VOL. 53 | ISSUE 3

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Abstract. *Notiolofos arquinotiensis* is the most abundant terrestrial placental mammal in the Paleogene of the Antarctic continent. Evidence suggests a South American origin of Sparnotheriodontidae, and an allopatric speciation event for the appearance of *N. arquinotiensis*. It was recorded exclusively on Seymour Island, through most of the La Meseta and Submeseta formations. Isotopic and paleomagnetic calibration of the units indicate a relatively continuous fossil record of at least 17.5 Ma. The stasis hypothesis is tested here as opposite to the possibility of a wider and previously non-identified specific diversity of Antarctic sparnotheriodontids. The material of *N. arquinotensis* available was compared in preservation, characters and dental occlusal areas to the more complete phylogenetic relative *Sparnotheriodon epsilonoides* and the North American *Meniscotherium chamense*. Despite there being no close phylogenetic relationship between *Notiolofos* and *Meniscotherium*, the morphological dental similarity between them suggests they could be interpreted as ecologically equivalent taxa. The analysis allows the reassignment of some *N. arquinotensis* teeth to other dental loci. The results indicate that there are no reasons to justify the presence of different species through the stratigraphic sequence or to refute the morphological stasis in *N. arquinotensis*. Stasis among Antarctic Eocene vertebrates is also recorded among Eocene penguins. The "*Plus ça change*" model indicate that morphological stasis and punctuated equilibrium were detected as the usual responses to widely fluctuating physical environments such as those characteristic of temperate regions and shallow waters. This model fits well with inferences on Antarctic paleoclimate and paleogeography and the land fossil record.

Key words. Antarctica. Eocene. Sparnotheriodontidae. Evolutionary stasis. *Plus ça change*.

Resumen. CONSIDERACIONES SOBRE LA ESTASIS EVOLUTIVA DE *NOTIOLOFOS ARQUINOTIENSIS* (MAMMALIA), EOCENO DE LA ISLA SEYMOUR, ANTÁRTIDA. *Notiolofos arquinotiensis* es el mamífero placentario más abundante del Paleógeno del continente antártico. La evidencia sugiere un origen sudamericano de los Sparnotheriodontidae y un evento de especiación alopátrica en la aparición de *N. arquinotiensis*. Esta especie ha sido registrada exclusivamente en la Isla Seymour, en la mayor parte de los niveles de las formaciones La Meseta y Submeseta. La calibración isotópica y paleomagnética de estas unidades indican un registro fósil continuo de al menos 17,5 Ma. La hipótesis de un evento de estasis evolutiva fue testeada en contraposición a la posibilidad de una diversidad específica mayor en el registro de sparnotheriodontidos de la Antártida. Los materiales disponibles de *N. arquinotensis* fueron comparados en sus distintos estados de preservación, caracteres y las áreas oclusales de sus dientes, con el más completo representante de la familia, *Sparnotheriodon epsilonoides* y con *Meniscotherium chamense* de América del Norte. Aunque no existe una relación filogenética próxima entre *Notiolofos* y *Meniscotherium,* la similitud en la morfología dental sugiere una probable equivalencia ecológica. El análisis realizado ha permitido reasignar los locus de algunos elementos dentales de *N. arquinotensis*. No existen elementos para justificar la presencia de otras especies a lo largo de la secuencia estratigráfica o para refutar la estasis morfológica de dicho taxón. Eventos de estasis se registran también en otros vertebrados del Eoceno de Antártida tales como los pingüinos. El modelo "*Plus ça change*" indica que la estasis morfológica y el equilibrio puntuado son una respuesta usual en ambientes con fluctuaciones físicas, como aquellos de regiones templadas o aguas someras. El modelo es una buena explicación para integrar el registro fósil terrestre y las inferencias sobre el paleoclima y la paleogeografía de Antártida.

Palabras clave. Antártida. Eoceno. Sparnotheriodontidae. Estasis evolutiva. *Plus ça change*.

SPARNOTHERIODONTIDAE is a Paleogene group of ungulates recorded in South America and Antarctica. Their phylogenetic relationship with other South American native ungulates remains contentious, since most of the authors

consider them as part of the order Litopterna (*e.g.*, Soria, 2001; Bond *et al.*, 2006; Gelfo *et al.*, 2015), while others suggest placing them within "Condylarthra" (Cifelli, 1993; Bergqvist, 1996, 2008). The main problem in order to iden-

tify the systematic position of sparnotheriodontids is that their alpha taxonomy was defined on the basis of isolated teeth and a few jaw remains. The last revision of the family considered them as part of the Litopterna (Soria, 2001; Bond *et al.*, 2006) and this interpretation is briefly discussed and followed here.

Updated biochronological and isotopic studies (Clyde *et al.*, 2014; Woodburne *et al.*, 2014) indicate that sparnotheriodontids are known in Brazil from early Eocene fissure fills in Itaboraí, Río de Janeiro; in middle Eocene localities in Argentina, *i.e.* Cañadón Vaca, Paso del Sapo and coeval localities in Patagonia and Divisadero Largo, Mendoza; and the Eocene of Seymour Island in Antarctica.

Bond *et al.* (1990) first identified the sparnotheriodontid affinities of one isolated upper molar (MLP 90-1-20-1) from the Eocene of Antarctica. This, and other remains collected in successive DNA-IAA field trips, were identified as a new species of *Victorlemoinea* (Marenssi *et al.*, 1994; Vizcaíno *et al.*, 1997), a well-known taxon from the early Eocene of South America represented by *V. labyrinthica* from Cañadón Vaca, Chubut Province, Argentina (Ameghino, 1901) and *V. prototypica* from São José de Itaboraí, Brazil (Paula Couto, 1952). Further studies indicated that the Antarctic sparnotheriodontid was endemic at the generic level (Bond, pers. com, in Reguero *et al.,* 1998) and so, described as *Notolophus arquinotensis* (Bond *et al.,* 2006). The monotypic genus was later replaced by *Notiolofos* (Bond *et al.*, 2009) because the first was a preoccupied name.

Two biogeographic hypotheses were proposed in order to explain the early Eocene Antarctic record of sparnotheriodontids and astrapotherians, which were also recorded in this continent (Hooker, 1992; Bond *et al.*, 2011). A dispersal event across a land connection (Weddellian Isthmus) between South America and Antarctica and a vicariance event resulted both from a pan-Gondwanan distribution prior to the fragmentation of the Gondwanaland mass (Reguero *et al.*, 2013).

Notiolofos arquinotensis includes isolated teeth recorded through the La Meseta Formation allomembers, formed from base to top by the Acantilados II, Campamento, Cucullaea I, and, Submeseta Formation (Bond *et al.*, 1990; Gelfo *et al.*, 2015). Isotopic and paleomagnetic calibration of the La Meseta and Submeseta formations (Montes *et al.*, 2013) indicates the presence of *N. arquinotensis* during a minimum

time of 17.5 Ma. Well known sequences and large data sets of other Eocene mammals (*e.g.*, *Hyopsodus*) also show little change in size or morphology but in a shortened period of not more than one million years (Gingerich, 1976; West, 1979). In contrast, this duration is longer for *N. arquinotensis* than for most known mammal species considering all the Cenozoic. The average duration of fossil mammal species –or, in other terms, the presence of morphological stasis– indicates that average species durations are in the order of 2–4 Ma (Prothero and Heaton, 1996; Prothero, 2014). The extremely long species duration of *N. arquinotensis* can only be compared to that of Neogene genera and species of small Old World mammals (Insectivora, Rodentia, and Lagomorpha), with a longevity range between 11–17 Ma (Liow *et al.*, 2008).

