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BODY MASS ESTIMATIONS IN LUJANIAN (LATE PLEISTOCENE-EARLY HOLOCENE OF SOUTH AMERICA) MAMMAL MEGAFAUNA

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ABSTRACT: In this paper a data base is initiated, with the body mass estimations for a number of xenarthran and epitherian species of the Lujanian Land Mammal Age (late Pleistocene - early Holocene of South America). For doing that, a set of allometric equations was used, which had been previously developed from craniodental and limb bone dimensions in modern mammals. The results were analysed statistically. The dispersion of body mass estimations was remarkable in the totally extinct xenarthran groups. Certain measurements (particularly, the posterior jaw length in glyptodonts and the transverse diameter of the femur in ground sloths) gave spurious predictions relative to non-xenarthran mammals. New equations specifically for xenarthrans should be developed to use these measurements. The dispersion of the epitherian mammals was lower than in the studied xenarthran. It is suggested that arithmetic mean should be used in those studies in which large size is the conservative hypothesis, and another statistic (such as the geometric mean, median or mode) in the opposite case. This database is intended to be the starting point for many autecological and synecological studies of this extinct fauna.

RESUMEN: Estimaciones de masa de la megafauna de mamíferos Lujanenses (Pleistoceno tardío-Holoceno temprano de América del Sur). En el presente trabajo se comienza una base de datos con las estimaciones de la masa corporal de varias especies de xenartros y epiterios pertenecientes a la Edad Mamífero Lujanense (Pleistoceno tardío - Holoceno temprano de América del Sur). Para ello, fue usado un conjunto de ecuaciones alométricas que previamente habían sido desarrolladas en base a dimensiones craneanas, dentarias y del esqueleto apendicular en mamíferos modernos. Los resultados fueron analizados estadísticamente. La dispersión de los resultados fue notable en los grupos de xenartros, que están completamente extinguidos. Ciertas medidas (particularmente el largo posterior de la mandíbula en gliptodontes y el diámetro transverso del fémur en perezosos terrestres) produjeron estimaciones espúreas con respecto a mamíferos no xenartros. Nuevas ecuaciones específicas para xenartros deben ser desarrolladas para usar estas medidas. La dispersión de los resultados fue menor en aquellos casos en los que el taxón estudiado cuenta con representantes vivientes. Se sugiere usar el valor de la media aritmética en aquellos estudios en los cuales la hipótesis conservadora sea el tamaño mayor y alguna otra cantidad (por ejemplo, la media geométrica, la moda o la mediana) en el caso contrario. Esta base de datos es el primer paso para estudios auto y sinecológicos sobre esta fauna extinguida.

Key words: megafauna, mammals, Lujanian, Pleistocene-Holocene, South America, body size, allometric equations.

Palabras clave: megafauna, mamíferos, Lujanense, Pleistoceno-Holoceno, América del Sur, tamaño, ecuaciones alométricas.

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INTRODUCTION

Body size is both a feature capable of being observed in fossil mammals and a remarkable influence on an animal's life history (Peters, 1983; Schmidt-Nielsen, 1984; Damuth and MacFadden, 1990). Virtually all life traits are decisively influenced by or correlated to body size; for example, metabolism (Kleiber, 1932), limb bone dimensions and biomechanics of locomotion (Alexander et al., 1979; Alexander, 1985, 1989; Fariña et al., 1997), population density and home range (Damuth, 1981a, 1981b, 1987, 1991, 1993; Lindstedt et al., 1986; Reiss, 1988; Swihart et al., 1988; Nee et al., 1991), behaviour and social organisation (Jarman, 1974) and proneness to extinction (Flessa et al., 1986, Lessa and Fariña, 1996, Lessa et al., 1997).

This is especially valid for the case of very large mammals, as studied by Owen-Smith (1987, 1988). Since the descriptions of the collected first specimens, the members of the Lujanian Land Mammal fauna (late Pleistocene-early Holocene of South America, Pascual et al., 1965) have been regarded as impressive in their large size (Cuvier, 1804; Owen, 1838; Darwin, 1839; Burmeister, 1866-67, 1879; Ameghino, 1887, 1889; Lydekker, 1894; Kraglievich, 1940; Patterson and Pascual, 1972; Simpson, 1980), and particularly so in the case of xenarthran representatives. However, estimations of the body masses of these animals are scarce (see below).

Among South American mammals, xenarthrans constitute a very conspicuous group, characterised by the highest degree of endemism, their peculiar anatomy and their diversity of shapes and ways of life. Their record goes back over 60 million years to the Middle Palaeocene. Perhaps the most striking representatives are the gigantic Pleistocene ground sloths (Mylodontidae and Megatheriidae) and glyptodonts (Glyptodontidae). Their remains are among the most abundant, if not the most abundant, of the Lujanian megafauna. They must have played very important ecological roles within Late Pleistocene communities (see Fariña and Blanco, 1996; Lessa and Fariña, 1996). In the same fauna several other mammals, belonging to the Cohort Epitheria McKenna 1981, reached also very large sizes (Darwin, 1839; Burmeister, 1866-67, 1879; Ameghino, 1887, 1889; Kraglievich, 1940; Patterson and Pascual, 1972). They belong to five different orders: the native ungulates Litopterna and Notoungulata, and representatives of the boreal lineages Perissodactyla, Proboscidea and Carnivora.

In this paper we begin to build a data base of mass estimations for a number of xenarthran and epitherian species belonging to the Lujanian Land Mammal Age (Tonni et al., 1985; Bargo et al., 1986; Alberdi et al., 1989; Scillato Yané et al., 1995). This data base is intended to be the starting point for many autecological and synecological studies of this extinct fauna. In some cases, it proved difficult to establish accurately the stratigraphic provenance of the material studied. However, this is not a matter of crucial importance, since all the species studied here are well-known members of the Lujanian fauna.

METHODS

Seven species of xenarthrans (three glyptodonts and four ground sloths) and six species of epitherians (one notoungulate, one litoptern, one perissodactyl, one proboscidean and two carnivores) were measured. We selected specimens that were represented by a complete or almost complete skeleton, so all the measurements (cranial, dental and limb skeleton) for each species belong to the same individual, except for a couple of cases discussed below. When it was possible to make a given measurement on the fossil material, the appropriate allometric equation based on that measurement was used. Those equations were taken from the literature and had been defined for cranial, dental and limb skeleton measurements as well as total body length in modern mammals (Anderson et al., 1985; Janis, 1990; Scott, 1990, see **Table 1**).

In some cases (which will be detailed below), our estimates are compared with those obtained following the procedure Alexander (1985, 1989) used to appraise the masses of some dinosaurs using scale models. This procedure is based on Archimedes' Principle: when an object is immersed in a fluid an upward force acts on it, that is equal to the weight of fluid it displaces (Alexander, 1983). Consider an object of weight W (mass = W/g, where g is the acceleration of gravity) and density ρ

