

Morphology of the tympanic-basiscranial region in *Mirounga leonina* (Phocidae, Carnivora), postnatal ontogeny and sexual dimorphism

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Abstract

The auditory region of pinnipeds has seldom been described. Here we describe and analyze the ontogenetic trajectory of the tympanic bulla of the southern elephant seal, *Mirounga leonina* (Phocidae, Mammalia). This species is extremely sexually dimorphic and highly polygynous (organized in harems). We examined 118 specimens, arranged in three age classes (CI, CII, and CIII), ranging from newborn to adults (males and females). To analyze the overall size and shape of the tympanic bulla we performed a geometric morphometric analysis including 87 skulls. Females reach definitive shape and size of the bulla at earlier ontogenetic stages than males, in agreement with their earlier involvement in reproductive activities. The internal anatomy of the tympanic region (e.g. form and extension of the *paries*) does not show remarkable differences between sexes or age classes. The greatest differences between age classes are related to bone thickness, resulting from the apposition of new annual layers. An examination of possible sex-related external differences among age classes shows significant shape differences between males and females in CIII. The morphology observed in neonates is conserved across all individuals from CI, which included specimens up to 1 year old. Clear morphological differences were observed between CI individuals, on one hand, and CII individuals plus CIII females on the other. During cranial development of both male and females, the glenoid cavity expands and compresses the bulla; this condition reaches its maximum expression in CIII males. CIII males showed the greatest morphological differences, with respect to both CI and CII individuals, and CIII females.

Key words: dimorphism; ear region; ontogeny; southern elephant seal.

Introduction

Studies of the morphology of the otic region of pinniped carnivorans offer the opportunity to investigate the correlates of an aquatic habitat and phylogenetic transformations, but this region of the anatomy has not been analyzed in depth for most species of this group. The auditory region of the Carnivora in general has been widely studied by many authors (e.g. Van Kampen, 1905; Pocock, 1921, 1929; Van der Klaauw, 1931; Thenius, 1949; Hough, 1952; Ginsburg, 1966; Beaumont, 1968; Hunt, 1974; Arnaudo et al. 2014). It

is noteworthy that the analysis of auditory features, such as the presence or absence of the septum bullae (Hough, 1948; Ivanoff, 2000), has supported the classification of the members of Carnivora into three large groups: Arctoidea, Aeluroidea, and Cynoidea (Flower, 1869), currently recognized as different clades (Eisenberg, 1989; Wozencraft, 1989, 2005; Wyss & Flynn, 1993; Ivanoff, 2001).

Within the pinnipeds (Otariidae, Phocidae and Odobenidae) the auditory region has been briefly described for several Northern Hemisphere species (e.g. Thenius, 1949; King, 1964; Odend'hal & Poulter, 1966; Graham, 1967; Solntseva, 1972, 1973a,b, 1975; Hunt, 1974; Marsh, 2001; Berta et al. 2006) and a few Southern Hemisphere ones (e.g. Wyss, 1987, 1988), and other contributions on which the ears of pinnipeds are treated together with those of other groups of mammals (e.g. Repenning, 1972; Fleischer, 1978; Nummela, 1995, and references therein). In addition, studies using a physiological approach, i.e. hearing (Mohl, 1967,

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1968) and audiometric (Kastak & Schusterman, 1999) analyses, have been performed on several Holarctic species such as *Mirounga angustirostris* (Phocidae, Carnivora). Species of this genus offer a rich subject of investigation given the chance to integrate the anatomical studies with biological information on the species.

The southern elephant seal (*Mirounga leonina*) (Phocidae) is an extremely sexually dimorphic and highly polygynous species. Adult males are much larger and almost three times heavier than females; they possess an enlarged proboscis and large canines (King, 1983; Laws, 1993, 1994). The main reproductive events of this species take place during the spring of the Southern Hemisphere, along a wide latitudinal range (Carrick et al. 1962; Condy, 1979; Bester, 1980; Bester & Lenghart, 1982; Baldi, 1992; Campagna & Lewis, 1992; Campagna et al. 1993; Lewis et al. 1998; Galimberti & Boitani, 1999) that extends from Valdés Peninsula (42°S, 64°W) in the Argentinean Patagonia to Isla 25 de Mayo/King George Island (62°S, 58°W) in Antarctica (Laws, 1994; McMahon et al. 2005; Carlini et al. 2006; Mennucci et al. 2012). Many aspects of the biology of this species, such as demography and distribution (Carrick et al. 1962; Condy, 1979; Bester, 1980; Bester & Lenghart, 1982; Baldi, 1992; Campagna et al. 1993; Lewis et al. 1998; Galimberti & Boitani, 1999; McMahon et al. 2005) and even behavior (McCaann, 1981; Modig, 1996; Negrete et al. 2011) have been extensively studied. Furthermore, anatomical studies regarding its skull allometry and ontogeny have recently been published (Tarnawsky et al. 2013).

Materials and methods

The tympanic region was studied using the complete skulls of 100 specimens, as well as 18 isolated auditory regions (see Appendix 1), and some comparisons were made with specimens of *M. angustirostris* ($n = 3$), *Hydrurga leptonyx* ($n = 52$), *Phoca* sp. ($n = 90$), *Leptonychotes weddellii* ($n = 74$), *Lobodon carcinophagus* ($n = 49$), and *Ommatophoca rossii* ($n = 8$). We are focusing on the morphology of the tympanic bone (endotympanic and ectotympanic) either on its external and internal views, and on the change of shape and size along its postnatal ontogeny. In addition some aspects of the morphological and topographically related basicranial region were considered. The specimens are deposited in the following collections:

FMM: Fundación Mundo Marino (San Clemente del Tuyu, Argentina)

IAA: Instituto Antártico Argentino Departamento Biología Predadores Tope (Buenos Aires, Argentina)

LAMAMA, (*CENPAT*): Laboratorio de Mamíferos Marinos del Centro Nacional Patagónico, CONICET (Puerto Madryn, Argentina)

MACN: Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina)

MHNM: Museo de Historia Natural de Montevideo Uruguay (Montevideo, Uruguay)

MLP: Museo de La Plata (La Plata, Argentina)

MNHN: Muséum National d'Historie Naturelle, Collection de Anatomie Comparée (Paris, France)

MVZ: University of California Museum of Vertebrate Zoology (Berkeley, CA, USA)

NMB: Naturhistorisches Museum Basel (Basel, Switzerland)

USNM: United States National Museum of Natural History, Smithsonian Institution (Washington DC, USA)

ZM-UZH: Zoologisches Museum der Universität Zurich, Vertebrate Collection (Zurich, Switzerland)

Among the specimens with whole skulls, seven *M. leonina* individuals of both sexes of known ages were selected to be analyzed using high resolution computed axial tomography (CAT), to observe the internal morphology on 3D reconstructions. CAT scans were performed at the Centro de Imágenes Médicas (CIMED, in La Plata, Buenos Aires) using a Scan Philips Brilliance 64 with 0.56-mm resolution between slices. For comparative analyses, an additional CAT scan of an *M. angustirostris* female was obtained with permission from the Digimorph.org website and Tim Rowe's Digital Libraries Grant from NSF. The 3D reconstructions were made using the software programs MIMICS 10.01, and IMAGEJ 1.49f.

Different methods have been proposed to establish age classes for this species, consequently, different categories exist, which are in many cases not completely equivalent. For instance, external and behavioral characters are used for living individuals (see Laws, 1994), whereas in the case of skeletal materials, age is established on the basis of suture lines (see Morejohn & Brigs, 1973), growth lines observed in tooth sections (see Laws, 1953; Carrick et al. 1962; Loza et al. 2011) or sequence of tooth eruption, condyle-basal length and degree of extraoccipital bone fusion (see Tarnawsky et al. 2013). To be able to count the number of growth lines in tooth sections, we removed organic matter using H₂O₂ (100 vol. 1/10), then we cut thin sections mechanically after the sections were decalcified with 20% formic acid, and finally stained the sections with graphite; lines were counted under a binocular microscope (Fig. 1).

Prior to deciding which system for age-class separation would best fit the goals of this work and the characteristics of the morphological structures to be analyzed, we divided all the specimens in our sample into groups following the age-class criteria proposed by other authors (e.g. Tarnawsky et al. 2013). Thus, we were able to verify that the separation of postnatal specimens (from newborns to adults), and even full-term unborn individuals, into more categories than the ones used here, did not reflect the differences observed in a statistically significant manner. Therefore, in this work, and because only cranio-dental materials were available, age

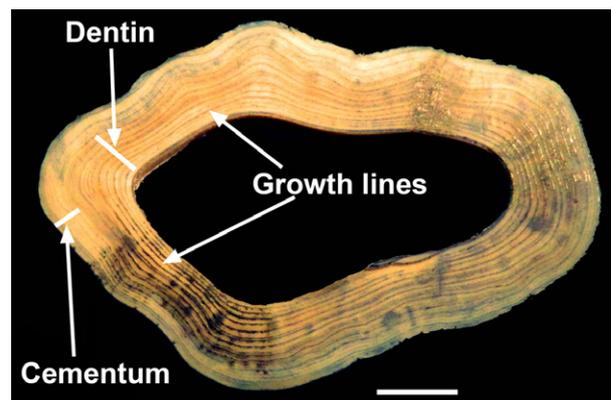


Fig. 1 Transverse section of an upper canine of a *Mirounga leonina* male, showing the annual growth lines in dentin and cementum. Scale bar: 5 mm.