The recognition of genera and species in paleontology is based on an arbitrary and subjective selection of traits. The assumed longevity of *N. arquinotensis* rests in the impossibility of detecting qualitative or quantitative morphological variation in the dental remains assigned to it (Bond *et al.*, 2006; Gelfo *et al.*, 2015). This stasis could be interpreted as an evolutionary pattern in which a character state remains unchanged through time (Burt, 2001) or the presence of little or no net accrued species-wide morphological change during the existence of a species-lineage (Eldredge *et al.*, 2005). In order to test morphological stability, a paleospecies requires a profuse fossil sample throughout the stratigraphic sequence. This is not the case of *N. arquinotensis,* which is known neither from a complete dental series nor abundant teeth, with a hypodigm including isolated teeth from different loci and stratigraphic levels.

The purpose of this work is to describe new remains here assigned to *N. arquinotensis*, to discuss the teeth loci of their hypodigm, assess their stratigraphic distribution, and the role of morphological stasis in this context.

Institutional abbreviations. **AMNH,** American Museum of Natural History, New York, USA; **DGM,** Divisão de Geologia e Mineralogia do Departamento Nacional da Produção mineral, Brazil; **DNA,** Dirección Nacional del Antártico, Ciudad Autónoma de Buenos Aires, Argentina; **DPV,** División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; **IAA,** Instituto Antártico Argentino, Universidad Nacional de San Martín, San Martín, Argentina; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Riva-

davia", Ciudad Autónoma de Buenos Aires, Argentina; **MCN-PV,** Museu de Ciências Naturais, Paleontologia de Vertebrados, Porto Alegre, Brazil; **MCT,** Museu de Ciências da Terra, Coleção de Mamíferos Fósseis, Rio de Janeiro, Brazil; **MLP,** Museo de La Plata, La Plata, Argentina; **MNRJ,** Museu Nacional, Rio de Janeiro, Brazil; **NMMNH,** New Mexico Museum of Natural History, Albuquerque, New Mexico. *Other abbreviations.* **CAV,** summer Antarctic fieldtrip; **HSB,** Hunter–Schreger Bands; **PDS,** profile of dental series; **Pre**

CAV, early summer Antarctic fieldtrip; **TELM,** Tertiary Eocene La Meseta.

MATERIALS AND METHODS

The hypodigm *Notiolofos arquinotiensis* and several specimens referred to it (Bond *et al.*, 2006; Gelfo *et al.*, 2015) are also included in the present analysis. All of them came from different levels of Seymour Island, Antarctica (Tab. 1) and are housed in the División Paleontología Vertebrados,

TABLE 1 – Notiolofos arquinotiensis *specimens.*

Stratigraphic and geographic location	Specimen	Locus	mesio-distal	labio-lingual	log10 area
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 94-III-15-3	i2	10.8	8	111 1.93
LMF. Cucullaea I Allomember (TELM 5) - IAA 3/96	MLP 96-I-5-9	left i3	12.45	10.4	2.11
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 12-XI-1-11	right p3	trigonid 8.08 talonid 7.32 max. 16.86	trigonid 11.67 talonid 12.64 max. 12.93	2.33
LMF. Cucullaea I Allomember (TELM 5) - IAA 2/95	MLP 08-XI-30-43	left p4	trigonid 10.28 talonid 8.57 max. 18.55	trigonid 12.54 talonid 11.5 max. 24.04	2.40
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/95	MLP 04-III-3-1	right p4	trigonid 9.02 talonid 8.37 max. 17.5	trigonid 13.59 talonid 12.58 max. 13.5	2.37
LMF. Cucullaea I Allomember (TELM 4) - DPV 2/84	MLP 91-II-4-1	right m1	trigonid 9.7 talonid 11.87 max. 21.7	trigonid 11.56 talonid 12.86 max. 12.6	2.43
LMF. Acantilados II Allomember (TELM 3) - IAA 1/13	MLP 13-I-25-1[a]	right m1 or m2	-	-	-
LMF. Campamento Allomember (TELM 3) - IAA 1/92	MLP 92-II-2–135[b]	m3	-	-	-
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 01-I-1-1	right m3	trigonid 12.55 talonid 18.25 max. 31	trigonid 18.05 talonid 16.64 max. 16.8	2.71
LMF. Cucullaea I Allomember (TELM 5) - IAA 2/95	MLP 96-I-5-5	I1?	13.26	7.56	2.00
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 90-I-20-3	right I3	15.8	12.7	2.30
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/96	MLP 96-I-5-10	I3	17.2	13.8	2.37
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 91-II-4-5	right P1	10.91	6.87	1.87
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 90-I-20-5	P3	10.08	10.74[c]	2.03
LMF. Cucullaea I Allomember (TELM 5) - IAA 1/90	MLP 90-I-20-1	M1	20	20	2.60
SF (TELM 7) - DPV 16/84.	MLP 95-I-10-6	M3	25.6	25	2.80
LMF. Cucullaea I Allomember (TELM 5) - IAA 1-96	MLP 95-I-10-7	upper molar[d]	-	-	-

Abbreviations: LMF, La Meseta Formation; *SF,* Submeseta Formation; *max.,* maximum length; [a] talonid fragment; [b] labial portion of enamel; [c] lingual side broken; [d] molariform fragment.

Museo de La Plata. Comparisons were made with other Antarctic specimens housed in MLP; *Sparnotheriodon epsilonoides* MACN 18225 (holotype), an incomplete lower jaw with left and right i1-m3 from Cañadón Vaca, Oeste de Río Chico, in Chubut province; *gen. et sp. nov.* MLP 66-V-12-2 (Tejedor *et al.*, 2009) here considered as a right dP4-M2; *Victorlemoinea prototypica* right dP4: MNRJ 1477V, MNRJ 1476V and several postcranial remains from AMNH, DGM, and MCN-PV mentioned in the text.

The stratigraphy and isotopic dates of Seymour Island follow Montes *et al.* (2013). The timespans of the Antarctic taxa mentioned in the text are minimum values since isotopic dates were taken from the bases of the older and younger units were the taxon was recorded.

Dental terminology follows Soria (2001) but with modifications in order to establish homologies with the proposal for ungulate-like mammals in Nessov *et al.* (1998). The terms neoparaconid and neoparalophid (Bond, 1988; Bond *et al.*, 2006) were avoided because there is no cladistic evidence that they are in fact new structures and not the paraconid and paralophid respectively. Another important difference with dental descriptions of Bond *et al.* (2006) is the replacement of the term metalophid used by them for the lophid joining together metaconid and protoconid. The term metalophid does not advance the understanding of real homologies since it was used for different structures among ungulates. Following Nessov *et al.* (1998) the cristid, which distally closes the trigonid is the protocristid, so the normal derivation of this structure in a lophid should be protolophid, which is here preferred instead of metalophid.

Identification and differentiation between lower isolated molars and fully molarized premolars was based comparing measurements with *S. epsilonoides*. The ratio between the talonid and trigonid sizes in this species allows the differentiation of these dental types. The talonid of the molars is larger than the trigonid, whereas this relationship is reversed in the premolars (Tab. 2).

The measurements were taken with a Schwyz digital caliper. Mesio-distal and labio-lingual lengths of teeth were taken when possible. Several measurements are the minimum value since the specimens are broken. For lower molariforms the sum of the mesiodistal length of the trigonid plus the talonid could be different from the maximum length of the tooth. The area profile of the dental series was transformed in log10 and the statistics done with Microsoft Excel 2007. The profile of the dental series (PDS) is here proposed as a way to integrate dental information from different loci of a taxon. In the present work **PDS** indicates the occlusal area of each tooth of the lower or upper series. PDS for each taxon was built following the measurements in the tables (see Tabs. 1–3). Probably the area will not be always the best measure to consider in PDS comparisons, since the shape of the tooth could be very different between two compared taxa and even though still have a similar area. But, the uniformity of the dental morphology in sparnotheriodontids (Bond *et al.*, 2006) suggests that this is not the case and that the area differences could be a good predictor of the loci. Differences in size between trigonid and talonid were also considered.

