

A comparative analysis on cranial ontogeny of South American fur seals (Otariidae: *Arctocephalus*)

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Received 10 April 2014; revised 23 July 2014; accepted for publication 28 July 2014

We analysed the cranial ontogeny of male *Arctocephalus australis* (Zimmermann, 1783) ($N = 116$), *Arctocephalus gazella* (Peters, 1875) ($N = 69$), and *Arctocephalus tropicalis* (Gray, 1872) ($N = 51$) to study skull growth and its allometric patterns in the genus. We used 15 metric variables with bivariate and multivariate approaches to detect interspecific similarities and differences between growth trends, which we discussed in the context of phylogeny and life history. We found common trajectories in 20% of variables, detecting that the differences between adults were associated with size. We detected higher growth rates in *A. gazella* than in *A. australis* and *A. tropicalis*, which were associated with shape differences. Amongst the three species, *A. tropicalis* was morphologically intermediate, showing additional common trends with *A. gazella* and *A. australis*, and an intermediate position in the multivariate morphospace. Allometric patterns were also compared with growth trends described for *Otaria byronia* (Péron, 1816) and *Mirounga leonina* (Linnaeus, 1758). We detected positive allometry in *Arctocephalus* for the mastoid width (MW) but negative allometry in *O. byronia* and *M. leonina*. This could indicate that males of *Arctocephalus* exhibited a delayed development of MW. Finally, the presence of common growth trends for the skull length and the postorbital constriction could indicate a conservative pattern within otariids.

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doi: 10.1111/zoj.12197

ADDITIONAL KEYWORDS: *Arctophoca* – cranial morphometry – ontogeny – Pinnipedia – skull – taxonomy.

INTRODUCTION

Allometry describes the changes in relative dimensions of parts of the body that are correlated with changes in overall size (Gayon, 2000). According to Gould (1966), allometry is most often a non-adaptive source of evolutionary change. Such change is a mechanical consequence of the increase in size, which is itself adaptive. Thus, allometry will most often be a source of biological diversity (Gayon, 2000). Three types of evolutionary change in ontogenetic trajectories are recognized: ontogenetic scaling (neither slopes nor intercepts differ between species), which is indicative of change in growth duration; lateral shift (intercepts differ but

slopes do not), which indicates changes in prenatal development; and directional change (slopes differ), which indicates novel modes of postnatal growth (e.g. Weston, 2003; Cardini & O’Higgins, 2005; Marroig, 2007; Suzuki, Abe & Motokawa, 2011). In constant environments in particular, allometric parameters (slopes as well as intercepts) will be subject to natural selection (Gayon, 2000). Thus, allometry is another factor potentially influencing phylogeny and taxonomy.

Otariidae comprises 14 species of eared seals (Berta & Churchill, 2012), traditionally subdivided into two subfamilies: Otariinae (sea lions) and Arctocephalinae (fur seals). Recent publications (e.g. Yonezawa, Kohno & Hasegawa *et al.*, 2009; Nyakatura & Bininda-Emonds, 2012; Berta & Churchill, 2012), however, have stated that these subdivisions are no longer valid. Rapid radiations of species within Otariidae (Wynen *et al.*, 2001)

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make the resolution of relationships between species difficult and indicate the requirement for additional data (both genetic and morphological). Consequently, the number of species and their evolutionary relationships remain controversial within this family (e.g. Brunner, 2004; Berta & Churchill, 2012). For instance, the southern fur seals have been traditionally included in the genus *Arctocephalus*, which has been reported as paraphyletic in recent works (e.g. Wynen *et al.*, 2001; Árnason *et al.*, 2006; Fulton & Strobeck, 2006; Higdon *et al.*, 2007; Yonezawa, Kohno & Hasegawa, 2009). Indeed, in a recent taxonomic review Berta & Churchill (2012) transferred five out of six species formerly included in *Arctocephalus* to the genus *Artophoca*, limiting the genus *Arctocephalus* as monospecific [*Arctocephalus pusillus* (Schreber, 1775)]. In some phylogenies *Arctocephalus tropicalis* Gray, 1872 has been reconstructed as a sister taxon to *A. pusillus* (e.g. Yonezawa *et al.*, 2009) and, if this is confirmed, the former should be transferred to the genus *Arctocephalus* (Berta & Churchill, 2012). Nyakatura & Bininda-Emonds (2012) compiled a new supertree of the Carnivora, however, and concluded that this usage of *Arctophoca* may be premature, although they recover the genus as paraphyletic. Uncertainty remains about their phylogenetic relationships, so we return provisionally to use *Arctocephalus* for all the southern fur seals (see Committee on Taxonomy, 2013). Despite the abundant morphometric studies focused on taxonomy in this controversial genus (e.g. Repenning, Peterson & Hubbs, 1971; Drehmer & Ferigolo, 1997; Brunner, 1998; Oliveira, Malabarba & Majluf, 1999; Drehmer & Oliveira, 2000; Brunner, 2004), all reports showed a marked degree of variation and high overlaps in skull measurements within and among species (e.g. Sivertsen, 1954; King, 1983; Daneri *et al.*, 2005). This complex includes three species that occur along the Argentinean coast: *Arctocephalus australis* (Zimmerman, 1783), the South American fur seal; *Arctocephalus gazella* (Peters, 1875), the Antarctic fur seal; and *Arctocephalus tropicalis* (Gray, 1872), the Subantarctic fur seal. Rapid radiations, hybridizations, and morphological similarities lead to contradictory phylogenies and taxonomic problems, which highlight the importance of morphological studies of the fur seals in order to clarify the degree of individual variation both within and between species. Despite the reported interbreeding between species (e.g. Kerley & Robinson, 1987; Shaughnessy, Erb & Green, 1998; Brunner, 1998), interspecific morphological differences in adults are obvious. Skulls of *A. gazella* are the most robust, and possess postcanine dentition not seen in any other otariid, whereas skulls of *A. tropicalis* express more typical *Arctocephalus* morphology, including a less robust skull than *A. gazella*, a more slender rostrum, and narrower supraorbital processes and interorbital constriction.

Ontogeny and evolution are intimately and reciprocally interrelated (Klingenberg, 1998). Despite this, there is a lack of ontogenetic studies orientated to the taxonomic discrimination among fur seals species. In this context, we analysed in allometric terms the male skull ontogenies of *A. australis*, *A. gazella*, and *A. tropicalis*. Male intrasexual selection is commonly perceived to be an evolutionary force among sexually dimorphic species (e.g. Plavcan, 2001; Lindenfors, Tullberg & Biuw, 2002; Leigh *et al.*, 2008), so male cranial morphology is a particularly useful source of phylogenetic information (e.g. Gilbert, Frost & Strait, 2009). Our study was performed in order to detect interspecific similarities and differences between ontogenetic trajectories (i.e. growth patterns) in an allometric framework. Allometric comparisons are important in clarifying interspecific cranial shape differences, which can be dependent on size variation. We also aimed to clarify how skull shape evolved in this group along with size variation using linear allometric approaches. Although adults of these three species reach similar body size and weight (Payne, 1979; Bester & Van Jaarsveld, 1994), they exhibit great disparity in their lactation periods (Vaz-Ferreira, 1981; Kerley, 1985, 1987; Costa, Trillmich & Croxall, 1988; Phillips & Stirling, 2000; Nowak & Walker, 2003; Jefferson, Webber & Pitman, 2008): *A. gazella* wean at 4 months, *A. tropicalis* wean at 10 months, and *A. australis* wean at 1–2 years old. We expect that if the allometric growth trends are strongly associated with phylogeny, closely related species would exhibit more similar trajectories than distantly related species; however, if allometric growth trends are strongly associated with behaviour or feeding ecology, the resulting growth patterns would be different in closely related species, in order to acquire their physical, physiological, and behavioral adult characteristics. Finally, our results on fur seals skull growth were also compared with allometric trends detected in previous studies for other highly dimorphic pinnipeds, such as *Otaria byronia* (de Blainville, 1820) (syn. of *Otaria flavescens* Shaw, 1800; for a discussion on its name validity, see Rodriguez & Bastida 1993), the southern sea lion, and *Mirounga leonina* (Linnaeus, 1758), the southern elephant seal (Tarnawski, Cassini & Flores, 2014a, b). The comparison with other groups could detect common patterns in a conservative plan, as well as specific trends shared by common ancestry.

MATERIAL AND METHODS

STUDY MATERIAL

This work is based on the analysis of a complete ontogenetic series of male skulls of *A. australis* ($N = 116$), *A. gazella* ($N = 69$), and *A. tropicalis* ($N = 51$), deposited in the systematic collections of Argentina and Brazil

(see the Appendix). The condylobasal length (CBL) of *A. australis* ranged from 157.4 to 250.1 mm, whereas in *A. gazella* the CBL ranged from 184.5 to 254.7 mm, and in *A. tropicalis* the CBL ranged from 151.8 to 216.6 mm. Although *A. gazella* included larger specimens (in age and size) than *A. tropicalis* and *A. australis*, this fact did not alter our analysis as the elimination of younger *A. tropicalis* and *A. australis* showed similar results. Specimens were categorized into two general age stages (Fig. 1) by their dental formula and sutural index (e.g. Sivertsen, 1954; Brunner, Bryden & Shaughnessy, 2004; Drehmer, Fabian & Menegheti, 2004; Molina-Schiller and Pinedo 2004), and by their estimated age from canine teeth development (i.e. growth layer groups, GLGs, interpreted as 1 year of life; Schiavini, Lima & Batallés, 1992). Non-adult specimens were those with between zero and four GLGs and non-fused sutures

(i.e. occipitoparietal and sagittal sutures), with a sutural index (SI) ranging from 9 to 16. Specimens considered to be adults had more than four GLGs, with the occipitoparietal suture completely fused, fully erupted dentition, an evident sagittal crest with a totally fused sagittal suture, and an SI higher than 13.

