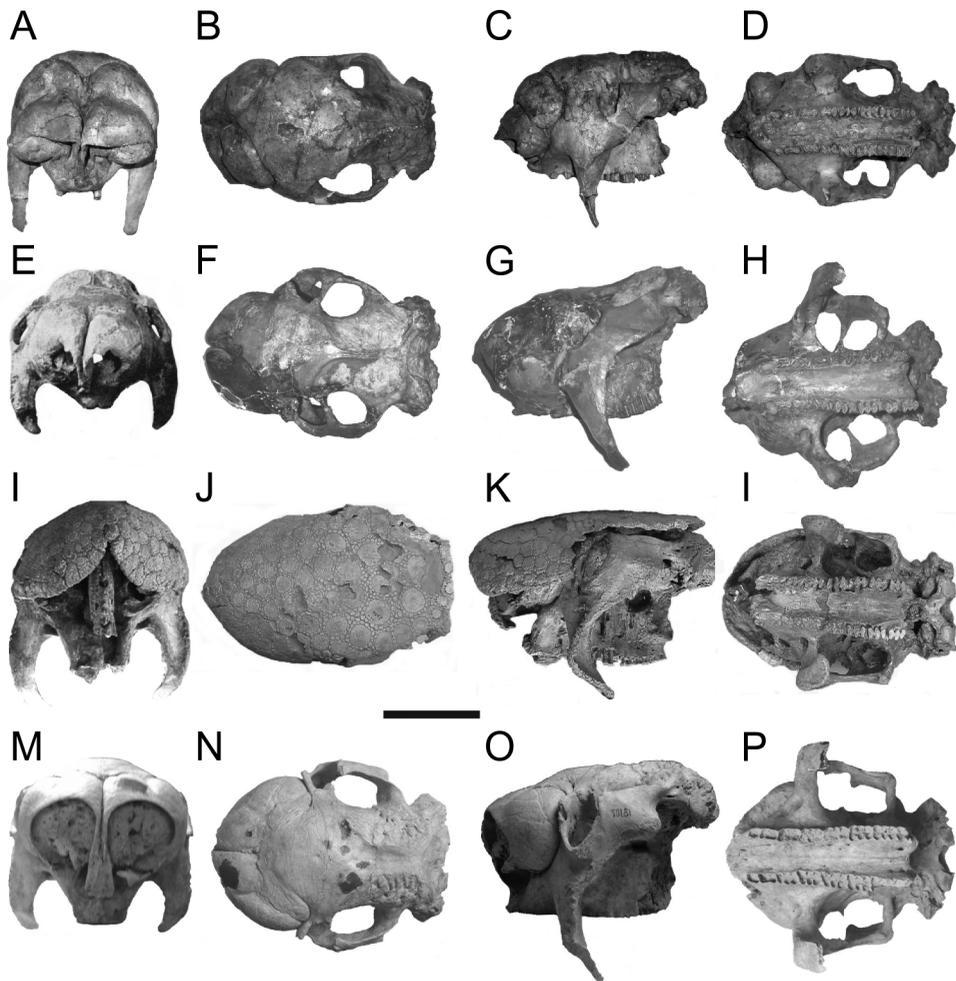
Figure 2. Skulls of *Neosclerocalyptus* spp. (A–D) *N. pseudornatus*; (E–H) *N. ornatus*; (I–L) *N. gouldi*; (M–P) *N. paskoensis*. First column: in frontal view; second column: in dorsal view; third column: in lateral view; fourth column: in occlusal view. Scale bar: 100 mm.

The number of components to use was determined using the "broken stick" model. This model is based on the estimation of expected values for each component and graphical comparison with the observed PCA values. The contact between the curves for expected and observed values is used as a cut-off point, and only the components whose observed value is greater than expected by the model are retained for further analysis.

Institution abbreviations. AGM, Archivo Gráfico y Museo Histórico de San Francisco y la Región, San Francisco, Córdoba; CORD-PZ, Córdoba-Paleozoología, Museo de Paleontología de la Universidad Nacional de Córdoba, Córdoba; Ctes-PZ, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes; GCF, Grupo Conservacionista de Fósiles, Museo Paleontológico Fray Manuel de Torres, San Pedro, Buenos Aires;

Table 1. Data matrix used in this work.

Taxa of *Neosclerocalyptus*	ML	TDR	MLDS	WPC	BD	MIW
N. pseudornatus (MFCA 107)	304	152	171	93	215	127
N. pseudornatus (MACN 8579)	295	161	160	103	213	129
N. pseudornatus (MACN 8773)	305	175	165	110	223	153
N. pseudornatus (MMP 234)	290	180	157	100	200	140
N. ornatus (MLP 16–28)	320	180	179	96	230	121
N. ornatus (MFCA 656)	320	170	176	102	223	140
N. ornatus (MACN 8091)	297	169	171	108	222	160
N. gouldi (MCA 2010)	310	190	175	114	205	170
N. paskoensis (MACN 18107)	289	197	183	110	233	153
N. paskoensis (AGM 002)	325	210	153	115	226	148

Notes: ML, maximum length; TDR, transversal diameter of rostral area, at level of vertical plane passing through middle lobe of M3; MLDS, maximum length of dental series; WPC, width of postorbital constriction; BD, bizygomatic diameter; MIW, minimum interorbital width.

LIL-PZ, Paleontología Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto "Miguel Lillo", Universidad Nacional de Tucumán, San Miguel de Tucumán; MACN, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires); MBM-PV, Museo Provincial de Ciencias Naturales "Bartolomé Mitre", Ciudad de Córdoba, Córdoba; MCA, Museo de Ciencias Naturales "Carlos Ameghino", Mercedes, Buenos Aires; MFCA, Museo Universitario "Florentino y Carlos Ameghino", Universidad Nacional de Rosario (ex Instituto de Fisiografía y Geología "Alfredo Castellanos") (Rosario, Argentina); MHIN-UNSL-GEO V, Museo de Historia Natural Universidad Nacional de San San Luís, Geología Vertebrados, San Luís; MHM, Museo Histórico Municipal de Arroyito, Córdoba; MLP, Departamento Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires; MMP, Museo Municipal de Ciencias Naturales del Mar del Plata "Lorenzo Scaglia", Mar del Plata, Buenos Aires; MNK-PAL, Colección Paleontología del Museo de Historia Natural Noel Kempf Mercado, Santa Cruz de la Sierra, Bolivia; MRFA, Museo Regional Florentino Ameghino, Río III, Córdoba; PV-UNS, Colección Paleontológica de la Universidad Nacional del Sur, Bahía Blanca, Buenos Aires.