Measurements of the archaic ungulate *Meniscotherium chamense* from NMMNH locality 203, Regina Member, San Jose Formation, San Juan Basin, New Mexico (Tab. 3), were taken from Williamson and Lucas (1992) and used to test the locus assignment made for *N. arquinotensis* (Bond *et al.*, 2006) and other unpublished remains. The rational basis for this comparison rests on two premises. There is a dental similarity between sparnotheriodontids and meniscotheriids, as already considered by Ameghino (1901) for *Victorlemoinea*, which allows them to be considered as ecological equivalents. They share the brachiodont structure of the molars, a similar lophoselenodont structure, strong W-shape ectolophs joining together the labial cusps of the upper molars, and a well-developed crushing protocone as the principal lingual cusp. The lower molars show a similar development of the paralophid and protolophid, and the entoconid is better distinguished from the hypolophid, particularly in the m3.

The second premise for the comparison rests on the similar lower PDS between *S. epsilonoides* –considered as a generalized sparnotheriodontid– and *M. chamense*. As a consequence the upper PDS of sparnotheriodontids could be similar to those described for *M. chamense*, if not completely in size at least in proportions. The loci of the isolated teeth of *Notiolofos arquinotiensis* were tested under these assumptions, analyzing their qualitative characters. No error or residual values were calculated because very few remains of sparnotheriodontid teeth are available for measuring.

319

TABLE 2 – Measurements of Sparnotheriodon epsilonoides *MACN 18225.*

Locus		mesio-distal	labio-lingual	mesio-distal mean	labio-lingual mean	$\log_{10}$ area
i1	right	6.76	10.12	6.095	8.925	1.73558
	left	5.43[a]	7.73			
i2	right	7.43	12.45	7.43	12.45	1.96616
	left	-	-			
i3	right	-	-	8.97	12.95	2.06506
	left	8.97	12.95			
c	right	16.14	14.43	16.45	15.535	2.40748
	left	16.76	16.64			
pm1	right	15.46	8.7	15.615	8.785	2.13728
	left	15.77	8.87			
pm2	right	trigonid 13.38	11.41	21.005	13.165	2.44174
		talonid 8.78	13.13			
		total 20.91				
	left	trigonid 12.01	11.78			
		talonid 8.57	13.2			
		total 21.1				
pm3	right	trigonid 10.43	12.97	20.58	14.32	2.46939
		talonid 9.85	14.19			
		total 20.39				
	left	trigonid 10.54	13.62			
		talonid 9.48	14.45			
		total 20.77				
pm4	right	trigonid 10.51	15.57	20.615	16.1	2.52101
		talonid 10.83	15.73			
		total 20.71				
	left	trigonid 10.36	16.25			
		talonid 10.25	16.47			
		total 20.52				
m1	right	trigonid 14.08[b]	17.06	26.785	17.465	2.67006
		talonid 13	17.37			
		total 27.1				
	left	trigonid 12.3	17.56			
		talonid 14.06	17.53			
		total 26.47				
m2	right	trigonid 14.66	19.11	30.79	19.315	2.7743
		talonid 16.79	18.63			
		total 31				
	left	trigonid 14.22	19.52			
		talonid 17.02	19.13[c]			
		total 30.58				
m3	right	trigonid 14.38	18.41	32.615	18.645	2.78398
		talonid 17.81	16.54			
		total 32.38				
	left	trigonid 14.44	18.88			
		talonid 17.14	16.86			
		total 32.85				

[a] a portion of the tooth is missing; [b] broken between the trigonid and the talonid, the measurement is approximated; [c] lingual side of the talonid is missing.

TABLE 3 – Meniscotherium chamense *dental measurements from Williamson and Lucas (1992).*

Locus	n	mesio-distal	labio-lingual	area	log area
i1	3	2.03	1.67	3.3901	0.5302
i2	3	2.4	2.07	4.9680	0.6962
i3	1	2.5	2.5	6.2500	0.7959
c1	3	2.93	2.9	8.4970	0.9293
p1	3	2.77	2.43	6.7311	0.8281
p2	5 -3*	3.4	2.43	8.2620	0.9171
p3	11	5.45	3.45	18.8025	1.2742
p4	17 -18*	7.79	trigonid 4.83 talonid 5.89	45.8831	1.6617
m1	23 - 19 -20*	7.86	trigonid 5.74 talonid 5.99	47.0814	1.6728
m2	23 - 22- 26*	8.95	trigonid 6.37 talonid 6.17	57.0115	1.7560
m3	15 - 17 - 17*	9.82	trigonid 6.08 talonid 5.29	59.7056	1.7760
l1	2	2.65	2.1	5.565	0.7455
l2	3	2.53	2.1	5.313	0.7253
l3	4	2.63	2.2	5.786	0.7624
C1	8	3.09	2.64	8.1576	0.9116
P1	1	3.6	2.8	10.08	1.0035
P2	9	4.24	3.33	14.1192	1.1498
P3	23 - 24*	6.04	6.43	38.8372	1.5892
P4	29 - 28*	7.59	8.95	67.9305	1.8321
M1	33 - 28*	8.95	10.56	94.512	1.9755
M2	26 -27*	10.27	12.29	126.2183	2.1011
M3	24 -23*	9.03	11.53	104.1159	2.0175

* Differences in the number of individual measured. In lower teeth, each n indicates specimens for mesio-distal and labio-lingual length of the trigonid, and, labiolingual length of the talonid respectively. In upper teeth each n indicates specimens for mesio-distal and labio-lingual length respectively.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758
Laurasiatheria Waddell, Okada and Hasegawa, 1999
Pan-Perissodactyla Welker *et al.*, 2015
Litopterna Ameghino, 1889
Sparnotheriodontidae Soria, 1980a

Comments. The systematic position of sparnotheriodontids is controversial, thus the whole family deserves attention. Ameghino (1901) related them with meniscotheriid condylarths. Simpson (1948) regarded *Victorlemoinea* Ameghino, 1901 as a primitive Macraucheniidae (Litopterna). This genus was later included in a new family, Sparnotheriodontidae, considered as a Notoungulata *incertae sedis* (Soria, 1980a).

Based on dental evidence, sparnotheriodontids were later considered as Litopterna (Soria, 1980b, 2001) closely related to Anisolambdidae (Soria, 2001). In contrast Cifelli (1983a, b, 1993) and Bergqvist (1996, 2008) argued that the Sparnotheriodontidae belongs to the paraphyletic order Condylarthra closely related to Didolodontidae.

The inclusion within the condylarths was based on the assignment of isolated postcranial remains to *Victorlemoinea prototypica* Paula Couto, 1952 from early Eocene rocks in the Itaboraí basin, Rio de Janeiro, Brazil. The novel idea developed by Cifelli (1983a) uses three independent methods −*i.e.*, morphology, relative size, and relative abundance− to associate isolated postcranial remains to species defined on dental elements. A right calcaneum DGM 890M and a right astragalus AMNH 55393 with alleged condylarthran characteristics were associated with doubts to *Victorlemoinea prototypica* (Cifelli, 1983a). As a consequence Sparnotheriodontidae were joined together with Didolodontidae in the new group of South American condylarths: Didolodontoidea (Cifelli, 1983b), which also includes the genera *Adiantoides* Simpson and Minoprio, 1949; *Indalecia* Bond and Vucetich, 1983; *Depaulacoutoia* Cifelli and Ortiz-Jaureguizar, 2014, and *Didolodus* Ameghino, 1897. The phylogenetic relationships of this group were ((*Victorlemoinea* (*Adiantoides-Indalecia*)) (*Depaulacoutoia* ((*Lamegoia-Didolodus*)) and it was supported (Cifelli, 1993) by two tarsal characters, *i.e.* the medial malleolar facet of astragalus extending onto the neck (character 43), and the presence of a dorsal "beak" in the distal end of calcaneus (character 44). In this analysis, sparnotheriodontids (and also Indaleciinae) traditionally placed as an Adianthidae subfamily (Bond and Vucetich, 1983; Cifelli and Soria, 1983) were removed from Litopterna. But the synapomorphies of Didolodontoidea depend exclusively on the previous association of isolated postcranial remains to the teeth of *V. prototypica*, as well as other associations assumed for the Didolodontidae (Cifelli, 1983a, 1993). Bergqvist (1996) denied the tarsal association of Cifelli (1983a, 1993) to *V. prototypica*, but associated to it ulnas (DGM 340M, DGM 341M, DGM 2423M, MCN-PV 1718), radii (DGM 343M, DGM 2431M, DGM 2433M) and humeri (DGM 889M, MCT 2314M, 2315M, 2327M). Even though the new phylogenetic analysis of Bergqvist (1996) also supported the Sparnotheriodontidae as part of "Condylarthra", the data matrix was built exclusively with post-cranial elements. As no dental characters were used the phylogenetic position obtained for *V. prototypica* depends on the taxonomic assignment of the postcranial remains.