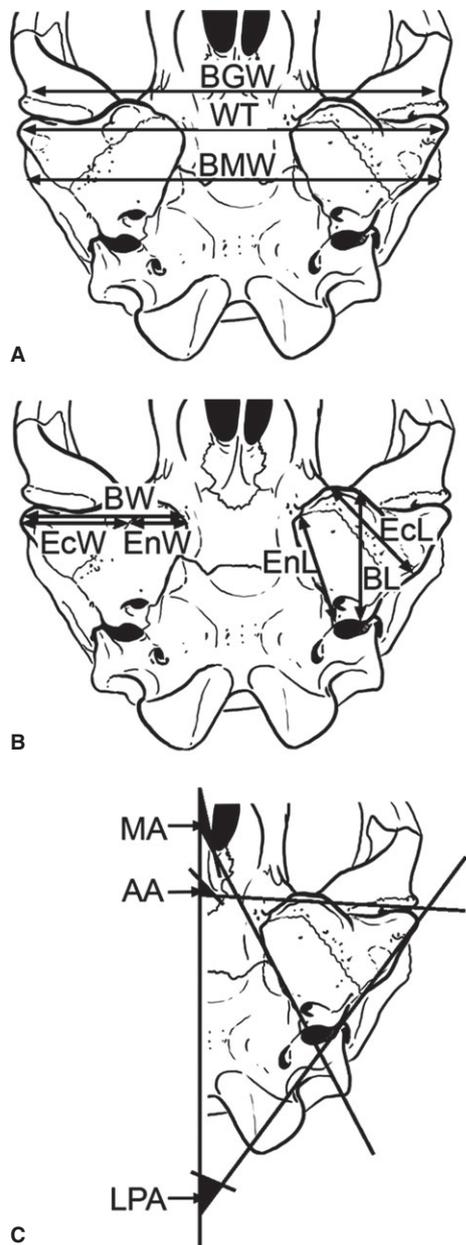


Fig. 2 A and B: Ventral view of the skull of *Mirounga leonina* showing measurements and angles used in this work; C: detail of left bulla showing the angles). Anterior base angle (AA), biglenoid width (BGW), maximum length of the bulla (BL), bimastoid width (BMW), maximum width of bulla (BW), length of ectotympanic bone (ECL), ectotympanic width (EcW), maximum length of endotympanic bone (EnL), endotympanic width (EnW), latero-posterior base angle (LPA), medial base angle (MA), width between tubers (WT).

classes (and consequently, assignation of specimen to them) were determined using the following criteria:

- Absolute age obtained by us (see Loza et al. 2011) from the count of growth lines in tooth sections (only for specimens deposited in the collections IAA, MACN, and MLP) (see Fig. 1).
- Sequence of tooth eruption of the permanent dentition.
- Condyle-basal length and degree of suture fusion (taken in part from Tarnawsky et al. 2013).

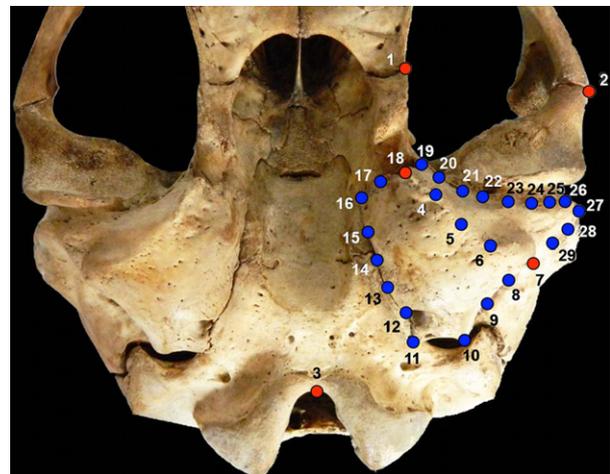


Fig. 3 Ventral view of the skull of a CIII female of *Mirounga leonina*, showing the used morphometric points; red dots (1, 2, 3, 7, 18), landmarks; blue dots, semilandmarks.

On the basis of these indicators, the following age classes were established:

Class I (CI). Specimens younger than 1 year old, with erupted incisors and postcanines, canines partially erupted in females and not erupted in males. Condyle-basal length < 234 mm; undoubtedly sexually immature (Ling & Bryden, 1981, and bibliography therein).

Class II (CII). Specimens 1–4 years old (females), and 1–7 years old (males); tooth series completely erupted, with condyle-basal length > 260 mm. As Ling & Bryden (1981, and bibliography therein) pointed out, most specimens (males and females) included in those time periods are not sexually mature or, if so, are not actively reproducing (Ling & Bryden, 1981, p. 302). For instance, sexual maturity in males of this species may be reached at ca. 4 years of age (Laws, 1956) but physically immature juveniles of this age are prevented from participating in breeding activities until they are 7–9 years old (Carrick et al. 1962), with very few and fortuitous exceptions (Negrete et al. 2012); a 1- to 3-year-old female was observed breeding on one occasion in Potter Peninsula (J. Negrete, personal observation).

Class III (CIII). Specimens both sexually and physically mature. Females: over 4 years old, condyle-basal length > 276 mm; males: over 7 years old, condyle-basal length > 400 mm.

The cranial regions studied here were measured in each specimen using digital calipers (accuracy 0.1 mm); angles were measured using a goniometer (accuracy 1°), and skulls were photographed in traditionally used views.

Nomenclature for foramina, ducts and canals follows the *Nomina Anatomica Veterinaria* (2012).

Measurements and morphometric landmarks

The auditory regions were measured with the goal of identifying variables that could be correlated with the previously defined age classes (Fig. 2). The following measurements were taken:

BGW (biglenoid width) – distance between lateral margins of articular surfaces of both glenoid fossae.

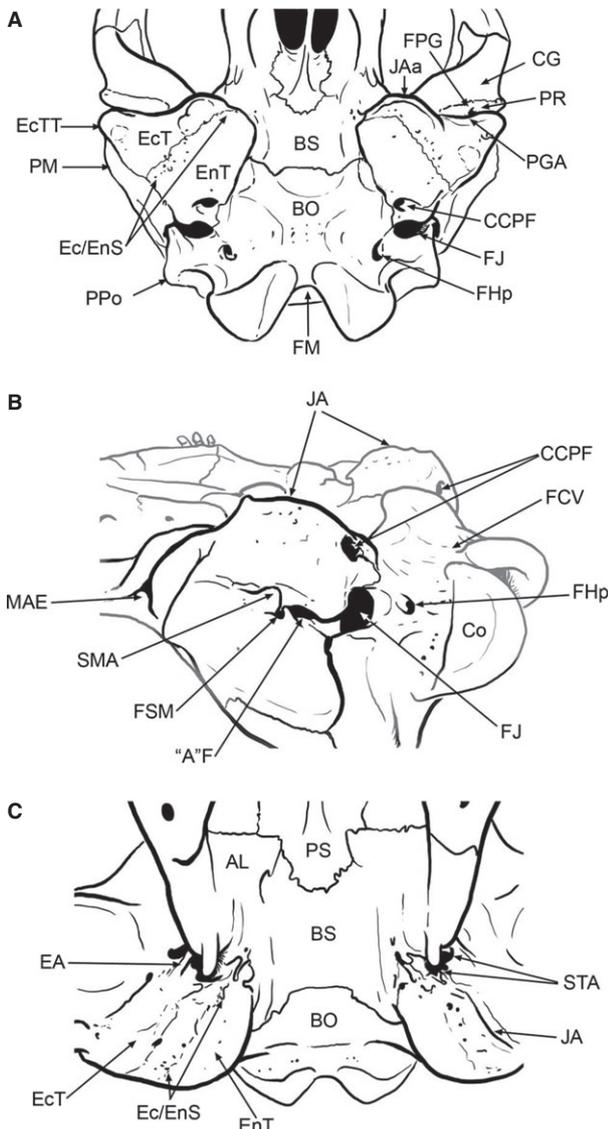


Fig. 4 Ventral views of the skull of *Mirounga leonina*, showing foramina and apophyses discussed in the text. (A) Ventral view, (B) latero-posterior view, (C) antero-ventral view. 'A'F; 'A' foramen; AL, alisphenoid; BO, basioccipital; BS, basisphenoid; CCPF, posterior foramen of *canalis caroticus*; CG, glenoid fossa; Co, occipital condyle; EA, Eustachian apophysis; Ec/EnS, ectotympanic/endotympanic suture; EcT, ectotympanic bone; EcTT, ectotympanic tubercle; EnT, endotympanic bone; FCV, *Fossa condylaris ventralis*; FHp, *foramen hypoglossis*; FJ, *foramen jugulare*; FM, *foramen magnum*; FPG, *foramen postglenoideum*; FSM, *foramen stylomastoideum*; JA, jugular apophysis; JAa, jugular apophysis; anterior crista; MAE, *meatus acusticus externus*; PGA, postglenoid apophysis; PM, *processus mastoideus*; PPO, *processus paraoccipitalis*; PR, *processus retroarticularis*; PS, parasphenoid; SMA, *stylomastoideum apophysis*; STA, *sulcus tubae auditivae*.

BL (maximum length of bulla) – antero-posterior distance between most anterior point of bulla (behind the glenoid fossa, not considering apophyses or processes that may or may not be present anteriorly to the posterior limit of this fossa), and most posterior point (which coincides with the

triple suture between ectotympanic, mastoid, and basioccipital).

BMW (bimastoid width) – distance between most lateral extremes of mastoid apophyses.

BW (maximum width of bulla) – distance between medial margin of endotympanic and most exterior point of *meatus acusticus externus*.

CBL (condylo-basal length) – distance between the condylar plane and the distal tip of the palate.

EcL (length of ectotympanic bone) – distance between most anterior point of ectotympanic and posterior margin of the *foramen stylomastoideum* (FSM, see below).

EcW (ectotympanic width) – distance between endo-/ectotympanic suture and most lateral margin of ectotympanic tuber.

EnL (maximum length of endotympanic bone) – distance between most anterior point of endotympanic and FCP.

EnW (endotympanic width) – distance between medial margin of endotympanic and endo-/ectotympanic suture.

WT (width between tubers) – distance between lateral ectotympanic tubers.

Angles

AA (anterior base angle) – between anterior face of bulla and the sagittal plane (Fig. 2c).

LPA (posterior base angle) – between a line passing through most lateral point of external auditory meatus and jugular foramen (FY) and extended on posterior wall of the bulla, and the sagittal plane.

MA (medial base angle) – between medial face of bulla and the sagittal plane.

Specimen information

The geometric morphometric analysis included the 87 *M. leonina* skulls with available sex data on their labels obtained from seven collections (see Appendix 1). Digital images in palatal view were obtained using a Nikon Coolpix L120 digital camera mounted on a stand. Each photograph included a scale in order to account for size in the analyses, and all skulls were placed in the same position. Both sexes were nearly equally represented (42 females, 45 males).

Morphometric analysis

We used landmark-based geometric morphometric methods to analyze overall size and shape of the tympanic bulla in *M. leonina* (Rohlf & Marcus, 1993; Adams et al. 2004, 2013; Zelditch et al. 2004). These methods quantify the shape of anatomical objects from the coordinates of homologous locations, after the effects of non-shape variation (i.e. orientation, position, and scale) are held mathematically constant (Adams et al. 2013; Kelly et al. 2013). Two-dimensional coordinates of five homologous landmarks were digitized. Additionally, 24 equidistant semilandmarks (Gunz & Mitteroecker, 2013) were placed along the boundary between the endo- and ectotympanic bones to capture the shape and curvature of this structure (Fig. 3).

