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ORIGINAL RESEARCH

Olfaction at depth: Cribriform plate size declines with dive depth and duration in aquatic arctoid carnivorans

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Abstract

It is widely accepted that obligate aquatic mammals, specifically toothed whales, rely relatively little on olfaction. There is less agreement about the importance of smell among aquatic mammals with residual ties to land, such as pinnipeds and sea otters. Field observations of marine carnivorans stress their keen use of smell while on land or pack ice. Yet, one dimension of olfactory ecology is often overlooked: while underwater, aquatic carnivorans forage “noseblind,” diving with nares closed, removed from airborne chemical cues. For this reason, we predicted marine carnivorans would have reduced olfactory anatomy relative to closely related terrestrial carnivorans. Moreover, because species that dive deeper and longer forage farther removed from surface scent cues, we predicted further reductions in their olfactory anatomy. To test these hypotheses, we looked to the cribriform plate (CP), a perforated bone in the posterior nasal chamber of mammals that serves as the only passageway for olfactory nerves crossing from the periphery to the olfactory bulb and thus covaries in size with relative olfactory innervation. Using CT scans and digital quantification, we compared CP morphology across Arctoidea, a clade at the interface of terrestrial and aquatic ecologies. We found that aquatic carnivoran species from two lineages that independently reinvaded marine environments (Pinnipedia and Mustelidae), have significantly reduced relative CP than terrestrial species. Furthermore, within these aquatic lineages, diving depth and duration were strongly correlated with CP loss, and the most extreme divers, elephant seals, displayed the greatest reductions. These observations suggest that CP reduction in carnivorans is an adaptive response to shifting selection pressures during secondary invasion of marine environments, particularly to foraging at great depths. Because the CP is fairly well preserved in the fossil record, using methods presented here to quantify CP morphology in extinct species could further clarify evolutionary patterns of olfactory loss across aquatic mammal lineages that have independently committed to life in water.

KEYWORDS

aquatic adaptations, cribriform plate, diving behavioral ecology, marine mammals, olfaction, skull morphology

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1 | INTRODUCTION

Mammals rely on their sense of smell to varying degrees and their olfactory systems have evolved to operate in distinct ecological contexts. As lineages, foraging landscapes, and chemical stimuli change over evolutionary time, species acquire and lose olfactory capacities (Gittleman, 2013; Hayden et al., 2010; Van Valkenburgh et al., 2011). For example, it is widely accepted that obligate aquatic mammals such as odontocete cetaceans, and to a lesser extent mysticetes, have lost some degree of olfactory anatomy, genes and behaviors relative to their living terrestrial relatives and ancestors (Kishida, Thewissen, Hayakawa, Imai, & Agata, 2015; Liu et al., 2019; Oelschläger, 1992; Oelschläger & Buhl, 1985). There is less agreement on the relative role smell plays in the life of aquatic mammals with residual ties to the land, such as marine arctoid carnivorans, the pinnipeds (seals, sea lions, and walrus) and sea otter (*Enhydra lutris*). Some studies (Harrison & Kooyman, 1968; Van Valkenburgh et al., 2011) have suggested that the olfactory apparatus of pinnipeds is generally reduced relative to their terrestrial carnivoran relatives, while another study found no significant difference (Pihlström, 2008). Support for a keen sense of smell in pinnipeds and sea otters comes from field observations of scent-driven behaviors, such as nose-to-nose nuzzling, genital sniffing, alarm responses to upwind biologists, and aversive reactions to con-specific carcass odors (Lowell & Flanigan, 1980; Peterson & Bartholomew, 1967; Riedman & Estes, 1990; Ross, 1970), all of which are also observed in terrestrial carnivorans. However, there is one olfactory dimension missing from this discussion. Unlike terrestrial species, aquatic carnivorans capture prey exclusively underwater and do so “noseblind.” With nostrils closed, diving mammals are shut off from all chemical cues except those they detect at the surface (Reidenberg, 2007; Riedman & Estes, 1990). It is thought that foraging pinnipeds use surface odors, such as dimethyl sulfide (DMS), to locate areas of high marine productivity in the same way mysticete whales and sea birds do (Bouchard et al., 2019; Kowalewsky, Dambach, Mauck, & Dehnhardt, 2006; Nevitt, 1999); however, once underwater, these diving carnivorans can no longer use the landscape of chemical cues relied on by terrestrial species to locate and capture prey (Smith, 1980; Ylönen, Sundell, Tiilikainen, Eccard, & Horne, 2003). For this reason, we pose a first, general hypothesis that aquatic carnivorans rely less on olfaction than closely related terrestrial species and predict that this will be manifested in reduced olfactory anatomy.

Secondly, dietary regimes vary widely across aquatic carnivorans and include pelagic and mesopelagic cephalopods and fish, benthic invertebrates, coastal zooplankton, penguins, and pinniped pups, among others (Bowen & Siniff, 1999; Pauly, Trites, Capuli, & Christensen, 1998). Coupled with this ecological diversity, pinnipeds and sea otters have evolved a wide range of diving behaviors, both the depth at which they pursue prey and the length of time spent diving (Ponganis, 2011; Schreer & Kovacs, 1997). For example, sea otters' dives average ca. 12 meters and last a little over a minute (Bodkin, Esslinger, & Monson, 2004; Tinker, Costa, Estes, & Wieringa, 2007), while northern elephant seals' dives average over

