THE OCCIPITAL REGION OF LATE PLEISTOCENE MYLODONTIDAE OF ARGENTINA

Luciano BRAMBILLA & Damián A. IBARRA

Boletín del Instituto de Fisiografía y Geología

Brambilla L. & Ibarra D.A., 2018. The occipital region of late Pleistocene Mylodontidae of Argentina. *Boletín del Instituto de Fisiografía y Geología* 88: 1-9. Rosario, 15-11-2018. ISSN 1666-115X.

Received 04/09/2018
Accepted 10/11/2018
Available online 15/11/2018

Editor
H. Parent

Abstract. In deposits of the late Pleistocene of Argentina the remains of ground sloths (Xenarthra, Folivora) are frequently represented by crania in which only the posterior region is preserved. In this work we characterize the occipital region of late Pleistocene Mylodontidae to allow a taxonomic identification of fragmentary specimens of *Lestodon armatus*, *Mylodon darwinii*, *Glossotherium robustum* and *Scelidotherium leptocephalum*. The available juvenile specimens were also included in this study and the ontogenetic shape changes are described. Additionally, the signs in the occipital region that allow the identification of juvenile specimens are discussed. The mylodontids *G. robustum* and *M. darwinii* have a significant variability in the occipital region which could be explained by sexual differences, or well as a result of palaeoenvironmental changes that took place during the Lujanian.

Keywords: Xenarthra ▪ Mylodontidae ▪ Ground Sloths ▪ Pleistocene ▪ South America

Resumen. ***La región occipital de los Mylodontidae del Pleistoceno tardío de Argentina.*** En los depósitos del Pleistoceno tardío de Argentina son frecuentes los perezosos terrestres (Xenarthra, Folivora) representados por cráneos de los que solo se preserva la región occipital. En este trabajo caracterizamos la región occipital de Mylodontinae del Pleistoceno tardío lo cual permitiría una identificación taxonómica de los restos de *Lestodon armatus*, *Mylodon darwinii*, *Glossotherium robustum*, y *Scelidotherium leptocephalum*. Los ejemplares juveniles fueron contemplados en este trabajo y se describen algunos cambios morfológicos ocurridos durante el desarrollo. Los signos en la región occipital que permiten identificar ejemplares juveniles son discutidos. En *G. robustum* y *M. darwinii* se destaca una significativa variabilidad en la región occipital que podría ser explicada por diferencias entre sexos o bien como el resultado de los cambios paleoambientales que tuvieron lugar durante el Lujanense.

Palabras clave: Xenarthra ▪ Mylodontidae ▪ Perezosos Terrestres ▪ Pleistoceno ▪ Sudamérica

L. Brambilla [lbrambilla@fbioyf.unr.edu.ar]: Facultad de Ciencias Bioquímicas y Farmacéuticas, Universidad Nacional de Rosario, Suipacha 531, 2000 Rosario, Argentina & Facultad de Ciencias Exactas, Ingeniería y Agrimensura, UNR, Pellegrini 250, 2000 Rosario, Argentina.

D.A. Ibarra: Facultad de Ciencias Bioquímicas y Farmacéuticas, Universidad Nacional de Rosario, Suipacha 531, 2000 Rosario, Argentina.

INTRODUCTION

The Mylodontidae were the most diverse group of ground sloths during the Pleistocene in Argentina (Esteban 1996, Deschamp et al. 2014), including representatives of the subfamily Mylodontinae such as *Mylodon darwinii* Owen, 1839, *Glossotherium robustum* (Owen, 1842) and *Lestodon armatus* Gervais, 1855, and the subfamily Scelidotheriinae such as *Scelidotherium leptocephalum* Owen, 1839 and *Catonyx tarijensis* (Gervais & Ameghino, 1880). Although there are Ensenadan records of these genera (Soibelzon et al. 2008, 2010), most records come from the late Pleistocene. The intraspecific variation observed in the cranium of the Mylodontidae is significant and has been addressed in previous studies (Esteban 1996, Brandoni et al. 2010, Czerwonogora & Fariña 2012, Miño-Boilini & Zurita 2015). However, the shape of the occipital region and its morphological variation have not been considered in detail. In a large number of cases the crania are represented by a posterior portion only, therefore, it is necessary to establish a detailed morphological description in order to obtain precise taxonomic identifications.

In this paper the ontogenetic, intraspecific and interspecific variations of the occipital region of the Mylodontidae are characterized.

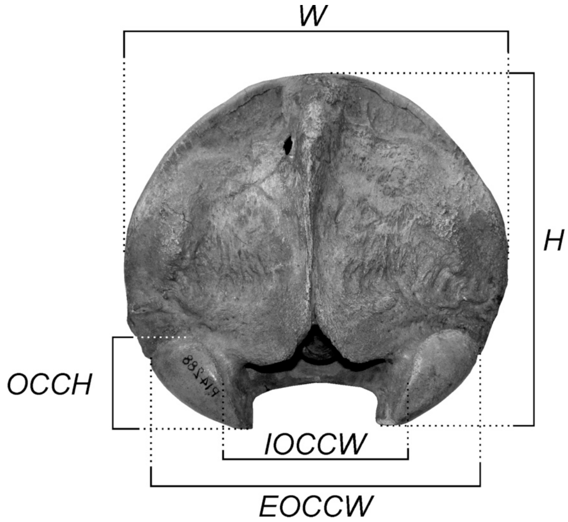

Figure 1. Measurements obtained from the occipital region (*Mylodon darwinii* FMNH-P14288). *H*: maximum height, *W*: maximum width, *EOCCW*: external occipital condyles width, *IOCCW*: internal occipital condyles width, *OCCH*: occipital condyle height.