Other abbreviations used: ML, maximum length: distance between anterior tip of nasals and upper margin of foramen magnum, taken on the sagittal plane; TDR, transversal diameter of rostral area, at level of vertical plane passing through middle lobe of M3; MIW, minimum interorbital width; WPC, width of postorbital constriction; BD, bizygomatic diameter; SH, skull height at level of (a) M1; (b) M4–5; (c) M8; MHN, maximum height of nares; MWN, maximum width of nares; MLBP, maximum length of bony palate: distance between anterior margin of premaxillae and posterior margin of palatine; MWP, maximum width of palate at level of (a) M1; (b) M4; (c) M8; MLDS, maximum length of dental series: distance between anterior tip of M1 and posterior tip of M8; LWM, length and width (at level of middle lobe) of molariforms; LGM, last glacial maximum; OIS, oxygen isotopic stages.
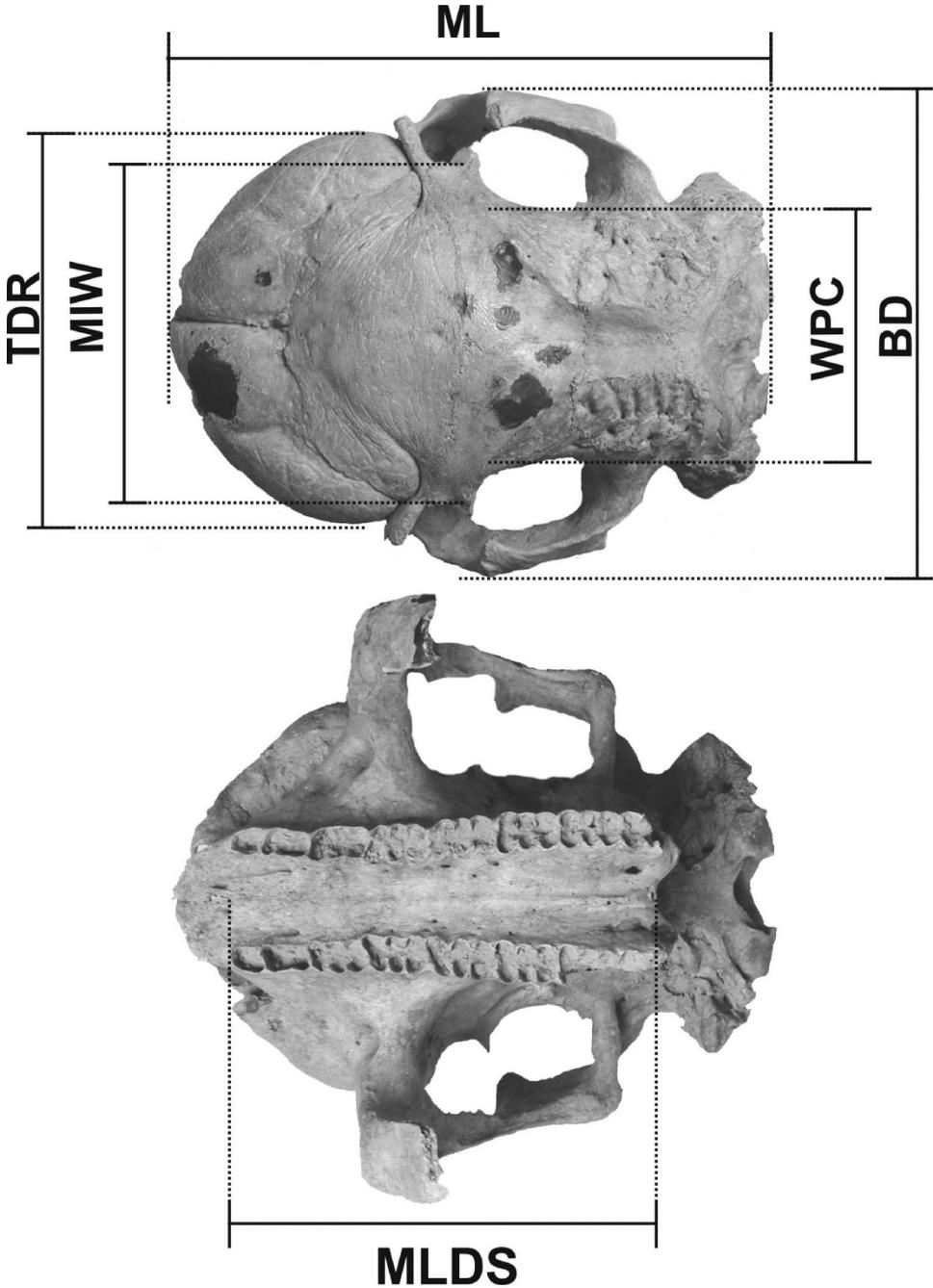
Figure 3. Diagram illustrating linear variables.

Results

The Pleistocene record of Neosclerocalyptus

Ensenadan (1.8–0.4 Ma) and Bonaerian (0.40–0.130 Ma) Stages (early Pleistocene to middle Pleistocene; OIS 64–5)

The oldest recorded species which shows pneumatization and development of the fronto-nasal sinuses is *N. pseudornatus* (Zurita et al. 2009). Its record is limited to the "Toscas del Río de la Plata" (Buenos Aires). At present these sediments are limited to scarce remnants (e.g. Anchorena Train Station of the "Tren de La Costa"; 34°29′5.8″ S, 58°28′49.9″ W), because of the expansion of Buenos Aires city (Soibelzon 2008; Soibelzon et al. 2008). Magnetostratigraphic analyses indicate that these sediments were deposited during times of normal polarity, referable to the Jaramillo event (Chron C1r1n; c. 1 Ma; see Soibelzon et al. 2008; Soibelzon et al. 2008).