500 meters and can last up to two hours (DeLong & Stewart, 1991; Robinson et al., 2012). We hypothesize that this diversity in diving behavior influences olfactory capacity for two reasons. First, because deeper and more extended dives remove underwater foragers from informative surface odorant cues that might be present at a dive's initiation site (Davis, Fuiman, Williams, Horning, & Hagey, 2003; Davis, Fuiman, Williams, & Le Boeuf, 2001; Harcourt, Hindell, & Bell, 2000), we hypothesize that among aquatic carnivorans, selection for keen olfactory performance is further reduced in more extreme divers. Additionally, cranial adaptations to the challenges of diving in low light (Welsch et al., 2001) under fluctuating pressure (Kooyman, 1973) include enlarged orbits and the reduction of air-filled skull cavities (Curtis, Lai, Wei, & Van Valkenburgh, 2015; King, 1983). These aquatic specializations likely constrain the space available for olfactory structures and tend to be more extreme in species that dive deeper (Debey & Pyenson, 2013). Consequently, we predict that within the aquatic carnivorans, reductions in olfactory anatomy will be inversely related to diving depth and duration.

Previous work on nasal turbinals in carnivorans suggested that aquatic species had reduced olfactory turbinal surface areas relative to their terrestrial relatives (Van Valkenburgh et al., 2011). However, only five aquatic species were sampled, making this conclusion tentative, and the authors did not examine any correlations with diving behavior. To further test the impact of aquatic foraging on olfactory anatomy, we expanded the number of aquatic species sampled to 19 and examined a different metric of olfactory anatomy, the area of the cribriform plate (CP). The CP is a bone in the posterior nasal cavity of mammals that is perforated with passageways for olfactory nerve bundles crossing from the periphery to the olfactory bulb of the brain (Negus, 1958) (Figure 1).

We chose to study the CP for several reasons. First, because its size varies with the amount of peripheral olfactory innervation found in a mammal's snout (Pihlström, Fortelius, Hemilä, Forsman, & Reuter, 2005), quantifying the CP provides an opportunity to gauge and compare relative olfactory investment across aquatic and terrestrial species (Bird, Amirkhanian, Pang, & Van Valkenburgh, 2014). Second, earlier work found that, across all superorders of mammals, relative CP size is closely correlated with the number of olfactory

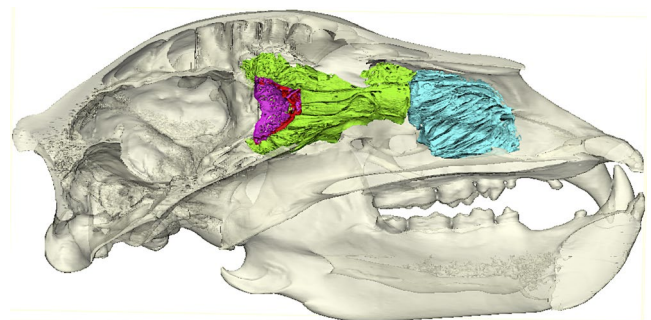


FIGURE 1 Nasal anatomy of grizzly bear (*Ursus arctos*). Left half of a sagittally sectioned skull. Pink, perforated cribriform plate bone separating nasal cavity from the brain case. Green, olfactory (ethmo-, fronto- and naso-) turbinals. Blue, respiratory (maxillo-) turbinals

receptor genes in an animal's genome, thereby establishing CP morphology as an informative metric of relative reliance on the sense of smell (Bird et al., 2018). Third, CP area is tightly correlated with the surface area of the ethmoturbinals, the bony plates that bear olfactory epithelium (Bird et al., 2014). Finally, CP area can be quantified in some fossil skulls (Bird et al., 2018), and so will enable future studies into the evolution of olfactory anatomy in extinct mammal lineages that have transitioned from land to water. Here, we perform the first extensive comparative and quantitative study of the CP morphology of arctoid carnivorans, a clade that has seen multiple independent invasions into the marine habitat and includes species at the intersection of terrestrial and aquatic life.

Our sample group, the arctoid carnivorans, is an ecologically rich clade that includes ursids (bears), mustelids (e.g., weasels, otters, and badgers), procyonids (e.g., raccoons and kinkajous), mephitids (skunks), and pinnipeds, among others (Figure 2) (Upham, Esselstyn, & Jetz, 2019). Within the arctoids, there were multiple independent, secondary entries into aquatic habitats (Berta, Sumich, & Kovacs, 2015), resulting in a diversity of closely related

species from disparate ecologies (aquatic, semi-aquatic, and terrestrial) along a spectrum of olfactory demands. According to the recent comprehensive mammalian phylogenetic analysis (Upham et al., 2019), pinnipeds diverged from the lineage leading to Musteloidea ca. 24–33 ma., and otters diverged from terrestrial mustelids more recently, ca. 8.5–12 million years ago. Studying Carnivora is advantageous, as the group has a fairly well-resolved phylogeny, allowing the application of comparative methods that account for phylogenetic relatedness in our study of ecological influences on olfaction.

2 | MATERIALS AND METHODS

Using high-resolution CT scans and 3D imaging software and methods developed in previous studies (Bird et al., 2014, 2018), we measured the surface area of the perforated region of the CP as well as the cumulative cross-sectional area of the CP foramina as proxies for relative olfactory innervation found in individual arctoid species.

