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Evolutionary biology

Sensory anatomy of the most aquatic of carnivorans: the Antarctic Ross seal, and convergences with other mammals

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Transitions to and from aquatic life involve transformations in sensory systems. The Ross seal, *Ommatophoca rossii*, offers the chance to investigate the cranio-sensory anatomy in the most aquatic of all seals. The use of non-invasive computed tomography on specimens of this rare animal reveals, relative to other species of phocids, a reduction in the diameters of the semicircular canals and the parafloccular volume. These features are independent of size effects. These transformations parallel those recorded in cetaceans, but these do not extend to other morphological features such as the reduction in eye muscles and the length of the neck, emphasizing the independence of some traits in convergent evolution to aquatic life.

1. Background

A glimpse of a Ross seal (*Ommatophoca rossii*) on an ice floe in the Antarctic summer, with its short flippers and thick neck, is vaguely whale-like, hinting at the eight months of the year it spends exclusively at sea [1,2]. Spending months at sea distinguishes this animal from the other three earless Lobodontini seals: the crabeater seal, leopard seal and Weddell seal. Ross seals leave the water for only two weeks to give birth and moult and have unarguable external specializations for their extreme aquatic lifestyle [3]. Until now, scarce sampling of these rare animals has inhibited further exploration of their internal anatomical specializations [3]. As species specialize for aquatic habitats, their sensory organs undergo major transitions, recorded for other carnivoran mammals besides the Ross seal [4]. Comparisons with groups that independently invaded marine environments, such as cetaceans (whales and dolphins) [5], provide insights on evolutionary convergences, even at the genomic level [6].

Specializations for aquatic habitats are reflected in vestibular anatomy, a complex area of the head that can be studied using virtual endocasts. Such endocranial volumes approximate the soft tissue morphology (e.g. ducts, vessels and nerves), and thus provide information useful to reconstruct sensory ecology, locomotion, behaviour and phylogeny [7,8]. Although the function of changes in the vestibular system—concerned with balance, orientation and motion sensation—in aquatic vertebrates are debated [9], reductions in marine vertebrates' semicircular canals have been associated with increased time in the water but not with axial body rotations [10]. The canals of the bony labyrinth of aquatic taxa are recorded to be shorter dorsoventrally and more elongate rostro-caudally than in terrestrial relatives [11]. Smaller semicircular canals may be related to reduced neck lengths [9]. Furthermore, the volume of the dorsal paraflocculus, a lobe of the cerebellum associated with the vestibular system,