STUDY OF GROWTH

Bivariate analysis of allometry

Ontogenetic allometry deals with covariation among characters along a growth series. The time frame is implicitly incorporated (size proxy), but not specified, in order to describe relative modifications in structures as the animal grows. For the bivariate allometric analysis, we employed 15 cranial variables (Fig. 2; for a list of the abbreviations used for characters

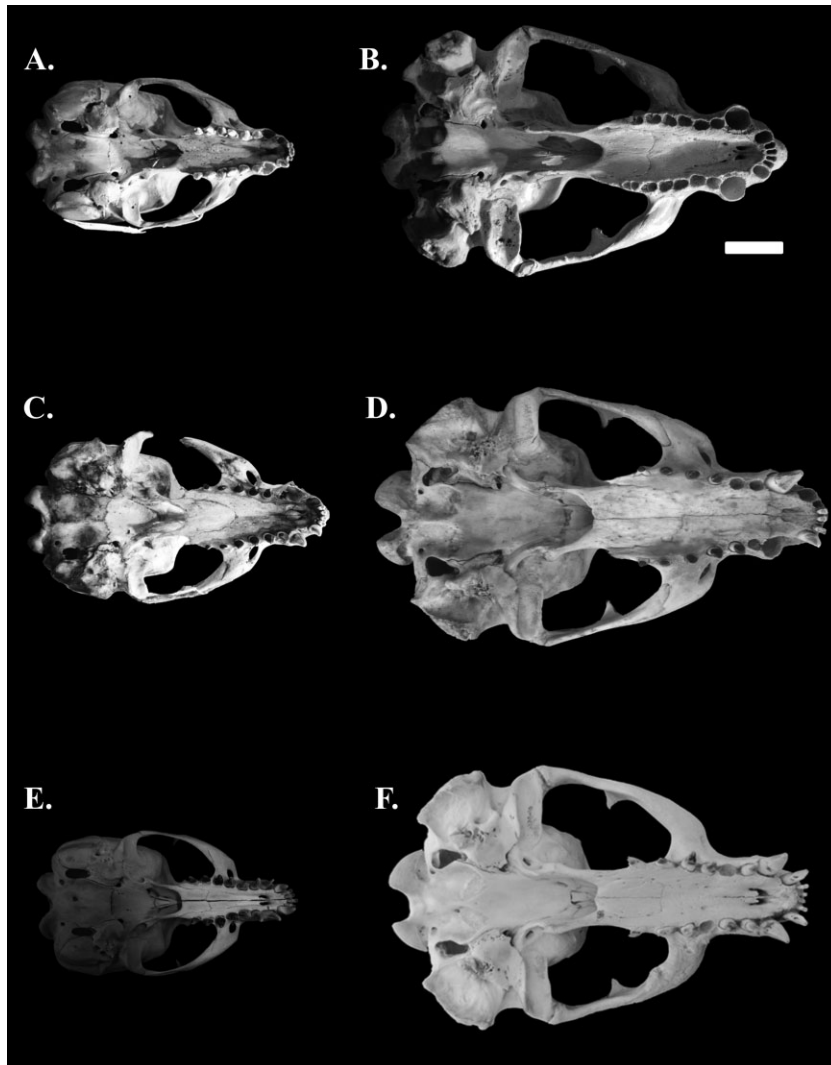


Figure 1. Ventral view of skulls of male *Arctocephalus australis* (A, B), *Arctocephalus gazella* (C, D), and *Arctocephalus tropicalis* (E, F). Ontogenetic series represent non-adult (left) and adult (right) specimens. Scale bar: 30 mm.

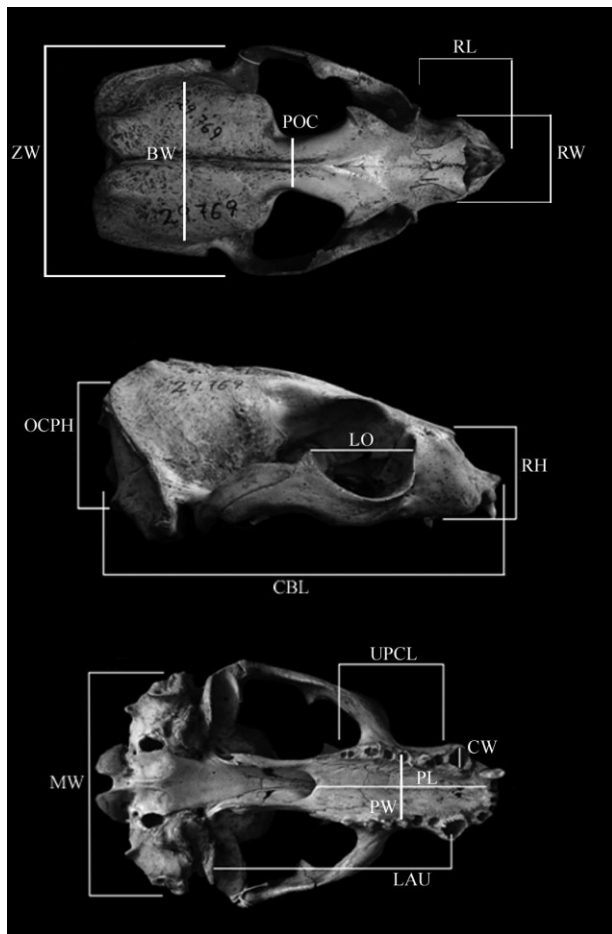


Figure 2. Cranial measurements of used in this study: BW, braincase width; CBL, condylobasal length; CW, alveolus width of upper canine teeth; LAU, load arm length at upper canine; LO, length of orbit; MW, mastoid width; OCPH, occipital plate height; PL, palatal length; POC, postorbital constriction; PW, palatal width; RH, rostral height; RL, rostral length; RW, rostral width; UPCL, upper postcanine length; ZW, zygomatic width.

throughout, see Table 1), including length, width, and height of neurocranial and splanchnocranial components. The geometric mean was used as the independent variable (e.g. Mosimann, 1970; Meachen-Samuels & Van Valkenburgh, 2009; Tarnawski *et al.*, 2014a, b) because the total length of the skull is not always isometric in pinnipeds (see Brunner *et al.*, 2004; Tarnawski *et al.*, 2014a, b). The relationship of each variable to the overall size (geometric mean) was examined with the logarithmic expression of the equation of allometry:

$$\log(y) = \log(b_0) + b_1 \log(x) + \log(e),$$

where y is any of the measured skull variables, $\log(b_0)$ is the y -intercept or constant of normalization (and b_0

is the constant term of the power growth function), b_1 is the slope of the line or coefficient of allometry, x is the geometric mean, and e is the error term (i.e. the residuals) (Alexander, 1985). The standardized major axis (SMA) regression determines an axis or line of best fit. Results have been presented as the bivariate allometry of a given cranial character with overall cranial size, and with overall size being measured by the geometric mean score. As most bivariate growth curves can be transformed into straight lines (Alberch *et al.*, 1979), ontogenetic vectors can be described by the slope, intercept, and length. The slope is referred to as the ontogenetic coefficient of allometry and represents the ratio of specific growth rates or the relative growth of the traits involved. As a first step, the significance of the coefficients of allometry was evaluated by a two-tailed Student's t -test at a significance level of $P = 0.01$. The relationship between the two variables was isometric when the slope was equal to one. Deviations from isometry were assessed by comparing the allometric coefficient with that expected under geometric similarity (Alexander, 1985). A coefficient value that was significantly <1 showed negative allometry, whereas a coefficient value that was significantly >1 showed positive allometry (Emerson & Bramble, 1993). For extensive overviews on the subject, see Tarnawski *et al.* (2014a).

Testing for a common coefficient of allometry (slope) among the trajectories of *A. australis*, *A. gazella*, and *A. tropicalis* was the second step in the bivariate analysis. Following the recommendations of Warton *et al.* (2006), a likelihood ratio test for a common SMA slope was used and compared against a chi-square distribution (Warton & Weber, 2002). If a common slope was shared, the significance of a common constant of normalization (y -intercepts) was compared using the Wald statistic for inference (Warton *et al.*, 2006). Finally, if both slopes and y -intercepts were shared, the data points were scattered around a common axis with no difference in elevation. To test the hypothesis that there might be a shift along the axis, the Wald statistic was followed, as in Warton *et al.* (2006). All these regression coefficients, statistical parameters, and tests were performed with R software (R Development Core Team 2009), using the SMATR package (Warton & Weber, 2002).

