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The ontogeny of shape disparity in three species of Otariids (Pinnipedia: Mammalia)

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Abstract: We compared skull ontogenies in three otariid species to identify evolutionary novelties and to understand their relationships with diversity. The species studied were *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. We analyzed evolutionary changes in three parameters of developmental trajectories of skull shape: shape at the outset of ontogeny, allometric pattern, and the amount of change undergone over the course of ontogeny, which depends on its duration (the length of the ontogenetic vector) and on the rate of development. Initial shapes were always very different among the species and the distances between shapes increased with time, independently from size. Furthermore, when the complete samples were considered, all the ontogenetic trajectories were significantly different concerning the directions of the allometric vectors during ontogeny. Ontogenetic trajectories also differed significantly among almost all compared pairs, except for the trajectories of males of *A. australis* and *C. ursinus*. However, these differences are expected by chance (considering the range of angles within each sample). A similar pattern was found when the subadults were compared in pairs of species, as well as adult males of *A. australis* and *O. byronia*. The correlation found between ontogenies of juveniles was expected by chance, with exception of *C. ursinus* and *O. byronia*. The ontogenetic trajectory of *C. ursinus* is the shortest and that of *O. byronia* is the longest, with the latter being near the triple of the former. *A. australis* has an intermediary length of ontogenetic trajectory. Considering all three species, disparity increased significantly over ontogeny since the disparity of the adults is near double that between juveniles. However, the pattern of disparity did not change considerably during ontogeny. For any ontogenetical stage, *O. byronia* is the species that most contributed to the disparity of the group, followed by *C. ursinus*. Finally, ontogenies examined herein are clearly not constrained (almost every developmental parameter of shape that could evolve was observed) and perhaps the differences in patterns have additive effects in the differentiation of the ontogenies.

Resumo: Objetivou-se comparar as ontogenias do crânio de três espécies de Otariidae para identificar novidades evolutivas na forma a fim de entender as relações destas com a diversidade. As espécies estudadas foram *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. Analisaram-se mudanças evolutivas em três parâmetros das trajetórias de desenvolvimento da forma dos crânios: forma no início do desenvolvimento, padrão alométrico e a quantidade de mudanças - que depende da duração (tamanho do vetor ontogenético) e da taxa das mudanças. As formas iniciais mostraram-se sempre diferentes entre todas as espécies e as distâncias entre as formas aumentou com o tempo, independentemente do tamanho. Em acréscimo, ao considerar-se toda a amostra, todas as trajetórias mostraram-se significativamente diferentes no que concerne às direções dos vetores alométricos. As trajetórias ontogenéticas diferiram significativamente entre praticamente todos os pares comparados, exceto para as trajetórias de machos de *A. australis* e *C. ursinus*. Estas espécies não se revelaram mais diferentes do que seria esperado ao acaso (considerando a distribuição dos ângulos em cada amostra). Um padrão similar foi encontrado quando os subadultos foram comparados entre pares de espécies e também quando foram comparados machos adultos de *A. australis* e de *O. byronia*. As correlações entre as ontogenias dos juvenis das três espécies enfocadas tampouco diferiram mais entre si do que o esperado ao acaso, excetuando-se entre os juvenis de *C. ursinus* e *O. Byronia.* A trajetória ontogenética de *C. ursinus* é a mais curta e a de *O. byronia* a mais longa (quase o triplo daquela de *C. ursinus*). *A. australis* apresenta um tamanho de trajetória intermediário. Quando as três espécies foram analisadas conjuntamente, verificou-se um aumento da disparidade ao longo da ontogenia (a disparidade dos adultos foi praticamente o dobro daquela entre os juvenis) e o padrão de disparidade não se altera significativamente ao longo da ontogenia. Para qualquer estágio ontogenético, *O. byronia* é a espécie que mais contribui para a disparidade do grupo examinado, seguida de *C. ursinus*. Finalmente, as trajetórias examinadas aqui claramente não são constringidas e talvez a diferença entre os padrões apresente efeitos aditivos na diferenciação das ontogenias.

Keywords: Otariidae, ontogeny, skull, disparity, geometric morphometrics.

Introduction

Disparity and taxonomic diversity provide insights into the expansion and contraction of variety, and the relationship between these two aspects of diversity also have important implications for evolutionary mechanisms. Disparity is measured as the total variance among forms in morphological space (proportional to the mean squared distance among forms) (Foote, 1993). This quantity is a measurement of the range of morphologies in a given sample of organisms, as opposed to diversity, which is expressed in terms of number (and sometimes ranking) of taxa.

The concept of biological and ecological diversity is familiar. It can be assessed by a variety of indices, usually depending upon the number of taxa present in a given sample. A related concept is the absolute morphological variety of a group, its variance in shape or the amount of morphological space that it occupies (Foote, 1992). On the other hand, the concept of disparity refers to how much the members of a group of organisms are morphologically different from each

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other, and then geometric morphometry provides a very objective assessment for these differences (Foote, 1992).

Furthermore, variation and disparity are similar terms related to the concept of variety, where disparity generally means the variety among a group. Disparity is the outcome of evolutionary processes and variation is the variety of individuals within a homogeneous group. Thus, it is the raw material to evolutionary processes (Zelditch *et al*., 2004).

The objective of this work is to compare ontogenies to identify divergent developmental features in the shape of the otariid skull with the purpose of understanding their relationships with diversity. The species studied were *Arctocephalus australis* Zimmermann, 1783, *Callorhinus ursinus* Linnaeus, 1758 and *Otaria byronia* Blainville, 1820[3]. Thus, we present a comparative study of the ontogeny of the skull of the two Otariidae species more frequently found on the coast of Rio Grande do Sul state, Brazil (*A. australis* and *O. byronia*). *Callorhinus ursinus* is also included because it is supposedly the extant otariid more closely related to the ancestral of this family (Berta *et al*., 2006). In this context, we analyzed evolutionary changes in three parameters of developmental trajectories of skull shapes: (1) shape at the outset of ontogeny, defined here as the starting point of the vector representing the ontogeny of shape; (2) allometric pattern and the direction of allometric vector in shape and space, and (3) the amount of change undergone over the course of ontogeny, which depends on the duration (the length of the ontogenetic vector) and rate of development.

That approach is justified by the fact that the study of disparity is a primordial step to understand how evolutionary novelties interact in those groups, which is particularly interesting considering the rapid (and poorly understood) radiation and speciation of the extant Otariidae (Demeré *et al*., 2003).

In addition, the shape disparity between different developmental stages was compared to check if the disparity level decreases during ontogeny (presence of novelties), which could indicate non-additive interactions between novelties (Zelditch *et al*., 2003a).