Table 1. Equations and their respective sources

Measurement	Equation	Source
sum of **humerus** + **femur** circumference (H9+F8)	mass = 0.000084 (H9 + F8)$^{2.73}$	Anderson *et al.* (1985)
humerus length (H1)	log mass = 3.4026 * log H1 -2.3707	Scott (1990)
humerus length (H2)	log mass = 3.3951 * log H2 -2.513	Scott (1990)
condylar width (H3)	log mass = 2.7146 * log H3 +0.2594	Scott (1990)
trochlear width (H4)	log mass = 2.4815 * log H4 +0.4516	Scott (1990)
distal width (H5)	log mass = 2.5752 * log H5 + 0.2863	Scott (1990)
transverse diameter (H7)	log mass = 2.485 * log H7 +1.0934	Scott (1990)
anteropost diameter (H8)	log mass = 2.4937* log H8 +0.876	Scott (1990)
radius length (R1)	log mass = 2.8455 * log R1 - 1.8223	Scott (1990)
distal articular surface width (R2)	log mass = 2.5894 * log R6 + 0.9092	Scott (1990)
distal articular surface height (R3)	log mass = 2.5894 * log R6 + 0.9092	Scott (1990)
distal width (R4)	log mass = 2.5894 * log R6 + 0.9092	Scott (1990)
maximum width (R5)	log mass = 2.5894 * log R6 + 0.9092	Scott (1990)
transverse diameter (R6)	log mass = 2.5894 * log R6 + 0.9092	Scott (1990)
anteropost diameter (R7)	log mass = 2.5038 * log R7 + 1.4661	Scott (1990)
ulnar length (U1)	log mass = 2.9762 * log U1 - 2.3087	Scott (1990)
femur length (F1)	log mass = 3.4855 * log F1 - 2.9112	Scott (1990)
femur length (F2)	log mass = 2.6886 * log F2 - 0.2471	Scott (1990)
3rd trochanter - distal end (F3)	log mass = 2.9405 * log F3 - 0.087	Scott (1990)
trochlear width (F5)	log mass = 2.782 * log F5 - 0.0107	Scott (1990)
transverse diameter (F6)	log mass = 2.821 * log F6 + 0.9062	Scott (1990)
anteropost diameter (F7)	log mass = 2.6016 * log F7 + 0.9119	Scott (1990)
tibia length (T1)	log mass = 3.5808 * log T1 - 3.1732	Scott (1990)
proximal width (T2)	log mass = 2.8491 * log T2 - 0.2495	Scott (1990)
proximal anteroposterior diameter (T3)	log mass = 3.1568 * log T3 + 0.137	Scott (1990)
distal transverse width (T4)	log mass = 2.6075 * log T4 + 0.4247	Scott (1990)
distal anteroposterior width (T5)	log mass = 2.8949 * log T5 + 0.642	Scott (1990)
transverse diameter (T6)	log mass = 2.7382 * log T6 + 0.8761	Scott (1990)
anteropost diameter (T7)	log mass = 2.906 * log T7 + 0.9909	Scott (1990)
occipital height (och)	log mass = log OCH * 2.783 - 0.42	Janis (1990)
basicranial length (bcl)	log mass = log BCL * 3.137 - 1.062	Janis (1990)
maseteric fossa length (mfl)	log mass = log MFL * 2.95 - 1.289	Janis (1990)
palatal width (paw)	log mass = log PAW * 3.27 - 0.196	Janis (1990)
muzzle width (mzw)	log mass = log MZW * 2.313 + 0.64	Janis (1990)
posterior skull length (psl)	log mass = log PSL * 2.758 - 0.973	Janis (1990)
mandibular angle height (dma)	log mass = log DMA * 2.448 - 0.331	Janis (1990)
posterior mandibular length (pjl)	log mass = log PJL * 2.412 + 0.031	Janis (1990)
width mandibular angle (wma)	log mass = log WMA * 2.803 - 0.352	Janis (1990)
lower molar row length (lmrl)	log mass = log LMRL * 3.265 - 0.536	Janis (1990)
lower premolar row length (lprl)	log mass = log LPRL * 2.673 + 0.438	Janis (1990)
anterior jaw length (ajl)	log mass = log AJL * 2.806 - 0.902	Janis (1990)
total skull length (tsl)	log mass = log TSL * 2.975 - 2.344	Janis (1990)
total jaw length (tjl)	log mass = log TJL * 2.884 - 1.952	Janis (1990)
2nd lower premolar length (SLPL)	log mass = log SLPL * 2.185 + 1.957	Janis (1990)
idem width (SLPW)	log mass = log SLPW * 1.99 + 2.636	Janis (1990)
3rd lower premolar length (TLPL)	log mass = log TLPL * 2.714 + 1.686	Janis (1990)
idem width (TLPW)	log mass = log TLPW * 2.224 + 2.389	Janis (1990)
4th lower premolar length (FLPL)	log mass = log FLPL * 3.203 + 1.533	Janis (1990)
idem width (FLPW)	log mass = log FLPW * 2.486 + 2.226	Janis (1990)
idem area (FLPA)	log mass = log FLPA * 1.398 + 1.913	Janis (1990)
1st lower molar length (FLML)	log mass = log FLML * 3.263 + 1.337	Janis (1990)
idem width (FLMW)	log mass = log FLMW * 2.909 + 2.03	Janis (1990)
idem area (FLMA)	log mass = log FLMA * 1.553 + 1.701	Janis (1990)
2nd lower molar length (SLML)	log mass = log SLML * 3.201 + 1.13	Janis (1990)
idem width (SLMW)	log mass = log SLMW * 2.967 + 1.932	Janis (1990)
idem area (SLMA)	log mass = log SLMA * 1.563 + 1.541	Janis (1990)

(Cont. Table1)

Measurement	Equation	Source
3rd lower molar length (TLML)	log mass = log TLML * 3.183 + 0.801	Janis (1990)
idem width (TLMW)	log mass = log TLMW * 2.933 + 1.991	Janis (1990)
idem area (TLMA)	log mass = log TLMA * 1.58 + 1.404	Janis (1990)
2nd upper molar length (SUML)	log mass = log SUML * 3.184 + 1.091	Janis (1990)
idem width (SUMW)	log mass = log SUMW * 3.004 + 1.469	Janis (1990)
idem area (SUMA)	log mass = log SUMA * 1.568 + 1.277	Janis (1990)
3rd upper molar length (M^3l)	log mass = log M^3l * 2.81 + 1.29	Damuth (1990)
idem width (M^3w)	log mass = log M^3w * 2.77 - 1.58	Damuth (1990)
idem area (M^3a)	log mass = log M^3a * 1.47 + 1.26	Damuth (1990)
7th lower molariform length	log mass = log 7LML * 3.201 + 1.13	Janis (1990)
7th lower molariform width	log mass = log 7LMW * 2.967 + 1.932	Janis (1990)
7th lower molariform area	log mass = log 7LMA * 1.563 + 1.541	Janis (1990)
lower postcranial row length (pcrl)	log mass = log PCRL * 3.15 - 1.28	Janis (1990)
lower postcranial row area (lpcta)	log mass = log LPCTA * 1.48 + 0.51	Janis (1990)
upper postcan row lgth (pcru)	log mass = log PCRU * 3.07 - 1.1	Janis (1990)
upper postcranial row area (upcta)	log mass = log UPCTA * 1.48 + 0.29	Janis (1990)
shoulder height (eqn. *a*)	mass = (shoulder hght * 1.02 * $10^{-4})^{3.11}$	Roth (1990; ref. therein)
shoulder height (eqn. *b*)	mass = (shoulder hght * 1.267 * $10^{-3})^{2.631}$	Roth (1990; ref. therein)
shoulder height (eqn. *c*)	mass = (shoulder hght * 5.07 * $10^{-4})^{2.803}$	Roth (1990; ref. therein)
shoulder height (eqn. *d*)	mass = (shoulder hght * 2.58 * $10^{-4})^{2.917}$	Roth (1990; ref. therein)
shoulder height (eqn. *e*)	mass = (shoulder hght * 3.96 * $10^{-4})^{2.890}$	Roth (1990; ref. therein)
shoulder height (eqn. *f*)	mass = (shoulder hght * 1.81 * $10^{-4})^{2.97}$	Roth (1990; ref. therein)
shoulder height (eqn. *g*)	mass = (shoulder hght * 8.234 * $10^{-4})^{2.711}$	Roth (1990; ref. therein)
shoulder height (eqn. *h*)	mass = (shoulder hght * 2.080 * $10^{-4})^{2.934}$	Roth (1990; ref. therein)
shoulder height (eqn. *i*)	mass = (shoulder hght * 3.071 * $10^{-4})^{2.917}$	Roth (1990; ref. therein)
shoulder height (eqn. *j*)	mass = (shoulder hght * 4.682 * $10^{-5})^{3.263}$	Roth (1990; ref. therein)
shoulder height (eqn. *k*)	mass = (shoulder hght * 3.24 * $10^{-5})^{3.356}$	Roth (1990; ref. therein)
shoulder height (eqn. *l*)	mass = (shoulder hght * 2.73 * $10^{-5})^{3.387}$	Roth (1990; ref. therein)
humerus length (HL, all carnivores)	log mass = 2.93 * log HL - 5.11	Anyonge (1993)
anteropost 2nd mom area (HIY, all carn)	log mass = 0.63 * log HIY - 0.61	Anyonge (1993)
transverse idem (HIX, all carnivores)	log mass = 0.6 * log HIX - 0.59	Anyonge (1993)
cortical area humerus (HCA, all carnivores)	log mass = 1.18 * log HCA - 0.99	Anyonge (1993)
humerus length (HL, felids)	log mass = 3.13 * log HL - 5.53	Anyonge (1993)
anteropost 2nd mom area (HIY, felids)	log mass = 0.64 * log HIY - 0.61	Anyonge (1993)
transverse idem (HIX, felids)	log mass = 0.63 * log HIX - 0.64	Anyonge (1993)
cortical area humerus (HCA, felids)	log mass = 1.25 * log HCA - 1.09	Anyonge (1993)
femur length (FL, all carnivores)	log mass = 2.92 * log FL - 5.27	Anyonge (1993)
anteropost 2nd mom area (FIY, all carn)	log mass = 0.67 * log FIY - 0.76	Anyonge (1993)
transverse idem (FIX, all carnivores)	log mass = 0.69 * log FIX - 0.77	Anyonge (1993)
cortical area femur (FCA, all carnivores)	log mass = 1.25 * log FCA - 1.04	Anyonge (1993)
articular area femur (FDA, all carnivores)	log mass = 1.31 * log FDA - 2.12	Anyonge (1993)
femur length (FL, felids)	log mass = 3.2 * log FL - 5.9	Anyonge (1993)
anteropost 2nd mom area (FIY, felids)	log mass = 0.69 * log FIY - 0.77	Anyonge (1993)
transverse idem (FIX, felids)	log mass = 0.69 * log FIX - 0.79	Anyonge (1993)
cortical area (FCA, felids)	log mass = 1.31 * log FCA - 1.18	Anyonge (1993)
articular area femur (FDA, felids)	log mass = 1.32 * log FDA - 2.16	Anyonge (1993)
m_1 length (M1L, all carnivores)	log mass = 2.97 * log M1L - 2.27	Van Valkenburgh (1990)
orbito-occiput length (OOL, all carnivores)	log mass = 3.44 * log OOL - 5.74	Van Valkenburgh (1990)
skull length (SKL, all carnivores)	log mass = 3.13 * log SKL - 5.59	Van Valkenburgh (1990)
m_1 length (M1L, felids)	log mass = 3.05 * log M1L - 2.15	Van Valkenburgh (1990)

(Cont. Table1)