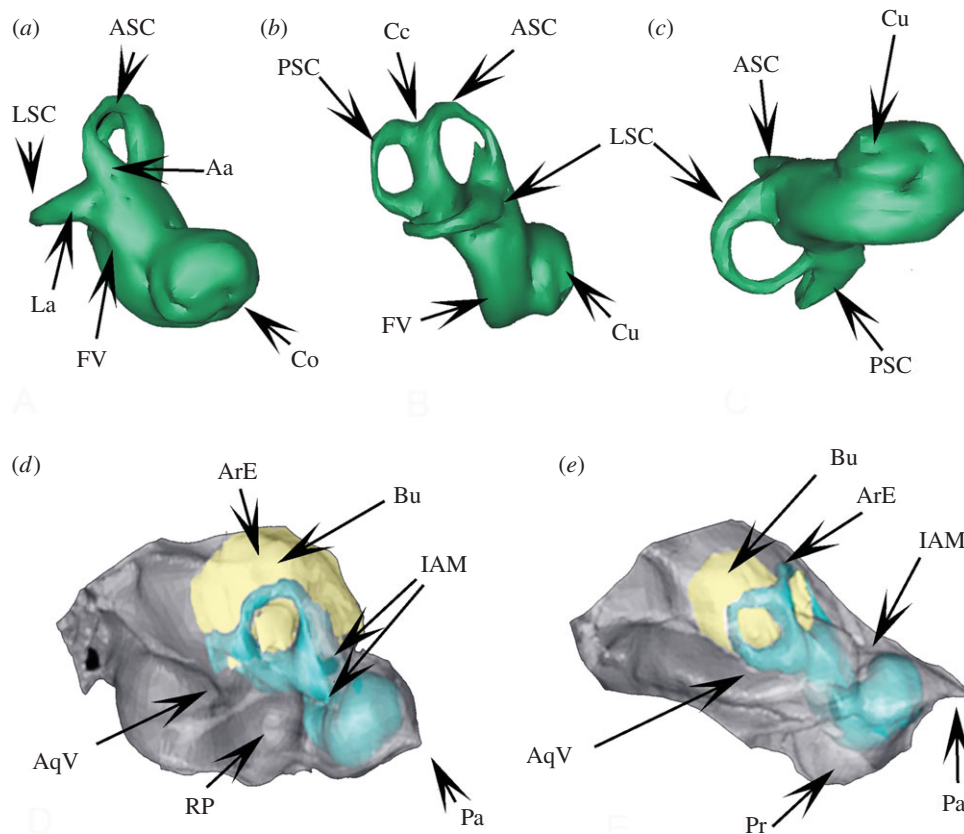


Figure 1. Virtual reconstruction of the right inner ear of the Ross seal, *Ommatophoca rossii* MACN 48.259 in isolation and within the petrosal bone: (a) anterior, (b) lateral, and (c) ventral view, and with the parafoveolus in (d) dorsal, and (e) medial views. Aa: anterior ampulla; AqV: vestibular aqueduct; ASC: anterior semicircular canal; Bu: subarcuate fossa housing the dorsal lobe of the parafoveolus; Cc: common crus; Cu: cupula; Co: cochlear canal; ArE: arched eminence; FV: vestibular fenestra; IAM: internal acoustic meatus; La: lateral ampulla; LSC: lateral semicircular canal; RP: Ross prominence; Pa: petrosal apex; Pr: promontorium; PSC: posterior semicircular canal.

is also reduced given its relation to agility and coordination of movements using vision and balance [12,13].

2. Methods

A list of museum sources and accession numbers of specimens examined is provided in the electronic supplementary material. A total of 68 petrosal bones from six species of phocids were investigated. All four members of the Lobodontini were sampled: two specimens of the Ross seal (an adult female MACN 48.259 and a newborn MACN 48.260), seven leopard seals (*Hydrurga leptonyx*), 11 Weddell seals (*Leptonychotes weddellii*) and 15 crabeater seals (*Lobodon carcinophagus*). The extant phylogenetic bracket is represented by 30 elephant seals (*Mirounga leonina*), one harbour seal (*Phoca vitulina*), one walrus (*Odobenus rosmarus*), one South American sea lion (*Otaria byronia*; Otariidae), a Tibetan wolf (*Canis lupus filchneri*), a hyena (*Crocuta crocuta*), and a sea otter (*Enhydra lutris*) (electronic supplementary material). We compiled body length data from the literature [14]. Statistics and graphs were generated using R [15]. We reconstructed the bony labyrinth and the petrosal in three-dimensional CT scans using VGStudio MAX v. 2.2, Mimics v. 10.1 and Avizo v. 6.2 (figure 1; electronic supplementary material).

We measured the volume of the subarcuate fossae, which houses the dorsal cerebellar parafoveolus, also called the dorsal portion of the petrosal lobe. Histological preparations confirmed the correspondence of the two structures (electronic supplementary material). The three-dimensional models are available at (<http://morphomuseum.com/>).

3. Results

The Lobodontini, in order of largest to smallest arc radius of the loops of the semicircular canals and common crus, are

leopard seals, crabeater seals, Weddell seals and Ross seals. The maximum diameter of each of the three semicircular canals and the length of the common crus of the Ross seal are significantly shorter than in other Phocidae (Welch *t*-test Ross seal = 0.7003617, other seals = 1.03011095, $t = -6.9386$, d.f. = 6.5762, $p = 0.0002965$; graph 1 in electronic supplementary material). Elephant seals exhibit less reduction of the semicircular canals versus the Lobodontini. In all Phocidae the horizontal canal is consistently the shortest and the anterior canal the longest.