The landmarks and semilandmarks were subjected to a generalized Procrustes analysis (GPA) (Rohlf & Slice, 1990). This procedure translates all specimens to the origin, scales them to unit centroid

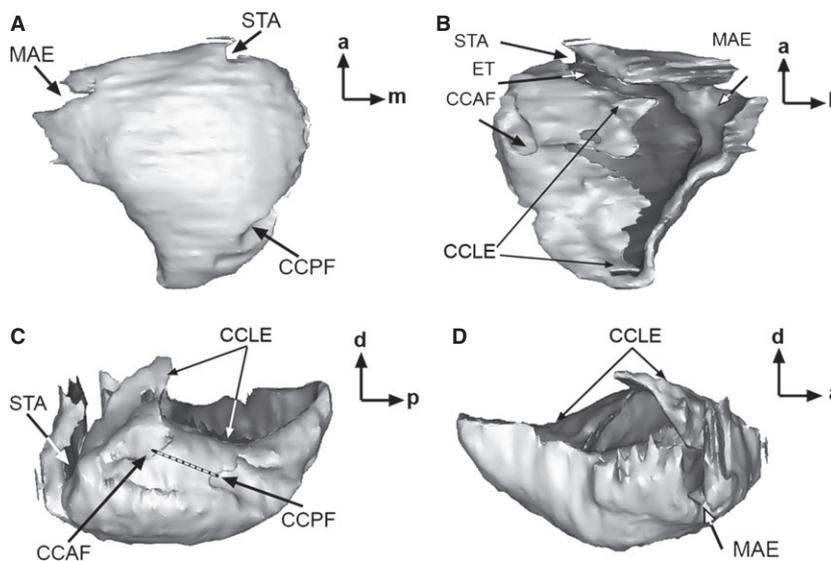


Fig. 5 Isolated tympanic bulla of *Mirounga leonina*; generated by 3D reconstruction of the CAT of a CI specimen showing its internal and external anatomy. (A) Reconstructed ventral view, (B) reconstructed dorsal view, (C) reconstructed medial view, (D) reconstructed lateral view. CCAF, anterior foramen of *canalis caroticus*; CCLE, lateral extension of *canalis caroticus*; CCPF, posterior foramen of *canalis caroticus*; ET, Eustachian tube; MAE, *meatus acusticus externus*; STA, *sulcus tubae auditivae*. a, anterior; d, dorsal; l, lateral; m, medial; p; posterior.

size, and optimally rotates them to minimize the total sums-of-squares deviations of the landmark coordinates from all specimens to the average configuration (Berns & Adams, 2013). During this procedure, semilandmarks are allowed to slide along their tangent directions (Bookstein, 1997; Bookstein et al. 1999) so as to minimize Procrustes distance between specimens (Pérez et al. 2006; Gunz & Mitteroecker, 2013). After superimposition, the aligned Procrustes shape coordinates are projected orthogonally into a linear tangent space yielding Kendall's tangent space coordinates (Dryden & Mardia, 1998; Rohlf, 1999; Claude, 2008; Berns & Adams, 2013), which are then treated as a set of shape variables to be used in the exploration of shape variation. Centroid size was also retained for further analyses.

The digitizing process was performed using TPSDIG2 (Rohlf, 2009) and morphometric analyses were performed in R 3.0.2 (R Development Core Team, 2013) using routines in the package 'geomorph' (Adams & Otárola-Castillo, 2013).

Analysis of size and shape

The main focus of this work is the examination of possible sexual shape dimorphism and ontogenetic allometry of the tympanic bulla in *M. leonina*. Two sets of analyses were performed to assess patterns of sexual dimorphism. Initially, a principal components analysis (PCA) of the tangent space coordinates was performed to visualize patterns of shape variation in the shape space. Secondly, a Procrustes ANOVA with permutation was used statistically to assess possible shape differences between males and females. Allometric patterns were visualized through a series of plots that describe the multivariate relationship between size and shape derived from landmark data. The abscissa of the plot is log (centroid size) and the ordinate represents shape, calculated as the common allometric component of the shape data, which is in turn an estimate of the average allometric trend within groups (Mitteroecker et al. 2004). In addition, a stylized graphic of the allometric trend was obtained for better visualization following Adams & Nistri (2010).

Results

External morphology of the tympanic region

Remarkably, the neonate specimens (IAA 01-14, LAMAMA ML024, LAMAMA ML026), defined as individuals ranging from newborn to 3 weeks old, did not show morphological differences with respect to CI individuals, and were therefore considered as part of the latter age class for these analyses (Figs 4 and 5).

The tympanic bulla of *M. leonina* presents the morphology characteristics of Phocidae (King, 1983; Wyss, 1988; Berta et al. 2006): it is primarily globose and triangular in outline, with a smooth surface and no markedly developed apophyses or processes (Figs 6 and 7). In contrast to the condition observed in Otariidae, the endotympanic bone is larger than the ectotympanic; the suture between these two bones is squamous and not always apparent, especially in the case of CIII individuals, in which it is completely obliterated and is represented only by a row of vascular foramina that indicate its approximate location. The mastoid region develops a rather evident pachyostosis (Berta et al. 2006), which grows in thickness concurrently with annual growth (and thus allows straightforward estimation of specimen age), hiding the sutures between the bulla, petrosal, mastoid, and squamosal. Only in some CI specimens is it possible with certainty to identify these boundaries in a CAT reconstruction (see Fig. 6).

The following foramina, ducts, and passages (which are characteristic of most members of Arctoidea) were recognized (Figs 4 and 5):

Meatus acusticus externus (MAE) (Fig. 4B) is the largest opening, located laterally; it is smaller relative to

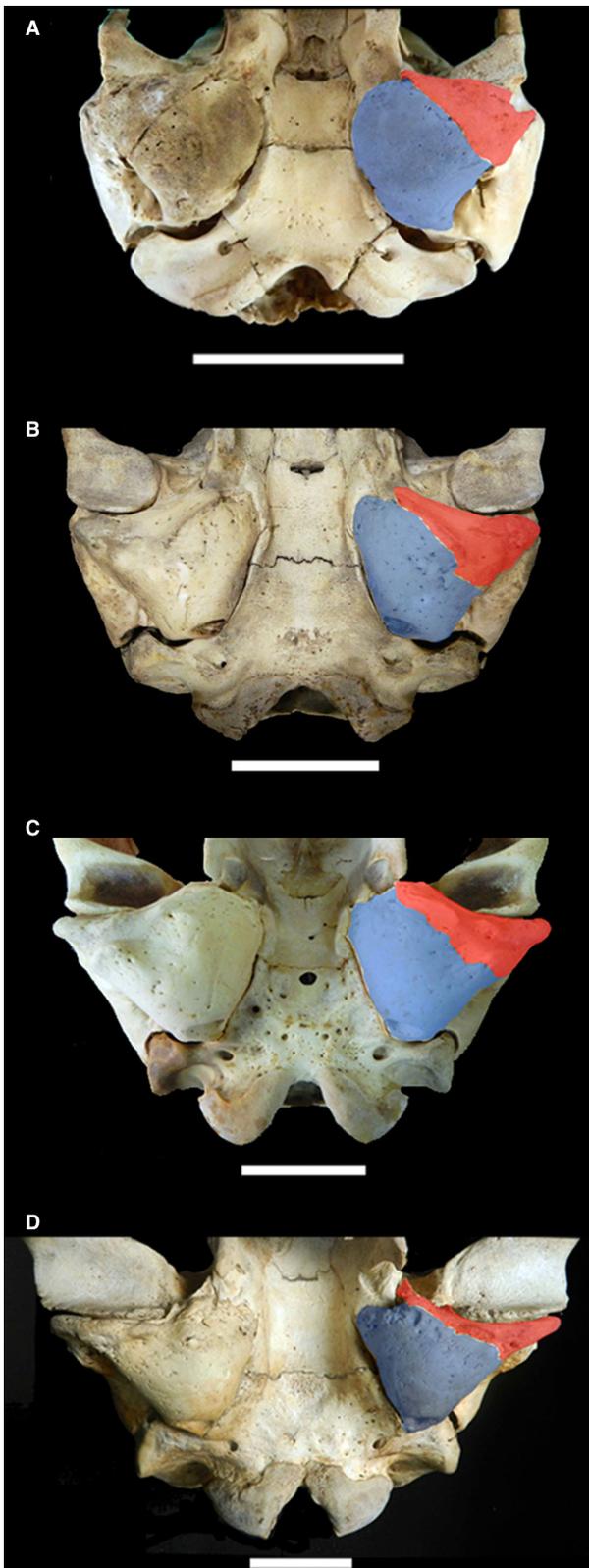


Fig. 6 External morphology of tympanic bulla of *Mirounga leonina* showing differences in development of the ectotympanic (red) and endotympanic (blue) bones in different age classes: (A) Class I, (B) Class II, (C) Class III female, (D) Class III male. Scale bar: 5 cm.

skull length in males than in females; its size is similar to that of *Lobodon*, *Phoca*, and *Leptonychotes*, but smaller than in *Ommatophoca*, and larger than in *Hydrurga*; its contour is mostly circular in males and oval in females (Table 1).

Sulcus tubae auditivae (STA), or (external foramen of the Eustachian tube) *sensu* Pocock 1916), is the anterior bony opening of the middle ear cavity continuous with the Eustachian tube (Fig. 4C). It is an obvious opening and generally oval in outline: relative to skull length, the foramen of males is the smallest of the family, whereas in females, its size is similar to those of *Lobodon*, *Leptonychotes*, and *Phoca*, and smaller than in *Ommatophoca* (Fig. 7). In other carnivorans, e.g. procyonids, hyaenids, and ursids, it is known as the 'anterior opening of auditory tube' (see Ivanoff, 2001) (Table 1).

Anterior foramen of the canalis caroticus (CCAF), or *foramen lacerum*, is located posterior to the alisphenoid and represents the opening for a branch of the internal carotid artery (Fig. 5B,C). In this species, the CCAF does not open on the basicranial surface and is therefore not visible in the ventral view of the skull, as in most species except *L. weddellii*. In some groups (e.g. Primates) it is known as the 'middle lacerate foramen' (MacPhee, 1981; Wible, 1991).

Posterior foramen of the canalis caroticus (CCPF) is the posterior opening of the endotympanic traversed by the carotid (Figs 4A and 5A,C). Frequently, this foramen is not identified as such because in some other mammals it opens into a common vestibule with the *foramen jugulare*, and is therefore included as part of the latter (e.g. Wible, 1991, 2010). However, this foramen is always separate in both Phocidae and Otariidae, and quite conspicuous especially in the former. In *M. leonina* it has a circular outline and is the largest foramen (Fig. 7; Table 1).