The selected focus was skull shape because these ontogenetic series are easily available and these data are especially well suited to studies of disparity (Zelditch *et. al*, 2003a). In addition, shape underlies the general statistical theory of modern shape analysis, the Procrustes distance. In fact, traditional morphometrics presents a major analytic problem caused by discrete characters: units of the same apparent magnitude are not necessarily equivalent (Zelditch *et al*., 2003a). However, any two samples that are separated by one unit of Procrustes distance differ from each other by the same amount as any other taxa. This aspect is important when the goal is to quantify the degree of difference among morphologies, especially when it concerns non-additivity of the interacting causes of disparity. Otherwise, this distance can be traced directly to the modifications in the place of homologous landmarks—the change in those locations is directly proportional to the difference in shape (Zelditch *et al*., 2003a).

Material and Methods

Sampling

Our samples comprise cross-sectional ontogenetic series of the skull of three otariid species: *A. australis* (n=76), *C. ursinus* (n=51) and *O. byronia* (n=84) (Appendix 1). We used the number of growth layer groups deposited in the dentine of the bisected canine as our estimate of chronological age (Schiavini, 1992) and the sutural ages to determine the ontogenetic stages (juvenile, subadults and adults) (Sivertsen, 1954). The analyses were performed considering species, sex and sutural age groups (juveniles, subadults and adults).

Our analyses were based on landmarks, discrete points that were recognizable and homologous on all species (and specimens) at different ages, in the study (Figure 1). The landmarks were chosen to provide the most comprehensive coverage of that view of the skull. Consistency of relative position, repeatability and coplanarity of the landmarks were also considered in the selection of these points. All landmarks were digitalized by one of the authors (D. Sanfelice). After that, the specimens were superimposed using the Generalized Least-Squares Procrustes superimposition (GLS).

Defining Morphological space and measuring morphological diversity

The approach here is to ordinate forms in a multidimensional morphospace and to base morphological differences on the array of points in morphospace (Cherry *et al*., 1982). Consequently, disparity is measured as the sum of univariate variances of all dimensions in morphospace, which is proportional to the mean squared Euclidean distance among points in morphospace (Van Valen, 1974).

The partial disparity is analogous to a variance, where the squared distances are taken relative to the overall centroid rather to the centroid of the subgroup. This permits access to the disparity contributions of subgroups. This has allowed morphological disparity analysis to address an issue that has long been addressed with taxonomic diversity data - concerning the relative contributions of different subgroups to overall morphological disparity. The method of disparity partitioning allows an assessment of the relative contributions of different taxa to the morphological disparity of the larger group containing them.

[3] Our use of the specific name *byronia* follows Drehmer (2005), Gardner and Robbins (1995) and ICZN Opinion 1962 (2000).

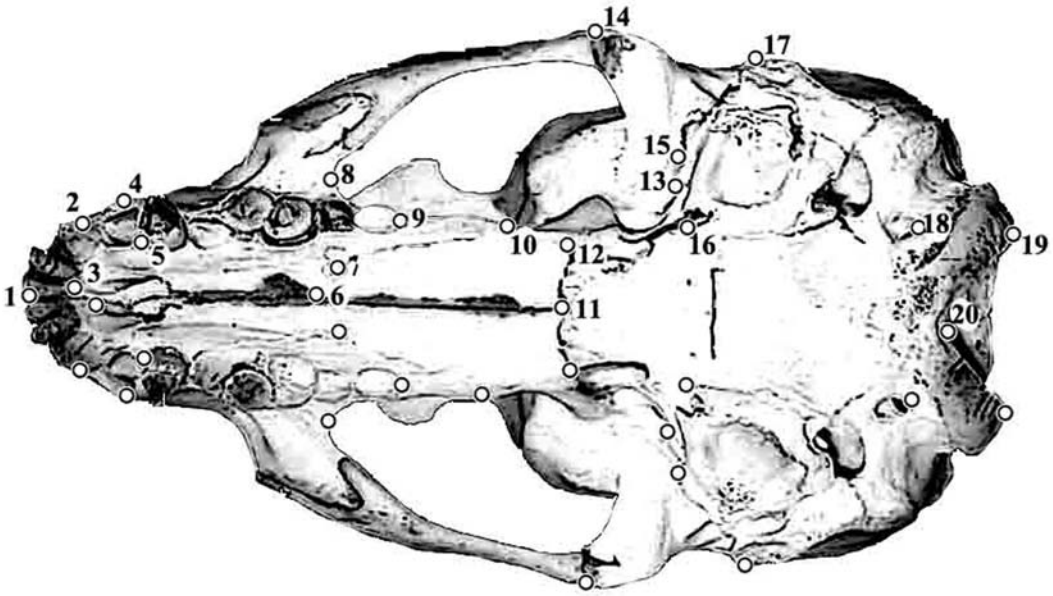

Figure 1. Landmarks shown on the ventral view of the skull of a juvenile of *Otaria byronia*. Descriptions of each landmark are given in Appendix 2.

Estimation and Comparisons among the Initial Shapes

The initial shape is estimated from the regression equation, which predicts the expected shape at each size or age. Here, we predicted the mean shape for each species at age zero. The sexes were pooled together considering that juveniles were not dimorphic in shape (Sanfelice and Freitas, 2008). Subsequently, the residuals from the regression were added to the predicted form, yielding a sample of shapes at each stage. Each individual specimen contributed with only one residual (*i.e.* the deviation of that individual from the predicted shape). To compare shapes, multivariate analysis of the variance (MANOVA) was performed and pairwise comparisons tested the differences between groups two-by-two. Otherwise, an experiment-wise error rate of 0.05 was maintained by dividing the number of unplanned comparisons (three) to obtain the critical a value of 0.016 (Bonferroni Correction). The misclassification rate of the discriminant function was also analyzed. The statistical significance of the pairwise differences was tested by a resampling-based *F*-test. The MANOVA and the misclassification rate were performed with CVAGen6j; pairwise *F*-tests were run in Two-Group6h. These programs belong to the Integrated Morphometrics Programs (Sheets, 2000) and they are freely available electronically at http://www.canisius.edu/;sheets/morphsoft.html.

Comparisons of the Allometric Trajectories

These parameters were assessed by multivariate regression of the partial warp plus the uniform component scores (dependent variable representing shape) on a measurement of geometric scale (the logarithm of the centroid size). For each species separately, the full set of shape variables was regressed on the independent variables considered. We assumed a linear relationship between shape and size since these estimates were based on linear regression.