All the postcranial associations assumed for *V. prototypica* were criticized (Wyss *et al.*, 1994; Soria, 2001; Gelfo and Lorente, 2012) and finally considered as invalid based on new regression models of a larger and statistically significant sample (Lorente, 2015). Summarizing, no certain sparnotheriodontid postcranial specimens were published; as a consequence, all the phylogenetic information still rests on dental characters, which indicate affinities with the Litopterna (Soria, 2001; Bond *et al.*, 2006).

Genus *Notiolofos* Bond, Reguero, Vizcaíno, Marenssi and Ortiz Jaureguizar, 2009

Type species. Notiolofos arquinotiensis (Bond, Reguero, Vizcaíno and Marenssi, 2006) [originally described as *Notolophus arquinotiensis* Bond, Reguero, Vizcaíno and Marenssi, 2006, p. 166–174, figs. 2–5].

Notiolofos arquinotiensis (Bond, Reguero, Vizcaíno and Marenssi, 2006)
Figures 1–2

Referred specimens. Two isolated premolars, MLP 12-XI-1-11 considered here as a right p3 and MLP 08-XI-30-43 which is assigned to a left p4.

Locality and age. Both remains came from Seymour Island, Antarctica. MLP 12-XI-1-11 from IAA 1/ 90 locality and MLP 08-XI-30-43 from IAA 2/ 95. The specimens came from
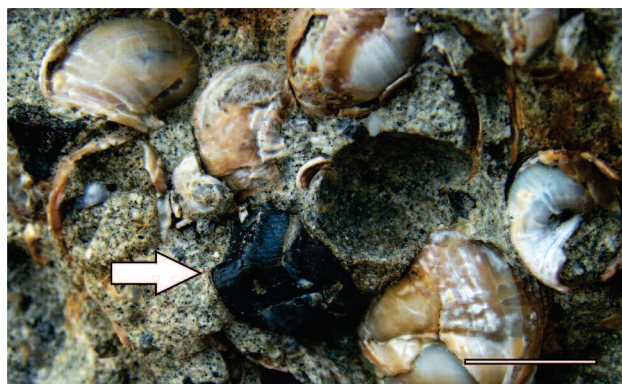
Figure 1. Rock of the naticid bank of Cucullaea I Allomember in La Meseta Formation. The white arrow indicates a right p3 of *Notiolofos arquinotiensis*, **MLP** 12-XI-1-11 as found during Pre CAV 2012, and several gastropods of the genus *Polynices.* Scale bar= 10 mm.
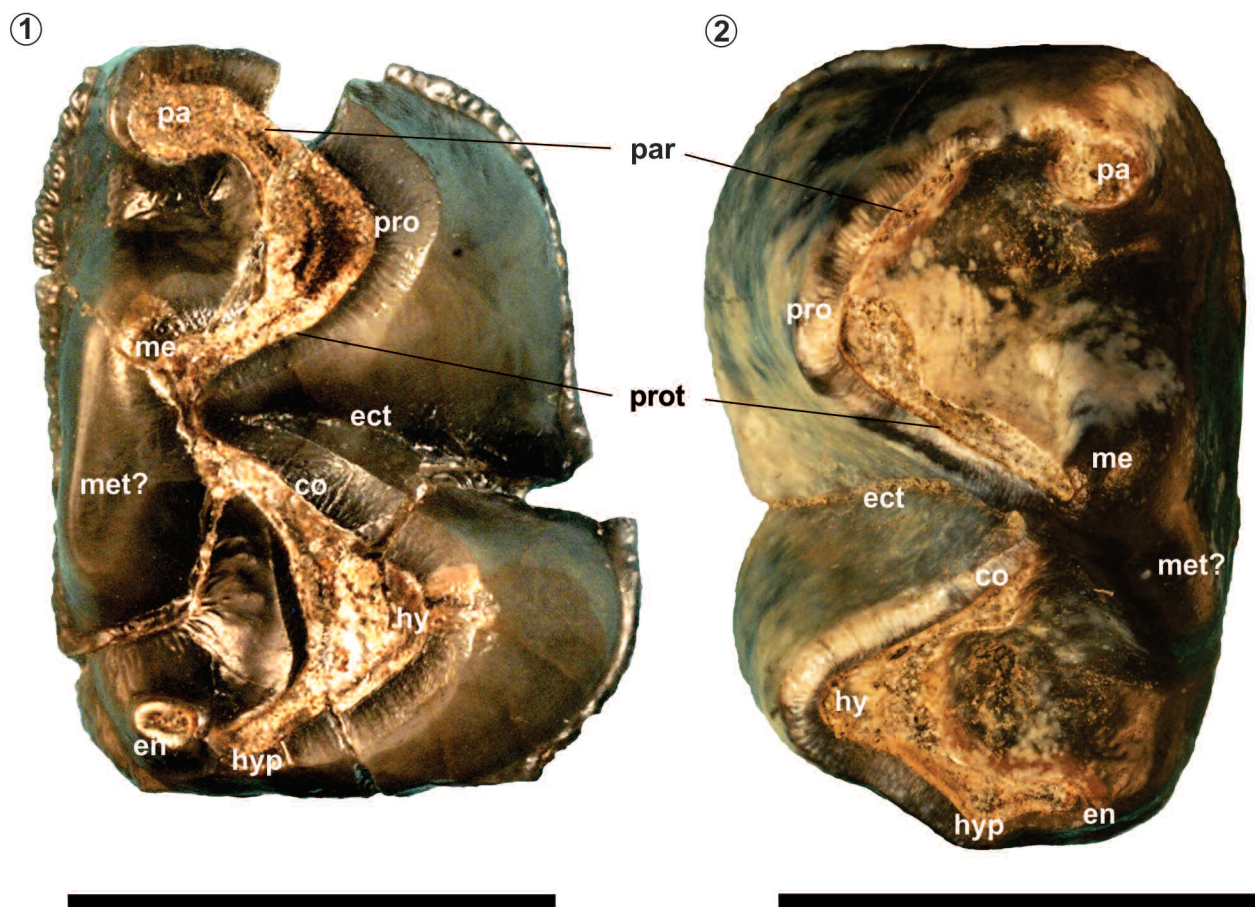
Figure 2. *Notiolofos arquinotiensis,* occlusal view of **1, MLP** 12-XI-1-11 right p3; **2, MLP** 08-XI-30-43 left p4. Abbreviations: **co,** cristid obliqua; **ect,** ectoflexid; **en,** entoconid; **hy,** hypoconid; **hyp,** hipoconulid; **me,** metaconid; **met?,** metastylid; **pa,** paraconid; **par,** paralophid; **pro,** protoconid; **prot,** protolophid. Scale bars= 10 mm.

the La Meseta Formation (Cucullaea I Allomember), early Eocene (Montes *et al.*, 2013).