Measurement	Equation	Source
orbito-occiput length (OOL, felids)	log mass = 3.54 * log OOL - 5.86	Van Valkenburgh (1990)
skull length (SKL, felids)	log mass = 3.11 * log SKL - 5.38	Van Valkenburgh (1990)
m_1 length (M1L,ursids)	log mass = 0.49 * log M1L + 1.26	Van Valkenburgh (1990)
orbito-occiput length (OOL, ursids)	log mass = 1.98 * log OOL - 2.38	Van Valkenburgh (1990)
skull length (SKL, ursids)	log mass = 2.02 * log SKL - 2.8	Van Valkenburgh (1990)
m_1 length (M1L, large carnivores)	log mass = 0.57 * log M1L +1.45	Van Valkenburgh (1990)
orbito-occiput length (OOL, large carnivores)	log mass = 1.51 * log OOL - 1.25	Van Valkenburgh (1990)
skull length (SKL, large carnivores)	log mass = 1.56 * log SKL - 1.6	Van Valkenburgh (1990)
head+body length (HBL, all carnivores)	log mass = 2.88 * log HBL - 7.24	Van Valkenburgh (1990)
head+body length (HBL, felids)	log mass = 2.72 * log HBL - 6.83	Van Valkenburgh (1990)
head+body length (HBL, large carnivores)	log mass = 2.46 * log HBL - 5.78	Van Valkenburgh (1990)
head + body length (all ungulates)	log mass = 3.16 * log HBL - 5.12	Damuth (1990)

immersed in a fluid of density ρ'. The volume of the object is *W/*ρ *g* so the weight of fluid it displaces is *W*ρ'*/*ρ. The net downward force on it, *W'*, is given by the equation

$$W' = W - W \rho'/\rho \quad (1)$$

The scale models are submerged in water, so ρ' equals 1 000 kg m^{-3}. For *Glyptodon clavipes*, commercial models sold by the British Museum of Natural History were used. When the particular species or genera had no model, they were made specifically for the purposes of this paper or the papers quoted. The appropriate displaced volume of water was weighed. The mass of the model obtained from the equation (1) was multiplied by the cube of the linear proportions (usually about 1/40). Further, it was assumed that the fossil mammals had a typical density of 1 000 kg m^{-3}. After that, the volumes of the mammals were obtained by multiplying those of the models by the cubes of the linear ratios, specifically 40^3 for some of them. A precision balance was used, the error in taking the model mass being less than 0.5 gram. Therefore, the final error introduced by multiplying by the scale should be less than 32 kg. Since the animals studied here had masses measured in hundreds of kilograms and tonnes, this source of error was not regarded as relevant.

For the specimens used in this data base, original catalogue data of both geographic and stratigraphic origins are taken from the literature, literally translated from, or quoted in, Spanish.

Abbreviations: MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. MLP, Museo de La Plata, La Plata, Argentina.

RESULTS

The results are summarised in Tables 1 to 7. In this section we will discuss each particular case.

CINGULATA
GLYPTODONTIDAE

Glyptodon reticulatus Owen (**Table 2, Fig. 1a**)

Specimen: MACN 200, complete skeleton and carapace. This specimen is the holotype of the species and was classified and figured by Burmeister (1874) as *Glyptodon asper*. It is mounted and exhibited at the Museo Argentino de Ciencias Naturales.
Locality: Salto, Buenos Aires Province, Argentina.
Stratigraphy: Upper Pampean "Formation".

Forty-three estimates of body mass were made for this species (**Table 2**). Several assumptions had to be made in the way certain measurements were taken, in this case and in those of the other glyptodonts, to overcome the difficulties posed by the lack of homology between xenarthran and placental masticatory anatomy. The cheek teeth in glyptodonts are not equivalent to those of the other placentals or even marsupials. Instead of a number of premolars and molars, the tooth row is composed of eight homodont molariforms. The first half of the molariform row was used in the

Table 2 Measurements and predictions for the three species of Lujanian glyptodonts considered.

	Glyptodon reticulatus		*Panochthus tuberculatus*		*Doedicurus clavicaudatus*	
Measurement	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**
sum of **humerus** + **femur** circumference	43	**1299**	45.5	**1516**	60	**3226**
humerus length (H1)	33.5	**658**	36.5	**881**	34	**692**
humerus length (H2)	31.5	**375**	35	**536**	32	**395**
condylar width (H3)	7.8	**480**	7.5	**431**	9	**708**
trochlear width (H4)	7.9	**478**	7.5	**420**	7.5	**420**
distal width (H5)	11.3	**996**	13	**1429**	15	**2065**
transverse diameter (H7)	5.6	**897**	4.7	**580**	8.4	**2456**
anteropost diameter (H8)	5	**416**	6.4	**770**	6.8	**895**
radius length (R1)	18	**56**	17	**48**	17	**48**
transverse diameter (R6)	2.8	**117**	2.5	**87**	3.5	**208**
anteropost diameter (R7)	2.8	**385**	2.5	**290**	2.8	**385**
ulnar length (U1)	26	**80**	28.5	**105**	26	**80**
femur length (F1)	42	**558**	46	**766**	51	**1098**
femur length (F2)	45	**595**	46	**635**	45	**595**
trochlear width (F5)	14.5	**1660**	17.5	**2802**	17	**2585**
transverse diameter (F6)	11	**6982**	7.5	**2370**	12.7	**10472**
anteropost diameter (F7)	5.7	**756**	10.5	**3703**	8.5	**2137**
tibia length (T1)	20.5	**33**	20	**31**	24	**59**
proximal width (T2)	14.7	**1192**	18	**2123**	17.5	**1959**
prox ant post diam (T3)	9.2	**1512**	8.5	**1178**	9.5	**1673**
distal width (T5)	9	**2538**	8.5	**2151**	12	**5836**
transverse diameter (T6)	3.3	**198**	4.5	**462**	6.5	**1265**
anteropost diam (T7)	9.6	**7005**	10.5	**9088**	10	**7887**
occipital height (och)	5.7	**48**	7	**85**	7	**85**
basicranial (bcl)	6.5	**31**	9	**85**	15	**424**
masset fossa length (mfl)	18	**260**	27	**858**	26	**768**
palatal width (paw)	4	**64**	6	**223**	6	**223**
muzzle width (mzw)	9.5	**797**	13.5	**1797**	10.5	**1005**
post skull length (psl)	11	**79**	18	**308**	18	**308**
mand ang height (dma)	23.5	**1060**	30.5	**2007**	21	**805**
post mand length (pjl)	- 0.7	**—**	3.5	**22**	1.5	**2.9**
width mand ang (wma)	7.5	**126**	7.5	**126**	9	**210**
molar row length (lmrl)	9.5	**457**	11.5	**846**	9.75	**493**
premolar (lprl)	9.5	**1126**	11.5	**1876**	9.75	**1207**
ant jaw length (ajl)	14	**206**	21	**643**	18.75	**468**
total skull length (tsl)	34.5	**351**	62	**974**	56.25	**729**
total jaw length (tjl)	23.5	**268**	47.5	**765**	39.75	**457**
7th low molariform lgth.	2.5	**253**	2.7	**324**	—	—
idem width	1.6	**345**	1.7	**413**	—	—
idem area	4	**303**	4.6	**377**	—	—
l postcan row lgth (pcrl)	19.8	**635**	21.1	**779**	—	—
idem area (lpcta)	29.7	**490**	34.4	**608**	—	—
up postcan row lgth (pcru)	18.5	**618**	19.9	**772**	—	—
idem area (upcta)	29.9	**298**	34.9	**374**	—	—

equations for premolar row, and the last four in the equations for molar row. In any case, this would alter the standard deviation of the sample but we assume that it will not modify essentially the averages. Also, the next to last lower molar dimensions (considered by Janis, 1990, as a good predictor) were obviously not those of the m2, but of the seventh molariform. One of the lengths of the femur (Scott's, 1990, F2) was measured as in equids, and, therefore, the appropriate equation for equids was used.

The arithmetic mean of the 43 estimates for this species was 862.3 kg, and the geometric mean reached the modest figure of 403 kg. Standard deviations differed markedly: in the first case it was as much as 1462.5 kg, while the equivalent for a log-normal distribution of the results was only 3.5 kg. This latter distribution was warranted (χ^2 = 6.8, degrees of freedom = 8, P > 0.54). Median and mode turned out to be, respectively, 457 kg and