Estimates and Comparisons between Allometric Patterns

The vector of allometric coefficients that describes morphogenesis is calculated using the multivariate regression of shape on size, as detailed above. To compare these vectors by multivariate analyses, we calculated the angle between them (the cosine of that angle is the vector correlation between the two ontogenetic trajectories of shape). That cosine was calculated as the inner product of vectors of allometric coefficients, normalized to the unit length. Thus, if two vectors pointed in the same direction, the angle between them would be equal to zero and the cosine would be 1. Since it would be too strict to consider an angle of 0 as the null hypothesis, here the null hypothesis states that the angles between species are no larger than we would expect from the variation within a single species or group (some variation is expected because individuals of the same species do not have identical ontogenies of shape). The subject here is whether or not the uncertainty of the estimation of each species trajectory (due to sampling) is very large, making it impossible to reject the null hypothesis of any significant difference. To estimate the range of angles within each species in congruence with the datasets (and thus to calculate the imprecision of the trajectory due to sampling) we estimate the residuals from the multivariate regression in a way that each individual gives a multi-

dimensional set of residuals describing its deviation from the expected shape at its size. Thus, a pair of bootstrap sets was constructed for species that will be used to calculate the angle between the trajectories in consideration. These pairs were constructed by resampling residuals (with replacement) and were randomly assigned to expected values of shape (derived from the original regression model) at values of the logarithm of centroid size (detected in the original data). This bootstrap approach is no more than a multivariate extension of the known procedure to estimation of uncertainties of regression slopes by resampling the covariance structure among variables (Efron & Tibshirani, 1993). Finally, the angles between the trajectories derived from the two within-species bootstrap sets were estimated and this procedure was repeated *N* times to produce a distribution of within-species angles. In the present study, we employed *N*=100. Since sample sizes were different among the species, the two bootstrap sets constructed from the species with largest sample size matched sample sizes of the two species in comparison (*i.e.* one set has the largest sample size of that species, while the other has the smallest sample size of the other species). The two bootstrap sets obtained from the data of the species with the smallest sample size have that sample size, since a bootstrap larger than the original data set cannot be constructed. If the interspecific angle exceeded the 95th percentile of the within-species range of angles, the interspecific difference was considered to be statistically significant. The multivariate regressions were performed using Regress6k and the comparisons between ontogenetic trajectories were carried out using VecCompare, both programs freely available in the IMP series (Sheets, 2000).

Estimations and Comparisons between the Lengths of Ontogenetic Trajectories

The length of the ontogenetic trajectory of shape is a function of the rate of shape change and the duration of development. To estimate this length, the Procrustes distance between the average shape in the juvenile stage and the shape at maximum body size was calculated. Confidence limits were placed on this measurement by bootstrap, considering the variability among individuals at the same size and the uncertainty of the regression. That is, the residuals estimated from the regression were drawn with replacement at random and were added to the expected shape, generating a bootstrap data set for each species. In the sequence, the same regression model was fitted to the bootstrapped sets and the size correction was carried out on these sets. The result was a bootstrap set for each species that incorporated the uncertainty of regression. These calculations were performed by DisparityBox6g, another freely available program in the IMP series (Sheets, 2000).

Measurement of the Level of Disparity

The level of disparity was calculated according to Zelditch *et al.* (2003a) for the different ontogenetical stages in each species and sexes (adults) and among species. To test the significance of differences in levels of disparity, we used the bootstrapping procedure explained in the previous section, since the analyses presented here were based on standardized data and the tests should take into account the uncertainties of the regression. Considering that one of the difficulties found in calculating the level of disparity was the differences in shape related to differences in size (allometry) and its influence on the disparity, the level of disparity was studied with and without correction for size. Therefore, we fitted a regression model to the data, determining the residuals and producing size-standardized data set. In the study without size correction, we measured disparity with correction to the mean size of each subsample and with correction using the same size for the two samples. The Partial Disparity, which is the contribution to disparity of each subsample analyzed, was calculated using Disparity Box6g (Sheets, 2000).

Analysis of the Pattern of Disparity

The dimensions and the distribution of shapes along the series where shapes are most disparate were described by principal components analysis, using the software PCAGen6n (Sheets, 2000). Such examinations are relevant because distinct ontogenetic stages may have the same level of disparity but present a different pattern, which hide the dynamic nature of disparity (Zelditch *et al,* 2003b). The patterns were examined for each subsample separately with the aim of finding one biological explanation to the direction of dominant variation within shape space (in addition to the fact that the morphospace resultant is different from sample to sample). The significance of the principal components was tested by Anderson´s test.

The sub-samples compared were: juveniles (specimens with sutural age between 9 and 10, including newborn and animals between 0 or 1 year of age), subadults (specimens with sutural ages between 11 and 18) and adults (specimens with sutural ages superior to 18). The adults were separated by sex, due to the dimorphism in the adult shape.

Results and Discussion

Comparisons among the Initial Shapes

All pairwise F-tests among species showed statistically significant differences in the initial shape (p=0.01), even after Bonferroni corrections for three comparisons (p=0.05). In addition, no specimens (n= 47) were incorrectly classified by the discriminant function. The pairwise distances between means are presented (Tables 1 and 2), suggesting a labile aspect in the initial shape of the otariid skull.

Performing the same analysis for the other ontogenetic phases, we detected that the differences tend to increase during ontogeny and that size does not have a great influence in the amount of difference.

Table1. Procrustes distances among the average initial shapes of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*.

	A. australis	*C. ursinus*	*O. byronia*
A. australis	0	0.0685	0.1003
C. ursinus		0	0.1444
O. byronia			0

All pairwise differences are statiscally significant for the Bonferroni-adjusted value of α=0.05.

We compared shapes with different standardizations (*e.g.* standardized by the minimum size of all specimens, by the maximum size of all the females, by the maximum size of all the males, by the range of size of the females of each correspondent species or even standardized by the range of size of the males of each corresponding species).

Allometric Patterns

When complete samples were considered, all the ontogenetic trajectories were significantly different concerning the directions of the allometric vectors during ontogeny. Here, the allometric patterns for each sex were presented separately, since patterns are distinct between males and females of the same species (Sanfelice and Freitas, 2008). Ontogenetic trajectories differed significantly among almost all compared pairs, except for the trajectories of males of *A. australis* and *C. ursinus*. The differences presented by this group are expected by chance considering the range of angles within each sample (Table 3). A similar pattern was observed when the subadults were compared between pairs of species, as well as for adult males of *A. australis* and *O. byronia*. Differences observed in juveniles were expected by chance (correlation between ontogenies in that phase was equal to one), with exception of *C. ursinus* and *O. byronia*, where angles ranged from 38.2° to 40.7° in females and from 38.1° to 48.8° in males. The most divergent trajectories found were those of *C. ursinus* and *O. byronia* for both sexes.

Table 3. Comparisons among ontogenetic trajectories of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. Vector correlations are above the diagonal, angles (in degrees) are below the diagonal.

	A. australis	*C. ursinus*	*O. byronia*
A. australis	-	0.766044	0.785857
C. ursinus	**40**	-	0.758134
O. byronia	**38.2**	**40.7**	-

	A. australis	*C. ursinus*	*O. byronia*
A. australis	-	0.772734	0.786935
C. ursinus	39.4	-	0.658689
O. byronia	**38.1**	**48.8**	-

Angles statistically significantly different from 0° are in bold.

Table 2. Procrustes distances among the average shapes of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*.