Multivariate analysis

In the multivariate generalization of simple allometry (Jolicoeur, 1963), the vector of the first principal component (PC1), extracted from a log-transformed variance-covariance matrix, details the pattern of allometric growth. In previous studies, multivariate analyses were performed in order to obtain coefficients of allometry (e.g. Tarnawski *et al.*, 2014a, b). Despite this, in this study the multivariate analysis

Table 1. Linear skull measurements taken from male fur seals in this study (measurements illustrated in Figure 2)

Acronym	Measurement	Definition
BW	Braincase width	Greatest breadth of braincase at the coronal suture, anterior to the zygomatic arches.
CBL	Condylobasal length	Skull length from prosthion to the posterior point on the occipital condyles.
CW	Canine width	Breadth of alveolus of upper canine teeth.
LAU	Load arm length at upper canine	Length from mandibular fossa to centre of Alveolus.
LO	Length of orbit	Greatest orbit length from maxilar to postorbital process of jugal bone.
MW	Mastoid width	Widest distance across the mastoid processes.
OCPH	Occipital plate height	Caudal skull height from basion to inion.
PL	Palatal length	Length from prosthion to palatal notch.
POC	Postorbital constriction	Breadth of the postorbital constriction.
PW	Palatal width	Breadth of palate at PC3, excluding the alveoli.
RH	Rostral height	Height from prosthion to anterior point of nasals.
RL	Rostral length	Distance from prosthion to the anterior margin of the infraorbital foramen.
RW	Rostral width	Greatest bicanine breadth.
UPCL	Length of upper postcanine row	Anterior margin of PC1 alveolus to the most posterior margin of PC6 alveolus.
ZW	Zygomatic width	Widest interzygomatic distance.

was principally focused on the spatial dispersion of the ontogenetic trajectories generated by the principal component analysis (PCA). The study of the morphospaces in morphologic disparity through ontogeny was recently addressed in mammals (e.g. Wilson & Sánchez-Villagra, 2010; Wilson, 2013); however, in our study this analysis was restricted to just a first round of PCA (i.e. PC1 and PC2) in order to examine the divergence of the ontogenetic trajectories of the three fur seal species. Although a strong association between the PC1 and size was expected, the position of the ontogenetic trajectories on the morphospace generated reflects the allometric relationships among the trajectories of the three species. A PCA was performed along the ontogenetic series of the three species, including all the cranial measurements. Mosimann shape variables were calculated for the raw measurements through geometric mean (GM) transformation of data prior to statistical analyses (e.g. Mosimann & James, 1979; Meachen-Samuels & Van Valkenburgh, 2009). These ratios provide an obvious way to study differences in body proportions, as ratios reflect geometric shape differences (Baur & Leuenberger, 2011). Many studies have found ratios to be statistically robust to statistical tests (e.g. Van Valkenburgh, 1987; Van Valkenburgh & Koepfli, 1993; Elissamburu & Vizcaíno, 2004; Meachen-Samuels & Van Valkenburgh, 2009). To standardize the data, each Mosimann variable was expressed as a logarithm. The PCA loading for each variable and the percentage of the variability explained by the most important components were obtained. The first and second components were plotted

and results for the three species were compared through the differences of the position of the multivariate ontogenetic trajectories.

RESULTS

BIVARIATE ANALYSES

Allometry in males of Arctocephalus australis

Regressions for males of *A. australis* (Table 2) showed high values of correlation in all dependent variables, except for the braincase breadth ($R^2 = 0.221$) and the postorbital constriction ($R^2 = 0.284$). Most of the observed allometric trends showed allometry, whereas isometry was detected for just two out of 15 cranial variables (i.e. 13.3%; e.g. OCPH, CW). Positive allometry was detected for eight out of 15 variables (i.e. 53.3% of variables; e.g. PL, PW, RH, RL, RW, LAU, MW, and ZW), whereas negative allometric growth trends were found in just four out of 15 variables (i.e. 26.7%; e.g. CBL, UPCL, BW, and LO). Finally, the POC showed enantiometry (i.e. the shortening of a measurement with skull growth; *sensu* Huxley & Teissier, 1936).

Allometry in males of Arctocephalus gazella

Bivariate regressions for males of *A. gazella* (Table 3) showed high values of correlation, except for breadth of the braincase ($R^2 = 0.068$), the postorbital constriction ($R^2 = 0.06$), and orbital and postcanine row lengths ($R^2 = 0.462$ and 0.463 , respectively). Allometric growth trends were positive for nine out of 15 variables (i.e. 60.0% of variables; e.g. PL, PW, UPCL, RL, RH, MW, LAU,

Table 2. Bivariate analysis of allometry in the ontogeny of male *Arctocephalus australis* ($N = 116$)

Var.	Regression		Intercept			Slope			
	R^2	$F_{(1,N-2)}$	$\log(b_0)$	$t_{(N-2)}$	P_{b_0}	b_1	$F_{\text{iso}(1,N-2)}$	P_{b_1}	Trend
CBL	0.982	6251.460	0.594	27.747	1.59E-52	0.952	15.376	1.51E-04	–
PL	0.940	1796.705	–0.125	–2.643	9.38E-03	1.148	36.511	1.96E-08	+
PW	0.860	702.744	–0.554	–7.530	1.29E-11	1.172	20.769	1.31E-05	+
ZW	0.980	5480.673	–0.053	–1.889	6.14E-02	1.175	146.230	0	+
UPCL	0.911	1172.133	0.173	4.064	8.89E-05	0.852	33.128	7.40E-08	–
OCPH	0.948	2058.192	–0.020	–0.502	0.617*	1.040	3.310	0.071*	=
BW	0.221*	32.381	1.455	35.308	3.24E-63	0.278	403.659	0	–
RL	0.940	1787.616	–0.575	–11.008	1.22E-19	1.270	110.644	0	+
LO	0.870	762.360	0.389	8.711	2.72E-14	0.736	84.923	1.89E-15	–
RH	0.945	1963.922	–0.386	–8.734	2.42E-14	1.122	27.808	6.44E-07	+
MW	0.978	5114.988	–0.501	–14.445	1.62E-27	1.397	606.964	0	+
POC	0.284*	45.315	2.799	27.093	1.69E-51	–0.727	16.791	7.84E-05	enan
LAU	0.968	3454.999	0.009	0.257	0.798*	1.144	64.890	8.56E-13	+
RW	0.966	3239.029	–0.898	–20.763	1.54E-40	1.396	387.352	0	+
CW	0.702	268.165	–0.755	–8.114	6.32E-13	1.013	0.068	0.795*	=

Parameters: R^2 , adjusted coefficient of determination (asterisks are low values); F , F -test for regression; $\log(b_0)$, intercept from standardized major axis; Student's t -test for intercept coefficients $\log(b_0)$; P_{b_0} , P value of $b_0 = 0$ (asterisks are significant values at 0.01); b_1 , slope from standardized major axis; F iso-test, no significant differences from expected value of one; P_{b_1} , P value of $b_1 = 1$ (P values significant at 0.01 level are in bold); growth trend is the summary allometry of each variable. Variable abbreviations are listed in Table 1 and illustrated in Figure 2. Symbols: =, isometry; –, negative allometry; +, positive allometry; enan, enantiometry.

Table 3. Bivariate analysis of allometry in the ontogeny of male *Arctocephalus gazella* ($N = 69$)

Var.	Regression		Intercept			Slope			
	R^2	$F_{(1,N-2)}$	$\log(b_0)$	$t_{(N-2)}$	P_{b_0}	b_1	$F_{\text{iso}(1,N-2)}$	P_{b_1}	Trend
CBL	0.916	731.817	0.720	12.303	7.51E-19	0.877	13.738	4.28E-04	–
PL	0.849	376.840	–0.242	–2.223	0.029*	1.219	17.623	8.12E-05	+
PW	0.791	253.475	–1.113	–7.241	5.60E-10	1.46	48.055	2.00E-09	+
ZW	0.917	744.667	0.139	1.979	0.051*	1.065	3.221	0.077	=
UPCL	0.463*	57.809	–0.656	–2.992	0.00387	1.299	8.744	4.29E-03	+
OCPH	0.729	180.606	0.133	1.176	0.243*	0.946	0.751	0.389	=
BW	0.068*	4.908	1.038	9.087	2.67E-13	0.514	36.841	6.71E-08	–
RL	0.702	158.205	–0.886	–4.988	4.57E-06	1.414	28.141	1.37E-06	+
LO	0.462*	57.430	0.592	5.460	7.50E-07	0.642	26.176	2.82E-06	–
RH	0.811	287.30	–0.681	–5.295	1.42E-06	1.284	22.611	1.09E-05	+
MW	0.873	462.330	–0.197	–1.960	0.054*	1.227	22.471	1.15E-05	+
POC	0.061*	4.338	3.864	13.947	1.72E-21	–1.24	3.378	0.070	enan
LAU	0.915	722.772	0.067	0.903	0.369*	1.099	7.064	9.83E-03	+
RW	0.905	635.787	–1.220	–10.973	1.31E-16	1.563	149.828	0	+
CW	0.644	120.968	–2.203	–8.988	4.03E-13	1.782	70.091	5.14E-12	+

Parameters: R^2 , adjusted coefficient of determination (asterisks are low values); F , F -test for regression; $\log(b_0)$, intercept from standardized major axis; Student's t -test for intercept coefficients $\log(b_0)$; P_{b_0} , P value of $b_0 = 0$ (asterisks are significant values at 0.01); b_1 , slope from standardized major axis; F iso-test, no significant differences from expected value of one; P_{b_1} , P value of $b_1 = 1$ (P values significant at 0.01 level are in bold); growth trend is the summary allometry of each variable. Variable abbreviations are listed in Table 1 and illustrated in Figure 2. Symbols: =, isometry; –, negative allometry; +, positive allometry; enan, enantiometry. Grey-shaded rows are non-significant regressions ($P > 0.01$).

RW, and CW). Three cranial variables (20%; e.g. CBL, BW, and LO) showed negative allometric growth trends, whereas two variables showed isometry (i.e. 13.3%; ZW, OCPH), and the remaining variable, the POC, showed enantiometry.

Allometry in males of Arctocepalus tropicalis

Most of the dependent variables showed high values of correlation in *A. tropicalis* (Table 4), although the braincase breadth and the postorbital constriction had low correlation values ($R^2 = 0.186$ and 0.080 , respectively). Six out 15 cranial variables (i.e. 40.0% of variables; e.g. PL, PW, ZW, RL, MW, and RW) showed positive allometry, whereas four variables (i.e. 26.7% of variables; e.g. CBL, OCPH, BW, and LO) showed negative allometry. Growth trends were isometric in another four variables (e.g. UPCL, RH, LAU, and CW). Finally, the POC showed enantiometry.