A comparison of the Ross seal with other phocids also reveals reduced parafoveolus volume with a simpler shape (figure 2). This difference persists after correction for body mass; a linear regression of the ratio of the parafoveolus volume to the natural log average mass for the species still results in significant differences (*t*-test $p = 0.03073$; electronic supplementary material). The parafoveoli of the other Lobodontini, besides being larger, have several individual digitiform projections extending around the horizontal semicircular canal, absent in the Ross seal (figure 2). The endocast of the subarcuate fossa of the Ross seal clearly exhibits less surface rugosity as well as greater simplicity and roundness.

The Ross seal has a double internal acoustic foramen, common to all phocids. The cochlea has two and a half turns, similar to the other Lobodontini, but it ends in a poorly demarcated cupula (figure 1). Additionally, Lobodontini and phocids have fewer cochlear turns than mustelids [17].

The Ross seal shares features characteristic of Cetacea that are absent in other lobodontines: a reduced parafoveolus volume and lack of surface projections. Both also share a secondary basal lamina on the first turn of cochlea [18,19] that is

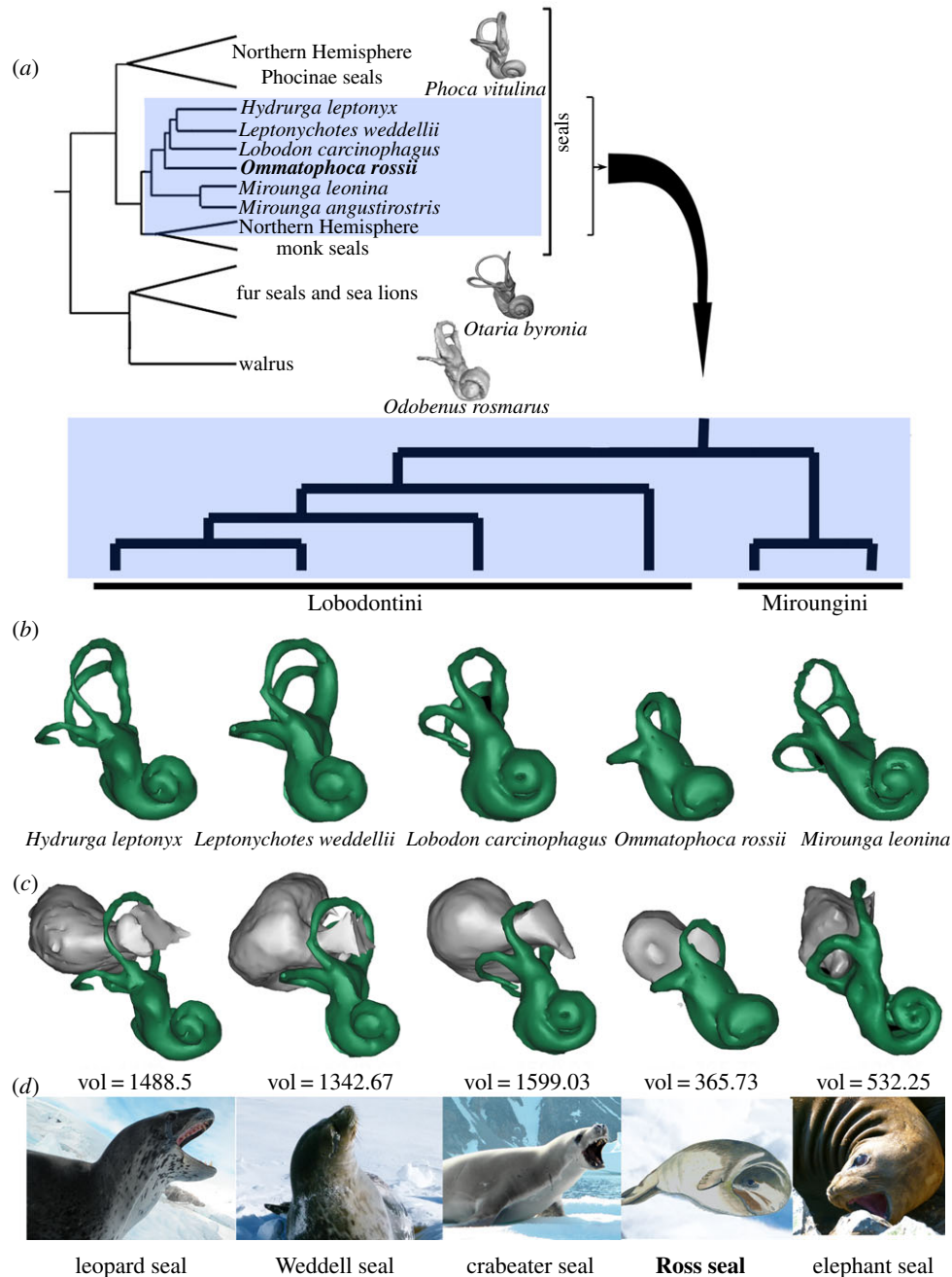


Figure 2. Three-dimensional models of relative labyrinth and parafloccular volume among the Antarctic true seals (Lobodontini) in the context of the phylogenetic relationships among pinniped carnivorans [16]. Photographs by C. M. Loza, drawing of the Ross seal by A. E. Latimer.

antero-ventral to the rest of the labyrinth, and is separated from the rest of the coil. An extremely thick squamosal portion of the temporal bone is present in Ross seals and cetaceans [3]. Likewise is a thickening of the anterior half of the petrosal which develops a rostral projection, a reduced arcuate eminence (probably due to the small size of the anterior semicircular canal), and an expanded medial side, as in some cetaceans [8]; see also electronic supplementary material. In the Ross seal the vestibular fenestra is visible on the lateral face of the vestibule, and the vestibule is smaller and more globular than in other species of phocids. Further anatomical comparisons are in the electronic supplementary material.

4. Discussion

The exceptionally aquatic lifestyle of the Ross seal among carnivorous mammals is reflected in anatomical specializations

that are hypothesized to be related to sensory function and which in some cases are similar to those recorded in whales. The semicircular canals of the Ross seal exhibit an extreme size reduction among phocids, as recorded also for cetaceans within Cetartiodactyla. This similarity does not extend to all other aspects of inner ear anatomy and correlated anatomical features.