SYSTEMATIC PALAEONTOLOGY

Anatomical abbreviations. fm: foramen magnum, exo: exoccipital, oc: occipital, occ: occipital condyle, occr: occipital crest.

Measurements (Fig. 1). *H*: maximum height, *W*: maximum width, *EOCCW*: external occipital condyles width, *IOCCW*: internal occipital condyles width, *OCCH*: occipital condyle height. *M1-cond*: distance measured from the anterior edge of the first maxillary molariform (M1) to the posterior edge of the occipital condyles. *M1-cond* is used as an estimator of the length of the cranium to include specimens that do not preserve the premaxilla or the anterior margin of the maxilla (Brambilla & Ibarra 2018). Mean, sample size (*n*), standard deviation and percent coefficient of variation (*CV* %) are computed from adults specimens and for species with at least three adult specimens. The specimens of Ensenadan age (Middle Pleistocene) are not included in the measurements, they are considered to refer to ontogenetic patterns and morphological considerations over time in the Scelidotheriinae.

Chronostratigraphy. The chronostratigraphic and biostratigraphic pampean schemes of Cione and Tonni (2005) are followed.

Institutional abbreviations. FMNH: Field Museum of Natural History (Chicago, USA); MACN-Pv: Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciudad Autónoma de Buenos Aires, Argentina); MARC: Museo y Archivo Regional de Castelli (Castelli, Buenos Aires, Argentina); MCA: Museo Municipal de Ciencias Naturales "Carlos Ameghino" (Mercedes, Buenos Aires, Argentina); MCL: Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (Belo Horizonte, Brasil); MCNP: Museo Municipal de Ciencias Naturales "Pachamana"; MLF: Museo de Ciencias Naturales "Florentino Ameghino" (Las Flores, Buenos Aires, Argentina); MLP: División Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata (La Plata, Buenos Aires, Argentina); MLS: Museo Legado del Salado (Junín, Buenos Aires, Argentina); MMCIPAS: Museo Municipal Centro de Investigaciones Paleontológicas y Arqueológicas de Salto "José Fernando Bonaparte" (Salto, Argentina); MPAHND: Museo Particular de Antropología e Historia Natural "Los Desmochados" (Casilda, Santa Fe, Argentina); MPLK: Museo de Ciencias Naturales "Lucas Kraglievich"(Marcos Paz, Argentina); MRS: Museo del Río Salado (Santa Fe, Argentina); MTZ: Museo Histórico Paleontológico "Tito Zuddas" (Andino, Santa Fe, Argentina).

Material. *Catonyx tarijensis*: MACN-Pv-994, MACN-Pv-995; *Glossotherium robustum*: MLF-420, MLF-442, MLS-68, MACN-Pv-11769, MCA-sala, MCA-2014, MRS-75, MLP-3-136, MPAHND-9, MPLK-w/o-n, MARC-15675.a.2/244, MTZ-12; *Lestodon armatus*: MACN-Pv-2323, MACN-Pv-10830, MACN-Pv-11687; *Mylodon darwinii*: MACN-Pv-14155, MLF-454, FMNH-P14288, MLP-36-VIII-12-1, MLP-3-122, MRS-74, MMCIPAS-B50-2458, MLP-54-III-8-1; *Scelidotherium leptocephalum*: MCNP-367, MACN-Pv-8633, MACN-Pv-13880, MACN-Pv-9625, MACN-Pv-13883.

Order Pilosa Flower, 1883
Suborder Folivora Delsuc, Catzeflis, Stanhope & Douzery, 2001
Family Mylodontidae Gill, 1872
Subfamily Mylodontinae Gill, 1872