Interspecific comparisons of bivariate analyses

Across all species, the character exhibiting the highest correlations with size (R^2) was CBL. In the SMA analyses (Tables 2–4), we detected common ontogenetic growth trends (i.e. the same allometric sign for all the species) in 13 out 15 of skull variables (i.e. 92.9%); however, the interspecific statistical comparisons of slopes and intercepts (Table 5) showed that the three species exhibited divergent patterns of cranial growth. On one

hand, in only 20% of cranial variables (i.e. PL, RL, and LO) all the species shared common slopes and also showed agreement among their intercepts. Nevertheless, these variables showed extensions of their common growth trajectories, being in all the cases greater for *A. gazella* than for the remaining species (Fig. 3A; Table 5). On the other hand, in 12 out 15 variables (i.e. 80%) we found significant differences between the coefficients of allometry (i.e. slopes) for all species (Fig. 3B). For instance, *A. australis* showed the highest slope values for neurocranial variables, such as CBL and POC, whereas *A. gazella* showed the highest values in our comparisons for BW and some splachnocranial variables (i.e. UPCL, RH, RW, and CW; Table 5). Slopes were higher in *A. australis* than in the other species mainly in variables related to muscle insertions (e.g. *A. australis* > *A. gazella* for ZW and MW; *A. australis* > *A. tropicalis* for OCPH); however, for PW both *A. gazella* and *A. tropicalis*, which shared slopes as well as intercepts, showed higher coefficients of allometry than in *A. australis* (Table 5).

The comparison between intercepts (i.e. no change of slopes, with change of intercepts) showed that *A. australis* had higher values than *A. tropicalis* for rostral widths (i.e. RW and CW), whereas intercepts were higher in *A. australis* than in *A. gazella* for OCPH and LAU (Table 5). Conversely, *A. gazella* showed higher intercepts than *A. tropicalis* for POC, whereas we did

Table 4. Bivariate analysis of allometry in the ontogeny of male *Arctocepalus tropicalis* ($N = 51$)

Var.	Regression		Intercept			Slope			
	R^2	$F_{(1,N-2)}$	$\log(b_0)$	$t_{(N-2)}$	P_{b_0}	b_1	$F_{\text{iso}(1,N-2)}$	P_{b_1}	Trend
CBL	0.978	2169.03	0.682	19.578	8.17E-25	0.9	24.841	8.17E-06	–
PL	0.931	664.689	–0.147	–1.839	0.071*	1.168	17.305	1.28E-04	+
PW	0.928	632.759	–1.075	–10.727	1.86E-14	1.435	92.845	6.80E-13	+
ZW	0.926	611.665	0.019	0.231	0.818*	1.145	12.176	1.03E-03	+
UPCL	0.861	303.386	–0.122	–1.223	0.227*	1.026	0.232	0.632	=
OCPH	0.926	615.905	0.346	5.830	4.27E-07	0.839	20.803	3.42E-05	–
BW	0.186*	11.206	1.397	18.369	1.29E-23	0.323	115.317	1.79E-14	–
RL	0.872	334.354	–0.767	–6.069	1.83E-07	1.357	36.766	1.87E-07	+
LO	0.766	160.133	0.222	2.099	0.040*	0.838	6.628	0.013	–
RH	0.899	436.463	–0.245	–2.822	6.88E-03	1.048	1.067	0.307	=
MW	0.921	567.509	–0.438	–4.344	7.02E-05	1.372	63.892	1.96E-10	+
POC	0.080*	4.275	4.298	11.003	7.66E-15	–1.56	11.348	1.48E-03	enan
LAU	0.968	1504.3	0.185	3.850	3.42E-04	1.04	2.405	0.127	=
RW	0.927	623.796	–0.921	–9.358	1.74E-12	1.399	78.783	9.03E-12	+
CW	0.642	87.798	–1.027	–5.740	5.87E-07	1.148	2.607	0.113	=

Parameters: R^2 , adjusted coefficient of determination (asterisks are low values); F , F -test for regression; $\log(b_0)$, intercept from standardized major axis; Student's t -test for intercept coefficients $\log(b_0)$; P_{b_0} , P value of $b_0 = 0$ (asterisks are significant values at 0.01); b_1 , slope from standardized major axis; F_{iso} -test, no significant differences from expected value of one; P_{b_1} , P value of $b_1 = 1$ (P values significant at 0.01 level are in bold); growth trend is the summary allometry of each variable. Variable abbreviations are listed in Table 1 and illustrated in Figure 2. Symbols: =, isometry; –, negative allometry; +, positive allometry; enan, enantiometry. Grey-shaded rows are non-significant regressions ($P > 0.01$).

Table 5. Interspecific comparisons of the bivariate allometric trajectories in *Arctocephalus australis* (A), *Arctocephalus gazella* (G), and *Arctocephalus tropicalis* (T)

Var.	L_r	P_{L_r}	Growth trend	$W(b_0)$	$P_{W(b_0)}$	Intercept	$W(\text{shift})$	$P_{W(\text{shift})}$	Shift
CBL	8.300	0.016	G = T; G < A; T < A All -	4.618	0.032	G < T			
PL	1.307	0.520	A = G = T All +	26.939	1.41E-06	A = G = T	174.651	0.000	A < T < G
PW	18.613	9.08E-05	G = T; A < G; A < T All +	2.620	0.106	T = G	56.553	5.47E-14	T < G
ZW	6.637	0.036	A = T; G = T; G < A All +	42.391 70.264	7.47E-11 0.00E+00	A < T G < T			
UPCL	24.801	4.12E-06	A < T < G A -; T =; G +						
OCPH	21.071	2.66E-05	A = G; G = T; T < A A +; G =; T -	42.133 11.473	8.53E-11 0.001	G < A G < T			
BW	17.739	1.41E-04	A = T; A < G; T < G All -	54.680	1.42E-13	A < T			
RL	3.249	0.197	A = G = T All +	111.242	0.00E+00	A = G = T	114.426	0.000	A = T; A < G; T < G
LO	5.608	0.061	A = G = T All -	55.833	7.52E-13	A = G = T	227.946	0.000	A < T < G
RH	8.275	0.016	A = T; A < G; T < G All +	3.213	0.073	A = T	10.595	0.001	A < T
MW	7.718	0.021	A = T; G = T; G < A All +	27.955 46.560	1.24E-07 8.89E-12	A < T G < T			
POC	28.516	6.42E-07	G = T; G < A; T < A All =	91.389	0.00E+00	T < G			
LAU	9.345	0.009	A = G; G = T; T < A All +	108.825 14.027	0.00E+00 1.80E-04	G < A G < T			
RW	7.264	0.026	A = T; A < G; T < G All +	23.288	1.39E-06	T < A			
CW	35.836	1.65E-08	A = T; A < G; T < G A =; T =; G +	17.710	2.57E-05	T < A			

Test for common slope, common intercept, and shift. Parameters: L_r , likelihood ratio (Warton *et al.*, 2006); P_{L_r} , P value of L_r parameter, (P -values significant at 0.01 level are in bold); $W(b_0)$, Wald statistic (Warton *et al.*, 2006) for intercept; $P_{W(b_0)}$, P -value of $W(b_0)$; intercept (b_0 com), common intercept from standardized major axis (values are in bold); $W(\text{shift})$, Wald statistic (Warton *et al.*, 2006) for shift; $P_{W(\text{shift})}$, P -value of $W(\text{shift})$; shift, shift along the regression axis. Growth trend is the summary allometry of each variable. Variable abbreviations are listed in Table 1 and illustrated in Figure 2. Symbols: =, isometry; -, negative allometry; +, positive allometry; enan, enantiometry. Differences are between the common slope trend and the slope observed for each species. Grey-shaded rows are designed to improve readability.

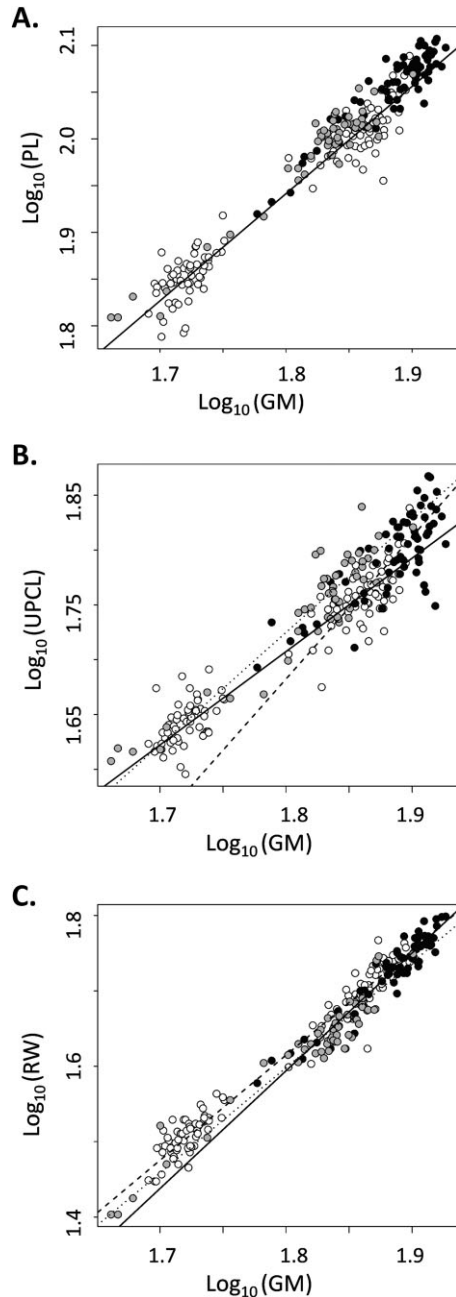


Figure 3. Bivariate standardized major axis (SMA) regressions for *Arctocephalus australis* (white circles and dashed line), *Arctocephalus gazella* (black circles and solid line), and *Arctocephalus tropicalis* (grey circles and dotted line): A, same slope and intercepts for *A. australis*, *A. gazella*, and *A. tropicalis*; B, different slopes between the growth trajectories; and C, same slope and different intercepts between species. Abbreviations as in Figure 2.

not detect differences between *A. gazella* and *A. australis* in this sense. Finally, *A. tropicalis* showed higher intercepts than *A. australis* and *A. gazella* for cranial widths associated with muscle insertions (i.e. ZW and MW).