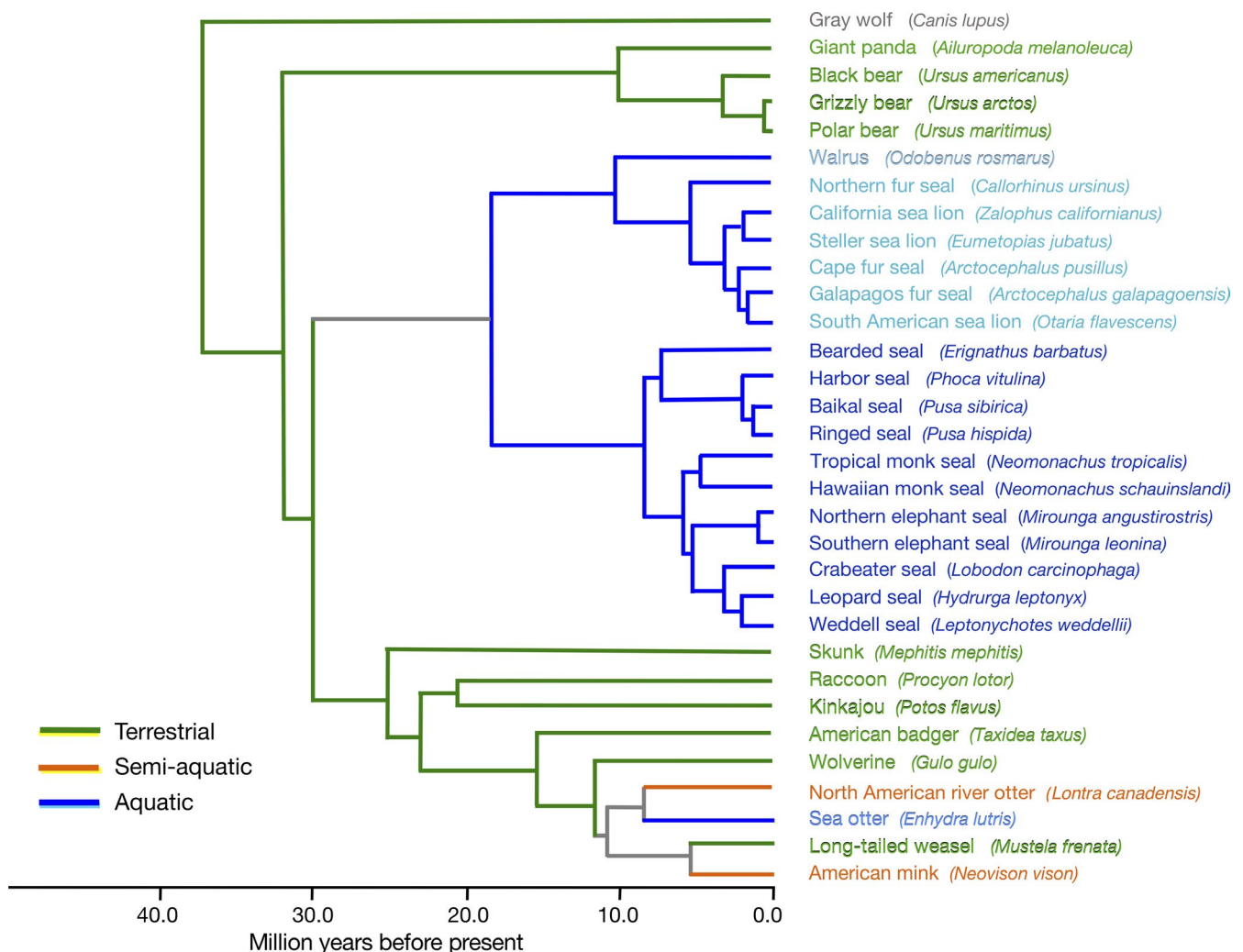


FIGURE 2 Time-calibrated phylogeny for arctoid carnivorans. All taxa except the gray wolf were sampled for this study. Topology and divergence estimates are taken from Upham et al. (2019)

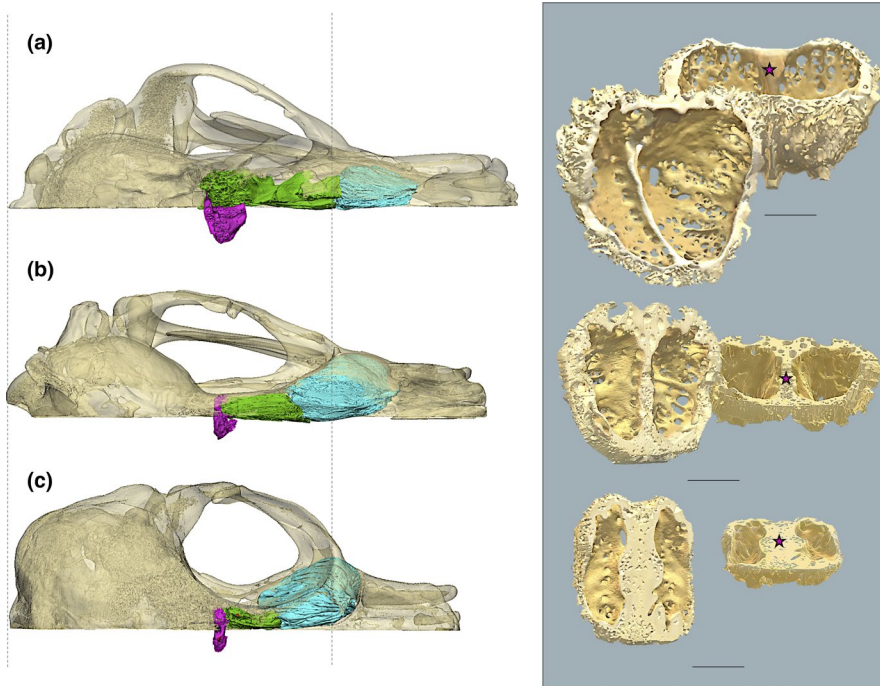


FIGURE 3 Cribriform plate morphology in terrestrial and aquatic carnivorans. (a) grizzly bear (*Ursus arctos*); (b) leopard seal (*Hydrurga leptonyx*); (c) northern elephant seal (*Mirounga angustirostris*). Left panel, dorsal view of left half of sagittally sectioned skull. Pink, entire cribriform plate (CP). Green, left olfactory turbinals. Blue, left respiratory turbinals. Dashed lines indicate landmarks for measurement of occipital condyle to orbit distance. Right panel: CP of each species enlarged. Left, posterior oblique view. Right, ventral oblique view: note large, densely perforated roof concavity in grizzly CP. Star, crista galli. Scale bar, 10 mm