Description. The p3 is a molarized tooth, with only a small portion of the mesial trigonid broken (Fig. 2). A cingulid surrounds the base of the complete tooth, and is interrupted by a distal and mesial notch in the enamel, due to the contact of the p4 and p2 respectively. The labial cingulid is not so crenulated as the lingual one, and is somewhat weaker. The protoconid is the largest cusp of the trigonid, but the metaconid is the highest due to the wear stage of the first cusp. The paraconid is differentiated from the paracristid and there is no metacristid, so the small trigonid valley is open lingually. The lingual side of the tooth is mostly formed by the metaconid with a flat lingual wall and a distal and rounded descending crest. The homology of this cristid —characteristic of sparnotheriodontids and some notoun-

gulates– with the metastylid described in archaic ungulates such as Phenacodontidae (Thewissen and Domning, 1992) and Didolodontidae (Gelfo and Sigé, 2011) needs to be tested. A strong ectoflexid separates the trigonid and talonid on the labial side. The talonid is lower and smaller than the trigonid and mostly formed by the hypoconid. From this cusp, a short cristid obliqua contacts the metaconid, and a hypocristid connection to the hypoconulid is not clearly differentiated. The entoconid is the smallest of the tooth cusps, and even when in contact with the hypoconulid it is separated from it clearly by a shallow furrow. A deeper wear of the entoconid could easily blur this cusp. The wear on the tooth is deeper in the labial than on the lingual side, so there is a very thick enamel border in occlusal view which runs distally from the hypoconulid up to the paraconid, around which the enamel is narrow. Vertically oriented HSB

are present and they are similar to those already described for sparnotheriodontids (Line and Bergqvist, 2005; Bond *et al.*, 2006).

The p4 is well preserved and shows little wear (Fig. 3). The roots are mostly missing except for a small portion of the mesial and distal ones in the lingual side. The premolar is fully molarized and crescentiform with the labial walls of the trigonid and talonid convex and the lingual side of the tooth flat and vertical. As in other specimens, the wear on the occlusal surface defines a strong and thick enamel border along the labial edge of the trigonid and the talonid structures, where vertical HSB could be seen. Only a faint mesial cingulid is present. It extends down from a small notch –formed by the preceding tooth to the mesial wall of the trigonid– to the mesiolabial base of protoconid. The trigonid is somewhat larger and higher than the talonid. The

trigonid basin is deep but not very wide, and opens lingually. A well-developed paraconid is distinguished from the paralophid, and is placed mesially and lower than the metaconid. The protoconid is represented by only a point at which the paralophid and protolophid join together. The metaconid is the highest cusp, with a robust and rounded distally descending crest, which does not close the talonid basin. The hypoconid is the largest cusp of the talonid and projects a cristid obliqua up to the metaconid, but contacts it below the contact of the protolophid, from which it is separated by a vertical furrow in the ectoflexid. A short hypocristid connects the hypoconid to a small hypoconulid. Wearing causes the entoconid to join the hypoconulid, but it is well delimited by the bend of the enamel along the distolingual side of the talonid. The talonid basin is similar to the trigonid one but larger and widely open lingually.
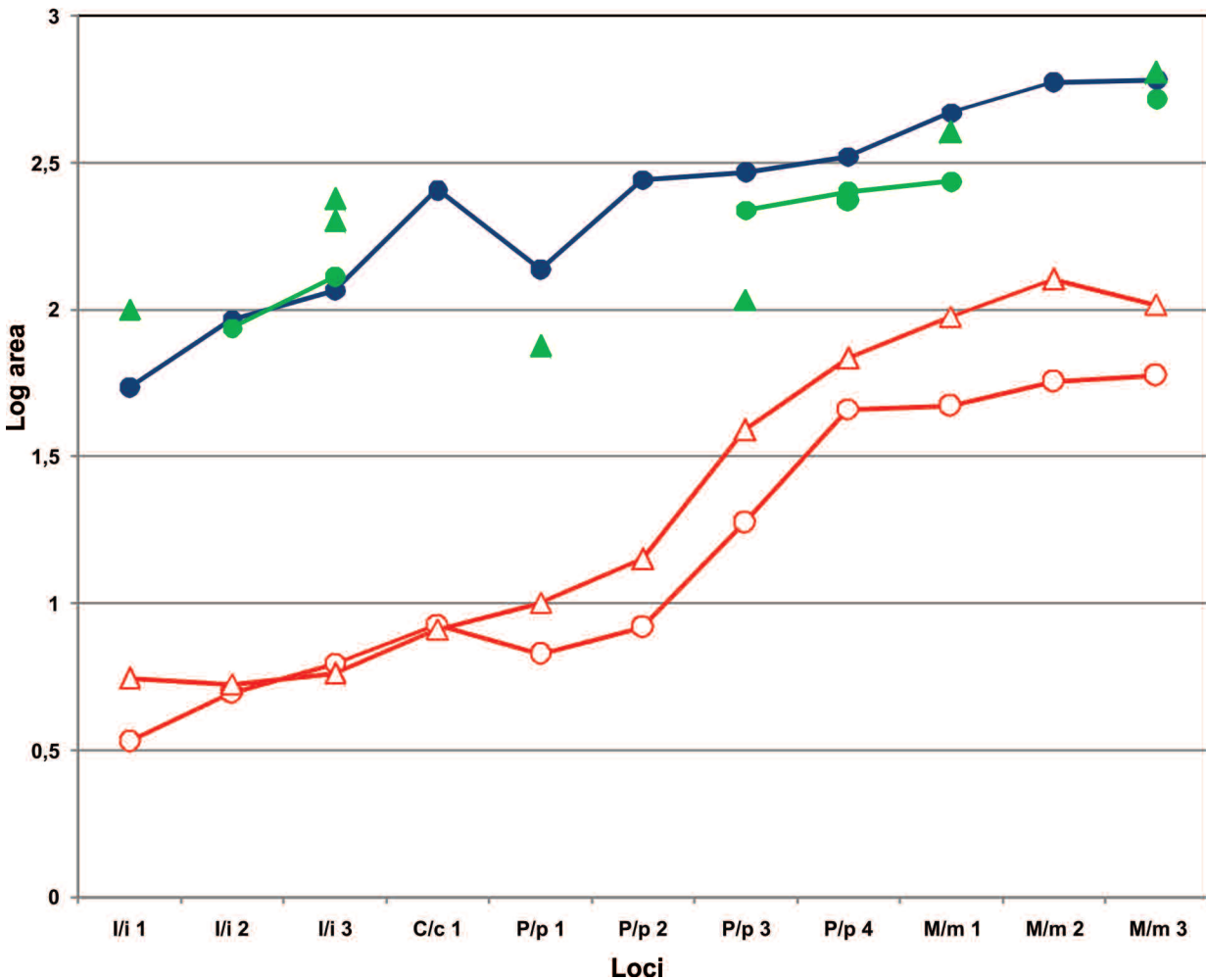
Figure 3. PDS of *Sparnotheriodon epsilonoides* in red, *Meniscotherium chamense* in blue and *Notiolofos arquinotiensis* in green. Circles are lower dentition and triangles upper dentition as indicated in the lower axis.

Remarks. The p4 specimen (MLP 08-XI-30-43) was recovered by Silvio Casadio during CAV 2008, while the p3 (MLP 12-XI-1-11) was found by the author *in situ* in a rock with naticid snails (Fig. 1) during Pre-CAV 2012.