We also found that *A. tropicalis* showed higher intercepts than *A. australis* for BW, whereas intercepts were higher in *A. tropicalis* than in *A. gazella* for CBL, OCPH, and LAU. We also detected additional differences (i.e. extensions over growth trajectory) between pairs of species with common slopes and intercepts. For instance, *A. gazella* showed the largest trajectories for PL, RL, and LO. Indeed, *A. gazella* also showed a greater offset than *A. tropicalis* in the growth trajectory of PW, whereas *A. tropicalis* showed a greater offset than *A. australis* for RH (Fig. 3C).

MULTIVARIATE ANALYSIS

The PCA analysis including the three species (Fig. 4) showed that PC1 and PC2 explained 92.3% of the total variation. Changes across PC1 were related to size on the ontogenetic trajectories, as the three species clearly occupied areas that correspond to the first component, placing non-adult and adult stages on positive and negative values, respectively. Hence, it provided a measure of the overall size variation. Eigenvectors of PC1 ranged from -0.500 to 0.301 , accounting for 79% of the total variation (Table 6). Variables with highest loadings on PC1 were RL and RH (-0.426 and -0.500 , respectively). Variation described by this PC indicated a strong rearrangement of the skull during growth, detecting that as male fur seals increased in size they develop larger and higher rostrums in comparison with the overall skull size (i.e. GM). The morphospace generated also showed overlapped trajectories for the three species across all their ontogenies, although adult *A. tropicalis* showed smaller overall size than adult *A. gazella* and *A. australis*. The divergence around juveniles of *A. gazella* may be a consequence of sample bias (see Material and methods). On the other hand, PC2 accounted for 13.3% of the total variation, and the highest loadings were LAU and CW (-0.534 and -0.477 , respectively). This PC also showed an overlap between the trajectories of the three species, showing low discrimination between them.

DISCUSSION

In this study we found that *A. australis*, *A. gazella*, and *A. tropicalis* shared common growth rates and intercepts for viscerocranial variables such as palatal and rostral lengths, as well as for the orbital length, suggesting the existence of a conservative pattern in the three species under study. Such conservatism in the skull morphology and in their ontogenetic variation is also reflected in multivariate space, in which the three trajectories highly overlapped. Indeed, genetic divergences between the major otariid clades suggested the period in which they diverged from each other represents a rapid radiation (i.e. 6.7 Myr, Wynen *et al.*, 2001;

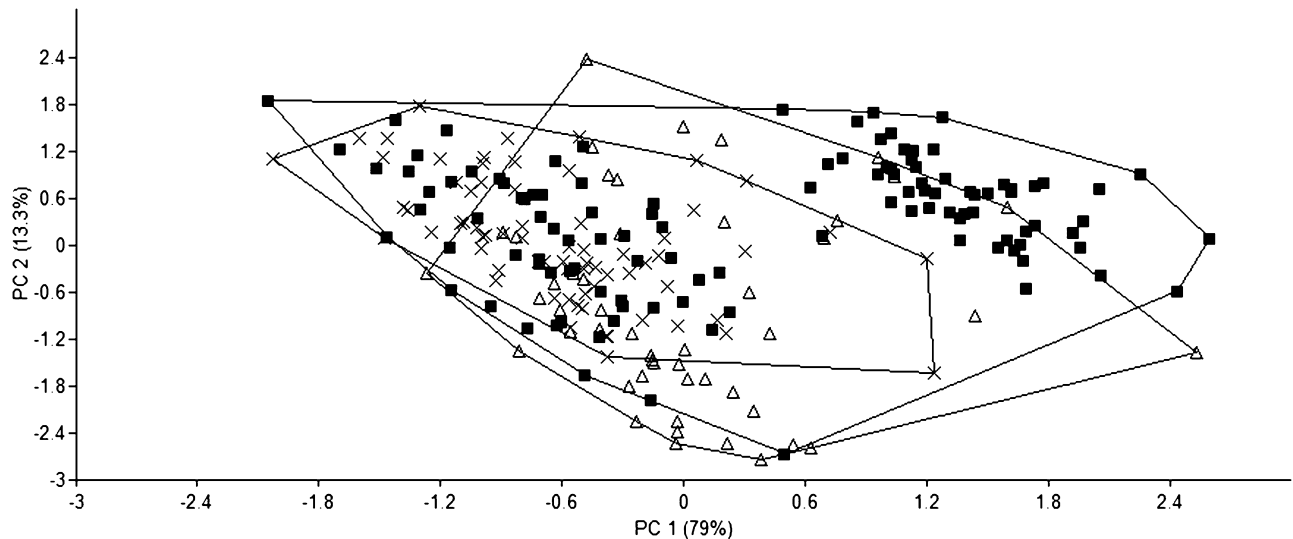


Figure 4. Pairwise comparison of factors 1 and 2 from the principal component analysis of the ontogenetic series of *Arctocephalus australis* (filled squares), *Arctocephalus gazella* (crosses), and *Arctocephalus tropicalis* (triangles).

Table 6. Eigenvectors for the principal component analysis of *Arctocephalus australis*, *Arctocephalus gazella*, and *Arctocephalus tropicalis*

	PC1 (79.0%)	PC2 (13.3%)
log (CBL/MG)	0.003	-0.017
log (PL/MG)	-0.210	-0.151
log (PW/MG)	0.0379	0.035
log (ZW/MG)	-0.232	-0.212
log (UPCL/MG)	0.093	0.039
log (OCPL/MG)	-0.259	-0.146
log (BW/MG)	0.219	0.109
log (RL/MG)	-0.426	-0.199
log (LO/MG)	0.301	0.061
log (RH/MG)	-0.500	-0.168
log (MW/MG)	0.272	-0.057
log (POC/MG)	-0.249	0.387
log (LAU/MG)	0.0695	-0.534
log (RW/MG)	-0.301	0.395
log (CW/MG)	0.142	-0.477

Variable abbreviations are listed in Table 1 and illustrated in Figure 2.

Yonezawa *et al.*, 2009). The rostrum morphology has been traditionally used for species identification in the genus (e.g. Repenning *et al.*, 1971; Brunner, 2004; Daneri *et al.*, 2005); however, in contrast to previous reports, our work highlighted that the differences in the relative proportions of the rostrum were not distinguishable in earlier ontogenetic stages, as differences were mostly related to growth extensions (i.e. size) in adult stages. This led to a larger rostrum in adult *A. gazella*

in comparison with adult *A. australis* and *A. tropicalis*, although this did not imply a greater rostral proportion, because differences in slope were not detected. This difference detected in the rostrum (PL, RL), a structure that is highly related with trophic functions, could indicate interspecific differences amongst prey-capture techniques. Although the three fur seal species capture fish and cephalopods by the pierce-feeding technique (e.g. Adam & Berta, 2002), *A. gazella* regularly employs another feeding technique. On one hand, according to Croll, Tershy & Newton (2008) the filter-feeding technique is almost exclusively used by *A. gazella* on Antarctic krill during the summer season. An elongated palate is possibly important to retain prey while water is expelled (e.g. Klages & Cockcroft, 1990). On the other hand, it is more likely that their elongated palate is used for suction feeding given the vestigial nature of the dentition. Indeed, Adam & Berta (2002) suggested that this technique was associated with the palate elongation detected in *Odobenus* and *Otaria*.

Similarly, the common trajectories (i.e. common slopes and intercepts) detected for the orbit length (LO) in the three species also indicated that these interspecific differences were related to size, again exhibiting the highest offset values in *A. gazella*. Recently, Debey & Pyenson (2013) stated that larger pinniped skulls, on average, had proportionately smaller eyes than smaller pinnipeds. This was also in agreement with our bivariate analyses, which indicated that orbits grew at a lesser rate than the overall skull size (i.e. LO/MG ratio decreases in adults in comparison with juveniles). Our results indicated that orbits grew at the same pace in the three fur seal species, but that *A. gazella* achieved a greater final size through an adult growth

extension. As a result, adult *A. gazella* have bigger orbits than *A. tropicalis* and *A. australis* (in that order), although the size of this structure is proportionately smaller in *A. gazella* than in the remaining species, by extension of its negatively allometric trajectory. It has been suggested that bony orbit size, a proxy for eye size, is linked to pinniped diving ability (e.g. Debey & Pyenson, 2013). Biological data support this hypothesis in the species under study, as the reported maximum diving depths for *A. gazella* (>350 m; Jefferson *et al.*, 2008) are deeper than those reported for *A. tropicalis* and *A. australis* (208 and 170 m, respectively; Schreer & Kovacs, 1997; Jefferson *et al.*, 2008). On the other hand, Debey & Pyenson (2013) reported a significant correlation between the orbit size and the zygomatic breadth, which was considered the best single predictor of orbit size for Pinnipedia. Our results are not in concordance with this finding, as for ZW we detected higher relative initial size in *A. tropicalis* than in the remaining species, and higher relative growth rates (i.e. slopes) in *A. australis* than in *A. gazella*. This fact could indicate that, although ZW can be associated with LO, this measurement is also related with other functions. For instance, the zygomatic arch not only protects the eye, but it also provides a base for the masseteric and part of the temporalis muscles in carnivores (Evans, 1993; Segura, Prevosti & Cassini, 2013). Both muscles raise the mandible, an action that has previously been linked with combat between males (e.g. Brunner *et al.*, 2004). Indeed, sexual dimorphism in ZW has been detected in other sexually dimorphic pinnipeds (e.g. Brunner *et al.*, 2004; Tarnawski *et al.*, 2014b).