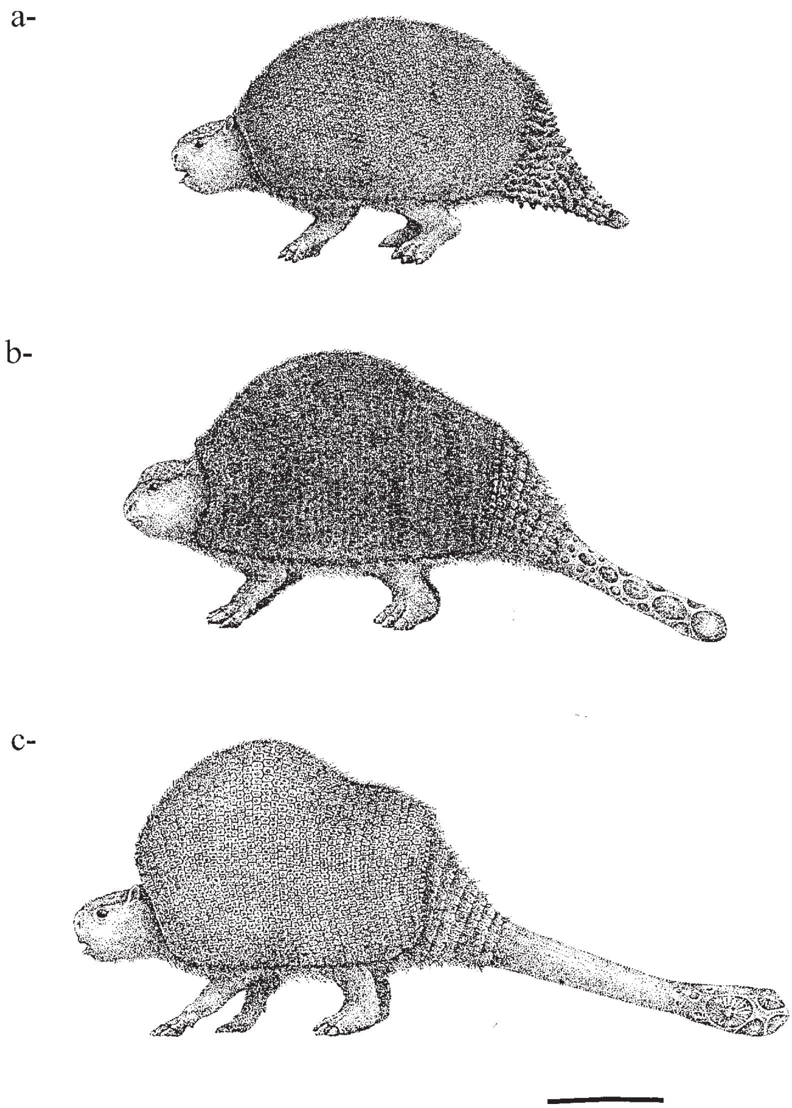

Fig. 1. Reconstructions of a) *Glyptodon reticulatus,* b) *Panochthus tuberculatus* and c) *Doedicurus clavicaudatus* (from Fariña and Vizcaíno, 1995). Scale: 1 m.

362 kg. Generally, limb bone dimensions tended to yield overestimations, with an average of 1271 kg, and a maximum of about 7 000 kg from the anteroposterior diameter of the tibia (Scott's, 1990, T7). Also the transverse diameter of the femur (F6) yields an estimate of almost 7 000 kg.

Skull, lower jaw and dental predictors tended to yield underestimations; the average was 391 kg, with several measurements yielding estimates under 100 kg, remarkably the basicranial length yielded only 31 kg. One measurement (posterior jaw length) had to be discarded because it had a negative value. These discrepancies (which made the dispersion larger) are easily explained by the peculiar anatomy of the glyptodont masticatory apparatus (Fariña and Parietti, 1983; Fariña, 1985, 1988), in which the ascending ramus emerges laterally and lets the tooth row pass medial to it. Among the dental measurements, Janis's (1990) conclusion about the goodness of the total lower molar row length as body mass predictor was not corroborated in this case, nor was it in the case of the other glyptodonts.

The mass of the larger species *Glyptodon clavipes* had been estimated by Fariña (1995), using two scale models in the way described above. One of them was a plastic one manufactured for and sold by the British Museum (Natural History) —actually, a 1/40 scale of a non-identified species of the genus *Glyptodon*, but very similar to *G. clavipes*— and another one made of a synthetic modelling clay specifically for the purposes of those papers, attempting a reconstruction of that species. The result obtained were 2 000 kg, which is congruent with the estimated average for the smaller *Glyptodon reticulatus* in this paper.

Panochthus tuberculatus Owen (**Table 2, Fig. 1b**)

Specimen: MLP 16-29, complete skeleton and carapace displayed in Sala IX of the Museo de La Plata. It had been figured by Lydekker (1894, Plates XX and XXIII).
Locality: Luján, Buenos Aires Province, Argentina.
Stratigraphy: Upper Pampean "Formation".

Forty-three estimates were obtained for this species. The arithmetic mean of those estimates was 1061 kg, and only 528 kg was obtained as geometric mean. The behaviour of the respective standard deviations was very similar to those of *Glyptodon reticulatus*: 1488.64 kg in the first case and only 3.5 kg for the geometric distribution. Log-normal distribution was warranted, although marginally ($\chi^2 = 16$, degrees of freedom = 9, $P > 0.07$). The median value was 701 kg. The distribution of predicted masses was bimodal. The values of these two modes were, respectively, 90.5 kg and 724 kg. Of course, the second mode seems more reasonable and it is higher than the first. Again, limb bone dimensions tended to yield overestimations, with an average of 1409 kg, and a maximum of slightly above 9 000 kg for one of the anteroposterior diameter of the tibia (Scott's, 1990, T7). As in the previous species, skull, lower jaw and dental predictors tended to yield underestimations; the average was 679 kg, with several measurements yielding estimates under 100 kg. Posterior jaw length yielded the minimum estimate, only 22 kg.

Based on a scale model, Fariña (1995) obtained an estimate for this species of about 1100 kg, which is congruent with the arithmetic mean.

Doedicurus clavicaudatus Owen (**Table 2, Fig. 1c**)

Specimen: MLP 16-24, skeleton and incomplete carapace. It is mounted and exhibited at Sala VII of the Museo de La Plata, and its skull had been figured by Lydekker (1894, Plate XXVII).
Locality: Luján, Buenos Aires Province, Argentina.
Stratigraphy: Upper Pampean "Formation".

Arithmetic and geometric means of the 37 estimates were 1468 kg and 613 kg, respectively, and their appropriate standard deviations were 2208 kg in the first case and 3.7 kg, similar to the other two species of glyptodonts. Log-normal distribution was not warranted in this case ($\chi^2 = 78$, degrees of freedom = 11, $P << 0.001$). However, if the exceedingly small estimate yielded by using the posterior jaw length (see below) is taken out, χ^2 is reduced to 3, and the appropriate P value rises to 0.99. Median and mode turned out to be, respectively, 708 kg and 512 kg. As usual, limb bone dimensions tended to yield overestimations, with an average of 2050 kg, and a maximum of almost 9 000 kg for the transverse diameter of the femur (Scott's, 1990, F6).

As in the previous species, skull and lower jaw predictors tended to yield underestimations (reliable dental measurements were not available); the average was 553 kg. As mentioned above, posterior jaw length yielded the minimum estimate, an absurd figure of less than 3 kg.

Based on a scale model, Fariña (1995) estimated the mass of this species as 1400 kg.

TARDIGRADA
MEGATHERIIDAE

Megatherium americanum Cuvier
(**Table 3, Fig. 2a**)

Specimen: MLP 27-VII-1-1, complete skeleton. It is exhibited in Sala VI of Museo de La Plata.
Locality: Río Salado, General Belgrano, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation".

The values of the arithmetic and geometric means of the 44 estimates of *M. americanum* were 6073 kg and 2745 kg, respectively. Their appropriate standard deviations were 14609 kg in the first case and 2.88 kg, repeating the pattern observed in the three species of glyptodonts. Log-normal distribution was not warranted (χ^2 = 25.1, degrees of freedom = 8, $P < 0.002$). However, most of the difference is explained by only one measurement (transverse diameter of the femur, Scott's, 1990, F6). If this value were not summed, the χ^2 would be reduced to 5.2, degrees of freedom 5, and the appropriate P value would rise to 0.3. Median and mode turned out to be, respectively, 2543 kg and 2896 kg. As usual, limb bone dimensions tended to yield overestimations, with an average of 9358 kg, and an incredible maximum of 97 000 kg for the transverse diameter of the femur (Scott's, 1990, F6). If this value were taken seriously, *Megatherium americanum* would find a match in size only in the really gigantic dinosaurs, as *Supersaurus* and *Argentinosaurus*. As in the previous group of species, skull, lower jaw and dental predictors tended to yield underestimations; the average was 2132 kg.

If the transverse diameter of the femur is taken out, the average will fall to 3950 kg. The mass of *Megatherium americanum* obtained through Alexander's procedure (Casinos, 1996) was 3800 kg.

MYLODONTIDAE

Lestodon armatus Gervais
(**Table 3, Fig. 2b**)

Specimen: MLP 3-3, complete skeleton, exhibited in Sala VII of the Museo de La Plata.
Locality: San Antonio de Areco, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation".

Forty estimates were obtained for this species. The arithmetic and geometric means were 3397 kg and 1784 kg, respectively. Standard deviations were 5990 kg in the first case and 3 kg in the second case. Median and mode turned out to be 1918 kg and 2896 kg, respectively. Despite the fact that transverse diameter of the femur yielded an incredibly high estimate (almost 38 000 kg), the frequency of the values obtained were not distinguishable from having a log-normal distribution (χ^2 = 12.4, degrees of freedom = 8, $P < 0.13$). The average of the limb bone dimensions was 4727 kg, and its maximum was the already mentioned transverse diameter of the femur (Scott's, 1990, F6), while tibial length T1 yielded an estimate of 205 kg. The skull and lower jaw average was 1401 kg, and the general average without F6 was 2517 kg.

Glossotherium robustum Owen
(**Table 3, Fig. 2c**)

Specimen: MLP 3-140, complete skeleton, exhibited in Sala VII of the Museo de La Plata.
Locality: Rio Luján, Olivera, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation".

The pattern of the results for *Glossotherium robustum* was similar to those for the previously studied species of ground sloths. Arith-

Table 3. Measurements and predictions for the four species of Lujanian ground sloths considered.