Genus *Mylodon* Owen, 1839
Type species: *Mylodon darwinii* Owen, 1839

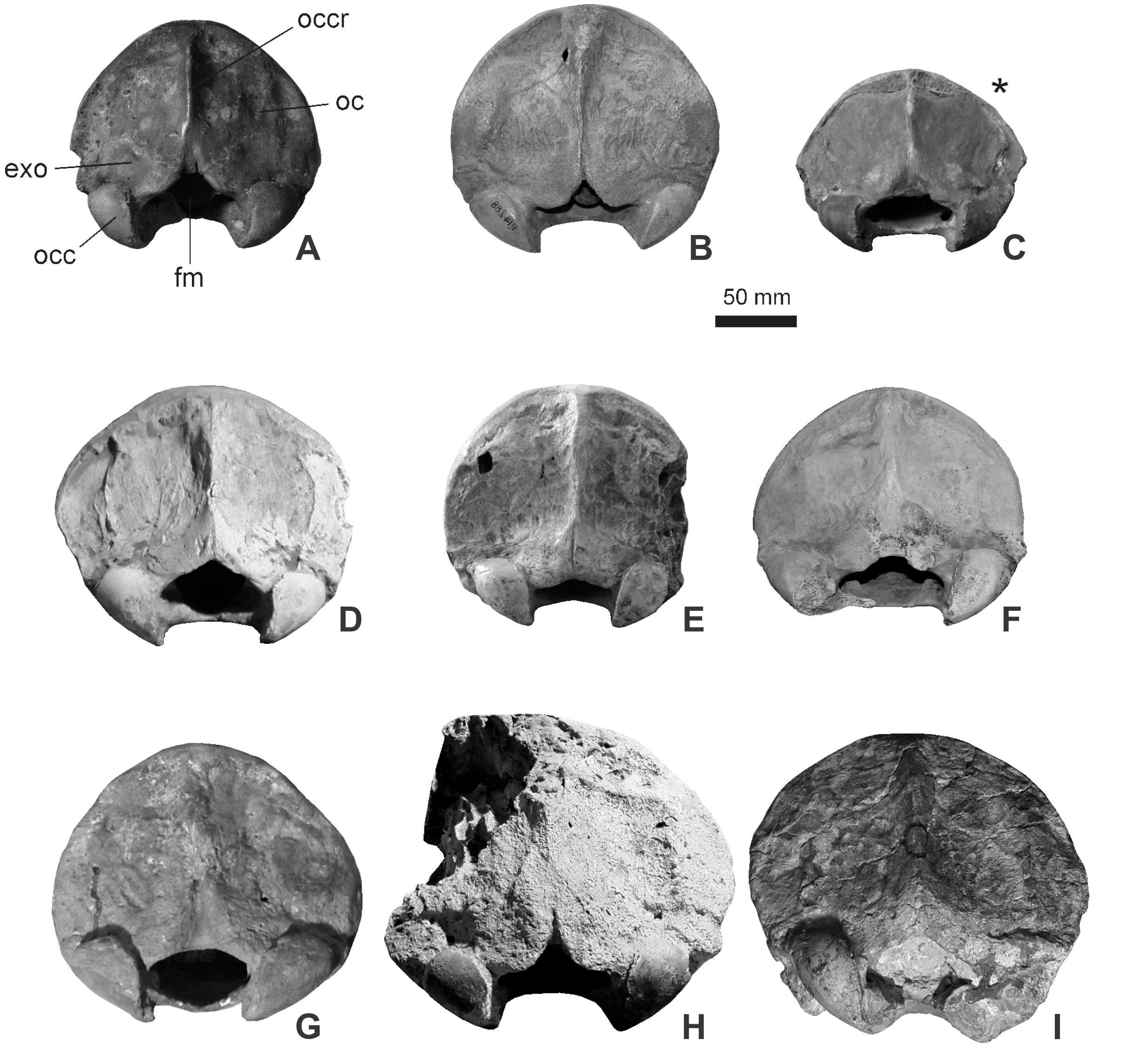

Figure 2. Occipital region of *Mylodon darwinii*. **A**: MACN-Pv-14155. **B**: FMNH-P14288. **C**: MTZ-6. **D**: MLP-54-III-8-1. **E**: MMCIPAS-B-50-2458. **F**: MLF-454. **G**: MLP-36-VIII-12-1. **H**: MRS-74. **I**: MLP-3-122. – All reduced x0.23. Subadult specimen marked with an asterisk.

Figure 3. Occipital region of *Lestodon armatus.* **A**: MACN-Pv-11687. **B**: MACN-Pv-2323. **C**: MACN-Pv-10163. – All reduced x0.23. Juvenil specimen marked with asterisk.