In addition to specimens added here to the hypodigm of *Notiolofos arquinotiensis*, unpublished specimens from DNA-IAA field trips housed in MLP deserve attention and are discussed here. A set of 10 isolated fragments of no more than a few millimeters and labeled as "Mammalia? indet." (MLP 91-II-4-297) from DPV 6/ 84 (= RV 8200 of Woodburne and Zinsmeister, 1984) include several unrelated remains: three unidentified elements (rock fragments?); three small dentine fragments; one element identified here as an indeterminate bone fragment; a small bone fragment measuring 5.13 mm long and 1.64 mm in cross-section; and two teeth, identified here as (a) and (b). The MLP 91-II-4-297 (a) tooth presents an isolated cusp laterally compressed with little wear in the apex, but the dentine is missing and some sediment fills it. There are two smooth crests which descend mesially and distally respectively. The specimen differs from *Sparnotheriodon* Soria, 1980a canines by being much smaller, more compressed and without the strong wear on the lingual side. The tooth is more comparable to an incisor of *Sparnotheriodon*, particularly I2; however, it is smaller and shows a different kind of wear. The last specimen, MLP 91-II-4-297 (b), is here interpreted as a portion of a left trigonid with the lingual portion broken. The enamel is thin, and in contrast to what is observed in *N. arquinotensis*, no vertical HSB are clearly seen. The protoconid is not distinguishable from the V-shaped lophid and the paraconid and metaconid portion are not preserved. The paracristid portion is peculiarly more elevated above the protoconid than the protocristid. At the base of the crown, a small remnant of a precingulid is present. The trigonid basin is very wide in contrast to those in molariforms of *N. arquinotensis*. At present there is no evidence to assign MLP 91-II-4-297 (a) and (b) to Sparnotheriodontidae.

A left lower second molar fragment (MLP 12-I-20-4) picked by Martín de los Reyes out of sediment from IAA 1/ 90, La Meseta Formation (Cucullaea I Allomember), resembles the morphology of sparnotheriodontids, particularly in the position and development of the entoconid, but differs from them and specially from *N. arquinotensis* by the presence of a labial pocket, the closed talonid basin, the absence of cingulids and ectoflexid, and a different inclination of the wearing surface between the cristid obliqua and the hypolophid (?). This molar was discussed in Gelfo *et al.* (2014), who arrived at this conclusion based on similar morphological arguments.

DISCUSSION ABOUT *NOTIOLOFOS ARQUINOTENSIS* TEETH LOCI

The comparison between the PDS in *Sparnotheriodon* and *Meniscotherium* shows that the main difference —despite the absolute size— is a proportionally greater area increment from p2 to p4 in *Meniscotherium* (Fig. 3). Thus, the slope in the lower premolar series is more pronounced in *Meniscotherium*.

The qualitative analysis of features present in the specimens indicates that under the mentioned assumption most of the loci previously assigned to *N. arquinotensis* (Bond *et al.*, 2006) match well with the proposal. Nevertheless, some of the teeth with previously uncertain loci identification and some with other interpretations are discussed herein.

MLP 90-I-20-1 is a left upper tooth broken mesiodistally into a lingual and a labial portion. At the time of this review, the distal part of the ectoloph where the metacone should occur was broken and lost. This specimen was described and interpreted as a left upper molariform, very probably an M1 or M2, although it could also represent a dP4 molariform. Given the incompleteness of the specimen and the circumstance of it being very worn and without root traces the possibility of it being a dP4 could not be discarded (Bond *et al.*, 2006). Differentiation between dP4 and P4 among Sparnotheriodontidae is not easy and no certain deciduous premolar has been described. An indeterminate sparnotheriodontid right maxillary fragment with three teeth (MLP 66-V-12-2) from the early Eocene of Paso del Sapo, Chubut Province, was interpreted as dP4-M2 (Bond *et al.*, 2006) and later as P4-M2? (Tejedor *et al.*, 2009: fig. 7D). If the dental replacement in sparnotheriodontids follows the same pattern as in most placental mammals a dP4 should have erupted before M1 and the last one, before P4. So, differences in the wearing facet and the relative height of the teeth could be used in order to compare these teeth. Despite the anterior molariform being broken mesially from the distal part of the paracone in the ectoloph up to the mesial side

of the protocone, a good comparison could be made with the M1. Wearing on these teeth is minor and only small differences can be observed in wearing facets. The prismatic wearing in the mesial face of the metacone in the ectoloph is strong and almost the same in both teeth. Nevertheless, two facets are absent in the M1 but present in the preceding tooth. There is a small and rounded facet on the hypocone and a facet in the postmetacristid portion of the ectoloph. The more intensive wear suggests that the tooth mesial to the M1 in MLP 66-V-12-2 is a dP4. In labial view, the higher position of the enamel-root contact in dP4 respect to M1 suggests that the former tooth erupted before the later, reinforcing the interpretation of it as a dP4 by Bond *et al.* (2006).

Other possible deciduous teeth for sparnotheriodontids belong to the *Victorlemoinea prototypica* specimen MNRJ 1477V which was considered as a right molariform (Paula Couto, 1952) and later as M1 or M2 or even dP4 (Bond *et al.*, 2006). The same size, cusp distribution and proportions are present in another right tooth of *V. prototypica* MNRJ 1476V and should be assigned to the same locus.

In *Meniscotherium* the dP4 closely resembles the M1 except that it is much smaller and with a stronger labial cingulum between the metastyle and the parastyle (Williamson and Lucas, 1992).

All mentioned dP4 share the presence of a longer axis labiolingually oriented. In contrast, the mesiodistal length of *N. arquinotiensis* MLP 90-I-20-1 (Tab.1) suggests the opposite and resembles more the M1 than dP4 of the sparnotheriodontid MLP 66-V-12-2, or the teeth of *V. prototypica* MNRJ 1477V and MNRJ 1476V. Also the area for this *N. arquinotiensis* tooth in the PDS matches well what is expected for an M1 and thus it is assigned to that tooth.

Specimen MLP 96-I-5-10 was not formally included in the hypodigm of *N. arquinotiensis* or the referred materials but it was described as such in the text and compared to a right incisiviform MLP 90-I-20-3, which is here interpreted as an I3. They were assigned to incisiviforms rather than a caninniform (Bond *et al.*, 2006), but the area size in the PDS in MLP 96-I-5-10 suggests that it could be also interpreted at least as a lower canine. No sparnotheriodontid upper canines are known but the area size for *Meniscotherium* is similar in upper and lower teeth. The area to compare in *S. epsilonoides* was calculated with measurements at the base

of the two canines (Tab. 2). In *S. epsilonoides* the labial outline of the canines is straight, not rounded as in the incisiviforms. A large, strong and pointed cusp is projected from the base and there is an almost straight and crenulated labial cingulid. The wear of the upper canine erased the mesiolingual part of the crown, and most of the enamel is present in the labial part of the canine. The root is probably the most diagnostic feature for this tooth, as it is larger compared to other teeth of the series. In contrast, in MLP 96-I-5-10 the cusp outline in labial view is more rounded and not as tall, the labial cingulid ascends distally and mesially over the enamel, the root is smaller and the wear restricted to the lingual tip, so there is a strong lingual rim which is in a higher position than the lingual cingulid. All these features suggest an I3 locus for the tooth, as Bond *et al.* (2006) suggested for MLP 90-I-20-3 and MLP 96-I-5-10.

MLP 96-I-5-9 was considered with doubts as an incisiviform and more probably as a left p1 (Bond *et al.*, 2006) but is here assigned to an i3. The area size matches well with a p1 (Fig. 3) but the mesiolingual length is very different from that of p1 (Tab. 1). The first premolars and the only root available are elongated in *Sparnotheiodon epsilonoides*, the labial rim is almost straight, the principal and highest cusp —the protoconid— is placed in the mesial half of the tooth, from where a short cristid descends mesially. A lingual bend in the labial enamel of the protoconid indicates the serial homology with the postvallid of the more molarized teeth, and so with the portion of the talonid represented by a distally projected cristid. In contrast to these features, MLP 96-I-5-9 presents a rounded and strong root; the labial cingulid is not straight but runs down from the mesial side and then goes up distally in order to contact the occlusal enamel edge, as in the incisiviforms of *S. epsilonoides*. Also, the wear of the occlusal surface more closely resembles i3 than p1 as the labial surface is well developed and the erased portion falls lingually.

Specimen MLP 94-III-15-3 —assigned to a lower right incisiviform, probably an i3 (Bond *et al.*, 2006)— is here assigned to the i2 locus, comparable to the area observed in the i2 of *S. epsilonoides* (Fig. 3).