	Megatherium americanum		*Lestodon armatus*		*Glossotherium robustum*		*Scelidotherium leptocephalum*	
Measurement	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**
sum of **humerus** + **femur** circumference	88	**9177**	79	**6836**	60	**3226**	59.5	**3153**
humerus length (H1)	65	**6279**	51	**2751**	37.5	**966**	34	**692**
humerus length (H2)	60	**3342**	52	**2056**	36.5	**618**	33	**439**
condylar width (H3)	11	**1376**	10.5	**1075**	7.7	**463**	8	**514**
trochlear width (H4)	15	**2543**	14	**1976**	12.5	**1491**	10.5	**968**
distal width (H5)	30	**11787**	25.5	**8099**	21	**4912**	19.5	**4059**
transverse diameter (H7)	11	**4800**	10.8	**4586**	8	**2176**	8.6	**2604**
anteropost diameter (H8)	7	**963**	7.7	**1221**	5.2	**459**	4.2	**270**
radius length (R1)	65	**2169**	35	**373**	26	**160**	27	**178**
transverse diameter (R6)	5	**524**	5	**524**	3	**140**	2.8	**117**
anteropost diameter (R7)	12	**14728**	9.8	**8870**	6	**2597**	6	**2598**
ulnar length (U1)	69	**1459**	46	**437**	36	**211**	25.5	**75**
femur length (F1)	62	**2169**	68	**2992**	45	**710**	40	**471**
femur length (F2)	62	**1546**	66	**1863**	44	**556**	38	**359**
trochlear width (F5)	28	**10358**	19.5	**3786**	15	**1825**	17	**2585**
transverse diameter (F6)	28	**97417**	20	**37706**	16	**20092**	8.5	**3374**
anteropost diameter (F7)	7	**1290**	8	**1825**	6.5	**1064**	4.2	**341**
tibia length (T1)	49	**757**	34	**205**	21.5	**40**	27	**90**
proximal width (T2)	27	**6739**	23	**4268**	14	**1037**	18	**2123**
prox ant post diam (T3)	16	**8673**	11	**2657**	8.5	**1178**	8	**972**
distal transverse wth (T4)	20	**7000**	15	**3100**	11.5	**1551**	14	**2590**
distal antpost width (T5)	17	**15997**	13	**7358**	9.5	**2968**	8	**1804**
transverse diameter (T6)	9	**3083**	9	**3083**	5.5	**801**	5.5	**800**
anteropost diam (T7)	11	**10404**	9	**5807**	7	**2797**	6	**1787**
occipital height (och)	14	**588**	18	**1411**	14.5	**758**	9	**172**
basicranial lenght (bcl)	27	**2680**	21	**1218**	20	**1046**	20	**1045**
masset fossa length (mfl)	38	**2352**	30	**1171**	23	**535**	23	**535**
palatal width (paw)	15	**3996**	7	**369**	6	**223**	2.9	**21**
muzzle width (mzw)	14	**1954**	16.5	**2858**	14	**1954**	8.6	**633**
post skull length (psl)	35	**2811**	36	**2086**	29.5	**1204**	26	**1358**
mand ang height (dma)	25	**2528**	14.5	**325**	14	**298**	12	**431**
post mand length (pjl)	15	**880**	18.5	**1223**	13	**522**	15	**880**
width mand ang (wma)	23	**2829**	22	**2656**	16	**1084**	14	**745**
molar row length (lmrl)	21	**5583**	12.8	**1200**	—-	**—-**	—-	**—-**
ant jaw length (ajl)	31	**1961**	22.4	**771**	—-	**—-**	22.5	**775**
total skull length (tsl)	87	**2645**	93.2	**3273**	51	**545**	53.9	**642**
total jaw length (tjl)	67	**2040**	71.7	**2508**	34.5	**304**	42.9	**570**
3th lower molariform lgth.	4.5	**1095**	2.7	**324**	4.7	**1912**	2.3	**194**
idem width	4.9	**2684**	1.9	**574**	2.4	**1148**	1.1	**113**
idem area	22	**1653**	5.1	**443**	11.2	**1513**	2.5	**145**
l postcan row lgth (pcrl)	18.2	**1095**	—-	—-	—-	—-	—-	**—-**
idem area (lpcta)	80.2	**2684**	—-	—-	—-	—-	—-	**—-**
up postcan row lgth (pcru)	17	**1653**	—-	—-	—-	—-	—-	**—-**
idem area (upcta)	78.6	**1095**	—-	—-	—-	—-	—-	**—-**

metic and geometric means of the 38 estimates obtained were 1713 kg and 891 kg, respectively, and their appropriate standard deviations were 3230 kg in the first case and 3 kg in the second case. Median and mode were 1041 kg and 1448 kg. Log-normal distribution was warranted (χ^2 = 11.1, degrees of freedom = 7, P < 0.13). Again, most of the difference is explained by only one measurement, namely, as in the previous species, the transverse diameter of the femur, which gave a maximum of more than 20 000 kg. As in the other two species of sloths, the arithmetic average of predicted values from limb bone dimensions (2168 kg) was higher than the global average, while the average for skull and lower jaw measurements was 932 kg. The average without considering the transverse diameter of the femur fell to 1216 kg.

Jerison (1973) reported an estimate of 1100 kg for the mass of one species of *Glossotherium* (*"Paramylodon" harlani*) from the Rancholabrean (late Pleistocene of North America), which was very close to our average.

Scelidotherium leptocephalum Owen
(**Table 3, Fig. 2d**)

Specimens: MLP 3-401, skeleton and MLP 3-420, skull. The specimen 3-401 is exhibited at Sala VII of Museo de La Plata. It was figured by Lydekker (1894, Plate LVI).
Locality: Buenos Aires Province, Argentina.
Stratigraphy: Upper Pampean "Formation".

This is the smallest of the four species of ground sloths considered here. We obtained 39 estimates, whose arithmetic and geometric means were 1057 kg and 594 kg, respectively. Standard deviations were 1060 kg in the first case and 3.4 kg in the second case. The distribution of the estimates was indistinguishable

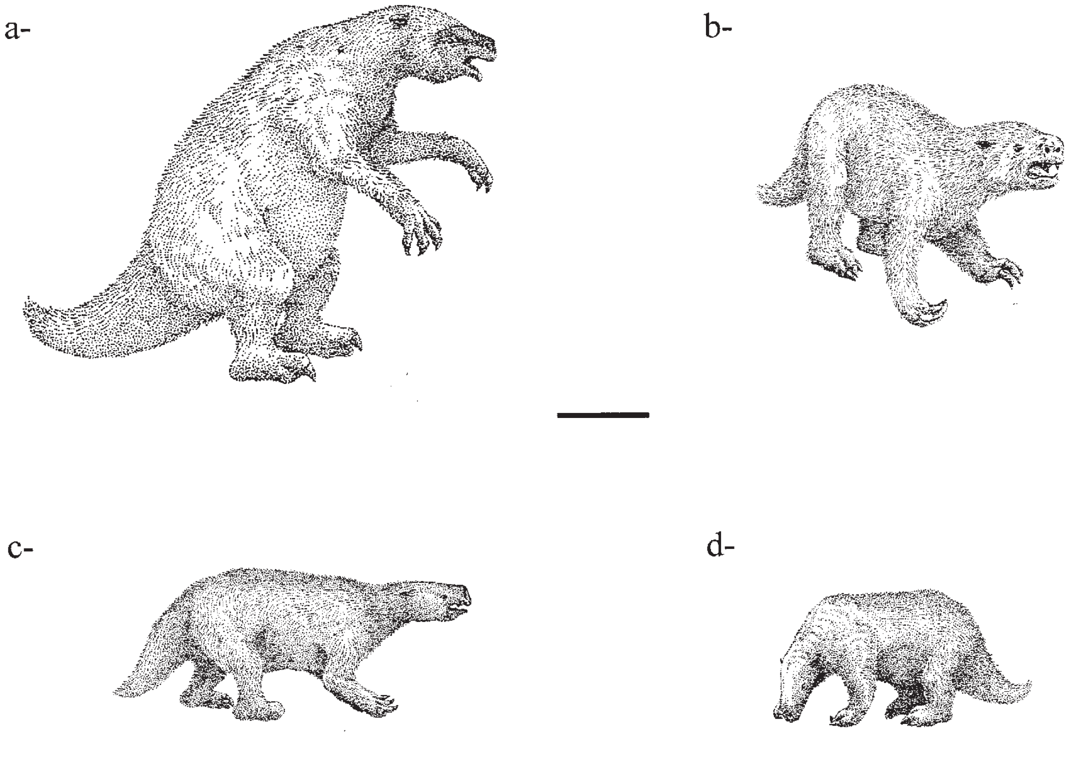

Fig. 2. Reconstruction of a) *Megatherium americanum*, b) *Lestodon armatus*, c) *Glossotherium robustum* and d) *Scelidotherium leptocephalum* (from Fariña and Vizcaíno, 1995). Scale: 1m.

from log-normal (χ^2 = 12.0, degrees of freedom = 7, P > 0.1). Median was 633 kg and mode was 724 kg. As usual, limb bone dimensions average (1373 kg) was higher than general average, but the measurement that yielded the maximum was the distal articular surface width of the humerus (Scott's, 1990, H5), more than 4 000 kg. Skull and lower jaw measurements yielded an average for the estimates of 551 kg.

LITOPTERNA
MACRAUCHENIIDAE

Macrauchenia patachonica
(**Table 4, Fig. 3a**)

Specimen: MLP 12-1424, complete skeleton. It had been figured by Sefve (1924: 5-14, 17-18). It is now mounted and exhibited at Sala VI of the Museo de La Plata.
Locality: Arrecifes, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation" (Lujanian Age).