2.1 | Specimen collection

We sampled 65 skulls from 31 species representing eight families of arctoid carnivorans (Figure 2) (Upham et al., 2019). Specimens and their source museums are listed in Table A1 in Appendix. All species are extant with the exception of the tropical monk seal (*Neomonachus tropicalis*). Body sizes span several orders of magnitude from <1 kg (long-tailed weasel, *Mustela frenata*) to at least 1,275 kg (male southern elephant seal, *Mirounga leonina*) (Irvine, Hindell, Van Hoff, & Den, 2000). Where possible, we sampled two wild-caught adult specimens, one male and one female, for each species.

2.2 | Morphological data

Thirty-five of the 65 skulls were scanned at the University of Texas High Resolution CT Scanning Facility (<http://www.ctlab.geo.utexas.edu>). The remaining 30 skulls were scanned on Phoenix nanotom s™ and Nikon Metrology XT H 225 ST machines at the Molecular Imaging Center of the Keck School of Medicine of USC in Los Angeles, on Phoenix v|tomex™ machines at General Electric's Inspections Technologies Facility in San Carlos, California, or on a Siemens Definition AS64™ scanner at Ronald Reagan Medical Center at UCLA. In order to maximize resolution, the field of view was restricted to the CP area of the skull in most cases, although a number of skulls were scanned in their entirety. Voxel size ranged from 0.044 to 0.5 mm. All scans are available upon request from either Digimorph (<http://www.digimorph.org>) or MorphoSource (<http://www.morphosource.org/>). Scans were imported into the 3D imaging software Mimics (v. 15.0-21.0, Materialise, Leuven, Belgium), segmented into two dimensional masks, and reconstructed as volumetric renderings. Edited 3D models of the CP constructed

for each specimen could be rotated and magnified for closer inspection and quantification. When needed, multiple regions of interest in the skull were segmented and rendered as separate 3D models to better visualize the CP in the context of its surrounding nasal anatomy (Figures 1 and 3). The first metric, CP surface area, includes only the section of the CP bone perforated by foramina that surround the olfactory nerves. We quantified CP surface area by generating a continuous surface in the imaging program 3-matic (v. 7.01-13.0, Materialise) with a wrapping function that fills all foramina in the CP model, then digitally cutting the surface at the perimeter of the perforated region and calculating its area in 3-matic (Bird et al., 2018) (Figure A1). To quantify the cumulative cross-sectional area of individual CP foramina, our second metric, we applied splines, or rings of coordinate points, to the perimeters of the CP foramina in Mimics. We imported the resulting splines into modeling software Rhinoceros-4 (McNeel and Associates), where surface areas for all foramina were calculated and tallied. While total foramina area may be the most direct estimate of the cross-sectional area of an animal's olfactory innervation, it cannot be resolved from low resolution scans, damaged skulls, or fossils. Therefore, because foramina area is closely correlated with CP surface area ($r^2 = .92$; $\text{pgls-}r^2 = .9$, $p < .001$, Figure A3), we used the latter to maximize sample size.

As a body size proxy, we used the skull metric, occiput-to-orbit length (OOL), defined as the distance between the posterior extent of the occipital condyles and the anterior most extent of the orbit (Figure 3). The correlation between OOL and body mass is similar to that between full skull length and body mass (Van Valkenburgh, 1990), and OOL offers advantages over skull length. First, OOL excludes the confounding influence of snout length, a feature that varies widely among arctoids independent of body size. Indeed, in our sample, relative snout lengths are shorter in aquatic species than terrestrials ($p = .036$, Table A1 and A3). OOL also allows the

inclusion of skulls with broken premaxillae and is better suited to analyze incomplete fossil skulls in the future. Using the skull metric OOL instead of body mass reduced the excessive influence of large fat stores in pinnipeds on body size estimates. For all specimens, in our sample, the skull metric OOL was measured from 3D skull reconstructions using Mimics or from skulls directly using digital calipers.

2.3 | Habitat groupings

We grouped the arctoids into three ecological categories, terrestrial, aquatic, and semi-aquatic. We defined terrestrial species as those that live and forage exclusively on land. These include ten species of ursids, procyonids, mephitids, and mustelids (Figure 2, Table A1). Species in the aquatic group ($n = 19$) forage exclusively underwater but also spend some time hauled out on land or pack ice and include eighteen pinniped species and the mustelid sea otter (*Enhydra lutris*). Semi-aquatic species forage both underwater and on land and include two mustelid species. Although the polar bear (*Ursus maritimus*) is often referred to as a semi-aquatic marine mammal and sometimes swims to stalk its prey (Berta et al., 2015), we chose to classify it as terrestrial, as it does not seek and capture its prey underwater (Stirling, 1974).