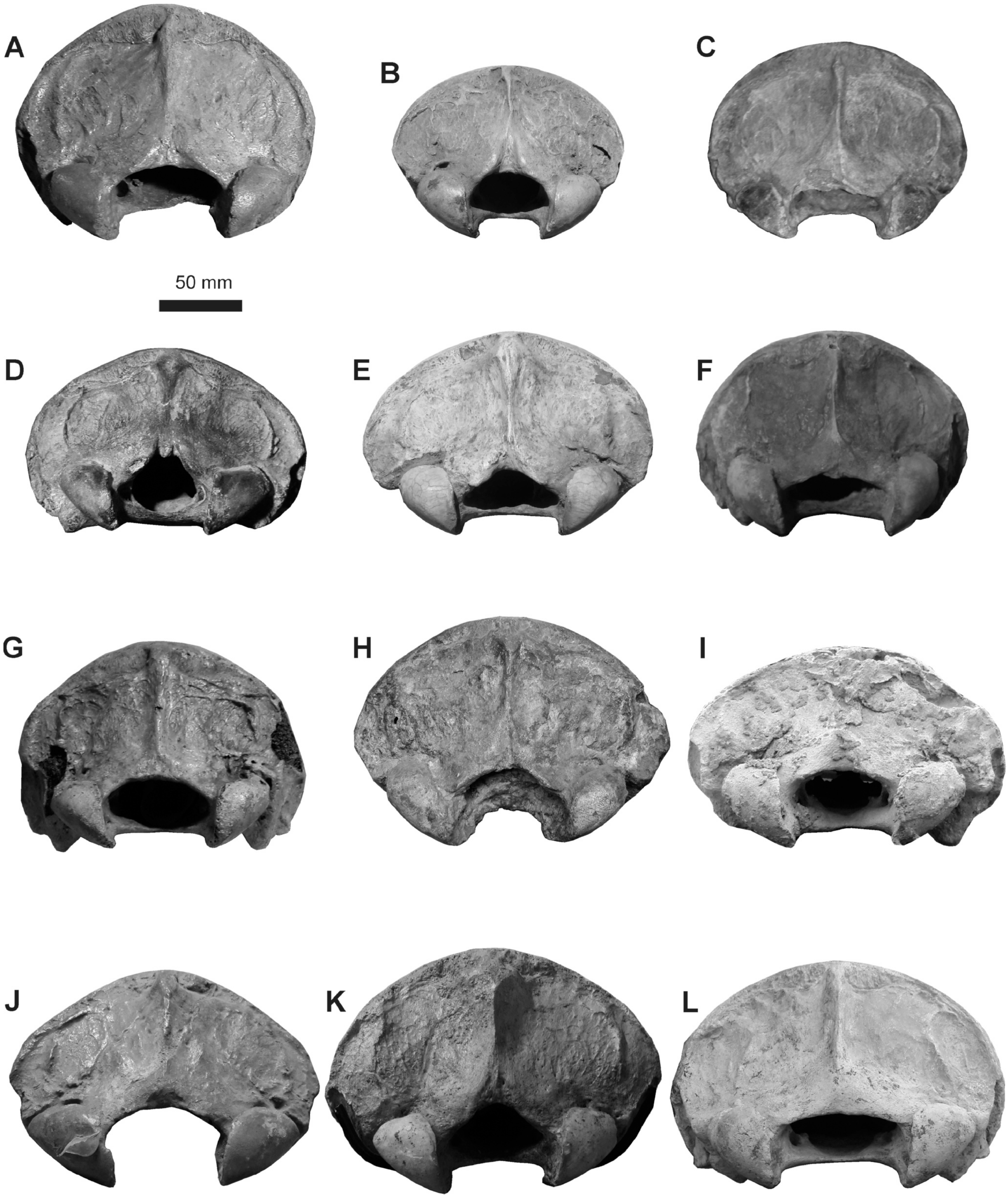

Figure 4. Occipital region of *Glossotherium robustum.* **A**: MACN-Pv-11769. **B**: MLF-420. **C**: MTZ-12. **D**: MRS 75. **E**: MLF-442. **F**: MARC-15675.a.2/244. **G**: MLP-3-136. **H**: MPAHND-9. **I**: MLS-68. **J**: MCA-sala. **K**: MCA 2014. **L**: MPLK-w/o-n. – All reduced x0.28.