One of the length of the femur (Scott's, 1990, F2) was measured as in equids, and, therefore, the appropriate equation for equids was used.

The arithmetic mean of the 66 estimates for this species was 988.1 kg, and the geometric mean was a bit lower, 830 kg. Standard deviations differed markedly, as was for xenarthrans: in the first case it was as much as 591.9 kg, while the equivalent for a log-normal distribution of the results was only 1.8 kg. This latter distribution was not warranted (χ^2 = 24.1, degrees of freedom = 4, P > 0.0001). However, if the lowest estimate is not considered, the rest of the estimates do show a log-normal distribution (χ^2 = 2.37, degrees of freedom = 3, P < 0.7). Median and mode turned out to be, respectively, 781 kg and 1024 kg. Generally, limb bone dimensions tended to yield overestimations, with an average of 1287.8 kg, and a maximum of about 2843.3 kg for the transverse diameter of the femur (Scott's, 1990, F6). Craniodental dimensions tended to yield underestimations, with an average of 757.5 kg, and a minimum of 123 kg for the palatal width.

In Fariña (1996), the mass of *Macrauchenia patachonica* was estimated by scaling up and averaging modern species of South American Camelidae, assumed to be morphologically similar to this extinct litoptern. Also, Fariña and Blanco (submitted) used a scale model. In both cases, a figure of 1100 kg was obtained.

NOTOUNGULATA
TOXODONTIDAE

Toxodon platensis
(**Table 4, Fig. 3b**)

Specimen: MLP 12-1125, complete skeleton. It is now mounted and exhibited at Sala VI of the Museo de La Plata.
Locality: Arrecifes, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation" (Lujanian Age).

The arithmetic mean of the 58 estimates for this species was 1642 kg, and the geometric mean was a bit lower, 1187 kg. Standard deviations differed markedly too: in the first case it was as much as 1347 kg, while the equivalent for a log-normal distribution of the results was only 2.3 kg. The distribution of the estimates was log-normal (χ^2 = 3.8, degrees of freedom = 5, P > 0.55), and it was bimodal: 724 kg and 2896 kg. Median was 1191 kg. Again, limb bone dimensions tended to yield overestimations, with an average of 1813.7 kg, and a maximum of about 6795 kg for the anteroposterior diameter of the tibia (Scott's, 1990, T7). Craniodental dimensions tended to yield underestimations, with an average of 1553.4 kg, and a minimum of 213 kg for the second lower premolar width.

A scale model had also been used to estimate the mass of *Toxodon platensis* (Fariña and Álvarez, 1994). Jerison (1973) reported similar estimates for the masses of *Toxodon*. Both estimates turned out to be the same, 1100 kg.

PERISSODACTYLA
EQUIDAE

Hippidion principale
(**Table 4, Fig. 3c**)

Specimen: MLP 6-64, a cast of the holotype of *H. bonaerense*, considered a junior synonym

Table 4. Measurements and predictions for the three species of Lujanian ungulates (*Notoungulata, Litopterna* and *Perissodactyla*) considered.

	Macrauchenia patachonica		*Toxodon platensis*		*Hippidion principale*	
Measurement	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**
sum of **humerus** + **femur** circumference	47	**1656**	51.5	**2126**	32	**580**
humerus length (H1)	33	**625**	38	**1011**	28	**446**
humerus length (H2)	33	**439**	44	**1166**	29.5	**429**
condylar width (H3)	8.8	**666**	10	**942**	8	**562**
trochlear width (H4)	13	**1644**	15	**2345**	9.2	**627**
distal width (H5)	14.2	**1793**	21	**4912**	9.5	**504**
transverse diameter (H7)	8	**2176**	9.5	**3335**	4	**432**
anteropost diameter (H8)	7	**963**	9	**1801**	5.5	**621**
radius length (R1)	59	**1647**	33	**315**	30.5	**339**
distal art surf width (R2)	9.7	**765**	—	**—**	9	**576**
distal art surf height (R3)	7	**1598**	—	**—**	5.2	**751**
distal width (R4)	9.7	**573**	—	**—**	9.8	**549**
maximum width (R5)	12	**1243**	—	**—**	9.1	**556**
transverse diameter (R6)	9.4	**2685**	5	**524**	4.8	**529**
anteropost diameter (R7)	4.2	**1063**	4.8	**1485**	2.8	**373**
ulnar length (U1)	68	**1397**	44	**382**	39.5	**361**
femur length (F1)	59	**1824**	54	**1340**	34	**337**
femur length (F2)	54	**1024**	42	**484**	37.5	**345**
3rd trochanter - distal end (F3)	29	**560**	—		27	**457**
trochlear width (F5)	13	**1225**	14.5	**1660**	9.5	**374**
transverse diameter (F6)	8	**2843**	8.5	**3374**	5.5	**673**
anteropost diameter (F7)	5.5	**689**	6.5	**1064**	5.5	**435**
tibia length (T1)	42	**436**	35	**227**	29.5	**307**
proximal width (T2)	13.5	**935**	14.8	**1215**	10.2	**409**
prox ant post diam (T3)	6	**392**	12.5	**3979**	5.4	**334**
distal transverse width (T4)	11	**1381**	8.5	**705**	8.9	**538**
distal anteroposterior width (T5)	7.8	**1677**	8.3	**2007**	5.4	**445**
transverse diameter (T6)	7	**1549**	4	**335**	4.9	**503**
anteropost diam (T7)	6.1	**1875**	9.5	**6795**	4.4	**586**
occipital height (och)	13	**479**	25	**3625**	11	**292**
basicranial (bcl)	22	**1410**	26.5	**2528**	20	**908**
masset fossa length (mfl)	18	**259**	33	**1551**	24	**607**
palatal width (paw)	5	**123**	13	**2796**	7.5	**647**
muzzle width (mzw)	6.7	**355**	10	**897**	6.4	**630**
post skull length (psl)	17	**263**	30	**1262**	23.5	**631**
mand ang height (dma)	16.5	**446**	37.5	**3328**	22.5	**691**
post mand length (pjl)	17	**997**	12.5	**475**	15	**746**
width mand ang (wma)	19.5	**1836**	20.5	**2113**	13	**416**
molar row length (lmrl)	11	**731**	16	**2486**	9	**473**
premolar (lprl)	12	**2102**	13.5	**2880**	9.5	**672**
ant jaw length (ajl)	17	**355**	24.5	**991**	23.5	**993**
total skull length (tsl)	45	**375**	67	**1226**	52.5	**633**
total jaw length (tjl)	45	**654**	53	**1049**	47.5	**822**
2nd low prem leng (SLPL)	2.4	**613**	1.9	**368**	3.5	**916**
idem width (SLPW)	1.2	**622**	0.7	**213**	1.7	**806**
3rd low prem leng (TLPL)	2.4	**522**	2.4	**522**	2.9	**568**
idem width (TLPW)	1.7	**797**	1.4	**518**	2.1	**949**
4th low prem leng (FLPL)	3	**945**	2.7	**687**	2.1	**193**
idem width (FLPW)	1.9	**830**	1.7	**629**	2.1	**767**
idem area (FLPA)	5.7	**933**	4.6	**691**	4.4	**395**

(Cont. Table 4)

	Macrauchenia patachonica		*Toxodon platensis*		*Hippidion principale*	
Measurement	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**	**Value (cm)**	**Prediction (kg)**
1^{st} low molar l^{gth} (FLML)	2.9	**701**	5.2	**4713**	2.7	**435**
idem width (FLMW)	1.9	**693**	1.8	**592**	1.9	**545**
idem area (FLMA)	5.5	**709**	9.4	**1630**	5.1	**488**
2^{nd} low molar l^{gth} (SLML)	4	**1141**	4.9	**2184**	2.4	**230**
idem width (SLMW)	2	**669**	1.5	**285**	2.1	**647**
idem area (SLMA)	8	**896**	7.3	**777**	5	**386**
3^{rd} low molar l^{gth} (TLML)	4	**522**	5.6	**1522**	2.6	**255**
idem width (TLMW)	1.8	**549**	1.8	**549**	1.6	**399**
idem area (TLMA)	7.2	**574**	10.1	**979**	4.2	**327**
2^{nd} upp molar l^{gth} (SUML)	4.5	**1482**	5.1	**2208**	2.7	**288**
idem width (SUMW)	2.9	**721**	4.5	**2699**	2.9	**479**
idem area (SUMA)	13.1	**1069**	22.9	**2287**	7.8	**371**
3^{rd} upp molar l^{gth} (M^3l)	3.8	**830**	—	**—**	2.5	**256**
idem width (M^3w)	2.6	**536**	—	**—**	2.4	**430**
idem area (M^3a)	9.9	**529**	—	**—**	6	**253**
head + body	315	**595**	290	**458**	250	**205**