According to the available evidence, *N. pseudornatus* was replaced by another species, *N. ornatus*, a taxon whose record is also limited to the Ensenadan of Mar del Plata city (Buenos Aires, 37°53′ S, 57°33′ W, from about 0.98 to 0.40 Ma; see Bidegain et al. 1998, 2003; Tonni et al. 1998; Soibelzon et al. 2009), and San Pedro (Buenos Aires 33°41′ S, 59°40′ W; from reverse-polarity sediments from the top of Matuyama; see Soibelzon, Carlini et al. 2008) but in sediments that correspond to the end of the Matuyama Chron (C1r1r; 0.98–0.78 Ma) and beginning of the Brunhes Chron (C1n; 0.78–0.40 Ma) (Figure 4). *Neosclerocalyptus ornatus* shows greater development and pneumatization of the fronto-nasal sinuses (Zurita et al. 2009).

So far, the only species recognized for the Bonaerian Stage (c. 0.40–0.13 Ma) is *N. gouldi* (see Zurita et al. 2008), whose development and pneumatization of the fronto-nasal sinuses is clearly more defined than that of *N. ornatus* (Figure 2). The only record corresponds to the type material (MCNA 2010), found in the vicinity of the locality San Andrés de Giles, Buenos Aires (34°26′ S, 59°26′ W). This specimen was exhumed from sediments of the Buenos Aires Formation which, while lithologically very similar to the Ensenada Formation, is formed mainly by alternating loess and paleosols. This has been traditionally interpreted as being the result of an alternating succession of arid cold climates and warmer, more humid pulses that gave rise to pedogenetic processes (Cione and Tonni 2001; Bidegain et al. 2007).

Lujanian Stage/Age (c. 130–8 ka; OIS 5-1): new records

The presence of one *Neosclerocalyptus* species, *N. paskoensis*, has been recognized; this is the most derived taxon of the genus and is characterized by maximum pneumatization and lateral expansion of the fronto-nasal sinuses (Figure 2).

In what is currently the Buenos Aires province of Argentina, numerous records are known from the northeast sector (MSP 33, San Pedro, La Postrera Fm.; see Nabel et al. 1993), the centre-south (Carhué, 37°11′ S, 62°45′ W; MACN 18107, MMP 540-M and MMP 232-S, Aurora Fm. of Fidalgo et al. (1975), formed by sands of aeolian origin synchronic with OIS 2) as well as from several southeastern localities (Lobería, 38°10′ S, 58°46′ W; MCNL 6.4; Bahía Blanca, 38°44′ S, 62°16′ W, PV-UNS 260 and Centinela del Mar, 38°26′ S, 58°13′ W, MCNL 6.2 and MCNL 6.3). The latter (MCNL and UNS) have been exhumed from sediments corresponding to the Lobería Formation. Recently, a complete dorsal carapace was exhumed in Mar del Plata from
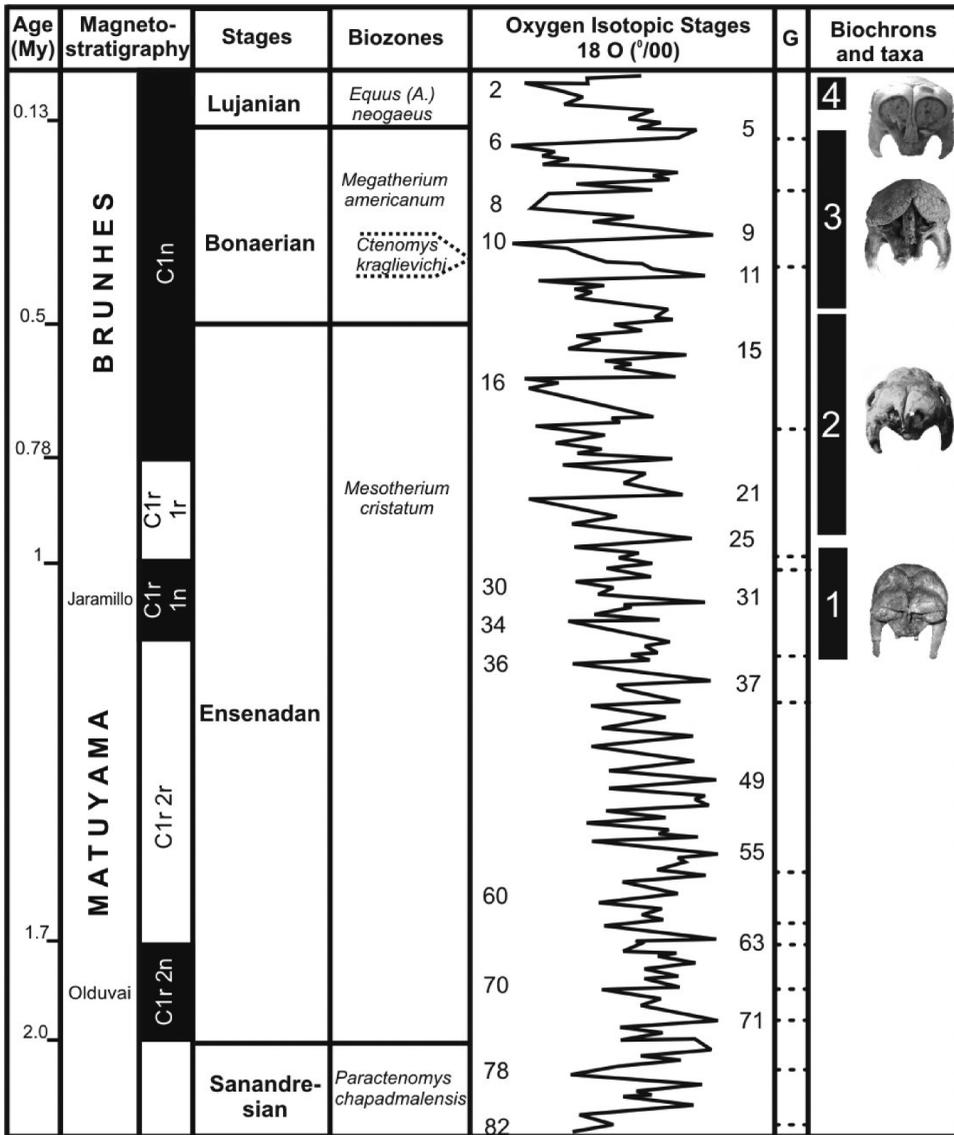
Figure 4. Chronological distribution of the species of *Neosclerocalyptus*. 1, *N. pseudornatus*; 2, *N. ornatus*; 3, *N. gouldi*; 4, *N. paskoensis*; G, Patagonian glaciations (*sensu* Rabassa et al. 2005). Oxygen isotopic stages (δ^{18}O curve for benthonic forams) according to Rabassa et al. (2005).