A. australis x C. ursinus	DISTANCE	95% CI	ST. MINIMUM	95% CI
JUVENILES	0.0685	0.0577-0.0861	0.0719	0.0628-0.0821
SUBADULTS	0.0647	0.058-0.08	0.0592	0.0551-0.0674
ADULT FEMALES	0.0673	0.0552-0.0793	0.0543	0.0478-0.065
ADULT MALES	0.0497	0.0444-0.0567	0.0573	0.909-0.1153
A. australis x O. byronia	DISTANCE	95% IC	ST. MINIMUM	95% IC
JUVENILES	0.0996	0.930-0.1125	0.1063	0.0989-0.1233
SUBADULTS	0.1444	0.1353-0.1528	0.1373	0.1299-0.1464
ADULT FEMALES	0.1387	0.1288-0.1459	0.142	0.1345-0.1488
ADULT MALES	0.1683	0.1578-0.1795	0.1662	0.1532-0.1747
C. ursinus x O. byronia	DISTANCE	95% IC	ST. MINIMUM	95% IC
JUVENILES	0.1445	0.1355-0.1566	0.1406	0.1356-0.1487
SUBADULTS	0.1842	0.1683-0.1989	0.16	0.1491-0.1703
ADULT FEMALES	0.1859	0.1747-0.1969	0.1717	0.1615-0.1807
ADULT MALES	0.1921	0.1839-0.2014	0.1745	0.1652-0.1841

All pairwise differences are statiscally significant for the Bonferroni-adjusted value of α=0.05. Distance is the Partial Procrustes Distance; 95% CI is the confidence interval; St. minimum is the PPD when the samples were standardized to the respective smallest size.

It may appear that the three species examined were more similar than expected by chance (*i.e.* the correlation is higher than zero) but they differed significantly (*i.e.* the correlations were lower than one). Additionally, the differences in the ontogenetic transformations of shape were visually conspicuous between sexes and overall between species (Figure 2).

Lengths of Ontogenetic Trajectories

The ontogenetic trajectory of *C. ursinus* was the shortest, while the longest was observed for *O. byronia*. *Arctocephalus australis* had an intermediary length of ontogenetic trajectory. In the three species, the females had the longest trajectories, but the confidence intervals of lengths of trajectories overlapped between the sexes of the same species. On the other hand, the lengths were significantly different between species (considering the sex pooling together or separately) (Table 4).

Shape disparity

In *A. australis* the disparity increased gradually and the disparity between the two sexes was the smallest in the adults, especially when we corrected for size (Table 5). The disparity between juveniles and subadults was nearly four times higher in *C. ursinus* than in *A. australis*, but the level of disparity between the different ontogenetic stages was more or less constant (the disparity between adults was nearly four times higher in *C. ursinus* that it was observed for *A. australis*) (Table 5). In the sea lion *O. byronia* (the species with a high level of disparity between males and females) the high level of disparity was found relatively early in ontogeny, between juveniles and subadults (Table 5 and 6). The subadults versus adult females presented the smallest disparity in morphology. In addition, it was observed that the disparity between the juveniles and the other ontogenetic stages was extremely striking, increasing gradually (Table 5). Moreover, standardization was not effective due to the small difference in size observed among the stages compared in the same species (Tables 5 and 6). For the sample comprising all three species, disparity increased significantly throughout ontogeny, since the disparity of the adults is near double the disparity found between juveniles (Table 7). Otherwise, for any ontogenetical stage, *O. byronia* is the species that most contributed to the group disparity, followed by *C. ursinus* (Table 8).

Comparing the two species of fur seals, the level of disparity is nearly static over the course of ontogeny, especially in females (but with some increment when we analyzed the disparity applying the size correction). In males we observed a decrease in disparity (Table 8). When *A. australis* and *O. byronia* were compared, the level of disparity increased early in ontogeny, but after the subadult stages it was almost stable. The disparity between *C. ursinus* and

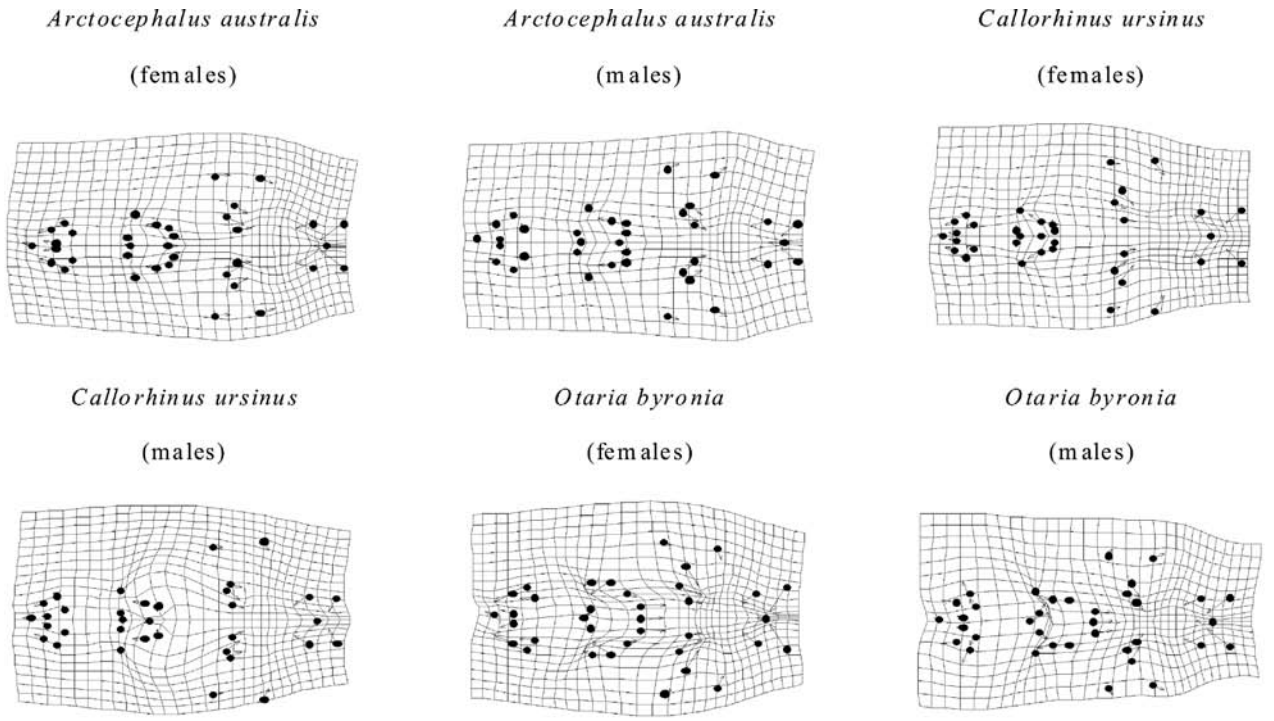

Figure 2. Ontogenetic transformations in shape. Each diagram depicts the regression of shape on log-transformed centroid size as a Cartesian transformation using the thin-plate spline.