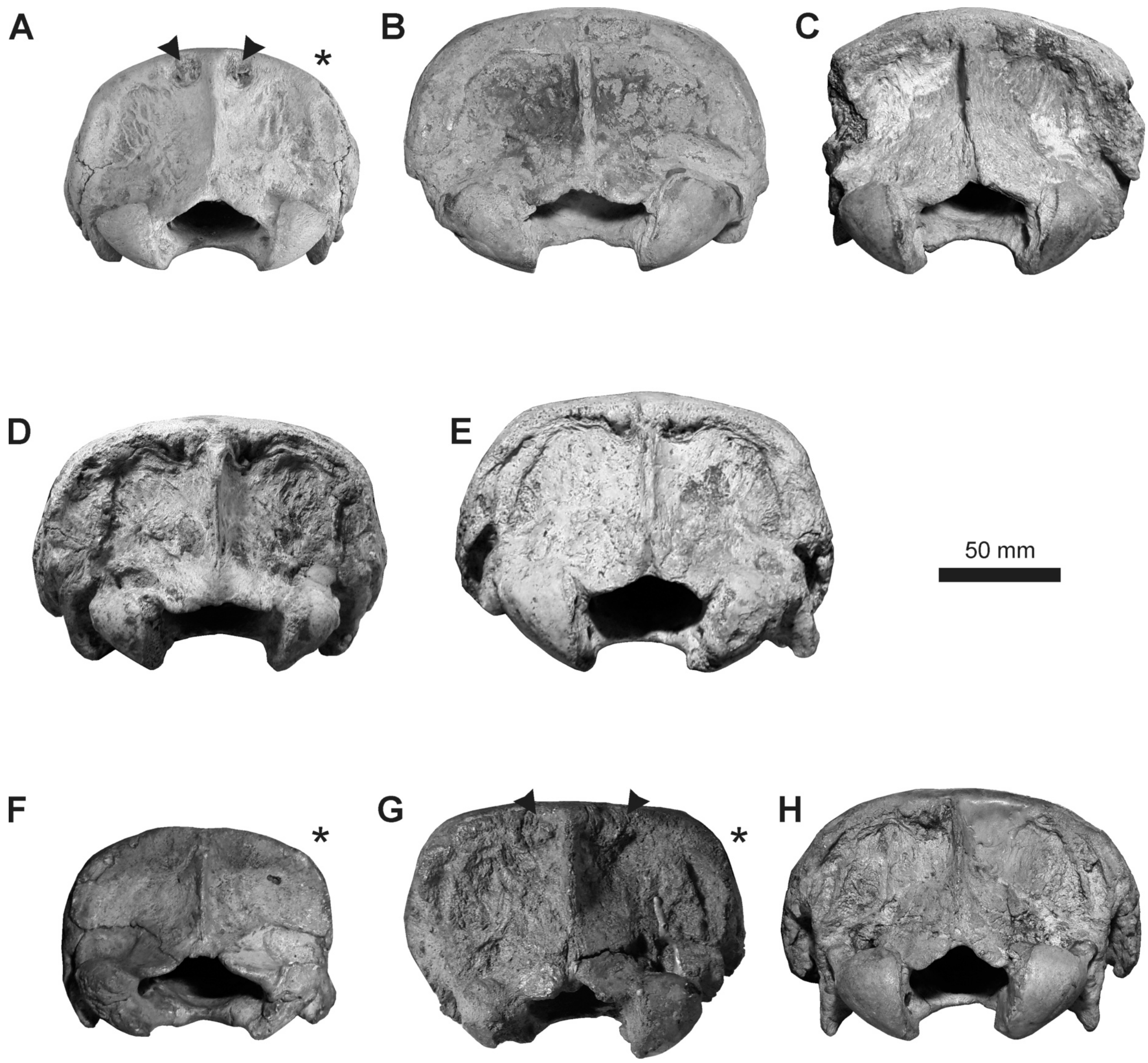

Figure 5. Occipital region of Scelidotheriinae. **A-E**: *Scelidotherium leptocephalum*. **A**: MCNP-367. **B**: MACN-Pv-8633. **C**: MACN-Pv-13880. **D**: MACN-Pv-9625. **E**: MACN-Pv-13883. **F-G**: *Catonyx tarijensis*. **F**: MACN-Pv-994. **G**: MACN-Pv-995. – All reduced x0.33. Juvenil and subadult specimens marked with asterisks. Arrow heads point the incomplete formation of the lamboidal ridge in subadult specimens.

***Mylodon darwinii* Owen, 1839**
Fig. 2

Description. The contour of the occipital region is almost circular, smaller than *L. armatus* if the adult stages are compared. The condyles are subtriangular, with its major axis oriented oblique and sometimes almost in dorsoventral direction. These reach 25-30% of the height of the occipital region. The size of the condyles in relation to the occipital area is smaller than in *L. armatus* and *G. robustum*. The occipital crest originates from a v-shaped groove near the foramen magnum in most of the specimens, even in the subadult MTZ-6 (Fig. 2C).

Genus *Lestodon* Gervais, 1855
Type species: *Lestodon armatus* Gervais, 1855

***Lestodon armatus* Gervais, 1855**
Fig. 3

Description. The occipital region is more expanded dorsoventrally than *G. robustum* and it has trapezoidal contour in the adult specimens while only in the juvenile specimen is depressed (Fig. 3A). The occipital condyles are large, prominent and expanded dorsoventrally. It differs from the occipital region of *M. darwinii* by the larger size of the occipital condyles. The occipital crest starts in the foramen magnum forming a nuchal tubercle or a v-shaped groove and extends to the dorsal edge of the occipital.

Genus *Glossotherium* Owen, 1839
Type species: *Glossotherium robustum* (Owen, 1842)

***Glossotherium robustum* (Owen, 1842)**
Fig. 4

Table 1. Measurements from occipital region in Mylodontidae from the late Pleistocene (all in millimeters). Abbreviations (see Fig. 1): *H*: maximum height, *W*: maximum width, *EOCCW*: external occipital condyles width, *IOCCW*: internal occipital condyles width, *OCCH*: occipital condyle height. Values estimated by symmetry marked with an asterisk.

	W	*H*	*EOCCW*	*IOCCW*	*OCCH*	*M1-cond*
Mylodon darwinii						
MTZ-6 (subadult)	140	112	113	65	35	-
MACN-Pv-14155	154	140	130	74	41	-
FMNH-P14288	164	151	140	79	40	536
MMCIPAS-B-50-2458	162*	147	119	56	42	444
MLF-454	166	147	149	74*	47	423
MLP-3-122	212	187	148*	60*	64	498
MLP-54-III-8-1	202*	161	144	75	50	-
MLP-36-VIII-12-1	189	171	162	69	54	505
MRS-74	226*	192	164	82	50	510
Mean (adults only)	184 (n = 8)	162 (n = 8)	145 (n = 8)	71 (n = 8)	49 (n = 8)	486 (n = 6)
Standard deviation	27	20	15	9	8	43
CV%	15	12	10	13	16	9
Glossotherium robustum						
MACN-Pv-11769	180	142	146	76	46	385
MLF-420	137	102	111	51	40	382
MTZ-12	155	119	125	64	34	-
MRS-75	166	110	127	53	44	364
MLF-442	175	123	134	68	43	399
MARC-15675.a.2/244	164	124	130	68	50	385
MLP-3-136	168	121	128	66	43	368
MPAHND-9	191	139	146	69	54	418
MLS-68	187	123	148	68	51	-
MCA-sala	188	132	164	70	50	-
MCA-2014	200	149	150	75	47	374
MPLK-w/o-n	198	138	163	84	49	-
Mean	176 (n = 12)	127 (n = 12)	139 (n = 12)	68 (n = 12)	46 (n = 12)	384 (n = 8)
Standard deviation	13	10	14	6	4	20
CV%	11	11	12	13	12	5
Lestodon armatus						
MACN-Pv-11687 (juvenile)	171	125	143	73	45	374
MACN-Pv-2323	201	175	158	78	67	-
MACN-Pv-10163	228*	116	192*	97*	74	-
Scelidotherium leptocephalum						
MCNP-367 (subadult)	122	92	95	50	28	-
MACN-8633	149	110	124	55	40	-
MACN-13880	144*	111	110	58	39	392
MACN-9625	144	104	103	58	32	394
MACN-13883	155	115	119	59	46	373
Mean (adults only)	148 (n = 4)	110 (n = 4)	114 (n = 4)	58 (n = 4)	39 (n = 4)	386 (n = 3)
Standard deviation	5	5	9	2	6	12
CV%	4	4	8	3	15	3

Description. The occipital region of *G. robustum* is always dorsoventrally depressed, allowing a clear distinction from *M. darwinii* and *L. armatus*. The condyles are subtriangular from posterior view, more laterally expanded than dorsoventrally in most of the specimens.