sediments assignable to the latest Pleistocene (MMP 4301); also, Lydekker (1894) illustrated a complete skull of this species, erroneously assigning it to *Neosclerocalyptus clarazianus*; regrettably, this material is currently missing. The latest Pleistocene is represented in Mar del Plata by Lobería Formation (of normal polarity and correlatable with La Postrera Formation of northeastern Buenos Aires), described by Kraglievich (1952), which crops out in the coastal cliffs of Mar del Plata and Miramar (Zanchetta 1995). It is important to remark that most of the palaeofauna known from

the late Pleistocene comes from the Guerrero Member of Luján Formation, and from the lower levels of La Postrera Formation (Prado et al. 2001). Recent dating of the Guerrero Member indicates that its sedimentation spanned an interval of between 21 and 10 ka, largely coincident with the LGM (Tonni et al. 2003).

In San Luis province there are two records assignable to this species. The first is from the area between the localities Merlo and Pasos Malos (32°21′ S, 65°02′ W) and was exhumed from Uspara Formation (MHN-UNSL-V 198). This unit shows clear predominance of loessic sediments assignable to the latest Pleistocene (Chiesa et al. 2000; Miño-Boilini et al. 2009). The second record is an almost complete specimen, reported by Chiesa et al. (2005) and found at the locality El Tala (MHN-UNSL V 487); it was exhumed from latest Pleistocene sediments, which mostly comprise fine sands and silts.

In Córdoba province there are two additional records (MBM-PV 112 and MBM-PV 113) from Córdoba city (31°24′ S, 64°10′ W), from Lujanian aeolian sediments belonging to the Upper Member of Río Primero Formation (see Santa Cruz 1972). The base of this unit was OSL dated, with a result close to 40,830 ± 3200 years (Sanabria et al. 1996). Another specimen comes from Despeñaderos locality (CORD-PZ 1734) and has been tentatively assigned to the Río Primero Formation (A. Tauber, personal communication to A.E.Z). Recently, two specimens (AGM 007 and AGM 006) were found in the San Francisco locality, (31°0.5′ S, 62°11′ W). The fauna associated with these two remains of Hoplophorinae Hoplophorini, particularly the Equidae *Equus* (*Amerhippus*) cf. *E.* (*A.*) *neogaeus*, allows an age restricted to the Lujanian s.s. to be inferred for the bearing sediments, and comprises Pampean–Patagonian taxa (Zurita et al. 2007). Lastly, MNH 04 was exhumed from loessic sediments assignable to the late Pleistocene of the locality Arroyito (see Iriondo 1999a). The mammals exhumed in these latter localities belong to the Tezanos Pinto Formation, whose loessic sediments were deposited during the LGM, OIS 2 (Iriondo 1996) between 36,000 and 8,000 years ago (see Kröhling and Orfeo 2002). Lastly, there is one record from the Lujanian of the locality Río III (MRFA 1009; 32°10′ S, 64°06′ W) (see Castellanos 1944).

At Santa Fe province, two records are known from Lujanian sediments. One corresponds to a poorly preserved skull (MFCA 901) found at the locality Puerto San Martín (32°42′ S, 60°42′ W); the second was found in the vicinity of the locality Granadero Baigorria, Santa Fe (32°51′ S, 60°42′ W). The latest Pleistocene of the greater part of central and southern Santa Fe province is represented, as mentioned above, by the Tezanos Pinto Formation, comprising basically aeolian silt deposited during the OIS2 (c. 35.8–17.6 ka) (Iriondo 1996, 1999b). According to Krohling and Iriondo (1999), the lower and upper members of this Unit were deposited during the LGM (36–15 ka) and the cold arid period spanning the latest Pleistocene–Holocene (14–8 ka) (see Kemp et al. 2004).

At least three records (Ctes-PZ 5878, Ctes-PZ 5879 and Ctes-PZ 5877) can be recognized for Chaco province, all from the locality Avia Terai (26°41′ S, 60°44′ W) (Zurita 2002) and exhumed from loessic sediments (see Iriondo 1988). These sediments are within the area of influence of the Bermejo river fluvial fan, and are probably part of what Iriondo (1980) formally named as Urundel Formation, deposited during the LGM, possibly between 36 and 8.5 ka (Iriondo 1999b). To date, all the palaeofauna exhumed in Chaco province corresponds to Pampean–Patagonian elements, with the absence of taxa of intertropical origin (see Zurita et al. 2004).

In Corrientes province there is one record from the Toropí-Yupoí Formation (Ctes-Pz 1677). Recent OSL dating has yielded ages between 50 and 35 ka (Tonni et al. 2005).

In Tucumán province, the scarce records are from the localities Tafí Viejo (LIL-PZ 4500; 26°44′ S, 65°15′ W) and San Miguel de Tucumán (LIL-PZ4500; 26°48′ S, 65°13′ W). These specimens were exhumed from sediments of aeolian origin belonging to Tucumán Formation (see Bonaparte and Bobovnikov 1974). In this province, the best known Lujanian sediments are basically represented by two units: Tafí del Valle Formation (27–18 ka) and Tucumán Formation (see Collantes et al. 1993; Sayago et al. 1998). These sediments, like those of the Pampean region, are formed by a complex of loess intercalated with palaeosols (Sayago et al. 1998), which also have the same mineralogical composition (Collantes et al. 1993).