O. byronia was high and constant during the development, with a very inconspicuous increment in the early ontogeny. In addition, this level was almost two times higher in adults of both sexes when the size correction was performed. The disparity between the sea lion and the other two species was similar, considering the range of the confidence intervals (and when the size correction was not applied).

Pattern of shape disparity

When we considered the three species together, the pattern of disparity did not show a considerably change during ontogeny (Figure 3). In the variance of juvenile shape, two significant components were found: the first separate the fur seals species from the sea lion species (Figure 3A). *Otaria byronia*, which presents high scores in that component, is differentiated from those with low scores by the great extension of the palate (and by consequence, the shorter choanes), the deepening of the braincase, and the comparison of the braincase with the rostrum. The second component describes the enlargement of the rostrum and the forward displacement of the choanes, but the most conspicuous pattern of changes in shape explained by this component is the postero-distal expansion lateral and posterior to the braincase. *Arctocephalus australis* had the lowest scores in that component and *C. ursinus* the highest. In subadults, the first principal component is responsible for the enlargement of the rostrum and the mastoid process region, and the second principal component expressed the enlargement of the posterior region of the bone palate.

In adults of both sexes, the enlargement in length and width is expressed largely by the first principal component (except in the condyle region), and the second principal component is related to changes in the posterior regions of the bone palate (females) or modifications in the posterior regions of the alveolar process (males).

Table 4. Lengths of ontogenetic trajectories in units of Procrustes distance for *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*.

SPECIES	ALL SPECIMENS (95% CI)	(95% CI)	(95% CI)
A. australis	0.0099 (0.0084-0.0119)	0.0084 (0.0066-0.0106)	0.0062 (0.0052-0.0075)
C. ursinus	0.0053 (0.0040 – 0.00078)	0.0059 (0.0033-0.0081)	0.0038 (0.0020-0.0067)
O. byronia	0.0184 (0.0163-0.0217)	0.0162 (0.0131-0.0230)	0.0134 (0.0106-0.0167)

The confidence intervals are in parentheses.

Table 5. Level of disparity among ontogenetic and/or sex groups of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*.

	A. australis	***C. ursinus***	***O. byronia***
JUVENILES X SUBADULTS	0.00023 (0.00027-0.00077)	0.00117 (0.00069-0.00264)	0.00415 (0.00320-0.00077)
	0.0017 (0.0009-0.0034)	0.0028 (0.0012-0.0064)	0.0111 (0.0087-0.0218)
JUVENILES X ADULT FEMALES	0.00212 (0.00178-0.00280)	0.00163 (0.00116-0.00289)	0.00592 (0.00520-0.00830)
	0.0051 (0.0038-0.0076)	0.0035 (0.0026-0.0055)	0.0145 (0.0123-0.0261)
JUVENILES X ADULT MALES	0.00227(0.00186-0.003)	0.00316 (0.00239-0.00450)	0.00934 (0.00740-0.01289)
	0.0071 (0.0058-0.0104)	0.0063 (0.0050-0.0084)	0.0197 (0.0165-0.0300)
SUBADULTS X ADULT FEMALES	0.00116 (0.00091-0.00197)	0.00116 (0.00091-0.00197)	0.00033 (0.00029-0.00076)
	0.0016 (0.0013-0.0025)	0.0016 (0.0013-0.0025)	0.0008 (0.0006-0.0016)
SUBADULTS X ADULT MALES	0.00139 (0.00112-0.00208)	0.00128 (0.00101-0.00243)	0.00172 (0.00128-0.00274)
	0.0034 (0.0023-0.0048)	0.0018 (0.0010-0.0041)	0.0030 (0.0024-0.0042)
ADULT FEMALES X ADULT MALES	0.00037 (0.00038-0.00081)	0.00128 (0.00105-0.00151)	0.00146 (0.00108-0.00253)
	0.0013 (0.001-0.0027)	0.0019 (0.0012-0.0034)	0.0025 (0.0019-0.0040)
FEMALES X MALES	0.00011 (0.00015-0.00045)	0.00035 (0.00025-0.001)	0.0005 (0.00041-0.00133)

The values in the first line of each case are the unstandarized levels of disparity and the values in the second line are the corresponding level with the samples standardized with respect to size. The numbers in parentheses are the confidence intervals.

Table 6. Level of disparity (distance-based disparity based on the group means, working with all loaded groups-bootstrapped size correction between males and females) between males and females of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*.

	A. australis	***C. ursinus***	***O. byronia***
Standandized for the minimum size	0.0172 (0.0105-0.0376)	0.0214 (0.0171-0.0542)	0.0753 (0.0539-0.1212)
Standardized for the maximum size of the females	0.0129 (0.0098-0.0282)	0.0165 (0.0110-0.0389)	0.0246 (0.0154-0.0381)
Standardized for the maximum size of the males	0.0119 (0.0082-0.0239)	0.0154 (0.0122-0.0406)	0.0224 (0.0153-0.0376)
Standardized for the range of size of the females	0.0058 (0.0045-0.0076)	0.0061 (0.0036-0.0088)	0.0150 (0.0123-0.0194)
Standardized for the range of size of the males	0.0046 (0.0037-0.0060)	0.0079 (0.0051-0.0115)	0.0098 (0.0083-0.0123)

The numbers in parentheses are the confidence intervals.

Table 7. Shape disparity, measured as the square root of the average of the squared distances between the mean shape of each species and the centroid of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. Confidence intervals are obtained by resampling.

GROUPS	JUVENILE DISPARITY	95TH PERCENTILE OF THE WITHIN-SPECIES RANGE	SUBADULT DISPARITY	95TH PERCENTILE OF THE WITHIN-SPECIES RANGE	ADULT DISPARITY	95TH PERCENTILE OF THE WITHIN-SPECIES RANGE	ADULT DISPARITY	95TH PERCENTILE OF THE WITHIN-SPECIES RANGE
All species	0.00603 0.006	0.0054-0.0073 0.0056-0.012	0.0098 0.0089	0.0089-0.0113 0.0074-0.0108	0.0097 0.0116	0.00885-0.01074 0.0102-0.0138	0.01128 0.0123	0.0104-0.0124 0.0109-0.0145
A. australis x *C. ursinus*	0.00266 0.0026	0.0022 -0.004 0.0016 to 0.0046	0.0021 0.0015	0.0016-0.0032 0.0010-0.0032	0.0027 0.0038	0.00175-0.00352 0.0028-0.0065	0.00124 0.0022	0.001-0.0017 0.0016-0.0037
A. australis x *O. byronia*	0.00497 0.056	0.0043-0.0071 0.0042-0.0112	0.0104 0.0104	0.0095-0.0115 0.0094-0.0119	0.0096 0.01	0.00878-0.01075 0.0081-0.0132	0.01417 0.0134	0.0126-0.0162 0.0105-0.0167
C. ursinus x *O. byronia*	0.01047 0.0099	0.0095-0.0125 0.0086-0.0156	0.0169 0.0147	0.0146-0.0198 0.0113-0.0187	0.0172 0.0210	0.01551-0.01989 0.0159-0.0261	0.01846 0.0212	0.0168-0.0208 0.0184-0.0243

In the first line the disparity is presented without correction for size and in the second line the level of disparity is corrected for size, using a different size for each subsample.