Foramen jugulare (FJ) is located between the *bulla tympanica* and the occipital bone; this opening is traversed by the glossopharyngeal (IX), vagus (X), and accessory (XI) nerves and the internal jugular vein: in this species the greater axis of this foramen is perpendicular to the sagittal plane. In relation to skull length, this foramen is always larger in females than in males of *M. leonina*, and it is the smallest in *Hydrurga*. It is mentioned in some texts as the 'posterior lacerate foramen' (e.g. canids, ursids, procyonids) (Figs 4A,B and 7; Table 1).

Foramen stylomastoideum (FSM) is located postero-latero-dorsal to the bulla and posterior to the *meatus acusticus externus*, between the tympanic bulla and the mastoid process; it is traversed by the facial nerve (VII) and the stylomastoid vein (which goes through the inner ear) (Fig. 4B); it is always evident in both sexes and diverse age classes, but as in the case of

Table 1 Relative sizes of CCPF, FJ, FHp, MAE, and FSM with respect to LBC, AMA, and AMB on six species of phocids.

| | CBL/CCPF | CBL/FJ | CBL/FHp | CBL/MAE | CBL/FSM | CBL/STA |
|----------------------------------|----------|--------|---------|---------|---------|---------|
| <i>Mirounga leonina</i> (male) | 42–47 | 22–18 | 65–63 | 28–30 | 64–84 | 87 |
| <i>Mirounga leonina</i> (female) | 34–37 | 12 | 42 | 26 | 44–64 | 38–28 |
| <i>Leptonychotes weddellii</i> | 33 | 15 | 56 | 22 | 49 | 31 |
| <i>Lobodon carcinophagus</i> | 46 | 22 | 58 | 24 | 45 | 31 |
| <i>Ommatophoca rossii</i> | 31 | 23 | 41 | 14 | 59 | 24 |
| <i>Hydrurga leptonyx</i> | 43 | 30 | 78 | 43 | 389 | 59 |
| <i>Phoca</i> sp. | 42 | 13 | 71 | 25 | 102 | 40 |

| | BMW/CCPF | BMW/FJ | BMW/FHp | BMW/MAE | BMW/FSM | BMW/STA |
|----------------------------------|----------|--------|---------|---------|---------|---------|
| <i>Mirounga leonina</i> (male) | 26–34 | 14–13 | 46–41 | 18–21 | 41–38 | 52 |
| <i>Mirounga leonina</i> (female) | 26 | 9 | 30–35 | 18–13 | 32–46 | 20–24 |
| <i>Leptonychotes weddellii</i> | 22 | 10 | 38 | 15 | 33 | 20 |
| <i>Lobodon carcinophagus</i> | 26 | 13 | 33 | 15 | 26 | 216 |
| <i>Ommatophoca rossii</i> | 23 | 17 | 30 | 10 | 44 | 18 |
| <i>Hydrurga leptonyx</i> | 24 | 17 | 43 | 24 | 218 | 35 |
| <i>Phoca</i> sp. | 22 | 7 | 39 | 13 | 54 | 21 |

| | BW/CCPF | BW/FJ | BW/FHp | BW/MAE | BW/FSM | BW/STA |
|----------------------------------|---------|-------|--------|--------|--------|--------|
| <i>Mirounga leonina</i> (male) | 9–13 | 4 | 17 | 6–8 | 23–13 | 17 |
| <i>Mirounga leonina</i> (female) | 8–9 | 3 | 12 | 4–7 | 11–17 | 7–9 |
| <i>Leptonychotes weddellii</i> | 7 | 3 | 12 | 4 | 10 | 6 |
| <i>Lobodon carcinophagus</i> | 8 | 4 | 10 | 4 | 7 | 6 |
| <i>Ommatophoca rossii</i> | 8 | 6 | 11 | 4 | 16 | 7 |
| <i>Hydrurga leptonyx</i> | 7 | 5 | 13 | 7 | 66 | 10 |
| <i>Phoca</i> sp. | 7 | 2 | 13 | 4 | 18 | 2 |

the FJ, it is larger in females, and smallest in *Phoca* and *Hydrurga*.

Foramen post-glenoideum (FPG) is located immediately posterior to the postero-medial angle of the glenoid fossa, anterior to the tympanic bulla; it is the opening for the external jugular vein. This foramen tends to be small in the Phocidae, and in the case of *M. leonina* it is frequently absent in all age classes (Figs 4A and 7).

Foramen 'A' is located latero-posterior to the foramen stylomastoideum; it is not present in all specimens; when present, it may be well defined and separated from FSM, or joined to the latter, or appear as a blind depression (Fig. 4B).

Lastly, the foramina in the cranial base are:

Foramen hypoglossus (FHp): for the passage of the hypoglossal nerve (XII); due to its location close to the occipital condyles, it is also known as 'condylar foramen' (Figs 4A,B and 7). This foramen is relatively larger in females than in males (Table 1).

Foramen ovale (FOv) is located on the alisphenoid, for the passage of the mandibular branch of the trigeminal nerve (V₃).

The foramina and openings with the most consistent presence in this region are: *meatus acusticus externus*, foramen for the *canalis caroticus posterior*, *jugulare*, *hypoglossis*

(reduced compared with the condition in Otariidae), *stylo-mastoideum* and *postglenoideum* (reduced or absent), and the 'A' foramen of uncertain homology.

The *bulla tympanica* presents a small anterior crista (JAa) (Fig. 4A) on the ectotympanic that extends along the anterior third of the latter, and a posterior crista (CP) that extends parallel to the ecto-/endotympanic suture. These two structures probably correspond to the 'jugular apophysis' of Otariidae; under this assumption, they may be described as two cristae (portions) of the 'jugular apophysis' (JA), one anterior (JAa) and the other posterior (JAp).

The tympanic bone also has a postglenoid apophysis (PGA), or tympanic process, smaller than that of *Lobodon* and *Leptonychotes*, that surrounds the FPG posteriorly and extends perpendicularly to the sagittal plane (Fig. 7). This apophysis should not be confused with the *processus retroarticularis* (PR) of the glenoid fossa; the latter surrounds the fossa whereas the PGA corresponds to the ectotympanic (Fig. 4A). Another apophysis is located adjacent to the anterior opening of the Eustachian tube (Fig. 4C). The ectotympanic bone develops a lateral tuberosity (EcTT) whose tip is more pointed in adult males than females.

Furthermore, both the mastoid region with its *processus mastoideus* (PM) and the paraoccipital region with its *processus paraoccipitalis* (PPo) (Fig. 4A) are well developed in CIII males and females and in some CII males.

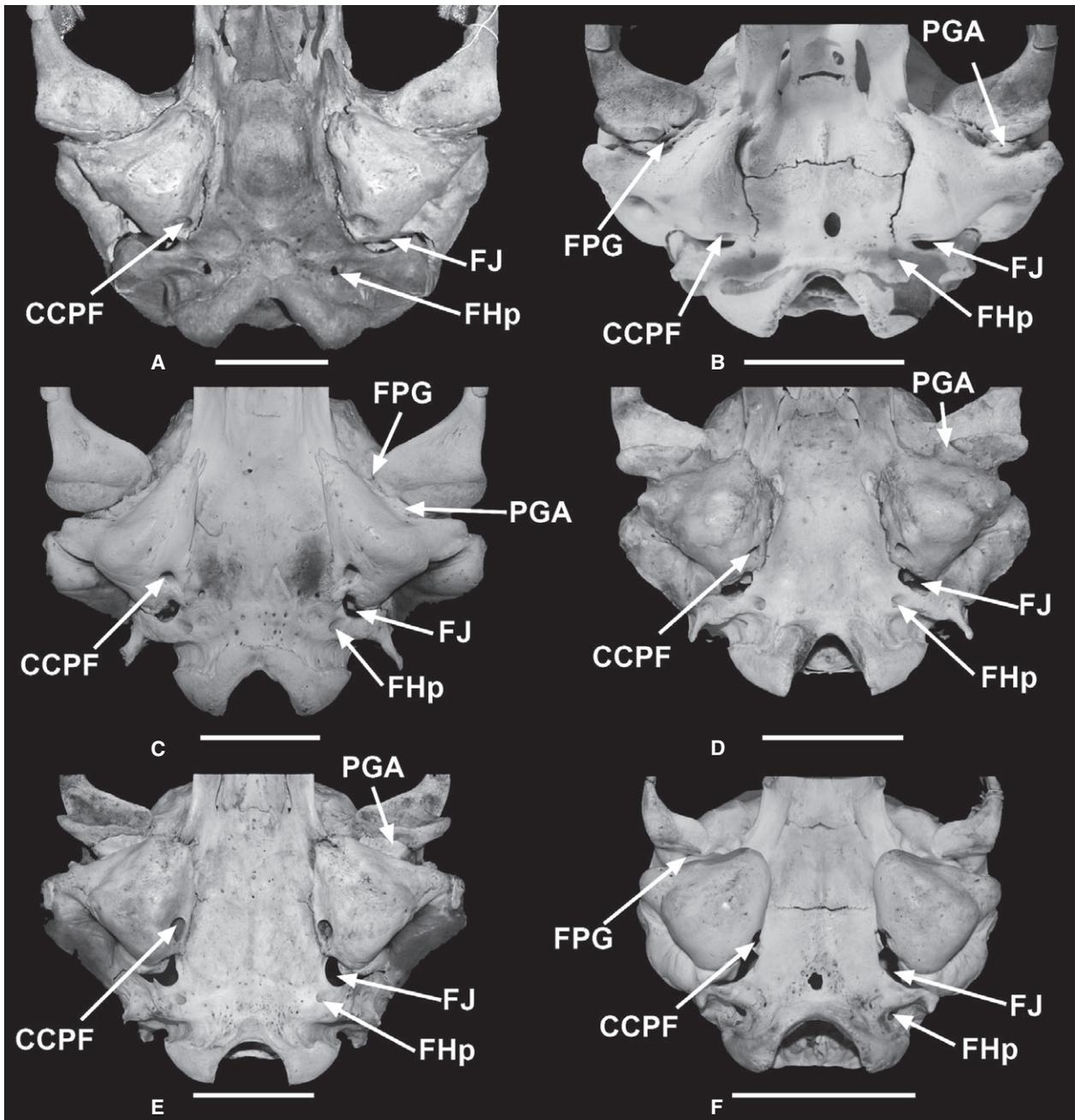


Fig. 7 Ventral views of the skull of: (A) *Mirounga angustirostris*, (B) *Ommatophoca rossii*, (C) *Hydrurga leptonyx*, (D) *Lobodon carcinophagus*, (E) *Leptonychotes weddellii*, and (F) *Phoca vitulina*. CCPF, posterior foramen of canalis caroticus; FHp, foramen hypoglossis; FJ, foramen jugulare; FPG, foramen postglenoideum; PGA, postglenoid apophysis.