Subfamily Scelidotheriinae Ameghino, 1904

Genus *Scelidotherium* Owen, 1839

Type species: *Scelidotherium leptocephalum* Owen, 1839

Scelidotherium leptocephalum Owen, 1839

Fig. 5

Description and remarks. The posterior view of the cranium shows an occipital region with rectangular contour. This is due to the straight lateral edges and the dorsal border more flattened than in Mylodontinae (Fig. 5). The occipital condyles extend mainly dorsoventrally than laterally, with the exception of the specimen MACN-Pv-8633 (Fig. 5B). A distinct lambdoidal crest is present in the dorsal region in adult specimens.

The rectangular contour of the occipital region is also observed in Scelidotheiinae of Ensenadan age, such as *Scelidotherium* sp. MACN-Pv-8678 (Fig. 5H) and *Catonyx tarijensis* MACN-Pv-995 (Fig. 5F) and MACN-Pv-994 (Fig. 5G).

Measurements of occipital region

All the measurements of the occipital region of *G. robustum* and *M. darwinii* show greater variability than the estimator of length of the cranium (*M1-cond*). Crania with similar *M1-cond* possess occipital regions of varied sizes in both species (Table 1). Maximum width and maximum height are the main variables that describe the size of the occipital region. In both species these are distributed over a wide range that give rise to occipitals of variable sizes (Fig. 6). *Scelidotherium leptocephalum* has lower variability in the occipital region compared to the Mylodontinae.

DISCUSSION

In *M. darwinii* and *L. armatus* the occipital region of the adults is dorsoventrally expanded and remarkably rounded in *M. darwinii*. The large size in the dorsoventral axis and posterior projection of the occipital condyle allows a clear identification of *L. armatus*.

An elliptical, depressed occipital region is present invariably in the studied specimens of late Pleistocene *G. robustum* of the Pampean region, and we consider it as a distinctive character of this species regardless the size of the specimens (Fig. 4). This condition is present since the Pliocene in *Glossotherium chapadmalense* Kraglievich, 1925 but not in some *Glossotherium* from Brazil (e.g. MCL-4303/01; see Pitana et al. 2013) or in *Glossotherium tropicorum* Hoffstetter, 1952 which have subcircular occipitals. The latter could provide evidence on the diversification of *Glossotherium* outside the Pampean region and the restriction of *G. robustum* to southernmost South America.

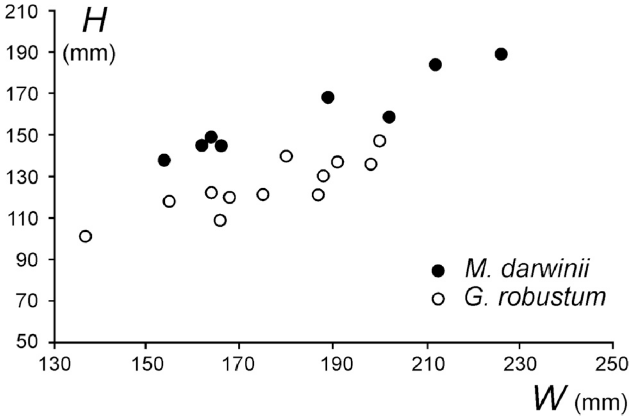

Figure 6. Scatterplot of occipital maximum width (*W*) versus maximum height (*H*) of *Mylodon darwinii* (full circles) and *Glossotherium robustum* (open circles).

The subrectangular shape of the occipital region of *S. leptocephalum* clearly differs from the occipital region of the Mylodontinae. In *S. leptocephalum* the occipital crest extends from the dorsal edge of the occipital and becomes more diffuse towards the foramen magnum due to a bulging of the peripheral region of the foramen magnum. On the other hand, in the Mylodontinae the occipital crest extends from the nuchal line, ending near the foramen magnum in a v-shaped fossa or a slight bulge of the dorsal region of the foramen magnum.

Remarks on the ontogeny in Mylodontidae. The relative height of the occipital region in *M. darwinii* and *L. armatus* increases towards the adult stage. The contour of the occiput and proportions of the occipital of the juvenile *L. armatus* MACN-Pv-11687 (Fig. 3A) and the subadult *M. darwinii* MTZ-6 (Fig. 2C) resemble those of adult *G. robustum*. For this reason the degree of ontogenetic development must be carefully considered when analyzing the shape of the occipital region in taxonomic determinations of Mylodontinae.

Although present specimens of *C. tarijensis* MACN-Pv-995 and MACN-Pv-994 (Fig. 5F-G) come from the Ensenada Formation (Middle Pleistocene; Tonni, Nabel et al. 1999) they add significant observations on the ontogenetic changes of the Scelidotheriinae. The specimens of *C. tarijensis* MACN-Pv-995 and MACN-Pv-994 have not reached the adult stage. The juvenile MACN-Pv-995 has smaller size, visible sutures, rounded and soft surfaces and porous occipital condyles due to the lack of ossification of the surface.