Outside the current Argentinian territory, records of *Neosclerocalyptus* are very scarce, especially in the East sector of southern South America (Zurita 2007), and are somewhat more common in the central-north area (see Zurita et al. 2009).

The absence or scarcity of *Neosclerocalyptus* records in areas that are geographically close to Argentinian Mesopotamia, such as western Uruguay (Sopas Fm.), is remarkable (see Ubilla and Perea 1999). The Sopas Formation includes a "mixture" of taxa with different ecological requirements (e.g. *Tapirus terrestris* vs *Rhea americana*). Recent ^{14}C and OSL dating suggest a deposition lapse of between 58 and 43 ka, which is congruent with the palaeoenvironmental conditions established for certain lapses of OIS 3 (Ubilla et al. 2004). In this setting, the most frequent Cingulata Glyptodontidae are the genera *Glyptodon*, *Panochthus* and *Neuryurus*, an association very similar to that found in the Mesopotamian region. Consequently, the palaeofaunal similarities established between Argentinian Mesopotamia and western Uruguay could be explained by the partial synchrony established between both areas (see Carlini et al. 2008).

This notable absence of *Neosclerocalyptus* extends northwards, in the late Pleistocene (c. 120?–10 ka; Rosa et al. 2000) of southern Brazil (Rio Grande do Sul state) where a large proportion of the fossil outcroppings are associated with taxa that have relatively humid and warm requirements (e.g. *Stegomastodon waringi*, *Eremotherium*, *Holmesina*, *Tapirus*, *Neochoerus*) (see Oliveira 1992, 1996).

In other areas of South America, *Neosclerocalyptus* seems to be a little more frequent. There is a record of *Neosclerocalyptus*, dated at 7070 years before present from central Paraguay (Carlini and Scillato-Yané 1999), which also represents the youngest record for this taxon. In Bolivia, *Neosclerocalyptus* has been cited for the locality Santa Cruz de la Sierra (17°47′ S, 63°11′ W) (MNK-PAL–), representing the northernmost record for the genus (Ameghino 1889; Zurita et al. 2009). Surprisingly, no records of *Neosclerocalyptus* have been found in one of the richest Pleistocene fossil beds of Bolivia, the Tarija Valley where, in contrast, *Glyptodon* is highly abundant (Zurita et al. 2009).

Principal components analysis

The application of the Broken Stick model as a retention criterion resulted in retaining the first two principal components, which are used as axes to visualize the observations in a new Cartesian space. Table 2 presents the principal components extracted through PCA of the morphological data matrix. Figure 5 shows a biplot (*sensu* Gabriel 1971)

Table 2. Variance explained by the principal components (PC) extracted from the principal components analysis (PCA).

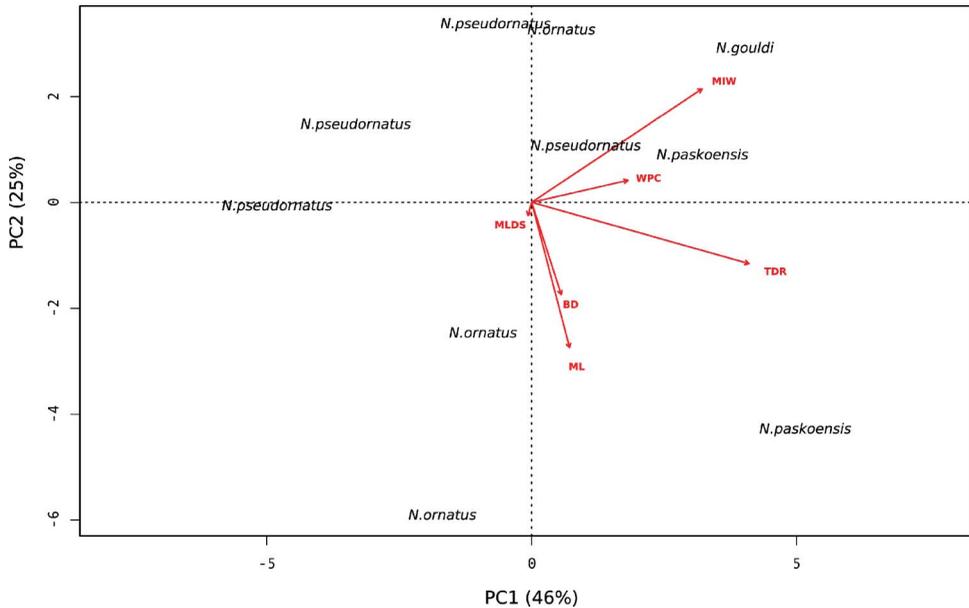|	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	21.24	15.52	11.69	9.9	6.58	1.94
Proportion of variance	0.46	0.25	0.14	0.1	0.04	0
Cumulative proportion (%)	46	71	85	95	99	100

Figure 5. Biplot of the principal components analysis.

of the observations in this new coordinate system and the vectors corresponding to each original variable.

It can be seen that a considerable portion of the data variance is explained by the first two principal components extracted from the analysis (71%).

Despite the scatter, one of the most outstanding features is the ordination of species along PC1 (46%), with *N. pseudornatus* and *N. ornatus* to negative values and *N. gouldi* and *N. paskoensis* at extreme positive ones. Furthermore, observation of the vectors for each variable clearly shows that the ones that most contribute to PC1 are MIW, TDR and WPC, namely "*Minimum interorbital width*", "*Transversal diameter of rostral area, taken at the vertical plane through the middle lobe of M3*", and "*Width of postorbital constriction*". All of these variables reflect different aspects of skull width and are positively correlated to PC1, whereas the variables BD and ML, namely "*Bizygomatic diameter*" and "*Maximum length*" load mainly on PC2 (25%). Remarkably, most of the measurements related to skull width contribute to PC1, whereas the variable "*Maximum length*" contributes to PC2. The vector representing the latter variable is almost orthogonal with respect to the variables that represent skull

Table 3. Matrix of variable loadings.