According to our results, *A. tropicalis* was morphologically intermediate between *A. australis* and *A. gazella*, as *A. tropicalis* shared several relative growth rates (regression slopes) with AUS and *A. gazella* separately. For instance, *A. tropicalis* shared six common relative growth rates with *A. australis*, which were all related to skull breadths (i.e. ZW, BW, RH, MW, RW, and CW; Table 5), and seven other common trends with *A. gazella* (i.e. CBL, PW, ZW, OCPH, MW, LAU, and POC; Table 5). Previous morphometric works are also in concordance with our results. Drehmer & Ferigolo (1997) also stated that *A. tropicalis* showed intermediate cranial characters in comparison with *A. australis* and *A. gazella*, although they only used adult skulls. Our results indicated that these morphological similarities between species in their skull proportions (shape) are evident along their entire postnatal ontogenies. Field data also support our findings, as *A. tropicalis* is known to have intermediate weaning times (i.e. lactating periods) and somatic growth rates (e.g. Kerley, 1985; Goldsworthy & Crowley, 1999; Phillips & Stirling, 2000; Luque *et al.*, 2007), compared with the other two species. In contrast, *A. gazella* and *A. australis* differed greatly

in growth rates, as our results indicated that they shared common slopes only for OCPH and LAU. Despite this, the recent phylogenetic analysis performed by Yonezawa *et al.* (2009) showed that *A. gazella* and *A. australis* were more closely related than with *A. tropicalis*. Thus, in contrast to this hypothesis, our results indicated that *A. gazella* and *A. australis* exhibited greater allometric differences between each other than with the latter species. The sister-taxon relationship of *A. gazella* and *A. tropicalis* proposed by other researchers (e.g. Higdon *et al.*, 2007; Agnarsson, Kuntner & May-Collado, 2010; Nyakatura & Bininda-Emonds, 2012) is in partial agreement with our results, however. Furthermore, in addition to ecological parameters (such as breeding and weaning), this may also explain some of the reported allometric similarities between *A. gazella* and *A. tropicalis*. Although the relationships of the species of the genus *Arctocephalus* are still controversial (e.g. Repenning *et al.*, 1971; Lento *et al.*, 1997; Wynen *et al.*, 2001; Berta & Churchill, 2012), the inconsistencies detected between the phylogenies and the allometric growth trends could indicate that the post-weaning skull development in males of *Arctocephalus* is more influenced by life history (i.e. life cycle, habitat, and polygynic behaviour) than by phylogeny. Given the recent radiation of the genus (Wynen *et al.*, 2001; Yonezawa *et al.*, 2009), it is not surprising that we detected a conservative pattern in allometric trends as well as within the multivariate morphospace.

In contrast to these common growth trends, we also detected that the UPCL showed a growth trajectory with different slopes for all the species. In proportion to the overall size of the skull, growth rates of UPCL were higher for *A. gazella* than for *A. australis*, being again intermediate in *A. tropicalis*. This could indicate a possible relationship with the larger space between the postcanine teeth in *A. gazella* and *A. tropicalis*, in comparison with *A. australis* (Fig. 1). In both species, tooth row is characterized by prominent diastemas, which tend to be larger between the posterior premolars and between the molars (e.g. Repenning *et al.*, 1971; Drehmer & Oliveira, 2000; Daneri *et al.*, 2005). On the contrary, in *A. australis* the postcanine teeth are typically abutting against each other (e.g. Brunner *et al.*, 2004), which is consistent with the negative allometry detected for UPCL in this species. Our results indicate that this character, which is also used to discriminate species of the genus (e.g. Brunner, 2004), is achieved as soon as the postcanine teeth erupt in juvenile stages. Future interspecific comparisons using non-adult specimens are still necessary to assess whether or not the postcanine tooth length is a useful character for species identification along the entire skull ontogeny.

Another character with taxonomic value is the PW because it is related to tooth row orientation in each

species. Tooth rows in *A. gazella* and *A. tropicalis* are characterized by a posterior divergence (especially at the level of the fifth postcanine teeth), whereas in *A. australis* they are roughly parallel (Fig. 1). Our results (Table 5) showed that these differences in PW were achieved as a consequence of a delayed development in comparison with *A. gazella* and *A. tropicalis*, whereas the wider palate of *A. gazella* was generated by an increase in the overall skull size of adult stages. Briefly, this showed that the relative PW could be another useful taxonomic character in order to discriminate *A. australis* from *A. gazella* and *A. tropicalis* along their entire ontogenies, as skull differences are evident not only in adults but also in non-adult stages.

The extent of the higher relative growth rates (i.e. slopes) in *A. gazella* compared with *A. australis* or *A. tropicalis* (Table 5) indicated that *A. gazella* exhibited more accelerated growth rates for several morphological traits, relative to the overall skull size, than the other species (mainly related to tooth eruption and brain development). The acquisition of a fully developed dentition and nervous system are both important in independent juveniles, when fur seals begin to forage and enhance their social skills through play. *Arctocephalus gazella* pups exhibited greater precocial growth than *A. australis* and *A. tropicalis*, as seen in their shorter lactation periods (116 days; Costa *et al.*, 1988) in comparison with *A. australis* and *A. tropicalis* (more than 300 days; e.g. Guinet & Georges, 2000 for *A. tropicalis*; Vaz-Ferreira, 1981 for *A. australis*). In addition, males of *A. gazella* reach sexual maturity earlier (i.e. at 3–4 years in *A. gazella*; Hoffman, Boyd & Amos, 2003, Nowak & Walker, 2003; at 8 years in *A. tropicalis*; Bester, 1990; at 7 years in *A. australis*; Vaz-Ferreira & Ponce de Léon, 1987), so rapid growth was expected in this species.

Finally, our comparison of intercepts pointed out that other skull shape differences between species already occurred in early ontogenetic stages, rather than in adult stages, by reorganizations of skull proportions along their ontogenetic trajectories. For instance, young *A. gazella* had a proportionately wider POC, relative to overall skull size, than young *A. tropicalis*, whereas the *A. tropicalis* had greater CBL, ZW, and OCPH than *A. gazella*. Broader interorbital constrictions have been described in adult *A. gazella* in comparison with other species of the genus (e.g. Brunner, 2004), but this has not been detected in juvenile stages. In addition, the PW exhibited similar proportions in *A. gazella* and *A. tropicalis* (i.e. the same slopes and intercepts for PW, but with different offsets; see Table 5), indicating that differences in this character between both species were not related to relative growth rates (slopes) or initial skull proportions (intercepts), but only arose from adult growth extensions. Thus, differences in the relative PW of adult stages were associated with size differences

(Fig. 4). Conversely, young *A. australis* showed proportionately wider rostrums (i.e. higher intercepts for RW and CW) than young *A. tropicalis*, whereas the latter showed wider dimensions related to the zygomatic arches, mastoid processes, and braincase (ZW, BW, and MW). This is partially in agreement with Brunner (2004) who stated that the ZW of adult *A. tropicalis* is the largest of the genus. In addition, our results demonstrated that this difference was also present in non-adult stages. The differences in ontogenetic growth trends of these variables, which are closely related to bite activity, head movements, and neurocranial components, demonstrate the complexity of the systems developed during the radiation of the genus. The proportionally higher ZW and BW of *A. tropicalis* could possibly reflect a compensation of the spaces generated for the temporal musculature. Its larger braincase causes a reduction in the space for this muscle, although its more expanded ZW creates additional space to accommodate it. Although MW and BW are structurally related variables, the higher intercepts detected in *A. tropicalis* suggest broader areas for muscle insertions related to neck movements from early stages.

COMPARISON WITH SOUTHERN SEA LIONS AND ELEPHANT SEALS

In two recent papers (Tarnawski *et al.*, 2014a, b) we have studied the skull ontogeny of *Otaria byronia*, the southern sea lion (Otariidae), and *Mirounga leonina*, the southern elephant seal (Phocidae). Although our studies of the ontogeny of sexual dimorphism in both pinniped species were based on functional grounds, we used similar methodological approaches for the three fur seal species studied. In this sense, comparisons of the ontogenetic patterns are important as recent molecular phylogenies (e.g. Nyakatura & Bininda-Emonds, 2012) support the monophyly of Southern Hemisphere otariids (i.e. *Otaria*, *Neophoca*, *Phocarctos*, and *Arctocephalus*). We note that in the bivariate analyses of allometry most variables (eight out of 15 cranial variables; i.e. 53.3%) showed the same growth trends in all otariid males, whereas 40% of the cranial variables showed common trends between otariids and phocid *M. leonina* (Table 7). These facts suggest a conservative growth pattern in pinnipeds. For instance, variables associated with the rostrum (e.g. PL, PW, RL, and RW) showed positively allometric growth trends in all the species considered, whereas those related to the neurocranium (e.g. BW and LO) showed negative allometry. Similarly, considering only otariids, *O. byronia*, and the three species considered herein showed enantiometry for the POC (i.e. reduction of the absolute size during growth). Enantiometry has seldom been detected in morphometric studies, but has been identified in the braincase growth of some primates (Corner

Table 7. Comparison the of bivariate allometric growth trends in *Arctocephalus australis*, *Arctocephalus gazella*, *Arctocephalus tropicalis* (this paper), *Otaria flavescens* (Tarnawski *et al.*, 2014a), and *Mirounga leonina* (Tarnawski *et al.*, 2014b)

Var.	<i>A. australis</i>	<i>A. gazella</i>	<i>A. tropicalis</i>	<i>O. byronia</i>	<i>M. leonina</i>
CBL	–	–	–	–	=
PL	+	+	+	+	+
PW	+	+	+	+	+
ZW	+	=	+	–	=
UPCL	–	+	=	–	–
OCPH	=	=	–	–	–
BW	–	–	–	–	–
RL	+	+	+	+	+
LO	–	–	–	–	–
RH	+	+	=	–	+
MW	+	+	+	–	–
LAU	+	+	=	+	+
RW	+	+	+	+	+
CW	=	+	=	+	+
CPO	enan	enan	enan	enan	=

Variable abbreviations are listed in Table 1 and illustrated in Figure 2. Growth trends of bivariate allometric analysis for each variable: =, isometry; –, negative allometry; +, positive allometry; enan, enantiometry. Shaded rows show similarities between all the species in their allometric growth trends.