External morphology and age classes

In external view, specimens of CI and CII do not possess well developed apophyses in the tympanic region; instead, they present markedly rugose areas. In CIII individuals the apophysis EA and the anterior process of JA are already visible (growth of the latter is already observable in CII). Remarkably, only JA shows a morphological trajectory that differs between males and females (see below and Fig. 6).

The EcTT was not observed in CI; this structure is well developed in CII and CIII, and its enlargement is accompanied by progressive elongation of the MAE.

In the course of ontogeny, the glenoid fossa reaches an apparently more posterior position so that it extends further onto the anterior wall of the tympanic bulla (Fig. 6). This seems to be brought about by the greater development of the retroarticular process from CII; this process becomes more vertical, thus providing stronger

support for the mandibular condyle, mainly in CIII males (Fig. 6D).

External morphology in males and females

In CI specimens, external morphology of males and females is similar, even though males are slightly larger; sexual dimorphism begins to be evident from CII onwards.

Given that this is a clearly dimorphic species, by CIII morphological differences are evident, and the size difference is quite marked. In females the surface of the endotympanic bone is evidently globose, whereas it is flatter in males (Fig. 6C,D); and the ectotympanic of males bears evident rugosities that become more marked in older specimens.

The outline of the tympanic bulla maintains a rather constant shape in females of the three age classes; in contrast, its characteristic angular outline changes from CI through CIII, and in CIII, the apex of EcTT is angular in males and rounded in females.

Angularity (referring to change in the angle formed by the anterior base of the bulla and the sagittal plane of the skull) decreases in males, so that the AJ reaches a position almost perpendicular to the sagittal plane, whereas in females this angle remains at values greater than 90° (close to the values for juveniles).

Internal morphology of the bulla

From an anatomical and functional viewpoint, the middle ear can be divided into three well differentiated parts: the *annexae mastoideae*, the *cavum tympani* and the Eustachian tube, or *Tuba pharyngotympanica* (Thomassin et al. 2008) (Figs 8–11). The middle ear is formed by a *pars petrosa*, a *pars tympanica*, and a *pars escamosa*; these three parts are also involved in the conformation of the external and inner ear (Fig. 8A).

Following the work of Gray (1858), below we describe the six walls that delimit the tympanic bulla and its *cavum tympani*.

1 *Paries tegmentalis* (tectum) (Fig. 8B) – formed by the ventral wall of the petrosal, the *tegmen tympani* in which the *recessus epitympanicus* is excavated; the latter is a conspicuous hemispheric cavity that contains the large incus.

In addition, this roof is also formed medially by a thin bone layer that extends from the lateral margin of the *canalis caroticus* and covers the petrosal ventrally, and the ventro-lateral surface of the petrosal; this conformation is visible in the most cranial portion of the bulla (Figs 8 and 9). Both parts separate the *cavum tympani* from the base of the skull. The thin bone plate of the *canalis caroticus* (a well developed channel that pierces the endotympanic bone in

an antero-dorsal to postero-ventral direction) is antero-posteriorly extended in the middle zone, forming the first third of the roof in the cranial medial half; due to the triangular outline of the bulla (which forms a wedge toward the rear), this bone plate forms all of the roof in the posterior or caudal half, with no participation of the petrosal (Fig. 9).

2 *Paries jugularis* (floor) (Figs 10B and 11A) – extends below the level of the lower wall of the MAE; its anterior region bears the *recessus hypotympanicus* (Fig. 10A) just below the *recessus epitympanicus*, the rest of its surface is slightly concave and smooth.

3 *Paries labyrinthica* (inner wall) (Fig. 11C) – includes the following structures: *fenestra ovalis*, *fenestra rotunda*, and *promontorium*. Gray (1858) also described a Fallopian aqueduct that we did not observe in *M. leonina*. Due to the enormous relative size of the petrosal, and to its oblique position (antero-medial and postero-lateral) with respect to the skull base, the *paries labyrinthica* is part of the dorsomedial and dorsolateral boundaries of the *cavum tympani* (at its anterior and posterior parts, respectively). This *paries* is completed medial by the lateral wall of the *canalis caroticus* (Fig. 12).

4 *Paries mastoidea* (posterior wall) (Fig. 11A,B) – contacts with the *annexae mastoideae* which are poorly developed in CI but are evident in CIII individuals, especially males; this may be due to the fact that the formation of the *annexae mastoideae* begins during fetal life, but takes place mostly after birth (e.g. *Homo*, see Tran Ba Huy & Teissier, 2011).

5 *Paries carotica* (anterior wall) (Fig. 11A,B) – circumscribes the posterior bony opening of the Eustachian tube, or *tuba pharyngotympanica*, in both adults and juveniles.

6 *Paries membranaceus* (external wall) (Fig. 11B,C) – defines the *meatus acusticus externus* (part of the external ear), which becomes proportionally narrower and longer during ontogeny. The *meatus acusticus externus* runs postero-ventrally from the *cavum tympani* to the exterior.

Morphometrics

The first two principal components explained 73% of the total shape variation, and showed several distinct clusters of specimens (Fig. 13). In general, males and females were at opposite extremes of the plot, with some degree of overlapping, implying that shape differences between sexes exist. A statistical evaluation was performed using Procrustes ANOVA with permutation, revealing significant shape differences both between sexes and between age stages, but the interaction term was marginally non-significant (Table 2).

Significant allometry was detected by means of a multivariate regression of shape on size (centroid size)

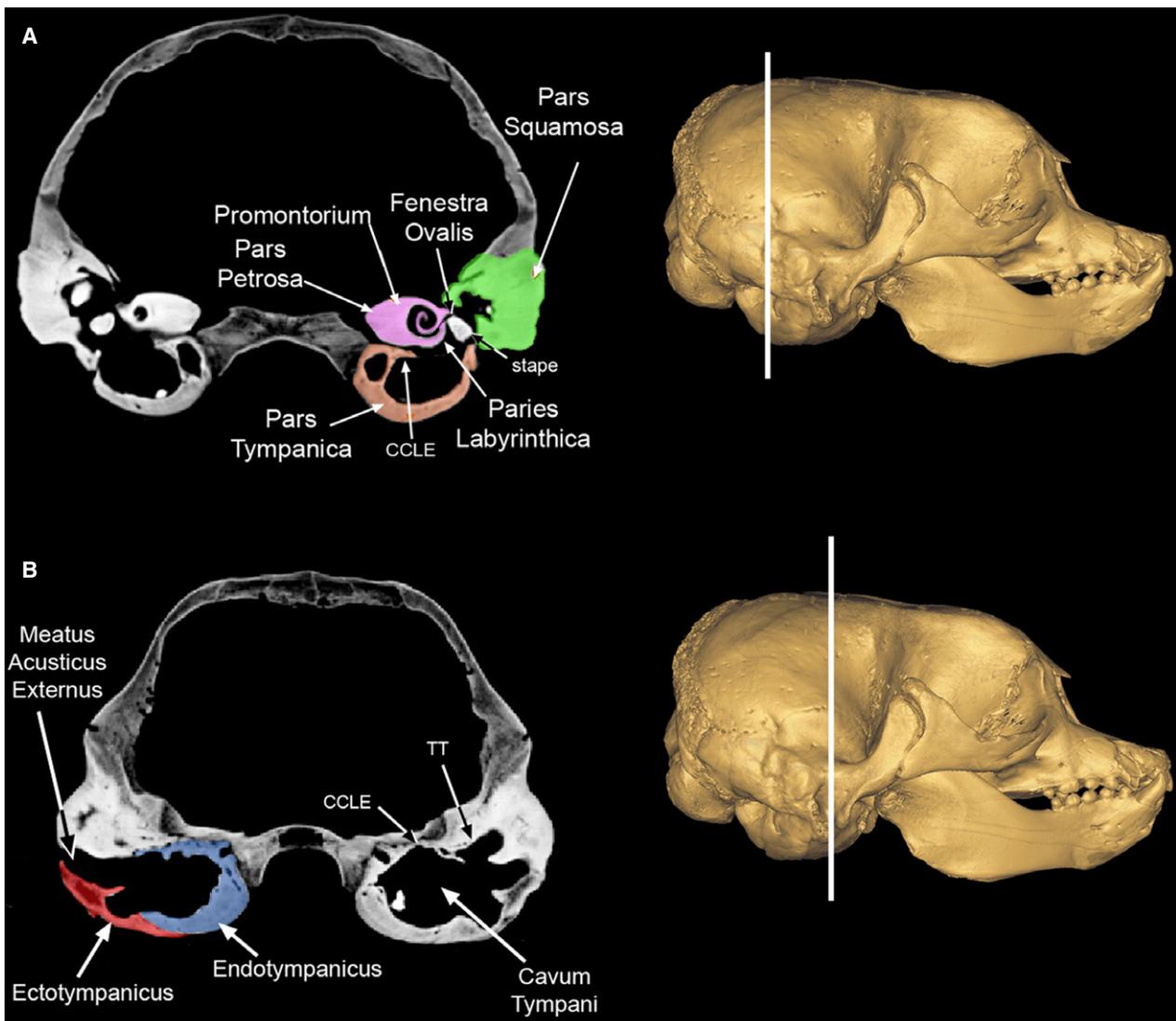


Fig. 8 Transversal section (TS) from CAT of the skull of *Mirounga leonina* at the auditory region level. (A) Posterior TS showing the paries labyrinthica, pars petrosa (pink), pars squamosa (green), and pars tympanica (brown). (B) More anterior TS showing the endotympanic/ectotympanic suture and the relationship of CCLE (lateral extension of *canalis caroticus*), as part of the *paries tegmentalis* or roof of the tympanic cavity. Skulls in lateral view show the precise line of each TS.

(P -value < 0.01). Males and females have approximately parallel trajectories, showing a common allometric pattern (Berge & Penin, 2004; Mitteroecker et al. 2004) (Fig. 14). However, when different age stages were taken into account, the patterns of allometric trajectories differed (Fig. 15). The allometric patterns as reported for stage C1 were clearly different compared with those of stages CII and CIII (Fig. 15).

Discussion

The study of a large sample of *M. leonina* made possible the characterization of the ear anatomy of this specialized carnivoran and the exploration of ontogenetic and sex dif-

ferences. Very few changes were detected after birth on the internal anatomy of the auditory region, between both sexes and age classes. However, significant differences between age classes were found in bone thickness, resulting from the apposition of new annual layers. Furthermore, there are possible sex-related external morphology differences among age classes that show significant shape differences in CIII. The external morphology observed in neonates is conserved across all individuals from C1 (including specimens up to 1 year old); however, morphological differences were observed between them, on one hand, and CII individuals plus CIII females on the other, and the CIII males showed the greatest morphological change, with respect to all the individuals regardless of age class or sex.