2.4 | Diving data

Four diving behavior variables are included in this study, maximum dive depth, mean dive depth, maximum dive duration, and mean dive duration. All dive data were compiled from published behavioral field studies (Table A2). If means were not directly reported in source literature, we derived these from supplemental raw dive data, data shared in personal communications, or in two cases by visually measuring from histogram distributions. We included as many studies as possible in calculating our means, weighting the contribution of each study by the number of animals recorded. Other potentially informative variables describing potential diving capacity or overall degree of aquatic specialization, such as magnitude and distribution of oxygen stores, at-sea durations, migration distances, haul-out durations, exist for some but not all sample species, and so could not be used for this study.

2.5 | Statistical analysis

Species means of all morphological and ecological variables were used for data analysis. To view scaling relationships between CP and body size and to derive values for size-adjusted relative CP size, we plotted \log_{10} absolute CP surface area against \log_{10} OOL using phylogenetic least squares regression (PGLS). Resulting residuals were used as relative CP size (RelCP) in all subsequent analyses. To test the influence of habitat on RelCP values, we performed pair-wise ANOVA and Tukey HSD post hoc tests. All regression plots include

regression lines from PGLS as well as general least squares regression (GLS). All analyses were performed in R (Team RC, 2015). For PGLS, we used Caper Package (Orme et al., 2013) and a time-calibrated mammal tree pruned to include only the species in our study (Upham et al., 2019).

3 | RESULTS

3.1 | Cribriform plate area and body size

Among all 31 species, absolute CP surface area is coupled to body size, as described here by the skull metric, occipital condyle to orbit length (OOL) ($\text{pgls-}r^2 = .7, p < .001$), and scales with negative allometry ($y = 1.37x - 0.1097$), (Figure 4, Table A3). Thus, large species have proportionally smaller CP for their body size. There is considerable scatter about the line with terrestrial species tending to fall above the line and aquatics below the line. Among the aquatic species alone the relationship between CP surface area and OOL is similar ($\text{pgls-}r^2 = .69, p < .001, n = 18$) and among terrestrials alone it is stronger ($\text{pgls-}r^2 = .84, p < .001, n = 10$).

3.2 | Cribriform plate in terrestrial, aquatic, and semi-aquatic species

To test the hypothesis that aquatic and semi-aquatic species have reduced olfactory morphology relative to terrestrial species, we performed a one-way ANOVA and Tukey HSD post hoc tests on mean relative CP size (RelCP) values from all three habitat groups. Aquatic species have significantly smaller mean RelCP than terrestrial species ($p < .001$). Mean RelCP of semi-aquatic species is smaller than that of terrestrials ($p = .014$) and does not differ significantly from that of aquatics ($p = 1$) (Table A3).

Similarly, when running a habitat analysis on CP surface area that is size-adjusted to full skull length (SkL) instead of OOL, comparable differences between groupings emerge (Appendix A1, Figure A2). As per Tukey HSD post hoc tests, again aquatics have significantly larger mean RelCP than terrestrials ($p < .001$), and there is no significant difference between semi-aquatics and aquatics ($p = .36$). The difference in mean RelCP (size-corrected to full skull length) between semi-aquatic species and terrestrials is less pronounced but significant ($p = .042$).

To consider whether the losses in olfactory anatomy in the aquatic mustelids occurred independently from those in the lineage leading to Pinnipedia, we analyzed RelCP in aquatics and terrestrials within the clade Musteloidea (mustelids, procyonids, and mephitid; $n = 9$) and within the family Mustelidae ($n = 6$) separate from Pinnipedia and Ursidae. A phylogenetically corrected ANOVA shows that the mean RelCP of the aquatic sea otter and semi-aquatic river otter and mink together are significantly smaller than the mean RelCP of terrestrial musteloids ($p = .007$) and terrestrial mustelids ($p = .014$). It is interesting that among the three terrestrial mustelid