MLP 91-II-4-1 and MLP 04-III-3-1 were described and tentatively assigned to molarized premolars which probably represent two right p4s or a p4 and a p3 respectively (Bond *et al.*, 2006). The first is here reassigned as an m1

since the mesiodistal and labiolingual size of the talonid is larger than in the trigonid. This is the observed relation among the lower molar elements in *S. epsilonoides*, while in the premolars the trigonid is larger than the talonid. In contrast, the second specimen is here considered as a p4.

MLP 92-II-2-135 is a very peculiar specimen considered as a fragment of a lower (?) molariform of *Notiolofos arquinotiensis* (Bond *et al.*, 2006). It is interpreted here as part of a labial portion of an m3. There is a strong basal rim, which continues with a long enamel surface (20.10 mm) with vertical HSB. The portion of labial cingulid is not crenulated as in the canines of *S. epsilonoides* and resembles more closely the structure in molars. In specimen MLP 91-II-4-1 here considered as an m1 there is a very light wear on the occlusal surface and none at all over the protoconid, in which the height of the crown is 13.48 mm. There is no available m2 to compare, but in the m3 MLP 01-I-1-1 the height of a much worn protoconid is 13.24 mm. So is it likely that MLP 92-II-2-135 is part of a labial portion of an m3.

PDS agree with the assignment of MLP 91-II-4-5 as a P1 –which was already fully described (Bond *et al.*, 2006) and here illustrated for the first time (Fig. 4)– as it is important for the discussion below. The loci interpretation in the present analysis is summarized in Table 1.

THE STRATIGRAPHIC DISTRIBUTION OF *NOTIOLOFOS ARQUINOTIENSIS*

All the remains of *N. arquinotiensis* were collected in localities of Seymour Island, East of the Antarctic Peninsula and part of ancient West Antarctica (see Reguero *et al.,* 2013 and literature therein). The sedimentary deposit where the remains were found is part of the Paleogene back-arc deposits comprising more than 1,000 meters of shallow marine to coastal fossiliferous clastic rocks, mainly of Paleocene and Eocene age (Elliot, 1988; Sadler, 1988; Marenssi *et al.*, 1998a). The Paleogene sequence in Seymour Island was deposited in incised valley settings. According to the last available geologic map (Montes *et al.*, 2013) it comprises –from base to top– part of the Marambio Group (Cretaceous/Paleogene), represented by the unit Klb 10 (earliest Danian) of the López de Bertodano Formation and Sobral Formation (Danian); and, the Seymour Island Group (Paleogene), with the Cross Valley Formation (Selandian–earliest Thanetian), La Meseta Formation (Thanetian–Lutecian) and Submeseta Formation (Lutecian–Rupelian). The last two formations are those with an important fossil mammal record. La Meseta and Submeseta formations included the seven lithofacies units of Sadler (1988) known in the scientific literature as Telm 1–7. Marenssi *et al.* (1998a) or-

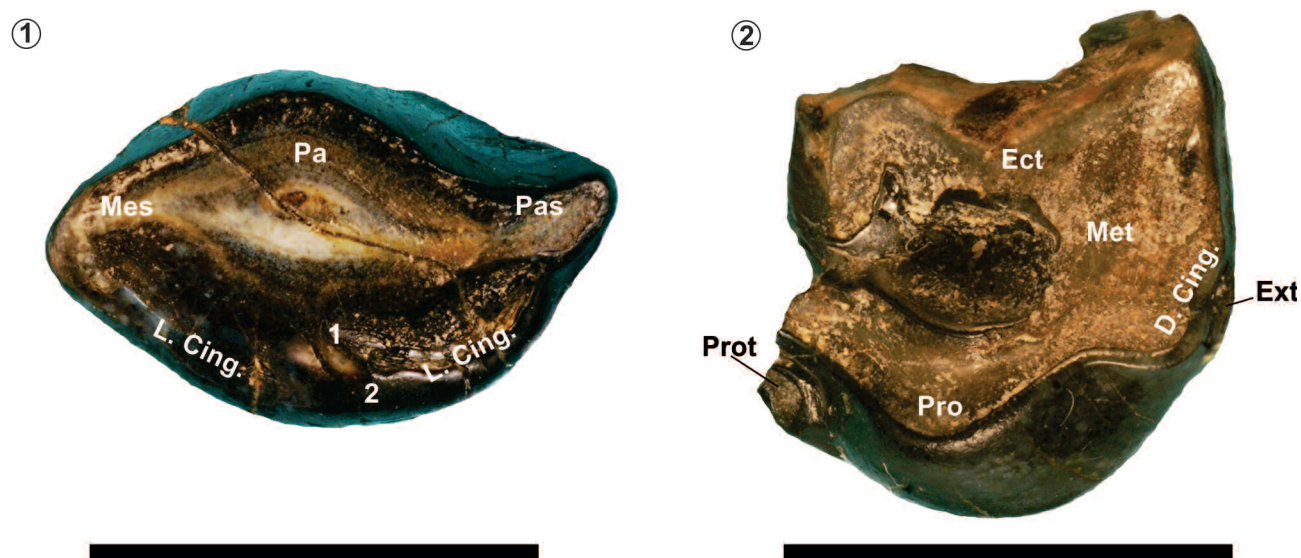Figure 4. *Notiolofos arquinotiensis,* occlusal view of **1, MLP** 91-II-4-5 right P1; **2, MLP** 90-I-20-5 left P3. Abbreviations: **D. Cing.,** distal cingulum; **Ect,** ectoflexus; **Ext,** extra distal cingulum; **L. Cing.,** lingual cingulum; **Mes,** mesostyle?; **Met,** metaloph; **Pa,** paracone; **Pas,** parastyle; **Prot,** protostyle; **1,** crest; **2,** lingual cuspule (= protocone?). Scale bars= 10 mm.

ganized these lithofacies into six erosionally-based internal allomembers, named from base to top Valle de Las Focas, Acantilados, Campamento, Cucullaea I, Cucullaea II and Sub-meseta, with the last one later recognized as Submeseta Formation (Montes *et al.*, 2013). These units were deposited in deltaic, estuarine and shallow marine settings, mostly within a northwest-southeast trending valley (Marenssi *et al.,* 1998a, b). No terrestrial facies are known for the Paleo-gene of Seymour Island, so the mammals and the rest of the land vertebrate fossils reported to date have been trans-ported within the marine settings and concentrated in paralic and shallow marine environments. The preserva-tion of leaves, tree trunks, and even a flower, indicate the proximity of a forested terrain (see references in Reguero *et al.*, 2013).

The oldest record of *N. arquinotiensis* is MLP 13-I-25-1, a small portion of talonid probably of an m1 or m2 (Gelfo *et al.*, 2015) that came from the basal marine horizon of the Acantilados II Allomember of La Meseta Formation (Telm 3), with its base dated at 55.3 Ma Ivany *et al.,* 2008; Montes *et al.*, 2013). The younger record –MLP 95-I-10-6– is a left M3 found in the upper third of Telm 7 (Vizcaíno *et al.*, 1997) equivalent to the Submeseta III Allomember of the Subme-seta Formation, with its base dated at 37.8 Ma (Montes *et al.*, 2013). As stated above, this stratigraphic distribution indicates a temporal span of 17.5 Ma through which *N. ar-quinotiensis* is present represented by teeth of different loci and distinct levels.