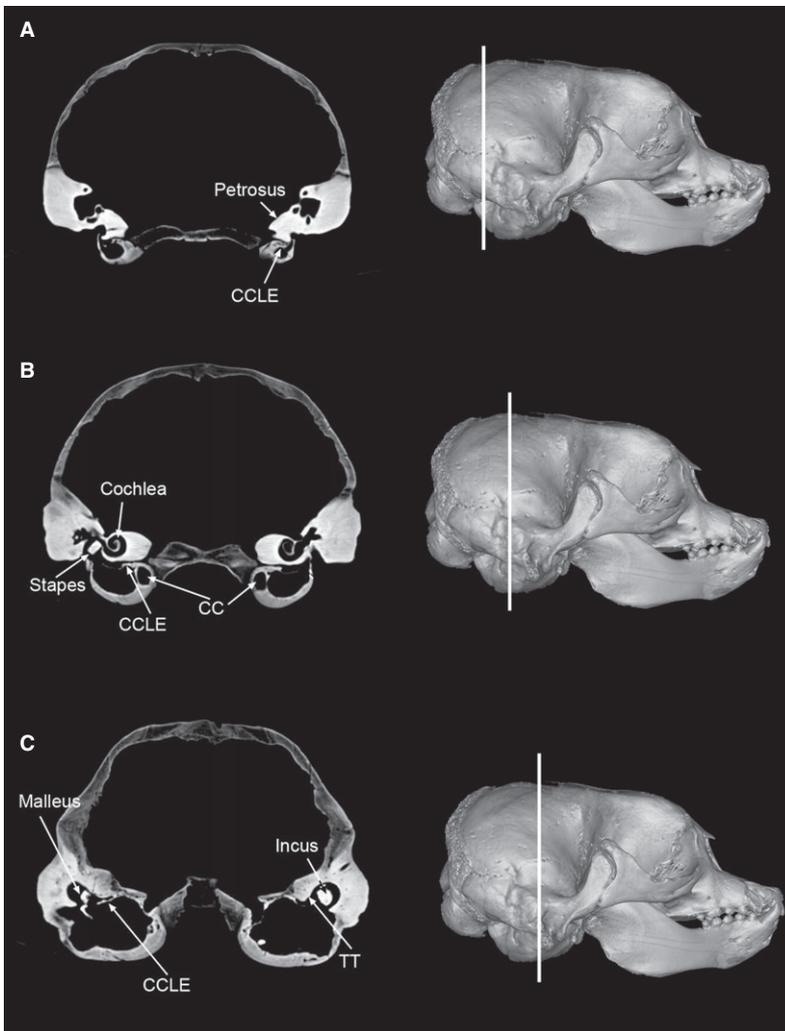


Fig. 9 Three consecutive TS views from CAT of *Mirounga leonina*, in postero-anterior sequence, from a CAT, showing variation in extension of the *paries tegmentalis* along the bulla and gradual reduction of the tympanic cavity. (A) Caudal TS, showing the petrosal excluded from the tympanic bullar roof, which is completely formed by the CCLE, and tympanic cavity restricted to a small space. (B) Middle TS, showing a bigger tympanic cavity, with a visible *tegmen tympani* (TT), and lateral extension of the *canalis caroticus* (CCLE). (C) Anterior TS, showing a large cavity, *recessus epitympanicus* that contains the *malleus* and *incus* (both large), and *tegmen tympani* (TT), associated to the lateral extension of the *canalis caroticus* (CCLE). Skulls in lateral view show the precise line of each TS.

Most foramina of the tympanic-basiscranial region of *M. leonina* are relatively smaller in adult males than in adult females in relation to skull length. In turn, the foramina of females are similar in relative size to those of *Leptonychotes* and *Lobodon*, but generally larger in relative size than in *Hydrurga* and generally smaller compared with *Ommatophoca*. The relative size of these foramina in *Phoca* is heterogeneous (Table 1).

The MAE is clearly evident in all age classes and both sexes. Although its outline may vary in shape between CIII males and females, this may be related to sex differences in growth patterns.

The STA is a large foramen in all classes and both sexes, probably in relation to the need to compensate for differential pressures at great depths, as this foramen is continuous with the Eustachian tube.

The CCAF and CCPF in all specimens examined are large and associated to the carotid ramus that brings blood to the encephalon and inner ear; their size could be related to the physiology of diving and the need for large volumes of

blood to be transported to avoid collapse of the circulatory system.

The FPG is absent or very reduced (probably due to the expansion of the post-glenoid process onto the tympanic bulla) and this has led to the assumption that the cephalic jugular drainage must follow a different path to ensure efficient venous return.

The large size of the foramina can be observed from early ages (CI); this could be associated to the short duration of nursing and parental dependence prior to their first independent feeding season. The foramina are also large in CII males and females and in CIII females. In contrast, in males the foramina are relatively smaller after sexual maturation (CIII males).

All preceding observations about the relative size of foramina were made with respect to skull length; the results are slightly different if the bimastoid width or tympanic width are used as reference. Nevertheless, in this case, again the foramina of *M. leonina* males (CIII) are relatively smaller than those of females (CIII), in accordance with the change

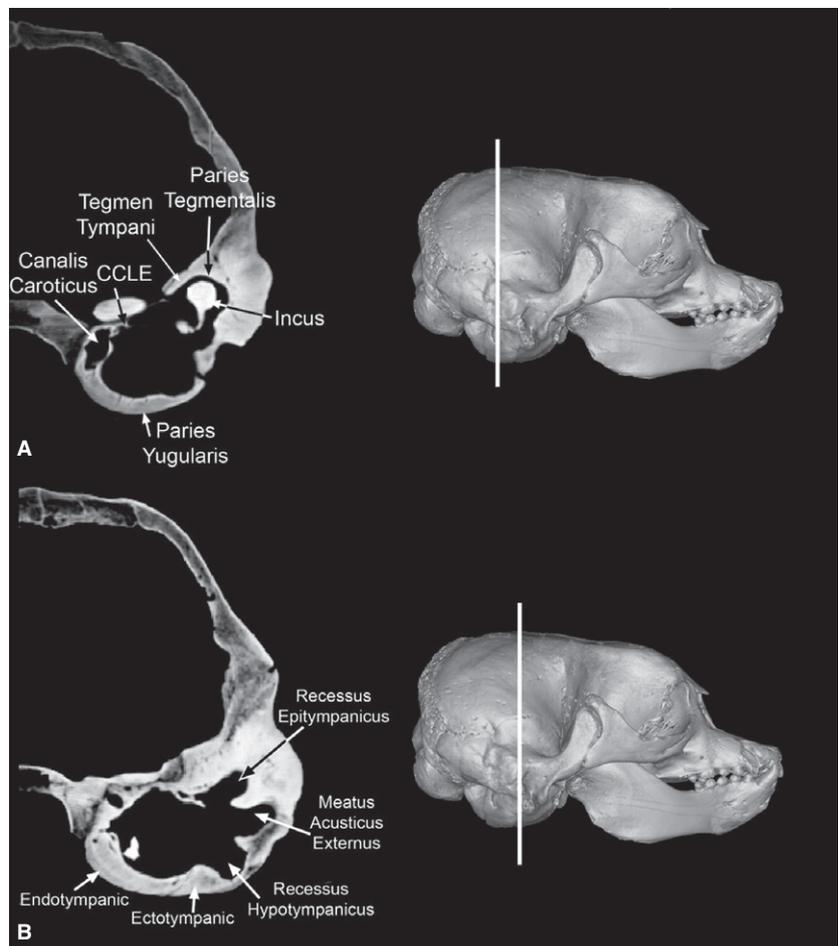


Fig. 10 Two consecutive TS views from CAT of auditory region of *Mirounga leonina* showing the *paries* that limit the tympanic cavity. (A) View of posterior TS. (B) View of more anterior TS. Skulls in lateral view show the precise line of each TS.

in male morphology associated to sexual maturity in a conspicuously dimorphic species. Also, the relative sizes of foramina in *M. leonina* females are similar to those of *Ommatophoca*, *Leptonychotes*, *Phoca*, and *Lobodon*, but *Hydrurga* consistently has the smallest foramina (Fig. 7; Table 1).

Finally, the homology of the FA is uncertain; it could either correspond to the vagal foramen or alternatively it could represent a deviation of the FSM, given that the FA is associated to the latter in all observed cases.

The large size of the apophyses and processes (e.g. PPO and PM together with the lambdoidal ridge of the skull) in CIII individuals is likely associated to the attachment of neck and mandibular muscles. The angle of JA changes as a consequence of the direction of growth of the ectotympanic, which becomes increasingly more perpendicular with respect to the sagittal axis (Fig. 6).

As stated above, the internal anatomy of the auditory region does not show great differences between sexes or age classes; however, bullar volume appears to decrease and some ducts increase in length and diameter (e.g. MAE, STA), surely as a consequence of the skull growth pattern of this species. The greatest differences between age classes

are related to bone thickness resulting from the apposition of new layers year after year.

The results of the Procrustes ANOVA show significant shape differences between sexes and age classes. Although the interaction term (sex : classes) is marginally non-statistically significant (P -value ~ 0.08), an examination of possible sex differences within age classes shows that there are significant shape differences between males and females in CIII. This is partly consistent with Mitteroecker et al.'s (2004) findings, in which individuals were rather similar in early ontogeny and subsequently diverged in adult morphology.