From the specimens of *L. armatus* MACN-Pv-11687 (Fig. 3A) and *C. tarijensis* MACN-Pv-995 (Fig. 5F) is possible to observe that the occipital condyles are not completely ossified when the specimen is still juvenile. In both cases, the occipital condyles are more ossified in the base attached to the exoccipital bone, while the cartilages are located in the surface of the condyles as can be judged by the presence of compact tissue under formation (Fig. 3A, 5F).

In the crania of *S. leptocephalum* MCNP-367 (Fig. 5A), *M. darwinii* MTZ-6 (Fig. 2C) and *C. tarijensis* MACN-Pv-994 (Fig. 5G) the lack of ossification in the nuchal crest is observed. The ossification of this region would have occurred after the complete ossification of the surface of the occipital condyles judging by the complete ossification of the occipital condyle of these specimens.

In juveniles the occipital crest is not marked, it is sinuous or irregular and its contact with the foramen magnum is diffuse. These characteristics also could be taken into account to determine the relative state of development of the specimens in which only the occipital region is preserved.

Intraspecific variation. The occipital region of *G. robustum* and *M. darwinii* have very different sizes among adult specimens (Figs. 2, 4, 6). In both species, all measurements from the occipital region have higher coefficients of variation than cranium length *M1-cond* (Table 1). This can be observed comparing the occipital region of the MLF-420 (Fig. 4B) and MACN-Pv-11769 (Fig. 4A) or MCA-2014 (Fig. 4K) which, despite having a comparable cranial length, they have very different dimensions in the occipital region. On the contrary, *S. leptocephalum* has less variable occipitals than the Mylodontinae, judging from the coefficients of variation (Table 1). Only the occipital condyle height *H* is as variable in *S. leptocephalum* as in *G. robustum* and *M. darwinii*.

The climatic and ecological oscillations during the Lujanian age (Tonni, Cione et al. 1999, Toledo 2011, Martinez et al. 2016) could have led to adaptive changes manifested in the cranial morphology of *G. robustum* and *M. darwinii*. Additionally, differences between sexes could contribute to the variation observed in the population. Nevertheless, these possibilities can not be evaluated here because the specimens used in this study come from localities with sediments of Lujanian age, but with no precise stratigraphic position. For this reason, it is not possible to order the specimens in temporal succession for correlating the observed variation with the climatic changes that occurred during the Lujanian age. Likewise, time-averaged samples (Hunt 2004) could prevent the discrimination between sexes since overlapping of populations of different ages would produce extended ranges of the variables, masking a bimodal distribution.

The differences observed between individuals in the development of the occipital region and consequently in the posterior region of the cranium could have impact on the internal morphology of the cranium of *G. robustum* and *M. darwinii*, an issue that could be evaluated from the analysis of the crania with extreme morphologies shown here.

CONCLUSION

The species of Mylodontinae can be clearly identified by the circular or elliptical shape of the occipital while the Scelidotheriinae are characterized by a subrectangular occipital.

Within the Mylodontinae the three late Pleistocene *L. armatus*, *M. darwinii* and *G. robustum* can be differentiated by the shape of the contour of the occipital region, and relative size and shape of the occipital condyles.

The absence of complete ossification of the surface of the occipital condyles is a clear sign of juvenil stages. This characteristic and the lack of preservation of the nuchal crests can be taken as signs of immaturity in specimens that do not preserve the anterior region of the cranium.

The variability observed in the occipital region of *S. leptocephalum* is low and contrasts with the significantly wide variability exhibited by the occipital region of *G. robustum* and *M. darwinii*. In light of the present results, a modular development is proposed between the anterior and the occipital regions of the cranium in *G. robustum* and *M. darwinii*.

The differences in size of the occipital region of adult specimens of *G. robustum* and *M. darwinii* are remarkable. The origin of this variability could be evaluated from collections with stratigraphic control.

Acknowledgments. We thank J.M. Marchetto and J.I. Zuccari (MLS), O.E. Vike (MPLK), H. Crispiani and E. Milicich (MLF), E. Aguirre (MPAHND), G. Acuña and H. Arsani (MCA), Y. Matos (MARC), J.L. Ramírez (MMCIPAS), M. Sioli (MRS), M. Reguero (MLP) and A.A. Kramarz (MACN), R.D. Scian and P.C. Straccia (MCNP) for facilitating access to collections of their institutions. R.K. McAfee for providing photographs of specimen FMNH P14288. M. Hidalgo, S. Bidart and staff of Biblioteca Florentino Ameghino (MLP) for providing relevant literature. The editor H. Parent contributed in many ways. The comments of Diego Brandoni (CICYTTP, Diamante, Argentina) and a further anonymous reviewer improved the manuscript of this article.

REFERENCES

Ameghino F., 1904. Nuevas especies de Mamíferos Cretáceos y Terciarios de la República Argentina. – *Anales de la Sociedad Científica Argentina* **58**: 131-137.

Brambilla L. & Ibarra D.A., 2018. *Archaeomylodon sampedrinensis* gen. et sp. nov., a new Mylodontine from the Middle Pleistocene of the Pampean Region, Argentina. – *Journal of Vertebrate Paleontology* - in print [DOI: 10.1080/02724634.2018.1542308].

Brandoni D., Ferrero B.S. & Brunetto E., 2010. *Mylodon darwini* Owen (Xenarthra, Mylodontinae) from the Late Pleistocene of Mesopotamia, Argentina, with remarks on individual variability, paleobiology, paleobiogeography, and paleoenvironment. – *Journal of Vertebrate Paleontology* **30**: 1547-1558.