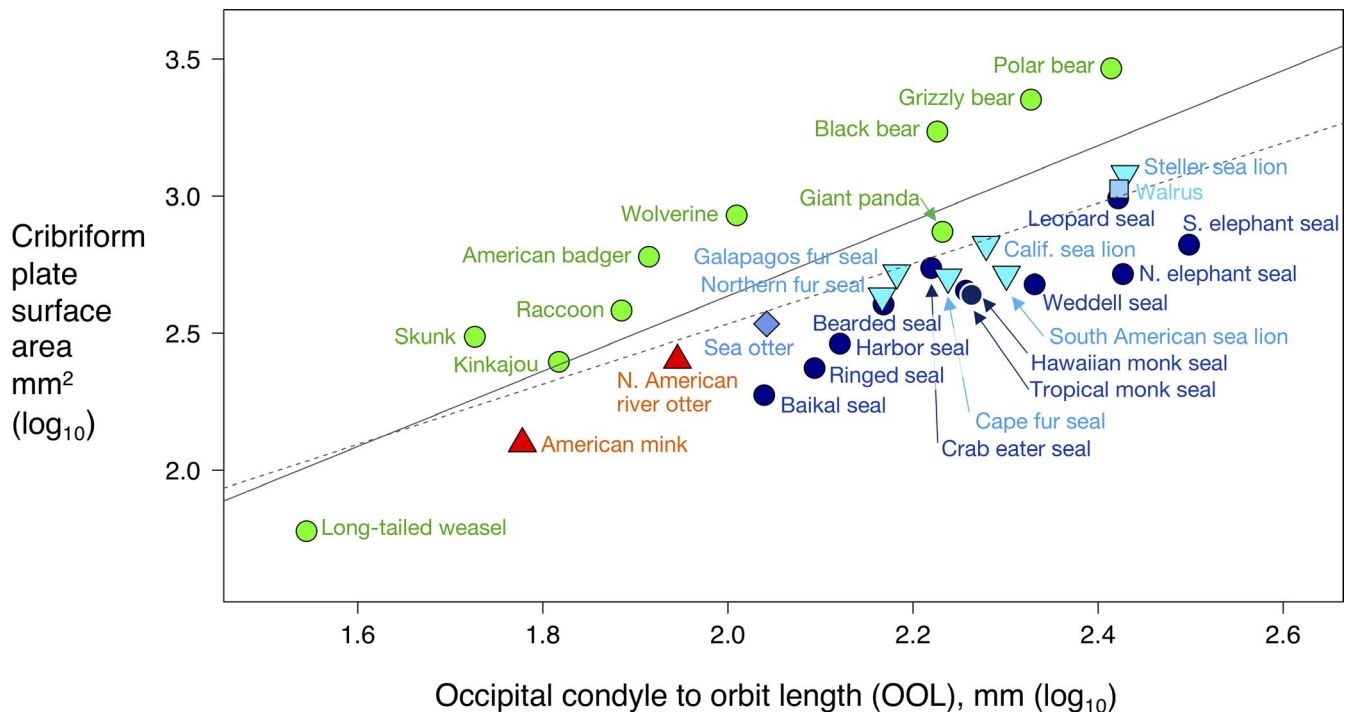


FIGURE 4 Log-log plot of CP surface area versus Occiput-orbit length (OOL) for three ecological groupings. Green circles, terrestrial species; red triangles, semi-aquatics; dark blue circles, Phocidae; turquoise inverted triangles, Otariidae; blue diamond, Mustelidae (sea otter, *Enhydra lutris*); light blue square, Odobenidae (walrus, *Odobenus rosmarus*); Solid line, best fit from phylogenetic generalized least squares (PGLS) regression; dotted line, best fit from generalized least squares regression (GLS)

species, the long-tailed weasel differs from the much larger badger and wolverine by having a reduced RelCP similar to that of the three more aquatic mustelids. This suggests that a reduced RelCP might be characteristic of smaller mustelids in general. Without a larger sample size of small mustelids, the diminutive RelCP of the long-tailed weasel is difficult to interpret.

3.3 | RelCP and diving ecology of aquatic carnivorans: dive depth and duration

To investigate possible interactions between diving behavior and olfactory morphology, we tested for correlations between RelCP and each of four diving parameters, mean dive duration, maximum dive duration, mean dive depth, and maximum dive depth within the 18 aquatic species for which we had published dive data (17 pinnipeds and the sea otter). We found strong inverse relationships between RelCP and three of the variables, mean dive depth ($r^2 = .75$, $p < .001$, $\text{pgls-}r^2 = .65$, $p < .001$), mean dive duration ($r^2 = .76$, $p < .001$, $\text{pgls-}r^2 = .61$, $p < .001$), and maximum duration ($r^2 = .66$, $p < .001$, $\text{pgls-}r^2 = .48$, $p < .001$), respectively (Figure 5a,b,d). This relationship is largely driven by the phocids; in all three cases, accounting for phylogeny weakens the coefficients of determination because the otariids tend not to follow the main trend and phylogeny exerts a strong influence on pinniped CP morphology independent of diving behavior. Phocids have on average smaller RelCP than either otariids alone ($p = .015$) and otariids and the odobenid walrus together ($p = .019$)

(Figure A4, Table A3). In the case of the fourth parameter, maximum dive depth, what appears to be a strong negative relationship with RelCP ($r^2 = .55$, $p < .001$), is barely significant after accounting for phylogeny ($\text{pgls-}r^2 = .22$, $p = .051$) (Figure 5c, Table A3).

The true seals, phocids, display a far wider range of mean dive depths (~17–505 m) and mean dive duration (~3–28 min) than their sister clade of otariids and odobenids (15.4–44 m, 1.7–5.1 min, respectively) (Figures 5 and 6a,b, Table A2), suggesting more extensive ecological diversity among the true seals, and so we examined them separately. We calculated RelCP values for phocids alone using residuals from the PGLS regression of CP surface area against OOL among the ten phocid species. Within the phocids, there is a strong negative correlation between RelCP and three diving metrics: mean dive depth ($r^2 = .75$, $p < .001$, $\text{pgls-}r^2 = .82$, $p < .001$), mean dive duration ($r^2 = .79$, $p < .001$, $\text{pgls-}r^2 = .88$, $p < .001$), and maximum dive duration ($r^2 = .76$, $p < .001$, $\text{pgls-}r^2 = .78$, $p < .001$) but no significant relationship with maximum dive depth (Figure 6a–d, Table A3).

4 | DISCUSSION

Results from our study point to reduced reliance on olfaction as a secondary adaptation to marine habitats, and in particular to foraging at depth. Among aquatic arctoid carnivorans, we found a pronounced loss of olfactory anatomy, specifically a reduction in relative cribriform plate size (RelCP), that mirrors established reductions in olfactory turbinal surface area (Van Valkenburgh et al.,