The shape observed in neonates was the same as that of individuals in CI, a result that is quite striking because these two classes differ markedly in size and because newborn pups suckle milk, whereas CI individuals have already spent a season feeding independently from their mothers. No statistically significant differences in tympanic-basiscranial structure were found in CI; all individuals were characterized by a markedly globose bulla without well developed apophyses or processes; the endo-/ectotympanic suture was visible in some specimens; bones presented a spongy or porous structure, and the bullar wall was thin because its thickness increases due to consecutive deposition of annual

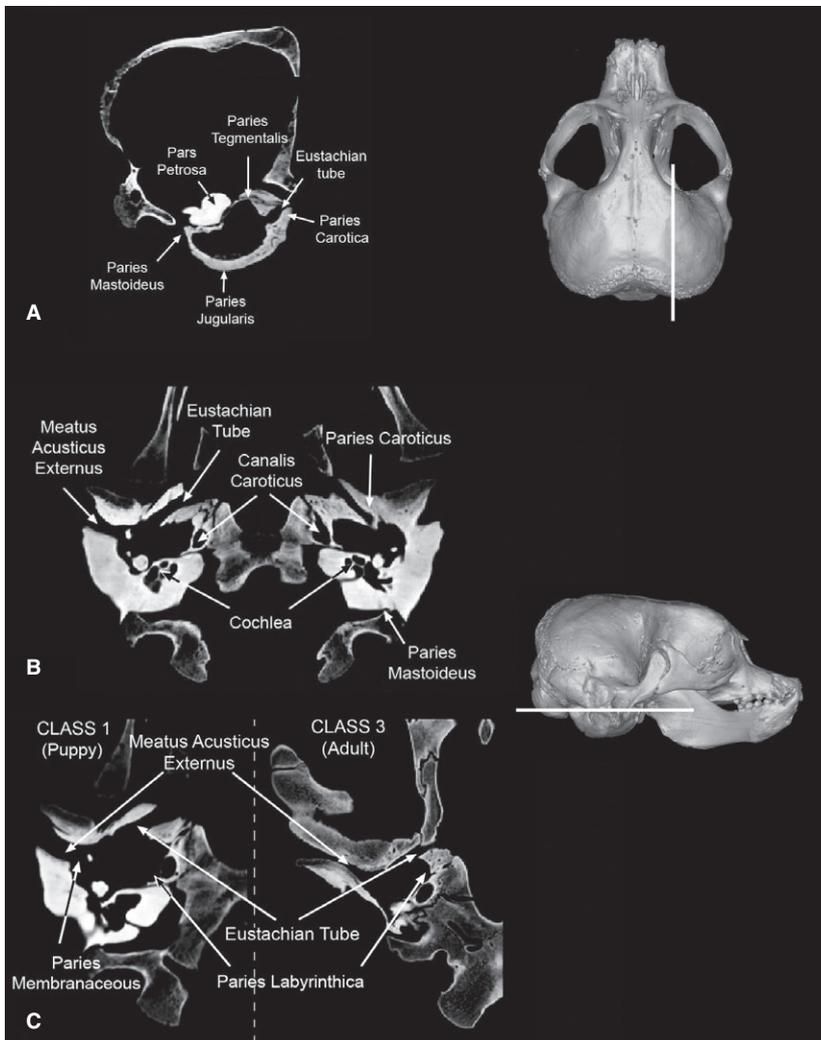


Fig. 11 Three views from CAT of auditory region of *Mirounga leonina* showing the *paries* that limit the tympanic cavity. (A) View of a lateral, parasagittal section. (B) View of section through a ventral horizontal plane. (C) View of section through ventral horizontal plane comparing two specimens of different age classes CI (to the left) and CIII (to the right), showing the difference in relative development of the *meatus acusticus externus* and the Eustachian tube, as well as different internal morphology of the bulla. Skulls in dorsal and lateral view show the precise line of each section.

layers (Fig. 16). The specimens that were subjected to CAT showed agreement as to their age as determined from bullar growth lines and the absolute age determined *a priori* from tooth sections.

CII specimens showed relatively less development of the ectotympanic and more compact bone structure than CI specimens. CII specimens of both sexes did not differ greatly from CIII females regarding bullar morphology. Furthermore, CII individuals already presented most of the characteristics observed in CIII specimens. Thus, there are clear morphological differences between CI individuals on one hand, and CII individuals plus CIII females on the other. Some of the most noticeable differences are the smaller size of the ectotympanic relative to the endotympanic, the formation (and growth) of rugosities on the ectotympanic surface, clear development of a more triangular outline, and distal growth of the retroarticular process (PR) of the glenoid cavity (CG), which becomes more posterior and vertical. Likewise, as a result of the mesio-distal growth of the CG, the latter ends up resting on the anterior surface of the

bulla, partially compressing it; this condition reaches its maximum expression in CIII males.

Females attain the definitive shape and size of the bulla at earlier stages of ontogeny compared with males, in agreement with their earlier involvement in reproductive activities. Thus, the bullar morphology of females is similar in all age classes; this could be related to the depths reached when diving in search of food (Boyd & Arnborn, 1991; Campagna & Lewis, 1992; Hindell & Bryden, 1992; McConnell et al. 1992, 2002; Campagna et al. 1993, 1995, 1998, 1999, 2000, 2007; Jonker & Bester, 1998; Hindell et al. 1999; Lewis et al. 2006; Field et al. 2007; Eder et al. 2010; McIntyre et al. 2010a,b). CIII males showed the greatest morphological differences, with respect to both CI and CII individuals and CIII females. CIII males dive to the greatest depths recorded so far for the species, more than 2000 m deep, whereas females and CII males have not been recorded below 1500 m depth, and CI individuals (males and females) make short shallow dives, reaching ca. 100 m depth (McIntyre et al. 2010a).

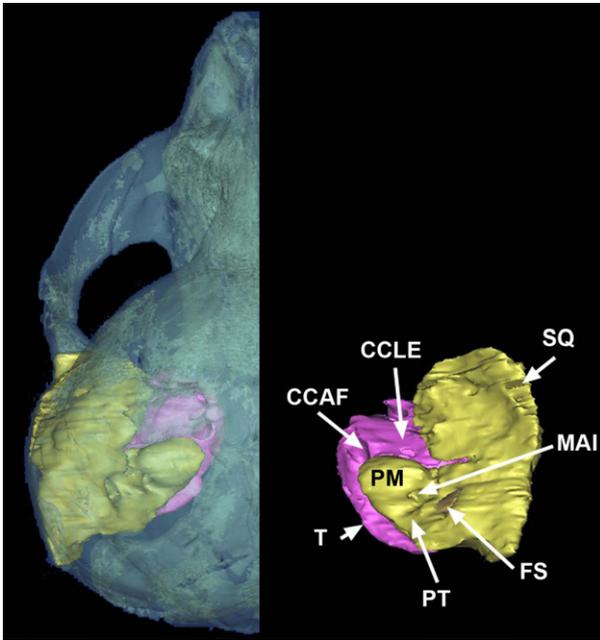


Fig. 12 3D reconstruction of a skull of a dorsal view of *Mirounga leonina* with left auditory region, and detail of right auditory region, showing the tympanic bulla (pink) and the petrosal fused to the squamosal (yellow). CCAF, foramen of the *canalis caroticus* anterior; CCLE, lateral extension of the *canalis caroticus*; FS, *fossa subarcuata*; MAI, *meatus acusticus internus*; PM, *promontorium*; PT, petrosal; SQ, squamosal; T, tympanic.

The morphological differences between the bullae of males and females could be related to the different behavior of the sexes during the breeding season, too. Whereas females must be able to recognize the call of their pup in the harem (at short range), males participate in agonistic

interactions, for which the recognition of vocalizations emitted by other males at greater distances is essential. In addition, males engage in intraspecific combats, during which the posterolateral region of the skull is hit quite often.

Mirounga leonina did not show remarkable differences compared with specimens of its sister species from the Northern Hemisphere, *M. angustirostris* (USNM 260867 and USNM- A21890), and compared with a CAT from the Digimorph.org website (MVZ 184140), in either its internal or external morphology and proportions, despite the larger size of *M. leonina*. Moreover, if the values for the *M. angustirostris* female are included in the morphometric analysis and PCA, the specimen falls within the CI–CII range.

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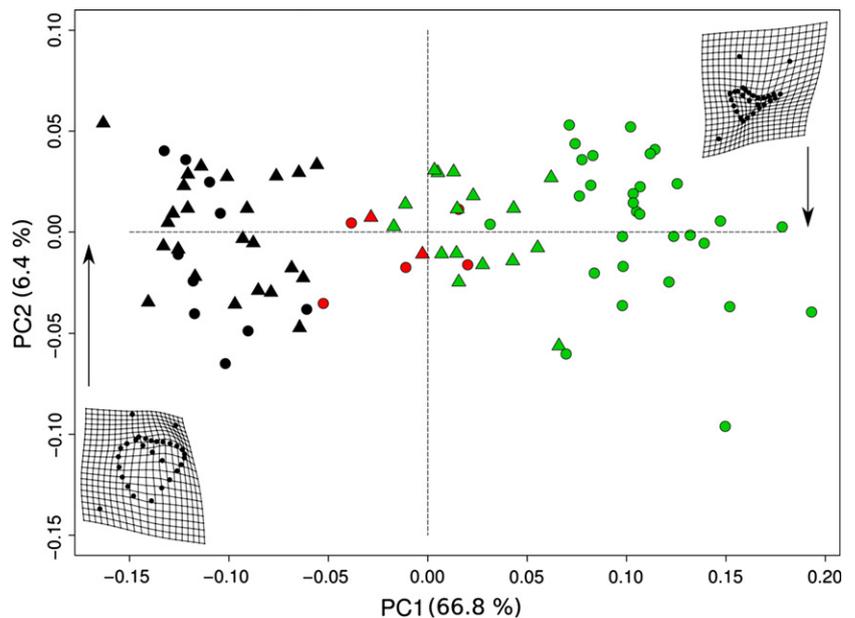


Fig. 13 Principal components analysis of shape variables in tangent space showing shape variation. Deformation grids display the shape of specimens of *Mirounga leonina* at the ends of the range of variability along PC1. Black, CI. Red, CII. Green, CIII. Circles correspond to males and triangles to females.

Table 2 Table listing results of statistical analyses on the *Mirounga leonina* specimens. For further details, see Materials and methods.

| Factor | df | SS.obs | MS | F | P-value | R ² |
|-------------|----|--------|-------|--------|---------------|----------------|
| Sex | 1 | 0.208 | 0.208 | 38.530 | 0.0001 | 0.1746 |
| Stage | 2 | 0.495 | 0.247 | 45.672 | 0.0001 | 0.4140 |
| Sex : Stage | 2 | 0.052 | 0.026 | 4.878 | 0.0891 | 0.0442 |

df, degrees of freedom; F, F ratio; MS, mean squares; SS, sum of square. P-value in bold.

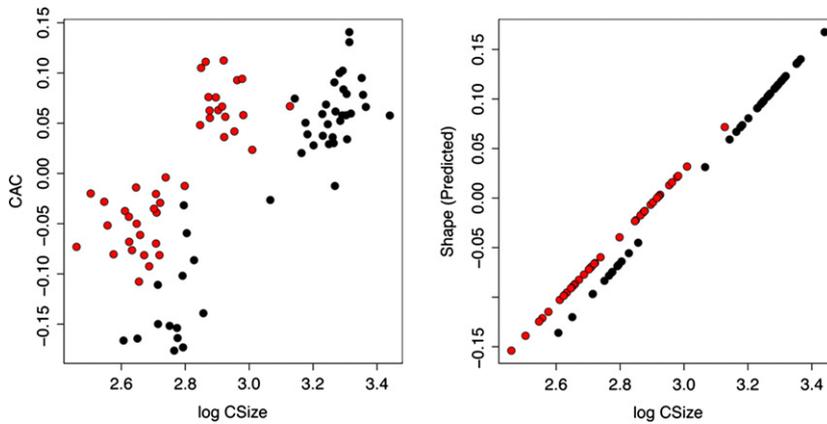


Fig. 14 Allometric trends of males and females of *Mirounga leonina* showing the multivariate relationship between size and shape. (A) The common allometric component (CAC) vs. size (log centroid size). (B) Stylized trend following Adams & Nistri (2010). Black, CI. Red, CII. Green, CIII. Circles correspond to males and triangles to females.