& Richtsmeier, 1991). Enantiometry could be associated with the generation of extra space to accommodate the temporal muscles, besides the growth of the zygomatic breadth. Indeed, temporal muscles are highly important in adult intra-male competition in pinnipeds. Future studies should analyse enantiometry in a phylogenetic context in order to test whether this unusual growth trend evolved in basal otariids, or even pinnipeds, or if it evolved by convergence in crown groups as a result of selective pressures, such as the polygynic behaviour. To date, the results obtained for male *M. leonina* (Tarnawski *et al.*, 2014b) indicated the absence of enantiometry in the POC. Furthermore, in contrast to *M. leonina*, all the otariid species also showed agreement between the allometric growth trends for CBL. Hence, the presence of these characters (i.e. enantiometry of POC and isometry of CBL) could be interpreted as possible synapomorphies of Otariidae if further studies detect these conditions in other otariids (e.g. *Callorhinus*, *Eumetopias*, *Zalophus*, *Neophoca*, and *Phocarcos*). Despite these similarities between the otariid species, we note that the detection of a positive allometric growth trend in *Arctocephalus* for the MW could indicate an important difference with other pinnipeds, as this character showed negative allometry in *O. byronia* and *M. leonina*. Our results indicated that males of the latter species exhibit precocial development of MW in comparison with the fur seals studied herein. Future studies should test whether this character is also present in other species of the genus *Arctocephalus* and, in that case, test if it is a

synapomorphy of the genus or a convergent character of fur seals. On the other hand, *O. byronia* and *M. leonina* also shared common growth trends with some of the *Arctocephalus* species. Both species shared an additional growth trend with *A. tropicalis* (e.g. OCPH), and two with *A. australis* (e.g. UPCL and LAU) and *GAZ* (e.g. LAU and CW). Moreover, *M. leonina* also showed a common growth trend with *GAZ* (i.e. ZW). These similarities could indicate that these pinniped species have similar ways of acquiring adult male morphology, despite their phylogenetic relationships.

In summary, our report revealed growth trends in the ontogenetic trajectories of males of three fur seal species, with some phylogenetic implications taking into account the male ontogeny of *O. byronia* and *M. leonina*. We detected differences in the ontogeny of the genus, and suggested that morphological differences could be important to avoid overlaps in life history during the evolution of the group, despite the strong overlap in morphospace. Information presented in this study confirmed earlier observations of fur seals (e.g. Brunner, 2004; Daneri *et al.*, 2005; Debey & Pyenson, 2013), and provided new information on skull growth useful for species discrimination, and also gave new information of interest for understanding life-history differences. Because ontogenetic allometry is a source of biological diversity, understanding how evolution proceeds in phenotypic space also requires an understanding of the evolution of development (Hall, 2000; Raff, 2000). Despite this, most of the previous studies on otariid taxonomy, systematics, and evolution have

focused on the adult stage (sampling only the end of their ontogenies). Future work on allometry should focus on sampling a greater variety of pinniped taxa and test whether patterns in ontogeny support existing phylogenetic hypotheses on pinniped phylogeny.

ACKNOWLEDGEMENTS

We thank Damián Romero and Natalia Martino (MMPMa), Daniela Sanfelice (MCN), Diego Verzi, and Itatí Olivares (MLP), Enrique Crespo and Néstor García (CNP), M.E. Marquez, Javier Negrete, and Javier Mennucci (IAA), Natalie Goodall and volunteers (RNP), Paulo Simões- Lopes and Mauricio Graipel (UFSC), Sergio Bogan (CFA), and Sergio Lucero (MACN), for allowing access to mammal collections. This work was financed by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

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APPENDIX

Specimens of *A. australis* (AUS), *A. gazella* (GAZ), and *A. tropicalis* (TRO) examined in this study.

Sp.	Collection no.	CBL	GM	Age class
AUS	UFSC 1335	157.4	49.72	NOAD
AUS	MCN 2834	159.5	49.24	NOAD
AUS	RNP 1311	159.7	47.99	NOAD
AUS	UFSC 1343	159.8	47.51	NOAD
AUS	UFSC 1043	160.0	50.89	NOAD
AUS	MCN 2498	160.8	48.84	NOAD
AUS	UFSC 1325	161.8	49.31	NOAD
AUS	MCN 2621	162.2	48.62	NOAD
AUS	MCN 2692	163.1	49.90	NOAD
AUS	UFSC 1363	163.6	49.98	NOAD
AUS	UFSC 1337	163.8	50.44	NOAD
AUS	UFSC 1380	165.0	50.14	NOAD
AUS	RNP 2271	165.1	48.12	NOAD
AUS	CNP Aa008	165.1	48.80	NOAD
AUS	MCN 2650	165.3	50.87	NOAD
AUS	MCN 2839	165.8	50.12	NOAD
AUS	MCN 2647	166.1	50.28	NOAD
AUS	MACN 28261	166.8	48.86	NOAD

APPENDIX *Continued*

Sp.	Collection no.	CBL	GM	Age class
AUS	UFSC 1263	167.0	51.06	NOAD
AUS	MCN 2507	167.8	48.70	NOAD
AUS	RNP 2337	168.6	49.44	NOAD
AUS	UFSC 1147	169.3	49.51	NOAD
AUS	RNP 1620	169.3	51.25	NOAD
AUS	RNP 2298	170.5	51.01	NOAD
AUS	UFSC 1096	170.6	52.78	NOAD
AUS	CNP Aa025	170.6	50.17	NOAD
AUS	RNP 2298	170.7	51.15	NOAD
AUS	MCN 2500	171.0	51.85	NOAD
AUS	RNP 1380	171.0	51.13	NOAD
AUS	UFSC 1272	172.1	51.32	NOAD
AUS	RNP 2680	173.2	51.50	NOAD
AUS	MMPMa 4085	173.3	53.02	NOAD
AUS	RNP 1796	173.3	49.82	NOAD
AUS	MACN 20570	173.4	51.90	NOAD
AUS	MCN 2684	173.5	51.95	NOAD
AUS	MCN 2634	173.8	52.21	NOAD
AUS	UFSC 1040	174.4	51.16	NOAD
AUS	MCN 2495	175.0	52.54	NOAD
AUS	MCN 2638	175.0	52.10	NOAD
AUS	UFSC 1283	175.3	52.99	NOAD
AUS	MCN 2537	175.5	51.48	NOAD
AUS	RNP 1581	175.9	50.16	NOAD
AUS	UFSC 1320	176.0	51.07	NOAD
AUS	UFSC 1111	176.4	52.52	NOAD
AUS	CNP Aa002	176.8	51.62	NOAD
AUS	MACN 20569	177.0	52.66	NOAD
AUS	CNP Aa030	177.4	52.97	NOAD
AUS	MMPMa 4154	177.9	53.25	NOAD
AUS	MCN 2628	178.2	52.53	NOAD
AUS	MMPMa 4084	178.2	52.02	NOAD
AUS	UFSC 1282	178.4	54.41	NOAD
AUS	CNP Aa007	178.6	52.18	NOAD
AUS	MCN 2529	178.8	53.95	NOAD
AUS	MCN 2606	179.3	54.49	NOAD
AUS	RNP 2574	180.8	51.87	NOAD
AUS	RNP 2574	180.8	51.87	NOAD
AUS	CNP Aa031	186.3	53.99	NOAD
AUS	CNP Aa026	209.3	62.48	AD
AUS	CNP Aa022	210	60.24	AD
AUS	UFSC 1378	217.1	67.46	NOAD
AUS	CNP Aa011	218	63.82	AD
AUS	UFSC 1156	219.6	62.48	AD
AUS	CNP Aa032	220.8	64.58	AD
AUS	UFSC 1274	221.0	64.49	AD
AUS	RNP 1524	221.0	63.96	AD
AUS	CNP Aa018	221.6	64.66	AD
AUS	UFSC 1143	224.8	65.17	AD
AUS	MCN 2706	225.0	68.07	AD
AUS	CNP Aa005	226	64.90	AD
AUS	CNP Aa020	227.3	67.24	AD
AUS	MCN 2685	227.5	69.59	AD
AUS	UFSC 1142	227.7	67.59	AD