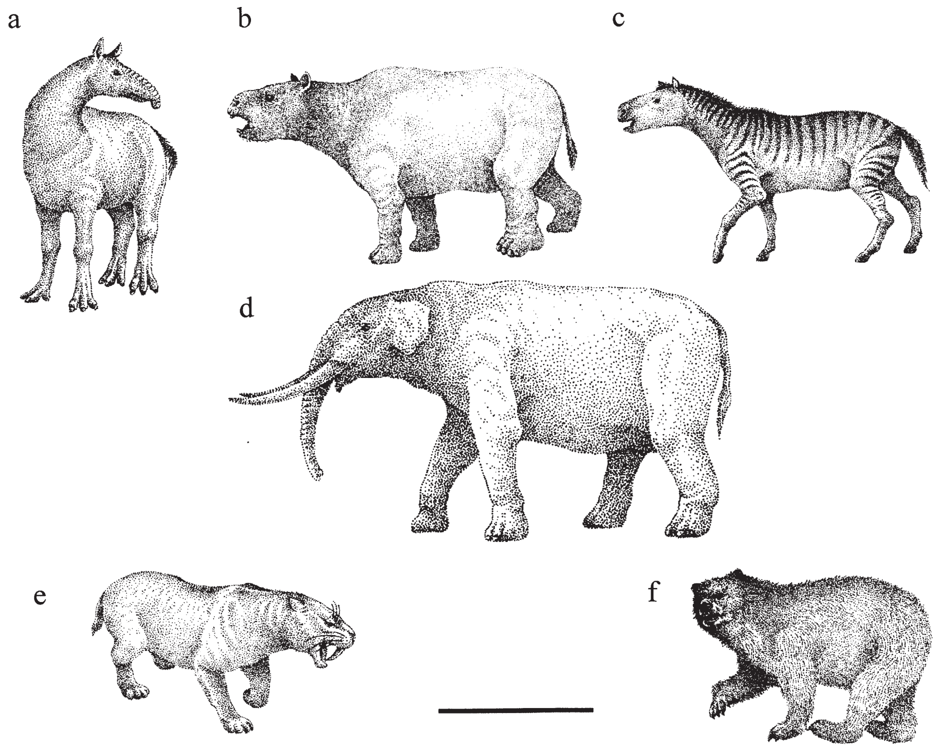

Fig. 3. Reconstructions of a) *Macrauchenia patachonica,* b) *Toxodon platensis*, c) *Hippidion principale*, d) *Stegomastodon superbus,* e) *Smilodon bonaerensis* and f) *Arctodus* sp. (from Fariña and Vizcaíno, 1995). Scale: 1m.

of *H. principale* by Alberdi and Prado (1993), exhibited at Sala VIII of Museo de La Plata.
Locality: Luján, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation" (Lujanian Age).

A total of 66 estimates was obtained, with more coherent results than in other Lujanian species. Its arithmetic mean was 511 kg, with a relatively lower standard deviation than in previous cases, 187 kg. Geometric mean was 476 kg, and its standard deviation only 1.5 kg. Median turned out to be 483 kg. Geometric and arithmetic modes were very similar too: 512 kg and 500 kg, respectively. Log-normal distribution of the estimates was not warranted (χ^2 = 10, degrees of freedom = 2, P < 0.01). Surprisingly, the estimates followed a normal distribution (χ^2 = 15.6, degrees of freedom = 8, P > 0.05). This (and also the higher coherence among the statistics) might be attributed to the fact that this species has very close modern relatives, whereas the others have not. Different from the other species considered here, the average of the limb derived estimates was lower than that from the craniodental measurements: 482 kg and 534 kg, respectively. The higher estimate was obtained from the anterior jaw length (933 kg), and the lower from the first lower premolar length (193 kg).

Alberdi et al. (1995) estimated the mass of *H. principale* as 460.35 kg using a different set of equations. The mass of another Lujanian equid, *Equus (Amerhippus) neogeus*, was regarded as not being very different from *E. caballus* (Prado and Alberdi, 1994), and conservatively estimated to be 300 kg in Fariña (1996).

PROBOSCIDEA
GOMPHOTHERIIDAE

Stegomastodon superbus
(**Table 5, Fig. 3d**)

Specimen: MLP 50-VII-1-2.
Locality: Chelforó Creek, Ayacucho, Buenos Aires Province, Argentina.
Stratigraphy: Pampean "Formation" (Lujanian Age).

Only 23 estimates were obtained for this species, probably the largest of the Lujanian fauna and rivalled only by *Megatherium*. It should be taken into account that one measurement (shoulder height, a very usual estimate for the mass of modern elephants) was used in 12 equations, identified as *a* to *l* in **Table 5**. The arithmetic mean turned out to be 7580 kg, and the geometric mean 4311 kg. The standard deviations were 11995 kg and 2.54 kg, respectively. Log-normal distribution of the estimates was not warranted (χ^2 = 20, degrees of freedom = 5, P < 0.001). The median was 2831 kg, and the mode 4096 kg. The maximum value was yielded by the equation for the muzzle width (more than 56 tonnes), and the minimum one by the femur length (1458 kg).

A mass estimate of 4 tonnes had been used for *Stegomastodon superbus* by Fariña (1996), based on a conservative comparison with modern African elephants, whose proportions were considered roughly similar to, or perhaps a bit smaller than, this extinct South American gomphotheriid.

Table 5. Measurements and predictions for the species of Lujanian proboscidean considered.

		Stegomastodon superbus
Measurement	**Value (cm)**	**Prediction (kg)**
sum of **humerus** + **femur** circumference	83.9	**8235**
humerus length (H1)	83.0	**1781**
femur length (F1)	96.0	**1458**
humerus circumference	45.9	**8420**
femur circumference	38.0	**7442**
shoulder height (eqn. *a*)	244.1	**2717**
shoulder height (eqn. *b*)	244.1	**2424**
shoulder height (eqn. *c*)	244.1	**2497**
shoulder height (eqn. *d*)	244.1	**2378**
shoulder height (eqn. *e*)	244.1	**2432**
shoulder height (eqn. *f*)	244.1	**2233**
shoulder height (eqn. *g*)	244.1	**2446**
shoulder height (eqn. *h*)	244.1	**2105**
shoulder height (eqn. *i*)	244.1	**2831**
shoulder height (eqn. *j*)	244.1	**2892**
shoulder height (eqn. *k*)	244.1	**3337**
shoulder height (eqn. *l*)	244.1	**3334**
muzzle width (mzw)	60	**5661**
palatal width (paw)	12	**2152**
masset fossa length (mfl)	75	**1748**
occipital heigth (och)	53	**2391**
posterior skull length (psl)	57	**7408**
basicraneal length (bcl)	38	**7830**

CARNIVORA
FELIDAE

Smilodon bonaerensis
(**Table 6a, Fig. 3e**)

Specimen: MACN 46, holotype, exhibited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" and figured by Méndez Alzola (1941). Cortical area of humerus was taken from the humerus MLP 62-VII-27-124, which is similar in size to the holotype, and that of femur, from the also similar-sized femur MACN 10037.
Locality: Luján, Buenos Aires Province, Argentina.
Stratigraphy: Upper Pampean (Lujanian Age)

A total of 27 estimates was obtained. Its arithmetic mean was 352 kg, with a relatively lower standard deviation than in previous cases, 161 kg. Geometric mean was 328 kg, and its standard deviation only 1.6 kg. Median turned out to be 347 kg. Geometric and arithmetic modes were 316 kg and 350 kg, respectively. Log-normal distribution of the estimates was not warranted ($\chi^2 = 27$, degrees of freedom = 4, $P << 0.001$), but the normal distribution was ($\chi^2 = 5.9$, degrees of freedom = 6, $P > 0.42$). As in this case of *Hippidion*, the smaller standard deviation, the higher coherence among the statistics and the fact that the estimates have a normal distribution might be attributed to the fact that this species has very close modern relatives. Some estimates derived from the same measurements using equations obtained for all carnivores, from felids and from large carnivores, respectively. When the felid equation was used, higher estimates were obtained. The highest estimate was obtained from the cortical area of the humerus using the equation for felids only (745 kg) and the lowest from the femoral length using the equation for all carnivores (127 kg).

Fariña (1996) used a figure of 300 kg for this species. Anyonge (1993) obtained an average mass of 352 kg for the smaller North American species of the genus, *S. fatalis*. When the average of our estimates using only Anyonge's equations (those derived from limb bone dimensions) for *Smilodon bonaerensis* are compared to those he presented for the giant North American lion *Panthera atrox*, a difference of 8 kg is obtained in favour of the latter. This difference is, of course, of no statistical or biological significance, and a femur larger than that of the holotype is kept in the Buenos Aires Museum (MACN 6195). The estimates obtained after this other specimen are substantially larger than those above, although of course much more partial. Therefore, it can be concluded that both species are the largest felids known to have existed.

CARNIVORA
URSIDAE

Arctodus sp.
(**Table 6b, Fig. 3f**)

Specimen: MACN 9645.
Locality: Partido de Tres Arroyos, Buenos Aires Province, Argentina.
Stratigraphy: "Right bank of the River Quequén Salado (yellowish sediment)".

As only three measurements were available, namely total skull length, postorbital length and m_1 length, the significance of the estimates is of less importance than in the other taxa under study. Once the appropriate equations for carnivores, ursids and large carnivores were applied, an overall average of 308 kg was obtained. The same set of equations was applied to the data in Van Valkenburgh (1990) for the *Arctodus* living closest relative, the spectacled bear *Tremarctos ornatus*. The actual mass of *Tremarctos ornatus* was given in Van Valkenburgh (1990) as 134.9 kg, and the average underestimated it as 94.2 kg. Therefore, it is reasonable to expect that a more complete data set will yield a higher average for *Arctodus*. In Fariña (1996), the mass of *Arctodus* had been tentatively judged to be 500 kg.