Neck mobility and neck length have been proposed to affect the morphology of semicircular canals. Reduced vertebral mobility restricts the degrees of freedom of the neck, and the semicircular canals reduce in size accordingly [9]. In pinnipeds, otarids have thinner canals and longer necks than phocids [20,21] and exhibit more neck mobility both during swimming and while moving on land [21]. However, among phocids including the Ross seal, correlation between the parallel reduction of the semicircular canals and neck length is not straightforward (electronic supplementary

material), and neck mobility may play a larger role. Among phocids, leopard seals have the longest neck and practice wide three-dimensional movements of the head, the fastest and most precise of which are related to prey capture [21–23]. Its large semicircular canals contrast with the reduction in the Ross seal.

Lobodontini have thick semicircular canals and ducts, as is characteristic of seals, but different from other aquatic mammals, e.g. sea lions, with thinner canals [20]. The semicircular canals in the Ross seal are smaller in radius than in other phocids, but larger than canals in cetaceans.

The Ross seal has a proportionally reduced paraflocculus with respect to other phocids; the simplicity of the paraflocculus and the semicircular canal may be coupled functionally, as is hypothesized for cetaceans. Not all the features of the Ross seal are consistent with whale anatomy. Reduced semicircular canals in cetaceans have been linked with a reduced need for the vestibulo-ocular reflex with reduction of extra-ocular muscles [24,25]. Ross seals, in contrast, have well developed ocular musculature and large eyes, and likely rely on vision for prey capture. The mechanism for the reduced

paraflocculus and semicircular canals therefore cannot be coupled solely on the musculature of the eyes.

Ethics. No special permission was needed to use the existing collections of skulls and histological materials in the museums visited, other than the agreement of the curators listed in the Acknowledgements.

Data accessibility. All specimens studied are in existing osteological and anatomical collections of universities. Data can be accessed at: <http://morphomuseum.com/>

Authors' contributions. All authors conceived the study, conducted analyses, contributed to interpretation of the data and preparation of the manuscript, approved the final version of the manuscript and agree to be held accountable for the content therein.

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