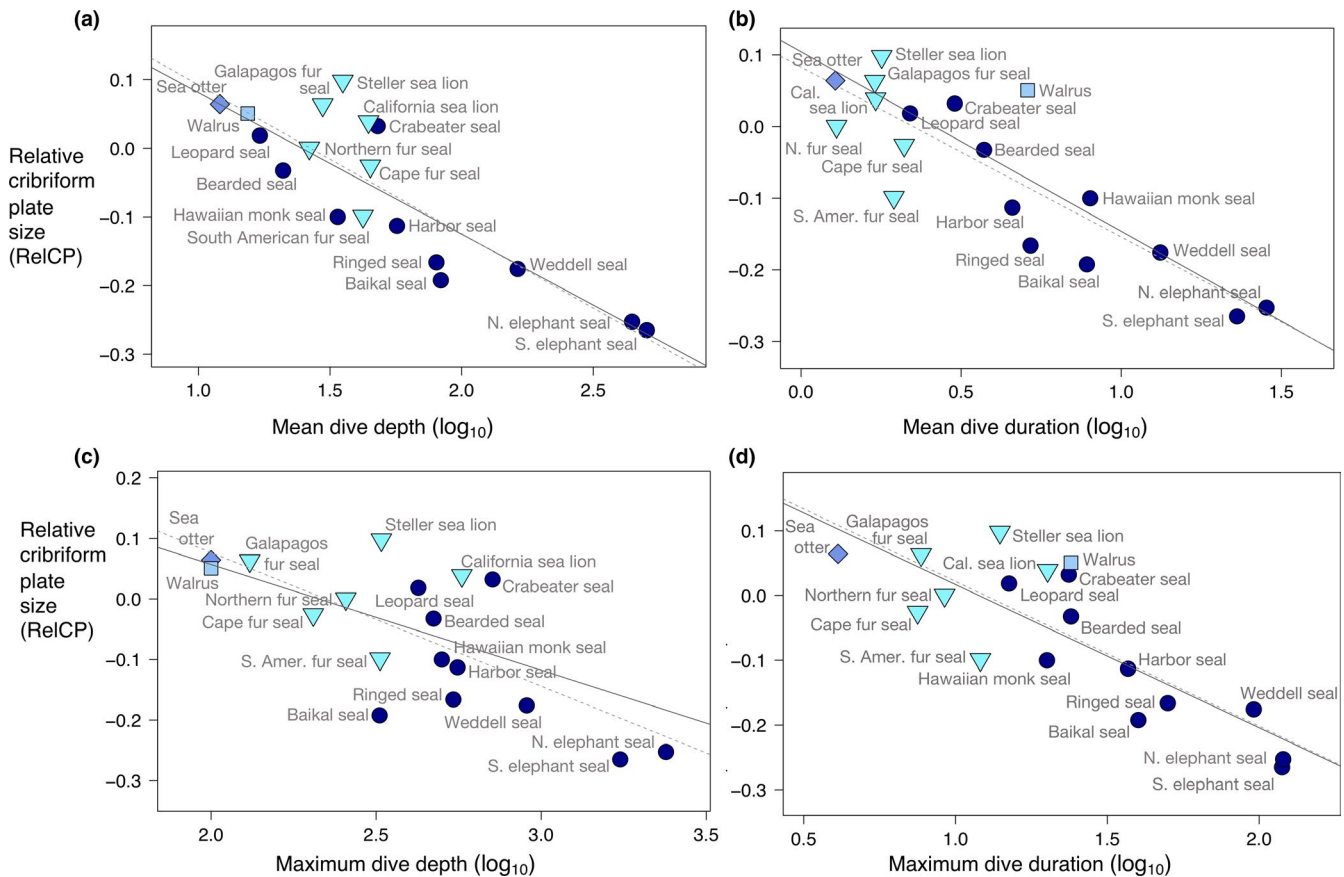


FIGURE 5 Significant correlation between relative cribriform plate size and three dive variables in the four families of aquatic carnivorans. (a) Relative CP size (RelCP) versus mean dive depth ($r^2 = .75$, $p < .001$, $\text{pgls-}r^2 = .65$, $p < .001$). (b) RelCP versus mean dive duration ($r^2 = .76$, $p < .001$, $\text{pgls-}r^2 = .61$, $p < .001$). (c) RelCP versus maximum dive depth ($r^2 = .55$, $p < .001$, $\text{pgls-}r^2 = .22$, $p = .51$). (d) RelCP versus maximum dive duration ($r^2 = 0.66$, $p < .001$, $\text{pgls-}r^2 = .48$, $p < .001$). Dark blue circles, Phocidae; turquoise inverted triangles, Otariidae; light blue square, Odobenidae (walrus); blue diamond, Mustelidae (sea otter). Solid line, best fit from PGLS regression; dotted line, best fit from GLS regression

2011). It is not surprising that both CP and olfactory turbinal surface areas are reduced in aquatic species, given their common developmental origin (Rowe, Eiting, Macrini, & Ketcham, 2005), and the fact that they are strongly correlated in size across all carnivorans (Bird et al., 2014). Our results accord with initial genomic studies reporting losses in the number of functional olfactory receptor genes in five aquatic arctoid species (two otter and three pinniped species) relative to terrestrial relatives (Beichman et al., 2019; Hughes, Gang, Murphy, Higgins, & Teeling, 2013; Liu et al., 2019). Our data show that pinnipeds and the sea otter, representing two lineages within Carnivora that independently reinvaded the marine environment, have likely undergone convergent reductions in relative cribriform plate size (RelCP) compared with closely related terrestrial species. Moreover, our findings go beyond previous work in revealing that, among aquatic carnivorans, species that dive deeper and for longer periods of time tend to have an even greater reduction in CP size.

Our finding of a smaller RelCP among aquatic arctoid carnivorans contradicts earlier work that concluded that CP size did not differ between pinnipeds and terrestrial carnivorans (Pihlström et al., 2005, 2008). There are several likely reasons for differences in our findings. First, Pihlström et al. (2005) used linear measurements to

calculate CP surface area, whereas we relied on digital quantification, a method that better captures the highly irregular shape of the CP (Bird et al., 2014). Second, their body size proxy, skull area, does not exclude snout length, which can lead to the underestimation of body size in the typically short-snouted pinnipeds and sea otter and a consequent inflation of size-adjusted CP size in aquatic species. Third, our sample represents a wider sampling of pinnipeds including species with relatively small CP, such as the northern and southern elephant seals (*Mirounga angustirostris*, *M. leonina*), the Weddell seal (*Leptonychotes weddellii*), Baikal seal (*Pusa sibirica*) and ringed seal (*Pusa hispida*).