GENERAL REMARKS

Most of the species considered in this contribution were megamammals in the strict sense **Table 7**, i.e. their adult body mass has to be

Table 6a. Measurements and predictions for *Smilodon banaerensis*, one of the two species of Lujanian Carnivora considered.

	Smilodon bonaerensis	
Measurement	**Value (cm)**	**Prediction (kg)**
sum of **humerus** + **femur** circumference	26.5	**347**
humerus length (all)	36	**240**
anteropost 2nd mom area (all)	5.7	**364**
transverse idem (all)	4.4	**693**
cortical area hum (all)	14.8	**563**
humerus length (felids)	36	**296**
anteropost 2nd mom area (felids)	5.7	**467**
transverse diameter (felids)	4.4	**693**
cortical area (felids)	14.8	**745**
femur length (all)	33.5	**127**
anteropost 2nd mom area (all)	3.3	**202**
transverse idem (all)	3.8	**225**
cortical area (all)	73.9	**352**
articular area (all)	46.8	**488**
femur length (felids)	33.5	**151**
anteropost 2nd mom area (felids)	3.3	**362**
transverse idem (felids)	3.8	**268**
cortical area (felids)	73.9	**378**
articular area (felids)	46.8	**484**
m_1 length (all)	3.3	**174**
orbito-occiput length (all)	25.5	**346**
skull length (all)	396	**347**
m_1 length (felids)	3.3	**303**
orbito-occiput length (felids)	25.5	**456**
skull length (felids)	39.6	**500**
m_1 length (large)	3.3	**207**
orbito-occiput length (large)	25.5	**242**
skull length (large)	39.6	**277**
head+body length (all)	210	**213**
head+body length (felids)	210	**161**
head+body length (large)	210	**247**

Table 6b. Measurements and predictions for *Arctodus* sp., one of the two species of Lujanian Carnivora considered.

		Arctodus bonaerense		
Measurement	**Value (cm)**	**Prediction (kg, all)**	**Prediction (kg, ursids)**	**Prediction (kg, large)**
m_1 length	4.1	**326**	**112**	**233**
orbit-occiput length	28.2	**488**	**296**	**282**
skull length	42	**418**	**316**	**304**

measured in tonnes or megagrams (see Owen-Smith, 1987, 1988). The only clear exception among the xenarthrans was the relatively small glyptodont *Glyptodon reticulatus*. Among the epitherians, the horse *Hippidion* and the two carnivores had body masses below the limit of the metric tonne, but far above 100 kg. Less clear are the cases of the two other glyptodonts studied, namely *Panochthus tuberculatus* and *Doedicurus clavicaudatus*. Some of the statistics obtained are above 1 000 kg, while some others are below this limit. Taking into account that the use of scale models yielded estimates of 1100 kg for *Panochthus tuberculatus* and of 1400 kg for *Doedicurus clavicaudatus*, it can be concluded that the former was near the limit of this category and that most individuals of the latter exceeded that limit.

However, it is noteworthy that the estimates were obtained using allometric equations that are not based on xenarthrans or other mammals of South American ancestry. As dimensions of varied sources are used, i.e. cranial, dental and limb bone measurements, the averages are not likely to be affected by this shortcoming. Certain dimensions and equations based on non-xenarthran mammals (e.g., posterior length of jaw in glyptodonts and transverse diameter of femur at midshaft in ground sloths) clearly give incorrect predictions of body mass when applied to extinct xenarthrans. This is due to specialisations of those parts of the skeleton in xenarthrans relative to other mammals. However, the scatter of estimates is decisively influenced, reaching an impressive range in all cases. The best solution to this problem would be to create such equations, as they were done for armadillos (Fariña and Vizcaíno, 1997). A major problem in doing that is the fact that most collectors do not record the body mass of the animal they collect. Therefore, there is a regrettable paucity of data on body mass of these and other South American mammals. We would like to encourage this practice for the future.

Another difficulty is posed by the lack of living representatives of many of those lineages. Certainly, an allometric equation yielded by modern sloths would be of virtually no use whatsoever to estimate body mass in the extinct ground sloths. The enormous differences in body size and in habits prevent the researchers from drawing too many conclusions about most features of the natural history of those fossil mammals. The living sloths *Bradypus* and *Choloepus* are so highly specialised to live in the trees, hanging from their legs with their backs facing the ground, that their morphology, physiology and behaviour may hardly give any idea on the ways of life of the ground sloth. Living sloths are almost unable to walk on the ground. Moreover, they are very small

Table 7. Summary of the results obtained.

	MASS ESTIMATIONS (kg)						
Taxon	**Number of equations**	**Arithmetic mean**	**Geometric mean**	**Median**	**Mode**	**Maximum value**	**Minimum value**
Glyptodon reticulatus	43	862.3	403	457	362	7005	31
Panochthus tuberculatus	43	1061	528	701	724	9088	22
Doedicurus clavicaudatus	37	1468	613	708	512	10472	3
Megatherium americanum	44	6073	2745	2543	2896	97417	524
Lestodon armatus	40	3397	1784	1918	2896	37706	324
Glossotherium robustum	38	1713	891	1041	1448	20092	40
Scelidotherium leptocephalum	39	1057	594	633	724	4059	21
Macrauchenia patachonica	66	988.1	830	781	1024	2843	123
Toxodon platensis	58	1642	1187	1191	724/2896	6795	213
Hippidion principale	66	511	476	483	512/500	993	193
Stegomastodon superbus	23	7580	4311	2831	4096	56606	1458
Smilodon bonaerensis	27	352	328	347	350	744	127
Arctodus sp.	9	308	—	—	—	—	—

animals (less than 10 kg) in comparison to the huge *Megatherium, Glossotherium, Lestodon* and *Scelidotherium*.

In the case of glyptodonts, their closest living relatives are the armadillos (Dasypodidae). Despite some anatomic differences, they seem to resemble each other better than living sloths do ground sloths. Nevertheless, there are some constraints to that comparison, the size being one of the most important. The biggest living armadillo, *Priodontes maximus*, is known to have masses up to 60 kg, which is obviously much less than that of the Lujanian glyptodonts. Besides, while glyptodonts are regarded as having been cursorial grazers, armadillos are mostly specialised for fossoriality and insectivory.

We expect to contribute to the better understanding of the fossil xenarthrans through this approach, which might be of interest to those working on the palaeobiology of such remarkable mammals. For instance, Bargo et al. (submitted) used the body masses of the ground sloths obtained here to generate allometric equations in order to analyse some aspects of their locomotion.

Although a thorough discussion about the palaeobiological implications of the body mass of extinct xenarthrans would be beyond the scope of this paper, some preliminary considerations can be drawn. For instance, McNab (1989) proposed that most extinct Lujanian mammals were poorer thermoregulators than modern mammals. Despite the fact that their physiological traits are still to be researched on, it can be stated that large size is by itself a way to maintain a constant body temperature. Metabolic energy is produced throughout the body tissues, and hence depends on body mass, which in turn depends on body volume if overall body density can be considered invariant from one mammal to another. Volume varies to the cube of linear dimensions. On the other hand, body heat is dissipated through surfaces, which vary to the square of linear dimensions. Therefore, if the animals are fairly geometrically similar (which can be safely assumed when land mammals are considered) the larger will dissipate less energy per unit body mass than the smaller.

Another conclusion is that arboreality can be ruled out for ground sloths, corroborating early impressions. Jaguars and leopards are among the largest modern arboreal mammals, their adult body mass being about 100 kg (Nowak, 1991). Even in the case of the smallest ground sloth studied here, *Scelidotherium leptocephalum*, juveniles must have attained this size very early in their lives.

The estimates obtained for the epitherians had smaller dispersion than those of xenarthrans. This must be due to the fact that the allometric equations used are not based on xenarthrans or other mammals of South American ancestry, but on mammals more closely related to those studied here. As one anonymous reviewer pointed out, this is another clear instance of how we cannot always extrapolate from living animals to extinct fossil groups. There are many features in the structure and biology of large extinct xenarthrans that were completely unlike those of the epitherians from which the equations were developed. Several of the body-mass estimates derived from the hind limb bones seem to be gross overestimates. It may be speculated that it is somehow related to unusual development of hind limb bone shape relevant to bracing the rear end while swinging the tail club in glyptodonts, or for standing bipedally (or tripodally with the heavy tail) in giant ground sloths. Certainly, these are questions to be addressed in the future palaeoecological and morphofunctional studies applying the predicted body masses.

As mentioned before, these estimations could be used as the starting point for palaeobiological studies of this extinct fauna, characterised for the very large size of many of its members. Some of them are congruent with previous estimations used in biomechanical and ecological analysis. That is the case of the studies on the escape strategy of *Macrauchenia patachonica* (Fariña and Blanco, submitted) and the locomotion and posture of *Toxodon platensis* (Fariña and Álvarez, 1994). On the other hand, some of the mass estimations used in the palaeoecological approach by Fariña (1996) show rather different figures, such us the ones of *Stegomastodon superbus* and *Arctodus* sp. Although they do not invalid the hypothesis defended in that paper, they deserve further studies based on more data.

Finally, it is noteworthy that most of the estimations in this paper were obtained on single individuals. Up to now only a few other complete specimens are available in different museums all over the world. It would be highly desirable to have a greater sample to analyse the individual variation for each species. This is one of many aspects of the palaeontological research that reopens the interest on the recovery of complete specimens from Quaternary sediments of the Pampean Region, rather abandoned during the last decades.

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