	PC1	PC2	PC3	PC4	PC5	PC6
ML	0.13	−0.67	−0.16	0.71	−0.07	−0.02
TDR	0.73	−0.28	−0.2	−0.48	−0.32	−0.09
MLDS	−0.01	−0.06	0.77	0.07	−0.6	0.21
WPC	0.32	0.1	−0.02	0.09	0.29	0.89
BD	0.1	−0.43	0.55	−0.24	0.65	−0.17
MID	0.58	0.52	0.22	0.45	0.14	−0.35

Notes: PC, principal component; ML, maximum length; TDR, transversal diameter of rostral area, at level of vertical plane passing through middle lobe of M3; MLDS, maximum length of dental series; WPC, width of postorbital constriction; BD, bizygomatic diameter; MIW, minimum interorbital width.

width, indicating a lower correlation of skull width with respect to its length. The variable loadings on each component are expressed in the rotation matrix or eigenvectors presented in Table 3.

Discussion

Palaeoclimatic aspects

From a palaeoclimatic perspective, at least 15 glacial–interglacial cycles have taken place in the last million years, especially since the Great Patagonian Glaciation (GPG, between OIS 30 and 34; c. 1.168–1.016 Ma, see Figure 4). Undoubtedly, the GPG had profound effects on the palaeofaunal composition of the Pampean region (more details in Rabassa et al. 2005; Soibelzon et al. 2008; Rabassa and Coronato 2009; Soibelzon and Tonni, 2009). According to Tonni, Cione et al. (1999), Rabassa et al. (2005) and Rabassa and Coronato (2009), the temperature of the Pampean region could have dropped by between 5 and 6°C during glacial periods. This cyclic climatic nature of the Quaternary had a profound impact on faunal and floral communities, allowing, among other things, the biostratigraphic recognition of the Ensenadan-Bonaerian-Lujanian Stages (Nabel et al. 2000).

The climatic conditions observed during the Ensenadan, which extended over a long interval (Lower–Middle Pleistocene; c. 1.8–0.4 Ma; Soibelzon, Tonni et al. 2008), were predominantly arid, and the numerous climatic–environmental changes affected the faunal composition and diversity of the region (Rabassa et al. 2005; Soibelzon and Tonni 2009). In this context, the earliest records of *Neosclerocalyptus* come from sediments of the "Toscas del Río de La Plata", which can be correlated with the Jaramillo event (see Soibelzon et al. 2008) and coincide with the maximum of the GPG (c. 1 Ma; see Figure 4). Morphologically, *N. pseudornatus* is characterized by an incipient degree of development and pneumatization of the fronto-nasal sinuses. Hence, an interesting correlation is observed between the appearance of this character and a cooling period represented by one of the largest glaciations of the Pleistocene (Rabassa et al. 2005).

Later on and during the last part of the Ensenadan (end of Matuyama Chron and beginning of Brunhes chron, c. 0.98–0.40 Ma, see Figure 4) *N. pseudornatus* is replaced by a different species, *N. ornatus*. This taxon is characterized by greater

pneumatization and lateral expansion of the fronto-nasal sinuses, which have a clear "funnel" shape. The palaeoclimatic–environmental evidence indicates that this interval coincides with a glacial period (see Tonni et al. 1999b; Nabel et al. 2000), which is in agreement with the palaeofaunal evidence (e.g. *Tympanoctomys cordubensis*; see Verzi et al. 2002). Moreover, Tonni et al. (1998) indicated that this could be associated with a cold global event that occurred in the interval 0.80–0.50 Ma, and with the Daniglacial event, fundamentally partly synchronic with the OIS 18–20 (Coronato et al. 2004).

During the Bonaerian (middle Pleistocene; 0.40–0.13 Ma, see Figure 4), the only species recorded is *N. gouldi*, which has, in comparison with previous forms, increased lateral expansion and pneumatization of its fronto-nasal sinuses. Although the Buenos Aires Formation shows clear alternation of loessic levels and palaeosols, the climate seems to have been mostly arid/semiarid and cold (Tonni et al. 1999; Rabassa et al. 2005). This is supported by sedimentological evidence (predominance of loessic sedimentation) and palaeofaunal evidence [taxa such as *Lestodelphis halli*, *Microcavia*, *Ctenomys*, *Zaedyus* and "*Chlamydophorustruncatus* (?) *fossilis*" (*Chlamyphorus* sp. indet.)] (see Tonni et al. 1999; Nabel et al. 2000). Unfortunately, the only record of this species is the holotype, for which there is no precise stratigraphic provenance within the Buenos Aires Formation (see Zurita et al. 2008).

The beginning of the late Pleistocene (Lujanian Stage) coincides with the maximum of the last interglacial (OIS 5e; c. 130–74 ka; Zachos et al. 2001). In present-day Argentinian territory, these sediments have been detected in some places. In the Pampean region, some authors have correlated La Chumbiada Member of Luján formation with a humid pulse of OIS 3 (c. 60 ka; Tonni, Cione et al. 1999), whereas others (e.g. Prado and Alberdi 1999) correlate it with OIS 5e, or alternatively, with a short warm humid period during the last glacial cycle (c. 30–25 ka; see Bonadonna et al. 1995). In southeastern Buenos Aires province (Pardiñas et al. 1996, 2004), there are no records of *Neosclerocalyptus*, while in the Mesopotamian region (central-western Entre Ríos province) the records of Glyptodontidae Hoplophorini (cf. *Neosclerocalyptus*) are very scarce (see Noriega et al. 2004; Noriega and Tonni 2007).