Cione A.L. & Tonni E.P., 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. – *In*: R.E. De Barrio, R.O. Etcheverry, M.F. Caballé & E. Llambías (*eds*.): *Relatorio del 16º Congreso Geológico Argentino (La Plata)*: 183-200.

Cope E.D., 1889. The Edentata of North America. – *American Naturalist* **23**: 657-664.

Czerwonogora A. & Fariña R.A., 2012. How many Pleistocene species of *Lestodon* (Mammalia, Xenarthra, Tardigrada)? – *Journal of Systematic Palaeontology* **11**: 251-263.

Delsuc F., Catzeflis F.M., Stanhope M.J. & Douzery E.J.P., 2001. The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil Eurotamandua. – *Proceedings of the Royal Society of*

London B **268**: 1605-1615.

Deschamps C.M., Esteban G. & Bargo M.S., 2014. El registro más antiguo del género *Lestodon* Gervais, 1855 (Xenarthra, Tardigrada, Mylodontidae) (Montehermosense, Plioceno Temprano). – *Ameghiniana* **38**: 151-156.

Esteban G.I., 1996. Revisión de los Mylodontinae cuaternarios (Edentata, Tardigrada) de Argentina, Bolivia y Uruguay. Sistemática, Filogenia, Paleobiología, Paleozoogeografía y Paleoecología. Unpublished doctoral thesis Universidad Nacional de Tucumán e Instituto Miguel Lillo, Tucumán.

Flower W.H., 1883. On the arrangement of the orders and families of existing Mammalia. – *Proceedings of the Zoological Society of London* **51**: 178-186.

Gervais P., 1855. Recherches sur les mammifères fossiles de l'Amérique méridionale. – *Comptes Rendus de la Académie des Sciences* **40**: 1112-1114.

Gervais H. & Ameghino F., 1880. Los Mamíferos de la América Meridional. Igon Hermanos, Buenos Aires. 225 pp.

Gill T., 1872. Arrangements of the families of mammals, with analytical tables. – *Smithsonian Miscellaneous Collections* **11**: 1-98.

Hoffstetter R., 1952. Les mammifères pleistocènes de la République de l'Équateur. – *Mémoires de la Société Géologique de France* **66**: 1-391.

Hunt G., 2004. Phenotypic variation in fossil samples: modeling the consequences of time-averaging. – *Paleobiology* **30**: 426-443.

Kraglievich L., 1925. Cuatro nuevos gravígrados de la fauna Araucana Chapadmalalense. – *Anales del Museo Nacional de Historia Natural de Buenos Aires* **33**: 215-235.

Martinez S., del Río C.J. & Rojas A., 2016. A Pleistocene (MIS 5e) mollusk assemblage from Ezeiza (Buenos Aires Province, Argentina). – *Journal of South American Earth Sciences* **70**: 174-187.

Miño-Boilini A.R. & Zurita A.E., 2015. Dimorphism in Quaternary Scelidotheriinae (Mammalia, Xenarthra, Phyllophaga). – *Palaeontologia Electronica* **18.1.12A**: 1-16.

Pitana V.G., Esteban G.I., Ribeiro A.M. & Cartelle C., 2013. Cranial and dental studies of *Glossotherium robustum* (Owen, 1842) (Xenarthra: Pilosa: Mylodontidae) from the Pleistocene of southern Brazil. – *Alcheringa* **37**: 147-162.

Owen R., 1839. Zoology of the Voyage of the Beagle, under the command of Captain R.N. Fitzroy during the years 1832-1826. Part 1. Fossil Mammalia. Smith, Elder & Co., London, 111 p.

Owen R., 1842. Description of the skeleton of and extinct gigantic sloth, *Mylodon robustus* Owen, with observations on the osteology, natural affinities, and probable habits of the Megatherioid quadrupeds in general. R. and J. Taylor, London, 176 p.

Soibelzon E., Gasparini G.M., Zurita A.E. & Soibelzon L., 2008. Análisis faunístico de vertebrados de las toscas del Río de La Plata (Buenos Aires, Argentina): un yacimiento paleontológico en desaparición. – *Revista del Museo Argentino de Ciencias Naturales nueva serie* **10**: 291-308.

Soibelzon E., Miño-Boilini A.R., Zurita A.E. & Krmpotic C.M., 2010. Los Xenarthra (Mammalia) del Ensenadense (Pleistoceno inferior a medio) de la región pampeana (Argentina). – *Revista Mexicana de Ciencias Geológicas* **27**: 449-469.

Toledo M.J., 2011. El legado lujanense de Ameghino: Revisión estratigráfica de los depósitos Pleistocenos-Holocenos del valle del Río Luján en su sección tipo. Registro paleoclimático en la Pampa de los estadios OIS 4 al OIS 1. – *Revista de la Asociación Geológica Argentina* **68**: 121-167.

Tonni E.P., Nabel P., Cione A.L., Etchichury M., Tófalo R., Yané G.S., San Cristóbal J., Carlini A. & Vargas D., 1999. The Ensenada and Buenos Aires formations (Pleistocene) in a quarry near La Plata, Argentina. – *Journal of South American Earth Sciences* **12**: 273-291.

Tonni E.P., Cione A.L. & Figini A.J., 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **147**: 257-281.