APPENDIX *Continued*

Sp.	Collection no.	CBL	GM	Age class
AUS	CNP Aa029	227.7	67.22	AD
AUS	UFSC 1166	229.7	66.07	AD
AUS	UFSC 1157	229.7	67.78	AD
AUS	MACN 24732	230.0	66.27	AD
AUS	RNP 2520	230.0	65.69	AD
AUS	UFSC 1159	231.0	67.90	AD
AUS	CNP Aa003	231.0	65.10	AD
AUS	UFSC 1158	231.8	69.78	AD
AUS	CNP Aa015	231.8	66.74	AD
AUS	CNP Aa021	231.9	66.13	AD
AUS	UFSC 1063	232.1	68.53	NOAD
AUS	UFSC 1163	232.1	69.98	AD
AUS	MMPMa 4143	232.8	71.08	AD
AUS	MACN 20566	232.9	69.59	AD
AUS	UFSC 1323	233.5	70.87	AD
AUS	MCN 2630	234.1	68.95	AD
AUS	UFSC 1160	234.2	68.54	AD
AUS	MMPMa 4014	234.4	68.55	AD
AUS	MLP 13.25	234.5	69.08	AD
AUS	CNP Aa016	234.7	69.10	AD
AUS	CNP Aa033	234.8	70.02	AD
AUS	MCN 2689	235.8	69.26	AD
AUS	MACN 20568	236.3	72.68	AD
AUS	UFSC 1169	236.6	70.49	AD
AUS	UFSC 1154	236.8	69.70	AD
AUS	MLP 1061	237.4	70.33	AD
AUS	MACN 29769	238.2	70.77	AD
AUS	CNP Aa 012	238.3	71.03	AD
AUS	MACN 21862	239.3	71.51	AD
AUS	CFA 12858	239.4	71.44	AD
AUS	MACN 21863	239.6	70.99	AD
AUS	CNP Aa 001	241.1	68.33	AD
AUS	MCN 2649	241.3	72.59	AD
AUS	RNP 914	241.8	72.73	AD
AUS	RNP 1365	242.0	74.11	AD
AUS	MCN 2688	242.2	71.70	AD
AUS	UFSC 1228	243.0	70.61	AD
AUS	MMPMa_a1	243.2	69.24	AD
AUS	CNP Aa023	243.3	70.66	AD
AUS	RNP 713b	245.0	72.43	AD
AUS	RNP 1995	246.0	74.81	AD
AUS	CNP Aa010	246.4	68.46	AD
AUS	RNP 1721	247.5	71.04	AD
AUS	CNP Aa019	250.1	71.53	AD
GAZ	MACN 16513	184.5	57.60	NOAD
GAZ	RNP 2675	197.8	59.51	NOAD
GAZ	RNP 2632	199.9	61.24	NOAD
GAZ	RNP 2674	203.7	62.83	NOAD
GAZ	RNP 2637	207.3	62.56	NOAD
GAZ	RNP 2643	208.7	64.42	NOAD
GAZ	RNP 2648	216.2	66.01	NOAD
GAZ	IAA 00.7	218.7	65.77	NOAD
GAZ	RNP 2771	220.0	68.49	NOAD
GAZ	RNP 2641	220.0	65.71	NOAD

APPENDIX *Continued*

Sp.	Collection no.	CBL	GM	Age class
GAZ	RNP 2673	221.2	67.28	NOAD
GAZ	MACN 21354	221.6	69.32	NOAD
GAZ	RNP 2634	224.0	68.41	NOAD
GAZ	MACN 21061	226.8	70.24	AD
GAZ	MACN 21352	227.8	70.12	NOAD
GAZ	RNP 2677	228.0	69.11	NOAD
GAZ	IAA 00.1	229.0	72.96	AD
GAZ	RNP 2630	229.5	71.69	AD
GAZ	MACN 21996	232.0	68.34	AD
GAZ	MACN 21350	232.3	73.64	AD
GAZ	MACN 20436	232.7	71.56	AD
GAZ	IAA 01.5	234.2	73.22	AD
GAZ	MACN 23666	235.0	71.95	AD
GAZ	IAA AA-4	236.0	73.64	AD
GAZ	IAA AA-1	236.1	71.41	AD
GAZ	IAA 01.10	237.6	72.86	AD
GAZ	IAA 01.2	238.5	73.16	AD
GAZ	MACN 16512	239.4	75.33	AD
GAZ	IAA 01.7	239.7	77.72	AD
GAZ	MACN 21858	240.2	71.73	AD
GAZ	RNP 1989	240.2	74.58	AD
GAZ	IAA 99.4	240.3	72.40	AD
GAZ	RNP 515	240.7	75.16	AD
GAZ	MACN 21859	241.0	75.14	AD
GAZ	MACN 21349	241.4	70.91	AD
GAZ	MACN 21756	242.4	75.83	AD
GAZ	IAA 97.1	243.2	74.55	AD
GAZ	IAA 00.3	244.0	73.48	AD
GAZ	RNP 1744	244.3	72.60	AD
GAZ	IAA 00.2	244.4	73.81	AD
GAZ	MACN 21351	245.0	75.16	AD
GAZ	IAA 00.5	245.3	73.11	AD
GAZ	MACN 21755	245.3	75.92	AD
GAZ	MACN 21860	245.5	75.04	AD
GAZ	IAA 01.1	245.7	77.59	AD
GAZ	IAA 01.9	245.9	75.83	AD
GAZ	MACN 21754	246.0	75.49	AD
GAZ	MACN 21760	246.2	75.48	AD
GAZ	IAA 99.2	247.0	77.48	AD
GAZ	IAA 01.12	247.0	76.46	AD
GAZ	MACN 21761	247.0	75.95	AD
GAZ	IAA AA-3	247.3	79.45	AD
GAZ	MACN 21857	247.7	73.38	AD
GAZ	MACN 21062	248.1	76.40	AD
GAZ	IAA AA-5	248.3	76.45	AD
GAZ	MACN 21757	248.3	73.05	AD
GAZ	MACN 24353	248.8	77.45	AD
GAZ	IAA 01.4	249.0	74.99	AD
GAZ	IAA 00.4	250.0	77.60	AD
GAZ	IAA 00.6	250.0	78.64	AD
GAZ	RNP 2627	250.1	78.32	AD
GAZ	IAA 01.6	250.3	75.23	AD
GAZ	IAA 01.11	250.3	79.59	AD
GAZ	IAA 99.3	251.9	77.15	AD

APPENDIX *Continued*

Sp.	Collection no.	CBL	GM	Age class
GAZ	IAA 01.8	251.9	77.93	AD
GAZ	MACN 21060	252.3	77.61	AD
GAZ	MACN 21759	253.1	74.10	AD
GAZ	IAA 99.1	254.6	77.18	AD
GAZ	IAA 01.3	254.7	75.68	AD
TRO	UFSC 1212	151.8	44.42	NOAD
TRO	UFSC 1280	154.0	45.22	NOAD
TRO	UFSC 1338	158.6	48.72	NOAD
TRO	UFSC 1237	159.3	46.06	NOAD
TRO	RNP 2406	162.8	49.67	NOAD
TRO	MCN 2499	175.8	52.76	NOAD
TRO	RNP 1683	181.0	55.23	NOAD
TRO	RNP 2682	189.5	58.78	NOAD
TRO	RNP 2715	203	61.56	NOAD
TRO	RNP 2638	205.7	61.93	NOAD
TRO	MCN 2631	207.8	60.45	NOAD
TRO	MCN 2617	208.0	63.52	NOAD
TRO	RNP 2686	209.6	62.54	NOAD
TRO	RNP 2642	210.1	63.30	NOAD
TRO	MCN 2520	210.2	63.20	NOAD
TRO	MCN 2613	210.8	64.09	NOAD
TRO	MCN 2503	211.7	64.23	NOAD
TRO	UFSC 1242	214.0	64.81	NOAD
TRO	MCN 2504	214.0	63.86	NOAD
TRO	MCN 2626	214.5	63.78	NOAD
TRO	UFSC 1277	214.6	61.66	NOAD
TRO	RNP 2647	214.8	64.23	NOAD
TRO	MCN 2615	216.3	63.68	NOAD
TRO	MCN2458	216.4	64.10	NOAD
TRO	RNP 2455	216.6	64.22	NOAD
TRO	UFSC 1132	216.6	64.82	NOAD
TRO	MCN 2620	217.0	64.74	AD
TRO	MCN 2608	217.0	65.06	AD
TRO	MCN 2607	217.5	63.03	AD
TRO	RNP 2516	217.8	64.75	AD
TRO	MCN 2640	218.0	64.69	AD
TRO	MCN 2646	218.6	65.42	AD
TRO	UFSC 1016	219.2	67.08	AD
TRO	MCN 2632	219.8	64.44	AD
TRO	RNP 2649	220.8	67.51	AD
TRO	MMPMa 4142	221.6	67.35	AD
TRO	UFSC 1120	223.5	66.23	AD
TRO	MCN 2605	223.5	66.80	AD
TRO	MCN 2502	223.5	65.70	AD
TRO	RNP 2655	224.3	70.99	AD
TRO	MCN 2463	225.5	67.83	AD
TRO	RNP 2624	225.6	67.06	AD
TRO	MCN 2642	228.0	66.24	AD
TRO	MCN 2510	229.3	67.16	AD
TRO	MCN 2511	230.0	68.36	AD
TRO	UFSC 1017	231.1	68.57	AD
TRO	MCN 2641	232.6	67.92	AD
TRO	RNP 2753	238.5	71.27	AD
TRO	RNP 2753	238.5	71.27	AD

APPENDIX *Continued*

Sp.	Collection no.	CBL	GM	Age class
TRO	RNP 2157	246.0	74.94	AD
TRO	UFSC 1319	216.6	65.90	AD

Institution acronyms: CFA, Colección Fundación Félix de Azara, Buenos Aires, Argentina; CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; IAA, Instituto Antártico Argentino, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCN, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MLP, Museo La Plata, La Plata, Argentina; MMPMa, Museo Municipal Lorenzo Scaglia, Mar del Plata, Argentina; RNP, Museo Acatushun de Aves y Mamíferos Marinos Australes, Ushuaia, Argentina; UFSC, Universidade Federal de Santa Catarina, Florianópolis, Brazil. Abbreviations: AD, adult; CBL, condylobasal length (mm); GM, geometric mean; NOAD, non-adult.