In this context, we could observe that those early ontogenies (allometric patterns) were similar, with early stages overlapping in shape space. By contrast, subadults compose a confuse age group that could, sometimes, affect the clarity of the results with its heterogeneity and high variance. In fact, it is important to highlight that mean shape of female and male subadults was close to the significance level (p=0.055) in *O. byronia,* which increased the heterogeneity of this subgroup.

Ontogenies examined herein were clearly not constrained: almost every developmental parameter of shape that could evolve was observed. The species differed in the initial and later shape of the skull, in the length of the ontogenetic trajectories, and in the allometric pattern. Thus, we observed a complex scenario where it was difficult to establish a relationship between the developmental processes with the phylogeny, mainly because we had sampled only three species. It may be possible that if all species in the family were examined we would have been able to determine the causal relations between ontogeny and phylogeny in otariids. Thus, it would be very interesting to analyze the relevance of evolution and development in the history of otariids. Since the species did not conserve the same ontogenetic trajectory, their evolution cannot be explained only by a heterochronic hypothesis.

The strongest differences in the repatterning of the allometry occur in the later ontogeny, but *C. ursinus* and *O. byronia* are extremely different during the entire process. The observed result where the disparity is higher when all the species are pooled together was logical. Similarly, the high partial contribution to disparity by the sea lion is congruent with all the other results regarding the comparisons between shapes in these species.

Table 8. Contributions to the disparity for each species, with and without size correction.

		PARTIAL DISPARITY	SE	PD WITH SIZE CORRECTION	SE
JUVENILES	*Aa*	0.00053	0.00143	0.00072	0.00115
	Cu	0.00236	0.00136	0.00216	0.00123
	Ob	0.00314	0.00150	0.00314	0.00104
SUBADULTS	*Aa*	0.00089	0.00259	0.00101	0.00217
	Cu	0.00307	0.00246	0.00242	0.00231
	Ob	0.00587	0.00262	0.00544	0.00218
ADULT	*Aa*	0.00072	0.00256	0.00071	0.00325
	Cu	0.00327	0.00271	0.00439	0.00263
	Ob	0.00574	0.00232	0.00648	0.00356
ADULT	*Aa*	0.00136	0.00344	0.00108	0.00343
	Cu	0.00279	0.00274	0.00370	0.00327
	Ob	0.00713	0.00271	0.00747	0.00343

Aa=Arctocephalus australis; *Cu=Callorhinus ursinus*; *Ob=Otaria byronia*; PD= Partial Disparity; SE=Standard error.

Concomitantly with the allometric repatterning, the lengths of the ontogenetic trajectories are also different; thus, complex changes are acting in the evolving ontogenies of these otariid species. However, the impact of each evolutionary pattern on disparity (counterbalance or amplification) is difficult to design without modeling hypothetical ontogenies.

The hypothesis of amplification predicts that the interaction among several novelties enhances disparity above the level we would anticipate for their separate effects while the hypothesis of counterbalancing predicts that the interaction among several novelties diminishes the impact of combined novelties. The most probable one is the occurrence of amplifications, since the ontogeny is not constrained and we did not fince evidence of counter-balancing in the disparity, which tended to increase during ontogeny.

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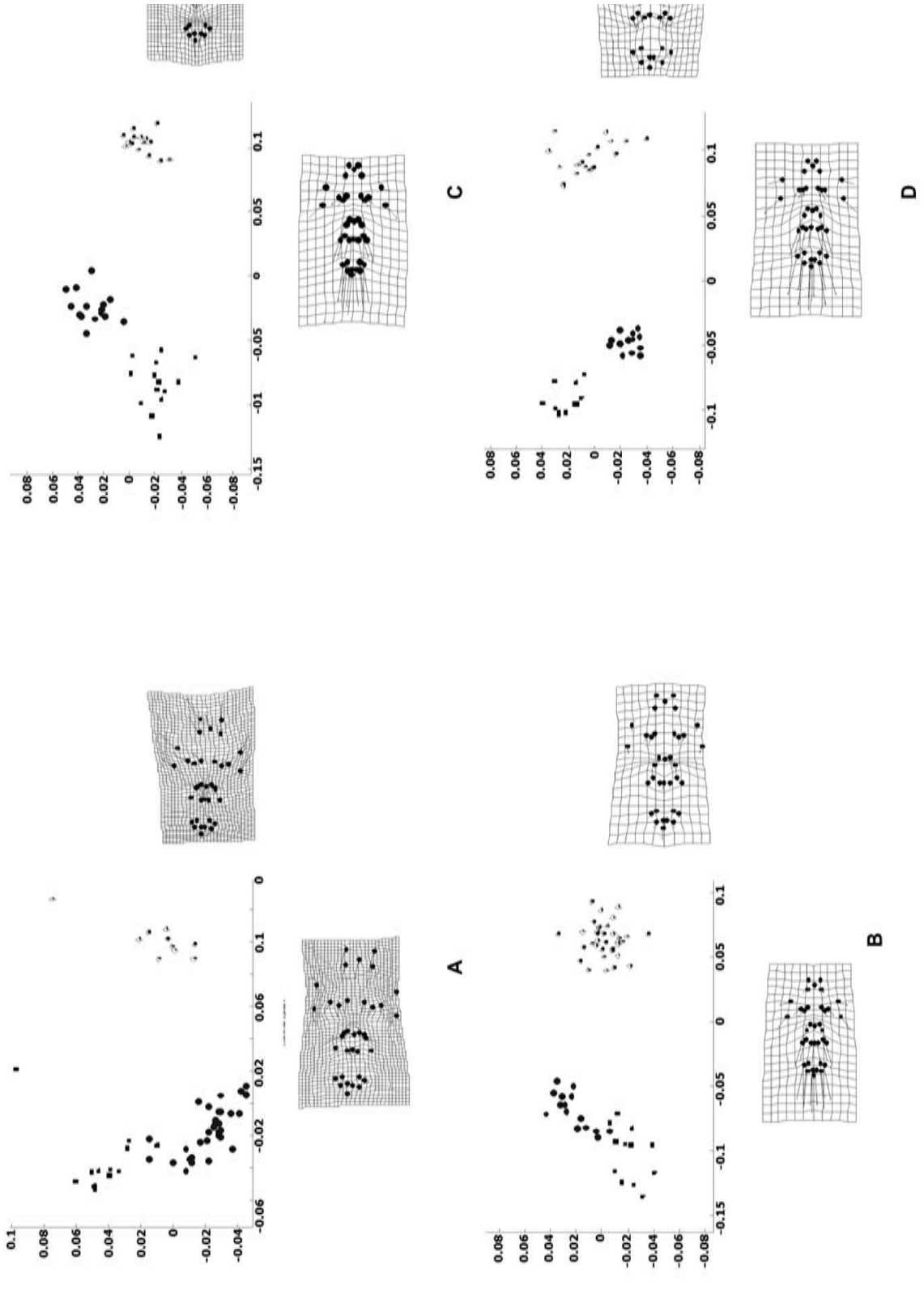

Figure 3. Principal components analysis of shape pooling all species together. (A) juvenile shapes; (B) subadult shapes; (C) adult females shapes; (D) adult males shapes. The difference between low and high scores on each axis is plotted as deformations using the thin-plate spline technique. Circles=*Arctocephalus australis*, Squares= *Callorhinus ursinus*, Diamond= *Otaria byronia*.