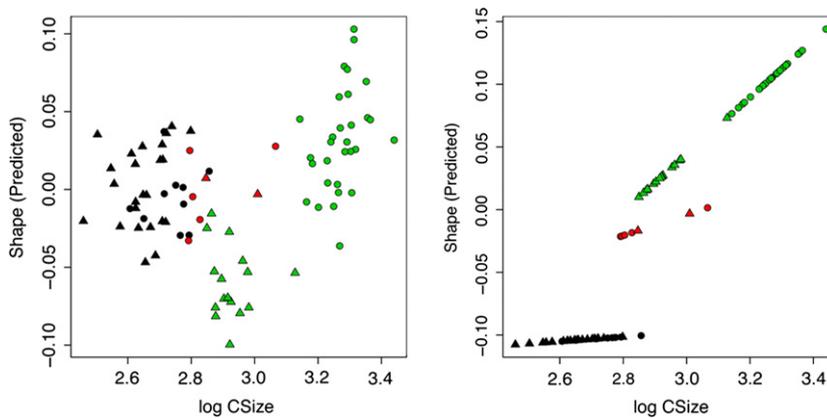


Fig. 15 Allometric trends of different age stages of *Mirounga leonina* showing the multivariate relationship between size and shape. (A) The common allometric component (CAC) vs. size (log centroid size). (b) Stylized trend following Adams & Nistri (2010). Black, CI. Red, CII. Green, CIII. Circles correspond to males and triangles to females.



Fig. 16 Four views from CAT of auditory region of *Mirounga leonina* showing the bone thickness resulting from the apposition of new layers year after year. (A) CI with no lines of growing, (B) CII with one line, (C) CII with three lines, (D) CIII with at least five lines.

scientific research in Antarctica, and was one of the fundamental pillars for the development of this and many other projects.

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Appendix 1 Specimens of *Mirounga leonina* examined in this study

| | Collection number | Sex | Age class | BL |
|----|-------------------|-----|-----------|--------|
| 1 | MACN 20608* | M | CIII | 89.88 |
| 2 | MACN 24.91* | M | CIII | 104.53 |
| 3 | MACN 13.26* | M | CIII | 107.76 |
| 4 | MACN 24.93* | M | CIII | 88.33 |
| 5 | MACN 24.49 | M | CIII | 92.48 |
| 6 | MACN 24.92* | M | CIII | 90.65 |
| 7 | MACN 22611* | F | CIII | 63.57 |
| 8 | MACN 26222* | M | CII | 63.18 |
| 9 | MACN 22614* | F | CIII | 70.45 |
| 10 | MACN 22612* | F | CIII | 73.48 |
| 11 | MACN 22613* | F | CIII | 69.32 |
| 12 | MACN 49.52* | F | CI | 60.31 |
| 13 | MACN 22615* | F | CI | 48.66 |
| 14 | MLP 947* | M | CIII | 109.63 |
| 15 | MLP 26.IV.00.13* | M | CII | 109.81 |
| 16 | MLP 1504* | M | CIII | 95.59 |
| 17 | MLP 14.IV.48.13 | M | CI | 57.15 |
| 18 | MLP 1966* | F | CI | 51.4 |
| 19 | MLP 1971* | F | CI | 49.49 |
| 20 | FMM 107 | M | CIII | 99.77 |
| 21 | FMM 109* | M | CIII | 80.01 |
| 22 | IAA AA-A* | F | CIII | 70.46 |
| 23 | IAA AA-B* | M | CI | 58.86 |
| 24 | IAA AA-C* | M | CI | 59.49 |
| 25 | IAA AA-7* | F | CI | 55.97 |
| 26 | IAA AA-6* | M | CI | 58.21 |
| 27 | IAA AA-8* | F | CI | 50.88 |
| 28 | IAA AA-2* | M | CI | 52.89 |
| 29 | IAA AA-11* | F | CI | 57.5 |
| 30 | IAA AA-10* | F | CI | 52.53 |
| 31 | IAA AA-9* | F | CI | 56.5 |
| 33 | IAA 02.14* | M | CI | 58.09 |
| 34 | IAA 02.19* | M | CI | 61.6 |
| 35 | IAA 02.25* | F | CI | 50.23 |
| 36 | IAA 02.18 | M | CI | 59.38 |
| 37 | IAA 02.30* | M | CI | 57.44 |
| 38 | IAA 02.28* | F | CI | 59.03 |
| 39 | IAA 02.22* | M | CI | 59.98 |
| 40 | IAA 02.29* | F | CI | 55.11 |
| 41 | IAA 02.20* | F | CI | 59.34 |
| 42 | IAA 02.26* | M | CI | 58.16 |
| 43 | IAA 02.23* | F | CI | 55.21 |
| 44 | IAA 02.24* | F | CI | 58.68 |
| 45 | IAA 02.17* | F | CI | 51.54 |
| 46 | IAA 02.21* | M | CI | 62.61 |

Appendix 1. (continued)

| | Collection number | Sex | Age class | BL |
|----|-------------------|-----|-----------|--------|
| 47 | IAA 02.12* | M | CIII | 78.92 |
| 48 | IAA 99.5* | M | CIII | 108.8 |
| 49 | IAA 00.8* | M | CIII | 112.43 |
| 50 | IAA 03.5* | F | CIII | 73.91 |
| 51 | IAA 03.4* | F | CIII | 73.55 |
| 52 | IAA 96.1* | F | CIII | 70.92 |
| 53 | IAA 00.9* | F | CIII | 70.34 |
| 54 | IAA 01.14* | F | CI | 44.64 |
| 55 | IAA 02.16* | M | CII | 63.85 |
| 56 | IAA 02.27 | M | CI | 53.52 |
| 57 | LAMAMA ML-25* | F | CII | 79.46 |
| 58 | LAMAMA CNP-105* | M | CIII | 108.33 |
| 59 | LAMAMA CNP-035* | M | CIII | 106.17 |
| 60 | LAMAMA ML-059* | M | CIII | 105.13 |
| 61 | LAMAMA CNP-102* | M | CIII | 97.91 |
| 62 | LAMAMA CNP-104* | M | CIII | 103.31 |
| 63 | LAMAMA CNP-111* | F | CIII | 73.21 |
| 64 | LAMAMA CNP-109 | M | CII | 64.56 |
| 65 | LAMAMA 103* | M | CIII | 100.12 |
| 66 | LAMAMA CNP-101* | M | CII | 65.06 |
| 67 | LAMAMA CNP-037* | F | CI | 61.98 |
| 68 | LAMAMA CNP-100 | F | CII | 64.54 |
| 69 | LAMAMA ML-32* | M | CIII | 107.43 |
| 70 | LAMAMA ML-34* | M | CIII | 96.92 |
| 71 | LAMAMA ML-28* | M | CIII | 100.55 |
| 72 | LAMAMA ML-35* | F | CIII | 75.94 |
| 73 | LAMAMA ML-36* | F | CI | 53.45 |
| 74 | LAMAMA ML-29 | M | CII | 71.04 |
| 75 | LAMAMA ML-30 | M | CII | 72.8 |
| 76 | LAMAMA ML-33 | F | CI | 42.85 |
| 77 | LAMAMA ML-23 | M | CI | 49.52 |
| 78 | LAMAMA ML-24* | F | CI | 47.43 |
| 79 | LAMAMA ML-26* | F | CI | 59.9 |
| 80 | LAMAMA ML-31* | F | CIII | 73.61 |
| 81 | LAMAMA ML-1* | F | CI | 53.77 |
| 82 | LAMAMA ML-4* | F | CI | 50.51 |
| 83 | LAMAMA ML-3* | M | CII | 71.39 |
| 84 | LAMAMA ML-9 | F | CIII | 74.82 |
| 85 | MHNM 5767* | M | CIII | 111.7 |

Appendix 1. (continued)

| | Collection number | Sex | Age class | BL |
|-----|-------------------|-------|-----------|--------|
| 86 | MHNM 5766* | M | CIII | 105.89 |
| 87 | MHNM 1277* | M | CIII | 104.2 |
| 88 | MHNM 5768* | M | CIII | 99.5 |
| 89 | MHNM S/N* | F | CI | 54.32 |
| 90 | MNHN 1972-647* | M | CIII | 107.72 |
| 91 | MNHN 1971-113* | M | CIII | 103.34 |
| 92 | MNHN 2012-983* | M | CIII | 112.9 |
| 93 | MNHN 1972-652* | M | CII | 82.21 |
| 94 | MNHN 2012-986* | M | CIII | 120.17 |
| 95 | MNHN 1978-347* | F | CIII | 73.85 |
| 96 | MNHN 2012-985* | F | CIII | 70.18 |
| 97 | MNHN 1972-651* | F | CIII | 75.46 |
| 98 | MNHN 1939-449* | M | CIII | 109.33 |
| 99 | MNHN 1972-142* | F | CII | 66.09 |
| 100 | MNHN 1977-20* | M | CIII | 110.8 |
| 101 | IAA AA-14 a | M | CII | n/a |
| 102 | IAA AA-14 b | M | CII | n/a |
| 103 | IAA AA-14 c | M | CII | n/a |
| 104 | IAA AA-14 d | M | CII | n/a |
| 105 | IAA AA-14 e | indet | CI | n/a |
| 106 | IAA AA-14 f | indet | CI | n/a |
| 107 | IAA AA-14 g | indet | CI | n/a |
| 108 | IAA AA-14 h | indet | CI | n/a |
| 109 | IAA AA-14 i | indet | CI | n/a |
| 110 | IAA AA-14 j | indet | CI | n/a |
| 111 | MLP 777-C | indet | CI | n/a |
| 112 | MLP 781-C | indet | CI | n/a |
| 113 | MLP 775-C | indet | CI | n/a |
| 114 | MLP 782-C | M | CIII | n/a |
| 115 | MLP 779-C | indet | CI | n/a |
| 116 | MLP 783-C | F | CIII | n/a |
| 117 | MLP 784-C | indet | CI | n/a |
| 118 | MLP 785-C | indet | CI | n/a |

F, females; M, males; n/a, not available data because of isolated, or partially broken, otic regions.

For museum abbreviations, see Materials and methods.

* Specimens used in the morphometric analyses.