In Corrientes province, the abundant Pleistocene fauna exhumed is limited to the Arroyo Toropí (28°36′ S, 59°02′ W; Toropí and Yupoí formations) which, as in the previous case, includes taxa with intertropical affinities (e.g. Cingulata *Holmesina paulacoutoi*; Proboscidea *Stegomastodon waringi*) together with other "Pampean" taxa (see Carlini et al. 2008). Tonni et al. (2005) indicates that this sequence was deposited between 50 and 35 ka, in an interval synchronic with OIS 3. Although the climate of this period is complex, at least two warm events are evident (c. 60 ka and 33–28 ka) (Rabassa and Clapperton 1990; Iriondo 1999a; Ubilla, 2004; Rabassa et al. 2005), and these could explain the presence of intertropical taxa in these deposits (Carlini et al. 2008). *Neosclerocalyptus* is rare in this setting in which other Xenarthra Cingulata are common, in particular the genera *Panochthus* and *Glyptodon* (Carlini et al. 2008).

In extreme central-northern Argentina (Formosa province), the palaeofauna exhumed from the coastal cliffs of the Bermejo river (26°36′ S, 58°40′ W) shows, as in the previous cases, a predominance of "Pampean-Patagonian" taxa (with high frequency of *Glyptodon* records and very scarce Hoplophorinae Hoplophorini) with some intertropical forms such as *Holmesina paulacoutoi*. OSL dating indicates an approximate age of 58,160 years before present (± 4390) (OIS 3) for this sequence,

which implies that its deposition could be partly coincidental with a humid pulse (Zurita et al. 2009).

The scarce abundance of *Neosclerocalyptus* during OIS 3, contrasts markedly with it subsequent abundance, especially during OIS 2 (c. 28–8 ka). During OIS 2 (c. 28–10 ka), *N. paskoensis*, together with *Glyptodon*, is the most frequently recorded taxon in the Chacoan-Pampean area, from 17°47′ S, 38°10′ S. Its geographical distribution clearly coincides with the distribution of loess (see Bidegain et al. 2007), deposited mostly under the cold and arid conditions characteristic of OIS 2 (see Tonni et al. 1999; Prado et al. 2001; Cione et al. 2003, among others) (Figure 6). OIS 2 represents a predominantly cold and arid interval (Tonni, Cione et al. 1999), associated with the expansion of glaciers, and including the LGM (c. 25–16 ka; Rabassa et al. 2005). Concurrently with this environmental deterioration, *N. paskoensis* exhibits the maximum degree of development and pneumatization of fronto-nasal sinuses, which again suggests strong correlation between climatic variables and morphological changes.

To sum up, from a palaeoclimatic and palaeobiogeographic viewpoint, the geographical distribution of *Neosclerocalyptus* during the Pleistocene (especially during the late Pleistocene–early Holocene), supports the hypothesis originally proposed by Oliveira (1996) and Cartelle and Lessa (1988). These authors affirmed that, in the south of South America and northwards to the central north of the continent, the megafauna of the late Pleistocene was associated with mostly cold and arid climatic–environmental conditions, but that, from 22°S and eastwards, its distribution corresponded to warmer and more humid environments. Indeed, the distribution of *Neosclerocalyptus* during the maximum of the Last Glaciation agrees with Clapperton's (1993) palaeoenvironmental reconstruction. There is close correlation between its palaeobiogeography and the development of arid/semiarid open environments (Figure 6). During this interval *Neosclerocalyptus* reaches its greatest latitudinal distributional range, concurrently with the great development of open areas (see also Cione et al. 2003; Tonni and Noriega 2001).

Skull morphology and evolution: a coincidence with palaeoclimatic conditions

An interesting aspect of *Neosclerocalyptus* is its progressive morphological evolution (especially regarding the fronto-nasal sinuses). Quantitatively, multivariate visualization techniques, like PCA, suggest that there is an increase in skull width because of the progressive widening of the rostral area from *N. pseudornatus* through *N. ornatus* and *N. gouldi* to *N. paskoensis*. This is consistent with the possibility of recognizing these four species in an interval of c. 1.07–0.008 Ma, during which each species seems to replace the previous one (see Zurita 2007).This appears to be at odds with some hypotheses that claim that glacial–interglacial cycles may have left some kind of "signal" in the genome of species, but were not enough to trigger cladogenetic processes (see Bennet 1990, among others); however, there is also evidence that some mammalian taxa that persist in environments that impose strong selective pressures may undergo rapid morphological evolution (Lister 2004). It is important to remark that Krmpotic et al. (2009) have observed significant differences in the cavity and glandular hairs on the osteoderms of *Eutatus* (Cingulata) between species of early Pleistocene and late Pleistocene, a situation very possibly linked to Pleistocene environmental change.
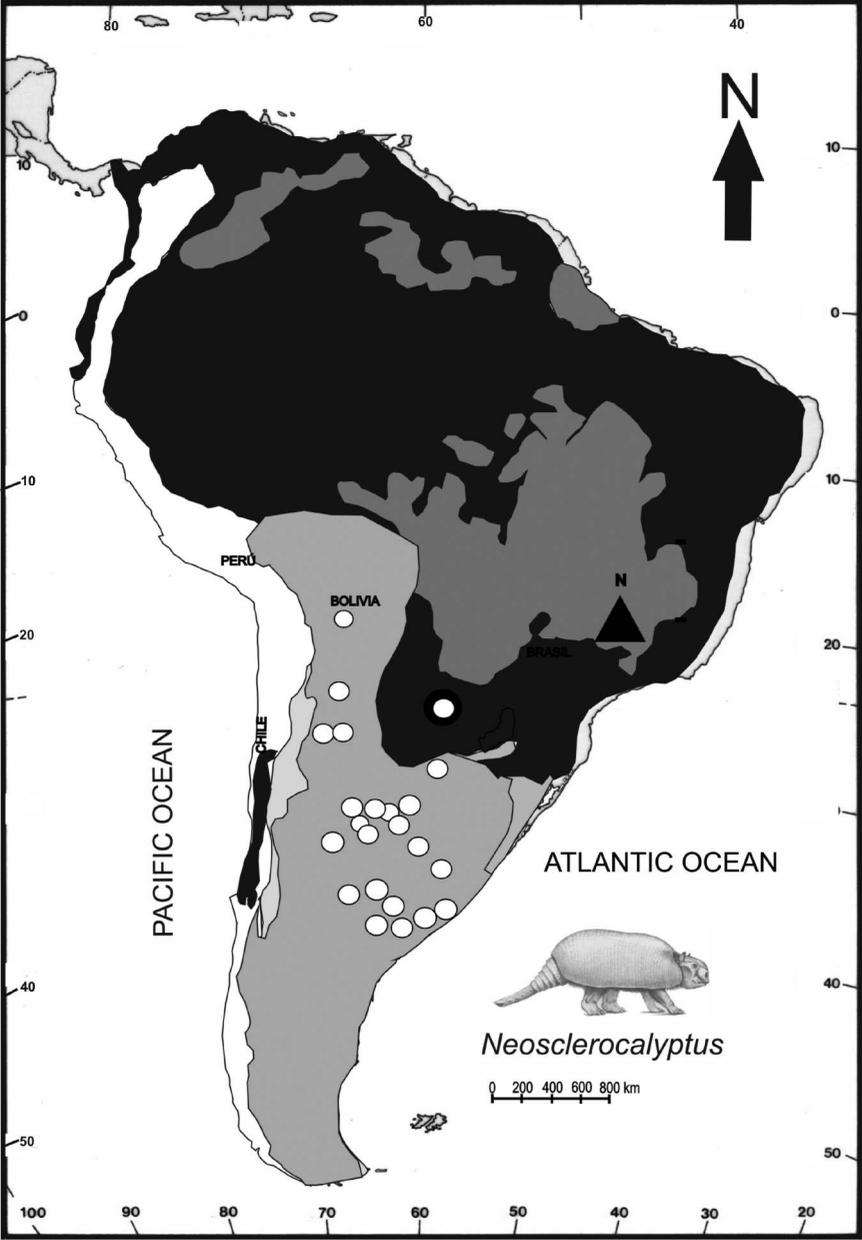
Figure 6. Geographical distribution of *Neosclerocalyptus* during Oxygen Isotopic Stage 2 (modified from Vivo and Carmignotto 2004).