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APPENDIX 1

LISTING OF THE SPECIMENS EXAMINED

Coll. N°= Collection Number; CS= Centroid Size in units of centroid size (cm); CCB= Skull Total Length (condylo-basal length); Sut. Age= Sutural Age; Age= age in years.
Institution Acronyms: AMNH= American Museum of Natural History (New York, USA); CAS= California Academy of Sciences (San Francisco, USA); CNP= Centro Nacional Patagónico (Puerto Madryn, Argentina); FCIEN= Facultad de Ciencias (Montevideo, Uruguay); GEMARS= Grupo de Estudos de Mamíferos Marinhos (Porto Alegre, Brazil); LAMAMA= Laboratorio de Mamíferos Marinos (Puerto Madryn, Argentina); MACN= Museu 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); MZV= Museu de Zoologia de Vertebrados (Montevideo, Uruguay); MVZ= Museum of Vertebrate Zoology (Berkeley, USA); NMNH= National Museum of Natural History (Washington D.C.); UAM= University of Alaska Museum; UFSC= Universidade Federal de Santa Catarina (Florianópolis, Brazil); UMICH= University of Michigan (Ann Arbor, USA). (*) Pictures by Dr. Sylvia Brunner (Alaska University Museum); (#) Information available only upon request.

Arctocephalus australis

Coll. Nº	Sex	CS	CCB	Sut. Age	Age
FCIEN A 21 DS 4		23.59	15.73	10	1
MCN 2834		25.18	15.97	9	1
MCN 2682		26.51	16.12	9	0
MCN 2692		26.88	16.22	9	0
MCN 2457		25.52	16.26	10	1
MCN 2647		26.94	16.42	10	1
MCN 2839		25.28	16.71	10	1
MCN 2702		26.13	16.77	9	0
UFSC 1147		29.28	16.85	9	1
MCN 2500		27.27	17.02	9	1
UFSC 1272		29.67	17.23	10	#
MCN 2684		28.69	17.35	10	1
MCN 2638		27.18	17.57	10	2
MCN 2537		28.96	17.59	9	3
UFSC 1111		29.54	17.67	9	#
MCN 2650		26.48	16.46	12	2
MZV 435		25.45	17.1	10	1
UFSC 1096		29.72	17.13	11	#
MCN 2634		28.37	17.35	9	1
MACN 20570		26.77	17.4	11	-
UFSC 1283		28.33	17.51	11	#
MCN 2628		26.60	17.84	13	1
UFSC 1282		27.76	17.89	11	#
MCN 2529		29.68	17.98	12	1
MCN 2606		29.34	18.12	13	3
UFSC 1135		35.67	22	8	-
UFSC 1156		34.22	22	18	#
UFSC 1143		36.93	22.2	19	#
UFSC 1157		37.28	22.4	19	#
UFSC 1153		35.75	22.54	18	-
UFSC 1142		38.02	22.7	19	#
UFSC 1158		39.12	23	26	#
UFSC 1163		40.79	23	29	#
UFSC 1063		36.64	23.2	25	-
UFSC 1160		39.53	23.2	18	#
UFSC 1170		38.36	23.4	29	#
UFSC 1154		37.66	23.5	20	#
UFSC 1169		38.43	24	21	#
MCN 2688		43.94	24.24	24	10

FCIEN 1584	18.93	13.19	9	-
FCIEN 434	21.62	14.49	9	0
UFSC 1139	24.68	15.11	9	#
MCN 533	23.68	15.14	9	-
MCN 2694	23.18	15.43	9	1
MCN 2690	23.51	15.44	9	0
FCIEN 433	23.16	15.57	12	0
MACN 25192	23.36	15.73	9	-
MCN 1531	23.41	16.06	9	1
UFSC 1137	24.81	16.11	10	-
MCN 247	26.24	16.19	9	1
MCN 2636	26.48	16.4	10	0
UFSC 1141	28.27	16.56	9	-
MCN 2683	25.95	16.9	9	1
UFSC 1131	29	17.04	9	-
MCN 2639	28.07	16.17	13	1
UFSC 1040	28.57	17.48	11	#
MACN 28261	25.16	17.73	11	-
MCN 2644	28.51	17.75	13	4
MZV 1517	31.63	18.2	16	4
MCN 2625	27.88	-	12	2
MZV 1523	30.43	19.19	29	-
FCIEN AL961	33.36	20	-	-
FCIEN 1538	30.83	20	30	14
MCN 2523	37.36	20	28	-
MCN 2833	34.41	20	28	10
MZV 1532	31.61	20.11	32	-
MCN 2614	34.92	20.3	27	14
MZV 1552	31.59	20.32	30	7
MZV 1580	31.07	20.5	39	-
MCN 2699	35.29	21.13	28	9
FCIEN 1527	30.91	21.19	25	-
FCIEN 336	31.72	21.72	29	11
FCIEN 1529	32.07	21.73	23	-
FCIEN 1550	37.01	24.39	26	11
UFSC 1133	35.33	29.54	19	#

Callorhinus ursinus

Coll. Nº	Sex	CS	CCB	Sut. Age	Age
MZV 114107		214.542	12.93	9	0
MZV 115223		342.167	19.28	10	3
CAS 22829		266.568	13.2	9	-
CAS 2323		254.386	13.55	9	0
CAS 26753		269.104	15.37	9	-
CAS 4655		296.989	16.93	9	2
CAS 3845		233.996	19.85	15	4
MZV 115218		332.438	18.44	14	3
MZV 115224		323.052	19.12	16	4
MZV 35085		331.588	18.95	16	3
CAS 3070		336.563	17.81	11	2
CAS 3696		384.514	19.26	15	-
CAS 4656		371.644	20.83	14	5
CAS 4468		404.831	20.71	15	4
CAS 3151		469.817	24.65	20	-
CAS 545		425.393	28.37	29	9
UMICH 114794		278.803	18.87	-	-
UMICH 114793		280.559	18.81	-	-
NMNH* 285726		364.135	23.06	33	-
NMNH* 285653		387.057	24.04	28	-
NMNH* 285665		419.181	25.33	30	-
NMNH* 47080		405.045	24.98	19	-