The integration of the available specimens of *N. arquino-tiensis* from distinct levels seems to match well with a sin-gle dental series. This would not be the case if *N. arquino-tiensis* had a size variation in their dentition along the strati-graphic section, which would refute the morphological sta-sis argument. Except for a few points, *N. arquinotiensis* and *Sparnotheriodon epsilonoides* follow a similar PDS in the lower dentition (Fig. 3). When comparing the absolute size of p3-m1 and m3, these are slightly smaller in *N. arquinotien-sis* (Tabs. 1–2) but both PDS shapes are very similar (Fig. 3). This similarity also agrees with the body size inference for *N. arquinotiensis*, estimated between 395–400 kg (Vizcaíno *et al.*, 1998) and the estimation of 400 kg for *Sparnotheriodon* (Vizcaíno *et al.*, 2012). This suggests that the jaw of *N. ar-quinotiensis* should be very similar in size and morphology to that of *Sparnotheriodon* MACN 18225.

A theoretical profile of the unknown upper dentition PDS of *S. epsilonoides* and *N. arquinotiensis* (indicating what are expected for them) could be compared to that of *Menis-cotherium* (Fig. 3). A proportionally larger area should be con-sidered for upper PDS in *S. epsilonoides* and *N. arquinotiensis* but with the same shape and size relation with lower PDS as in *Meniscotherium.* The main differences between expected and real values are the I3 areas of *N. arquinotiensis* (MLP 90-I-20-3 and MLP 96-I-5-10) which are much larger than the i3 (MLP 96-I-5-9). The same occurs with the P1 (MLP 91-II-4-5) of *N. arquinotiensis* (Fig. 4), which has a value different from what is expected for the *Meniscotherium* P1/p1 rela-tive area size (Fig. 3). The theoretical value for the P1 of *No-tiolofos arquinotiensis* should be higher than that of p1 in *Sparnotheriodon* (which is supposed to be a good predictor of *N. arquinotiensis* p1 size) and not, as it is, smaller. The value of the P3 (MLP 90-I-20-5) in *N. arquinotiensis* is also lower than expected but this tooth is broken and the measure is only an approximation (Tab. 1; Fig. 4).

A possible explanation for size differences between ex-pected and measured values in I3 and P1 could rest in a variation of *N. arquinotiensis* PDS through distinct strati-graphic levels, which should be indicative of a variation of size in their life span. This should be a good argument to re-fute the morphological stasis of *N. arquinotiensis*. But, despite both I3 and P1 having come from different locali-ties of Seymour Island, they were found in the same levels of the Cucullaea I Allomember (middle levels of the unit, Telm 5) of the La Meseta Formation. In fact, most of *N. ar-quinotiensis* specimens that are complete enough to be measured (Tab. 1) came from this level, which is one of the best sampled for land mammals during the past CAV (Reguero pers. com. 2014). Another possible explanation for the shift from the expected values of I3s and P1 in *N. arquinotiensis* PDS could be that they belong to teeth of another taxa. A possibility could be *Antarctodon sobrali*, an astrapotherian found in Allomembers Cucullaea I (basal levels of the unit, Telm 4) and Cucullaea II (highest levels of the unit, Telm 5) of the La Meseta Formation, with the same HSB structure than *N. arquinotiensis* (Hooker, 1992; Bond *et al.*, 2011). *Antarctodon sobrali* is only represented by MLP 08-XI-30-1, an isolated right p4 or m1, so more detailed comparisons are pending until new material is collected.

Summarizing, the few specimens available for testing

the stasis of *N. arquinotiensis* prevented the previous review and analysis from detecting variability through their stratigraphic distribution.

CONCLUSIONS

Despite the fact that no elements refute the morphological stasis of *N. arquinotiensis*, it is important to note also that there are very few specimens in each allomember to support it. A larger sample is desirable in order to re-assess it.

The examination of the phylogeny of sparnotheriodontids indicated the late Paleocene as the minimum time for the presence of a common ancestor for *N. arquinotiensis* and the rest of the family, which has a wide distribution in South America (Reguero *et al*., 2014). Probably by that time, the Antarctic sparnotheriodontids started to evolve in geographical isolation from their South American counterparts, since the Weddellian Isthmus –the land connection between both continents– was flooded by a shallow epicontinental sea (Reguero *et al*., 2014). This barrier should have prevented the faunal interchange for cursorial terrestrial forms and, at a microevolutionary scale, this event indicated the end of any possible genetic flow between South American and Antarctic sparnotheriodontids. A direct consequence of it was an increasing genetic drift among ungulate populations in West Antarctica. Drift and stabilizing selection were usually considered as responsible of avoiding the origin and establishment of morphological novelties within local populations and thus were also a good explanation for morphological stasis patterns (Eldrege *et al*., 2005; Haller and Hendry, 2013). Nevertheless, they were probably only first steps for explaining trait stability through a long time span. Stasis at the species level can be maintained by a complex pattern of selection imposed on geographically structured populations (Gould, 2002; Eldrege *et al*., 2005) and this seems to be possible in West Antarctica, according to analyses based on other vertebrates.

In contrast to mammals, penguins have a very detailed fossil record in the Eocene levels of Seymour Island (Reguero *et al*., 2013), with some good examples of long-lived taxa recorded (Acosta Hospitaleche, 2006). This is evident in the genera *Palaeeudyptes* and *Antrhopornis* which are well represented in Eocene sediments of West Antarctica. The penguin longevity of the recognized species distributed

along La Meseta and Submeseta Formations indicated minimum ranges of 12.9 Ma for *P. klekowskii,* 15.7 Ma for *A. nordenskjoeldi* and *A. grandis* and 17.5 Ma for *P. gunnari* (see Acosta Hospitaleche *et al*., 2013; Reguero *et al*., 2013 for a detailed stratigraphic distribution).

Notiolofos and *Palaeeudyptes* were recorded in the same levels through the Eocene sequence. As mentioned above *Notiolofos* remains represented by a monotypic genus, but *Palaeeudyptes* included two species based on the morphology of the tarsometatarsus (Jadwiszczak and Acosta Hospitaleche, 2013). Both apparently experienced stasis events through the Eocene. If the Antarctic fossil record is well interpreted, the question is: Why is stasis so common in Paleogene Antarctic vertebrates?

It was argued that in the same way that the Hardy-Weinberg equilibrium is an appropriate null model to understand population genetics and microevolution, evolutionary stasis should be the logical extension for macroevolutionary studies (Burt, 2001). But a null model by itself does not clarify the stasis in Antarctic vertebrates. Other explanations, like the "*Plus ça change*" model (Sheldon, 1996) which discuss gradual change versus stasis events, probably provides a better insight in relation to the interaction of environmental conditions and the evolution of lineages. This argumentation holds that morphological stasis is the usual response to widely fluctuating physical environments on geological timescales. Particularly, an intensification of stasis and punctuated equilibrium (Eldredge and Gould, 1972) would be expected in temperate regions and shallow waters, and gradual evolution on land more frequent in the tropics and in the deep sea (Sheldon, 1996; Gould, 2002).

The paleoclimates in Antarctica experienced a meaningful change from warmer and more seasonal conditions during the first half of the Cenozoic to cooler and gradually non-seasonal conditions in the second half. By the time *Notiolofos* was present in Seymour Island a cool and seasonal climate prevailed, as suggested by the paleofloral analysis for the early–middle Eocene of the Antarctic Peninsula (Gandolfo *et al*., 1998a, b; Francis *et al,* 2009). It was not until the end of the Eocene that Antarctica became permanently glaciated, so a cool albeit not glacial climate was suggested for at least the winter season in the early Cenozoic of Antarctica (see references in Reguero *et al*., 2013). By now, considering the Paleogene environmental conditions in

Antarctica, the "*Plus ça change*" model could be a plausible explanation for the evolutionary stasis of *N. arquinotiensis* and penguin taxa.

Despite the increase of the paleontological work in CAV and Pre CAV since the 1980s, there are plenty of gaps in the knowledge of the role played by Antarctica in the origin, evolution and extinction of biological entities. Particularly among the fossil land vertebrates, a more detailed and accurate fossil record is desirable in order to test phylogenetic and paleobiogeographical assumptions (Reguero *et al.*, 2014). Meanwhile, the morphological stasis hypothesis here discussed can be a helpful starting point to analyze patterns among Antarctic vertebrates.

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