In this sense, the restricted and peculiar latitudinal geographical range of *Neosclerocalyptus*, as well as the low continentality that characterized its distributional range, must be taken into account with regard to the rapid morphological evolution of this genus. As support for this hypothesis, it is worth highlighting that some Xenarthra (eg. Tardigrada: *Eremotherium*, *Valgipes*, *Catonyx*; Cingulata: *Holmesina*) that inhabited intertropical habitats during the Pleistocene tended to retain many primitive anatomical features (see Scillato-Yané et al. 2005; Carlini, Brandoni et al. 2006; Carlini, Scillato-Yané et al. 2006; Carlini, Zurita et al. 2008; Carlini, Brandoni et al. 2008). This phenomenon could be partly the result of the greater stability of intertropical environments and the low extinction rates that some authors have suggested for the mammals inhabiting those latitudes (Lister 2004).

Evidence such as the limited latitudinal distribution of the genus and the replacement of one species by another suggests the existence of a single successive lineage of species (see Barnosky 1987, 2005). This hypothesis has been also advanced for other Xenarthra (e.g. *Thalassocnus*; see De Muizon et al. 2003) which show some common evolutionary features with this Glyptodontidae clade. Nevertheless, a more complex evolutionary pattern cannot be dismissed.

Conclusions

The evidence available so far indicates that *Neosclerocalyptus* is as an endemic taxon (at a regional scale) for southern South America. Its latitudinal range extends from 17°47′ S, 63°11′ W (Santa Cruz de la Sierra, Bolivia) to 38°10′ S, 58°46′ W (Lobería, Buenos Aires province, Argentina).

Among the Pleistocene glyptodontids, the genus *Neosclerocalyptus* could be correlated with the cold arid Pleistocene cycles. This genus is scarce or absent in outcroppings that show evidence of relatively warmer and more humid climates, with "mixtures" of "Brazilic" and Pampean-Patagonian taxa (OIS 5e, OIS 3: Mesopotamia, southern Brazil, western Uruguay, La Chumbiada Member of Luján Fm.). During the last glacial cycle (c. 28–10 ka; OIS 2) *Neosclerocalyptus* is the Glyptodontidae with the highest frequency of records, together with *Glyptodon* and *Panochthus*. Its geographical distribution clearly agrees with the loessic sedimentation of southern South America and with the palaeoenvironmental reconstruction proposed by Clapperton (1993) for the LGM.

In this setting, the morphological evolution of *Neosclerocalyptus* is surprisingly fast: *Neosclerocalyptus pseudornatus* is restricted to the "Toscas del Río de La Plata" (c. 1.07–0.98 Ma); *N. ornatus* seems to be restricted to the top of Matuyama(c. 0.98–0.40 Ma), while *N. gouldi* is limited to the Bonaerian Stage (middle Pleistocene; c. 0.40–0.13 Ma). In turn, the records of *N. paskoensis* with reliable stratigraphic provenance are mostly limited to OIS 2 (c. 28–10 ka) of the Lujanian Stage.

This morphological evolution (especially regarding its fronto-nasal sinuses) could have been linked to its particular and limited latitudinal distribution and to the low continentality of its distribution range, which makes this territory very sensitive to the climatic–environmental fluctuations of the Pleistocene, subjecting the populations to selective pressures. On the contrary, evidence indicates that some intertropical xenarthran forms (e. g. *Eremotherium*, *Valgipes*, *Catonyx*) tended to retain more primitive characters.

One of the most evident autapomorphies of the genus is the progressive pneumatization and lateral expansion of the fronto-nasal sinuses. The appearance of this character is synchronic with the Great Patagonian Glaciation (OIS 30–34; c. 168–1.016 Ma). The greatest development of this structure occurs in *N. paskoensis*, widely distributed in loessic sediments of OIS 2, coincident with a marked climatic–environmental deterioration. In agreement with this, the use of multivariate visualization techniques (PCA), based on linear morphological variables, shows a progressive widening of the skull at the fronto-nasal region.

The restricted geographical range of this taxon, the possible absence of barriers during the Pleistocene (which would favour vicariance processes), and the absence of cases of sympatry, suggest the existence of a single continuous lineage of species. This hypothesis has been advanced for other xenarthrans (e.g. *Thalassocnus*; De Muizon et al. 2003).

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