MZV 43	343.644	24.01	26	-
NMNH* 285684	398.729	22.07	31	2
NMNH* 285694	387.280	23.72	20	4
NMNH* 285697	402.634	23.65	27	3
CAS 23153	406.728	12.85	9	-
CAS 23831	211.166	13.66	9	0
CAS 23145	211.166	13.58	9	-
CAS 23829	210.265	13.2	9	0
CAS 23835	235.537	13.94	9	-
CAS 26760	239.410	14.4	9	-
CAS 23832	236.604	14.16	11	0
MZV 115227	296.393	16.85	11	2
CAS 2322	307.635	16.36	11	1
CAS 4185	293.647	19.58	12	3
CAS 4682	292.519	17.03	12	-
CAS 4235	296.029	19.51	23	5
CAS115228	304.093	18.01	23	7
CAS 21497	381.839	20.18	34	-
CAS 23101	306.776	16.59	24	-
CAS 2329	386.688	19.51	19	6
CAS 4564	370.351	18.73	18	7
CAS 1894	305.949	19.25	25	7
CAS 2402	341.551	19.15	28	-
CAS 3081	320.004	18.06	21	10
CAS21243	343.078	18.3	30	-
UAM 11492*	290.226	17.92	20	-
UAM 11497*	312.306	19.44	25	-
NMNH 286143*	299.077	18.62	22	6
AMNH 3800*	270.482	17.16	18	-

Otaria byronia

Coll. Nº	Sex	CS	CCB	Sut. Age	Age
FCIEN 1202		220.856	15.11	9	0
CNP 115		257.928	15.49	9	0
MACN 30236		246.002	16.88	9	-
LAMAMA 62		236.171	17.16	9	-
LAMAMA 115		243.689	17.55	9	0
LAMAMA 134		274.455	18.43	10	0
MACN 125		295.501	21.14	9	-
MACN 20595		309.940	22.23	14	2
LAMAMA 555		332.540	23.95	-	-
LAMAMA 31		358.622	24.73	14	3
MACN50.52		363.366	24.85	13	3
LAMAMA 24		356.799	25.05	13	2
CENPAT 160		364.590	25.24	16	-
MCN 2610		462.272	25.88	15	5
MACN 21743		364.699	26.1	15	-
LAMAMA 487		397.021	26.21	17	-
LAMAMA 105		352.305	26.32	15	5
UFSC 1161		375.044	26.43	13	2
LAMAMA 270		355.093	26.55	14	0
LAMAMA 43		400.319	26.86	15	5
MACN 25.45		403.084	27.15	15	4
MCN 2525		427.622	27.35	14	5
UFSC 1168		395.835	28.64	15	2
MACN 20420		447.971	29.29	15	4
LAMAMA 337		412.758	29.69	15	7
GEMARS 667		540.036	32	17	-
LAMAMA 90		329.387	25.73	22	3
UFSC1152		379.361	26.56	15	1
MZV 28		525.993	29.67	23	7

LAMAMA 60	412.408	30.49	20	6
MACN 20583	542.353	30.98	26	8
MZV 87001	571.605	31.88	36	-
LAMAQ 1134	497.132	31.9	23	-
LAMAQ 1140	479.440	32	21	7
MCN 2990	552.200	32.27	33	9
MACN 41226	478.253	32.4	26	-
GEMARS 171	532.548	32.45	36	#
GEMARS 353	524.341	32.52	26	#
MCN 2505	558.594	32.95	20	7
MCN 2696	569.611	33.15	27	6
MZV 1181	543.199	33.43	21	9
UFSC 1171	538.996	33.5	36	-
MCN 2460	576.586	33.58	30	14
GEMARS 284	519.106	33.84	30	#
MACN 20168	446.280	34.34	32	-
GEMARS 658	543.883	34.39	31	-
CENPAT 111	158.295	9.98	9	0
MACN 21740	230.889	14.99	9	0
LAMAMA 70	250.979	16.53	9	0
MACN 21737	322.395	20.69	17	-
MACN 21741	148.127	9.58	9	0
MACN 10.30	157.847	12.21	9	0
LAMAMA 237	297.321	20.89	12	2
FCIEN 1196	282.251	22.4	15	-
LAMAMA 483	338.476	22.59	16	-
MACN 21738	337.451	22.69	16	-
LAMAMA 240	316.188	22.89	15	3
FCIEN 332	335.863	22.9	15	3
LAMAMA 243	339.389	23.44	15	7
LAMAMA 127	326.419	23.94	16	6
LAMAMA 251	326.602	24.12	16	-
LAMAMA 33	340.558	24.21	15	6
LAMAMA 536	330.940	25.25	15	-
LAMAMA 303	367.634	25.32	17	3
MACN 20573	340.015	25.33	15	-
MCN-M 2691	446.209	25.5	17	7
LAMAMA 61	371.000	25.12	29	10
MACN 25138	335.881	25.28	23	5
MACN 90.03	392.383	25.33	23	11
LAMAMA 478	351.266	25.34	-	-
MACN 20578	367.904	25.67	23	-
LAMAMA 89	377.546	25.83	30	-
LAMAMA 88	369.004	25.87	29	10
MCN 2701	449.707	25.96	22	8
MACN 20576	375.854	26.31	27	-
MACN 20596	443.583	26.7	28	12
MCN 2462	385.647	26.9	20	13
MCN 2703	470.011	27.48	24	9
MACN 13.11	409.025	27.8	27	9
MZV 1188	465.070	30.48	17	11
MACN 20572	352.886	26.75	29	-
GEMARS 428	533.254	33. 53	36	#

APPENDIX 2

ANATOMICAL DESCRIPTION OF THE LANDMARKS

1 Anteriormost point of the pre-maxilla tuberosity
2 Antero-lateral extremity of third incisive alveolus
3 Anteriormost point of incisive foramen
4 Lateral extremity of canine alveolus
5 Anteromedial point of first post-canine alveolus
6 Anteriormost point of the maxilla-palatine suture
7 Point that label the direction change of the maxilla-palatine suture
8 Posteriormost point of the root at the lateral limit at bone palate of zigomatic process of the maxilla
9 Posteriormost point of sixth post-canine alveolus
10 Posteriormost point of palatine extension of maxilla ("pterygoid" process of the maxilla)
11 Posteriormost point of interpalatine suture
12 Point that label the direction change of the posterior border of palatine
13 Posteriormost extremity of oval foramen
14 Lateral extremity of jugal-esquamosal suture
15 Medial extremity of the contact between the glenoid fossa and the ectotympanic
16 Anteriormost extremity of the anterior aperture of carotid canal
17 Antero-lateral corner of mastoid process
18 Posteriormost point of the condiloid foramen
19 Posteriormost point of occipital condyle
20 Anteriormost point of foramen magnum

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