Within aquatic carnivorans, we found marked variation in olfactory morphology that corresponds closely with diving behavior. Although there is no clearly significant association between maximum dive depth and RelCP that persists after phylogenetic accounting, there are strong inverse correlations between RelCP and the following three dive variables: mean dive depth, mean dive duration, and maximum dive duration. These relationships are even more pronounced when considering the phocids, or true seals, alone. The absence of a significant relationship between maximum dive depth and RelCP was surprising given that maximum dive depth values exhibit

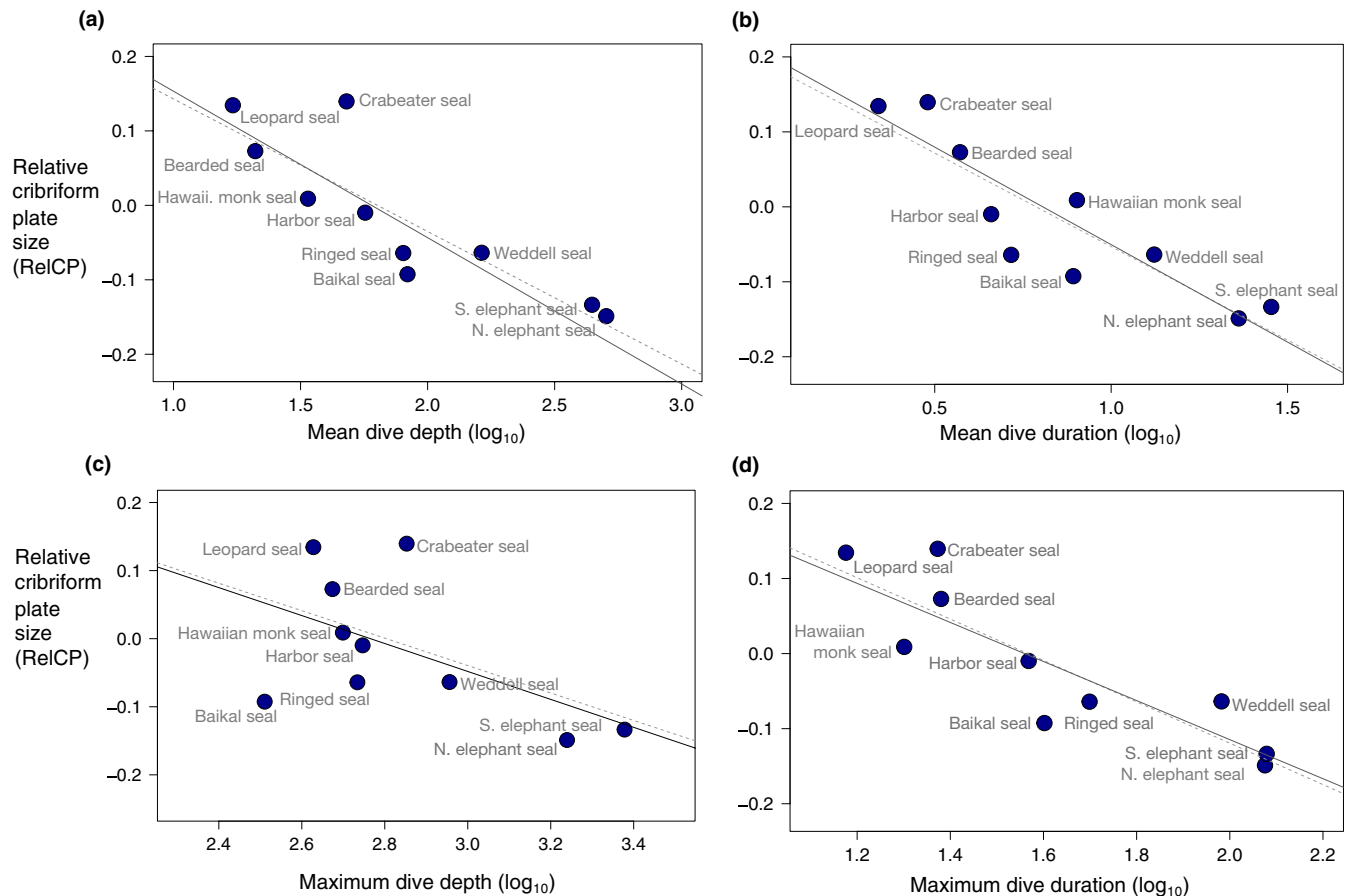


FIGURE 6 Relationship between RelCP and dive behavior among the phocids. Regression plots of relative CP size versus (a) mean dive depth ($r^2 = .75$, $p < .001$, $\text{pgls-}r^2 = .82$, $p < .001$); (b) mean dive duration ($r^2 = .79$, $p < .001$, $\text{pgls-}r^2 = .88$, $p < .001$); (c) maximum dive depth (ns: $r^2 = .3$, $p = .17$, $\text{pgls-}r^2 = .22$, $p = .17$); (d) maximum dive duration ($r^2 = .76$, $p < .001$, $\text{pgls-}r^2 = .78$, $p < .001$). Solid line, best fit from PGLS regression; dotted line, best fit from GLS regression

the widest range of the four diving parameters and because the smallest RelCP values by far belong to the most extreme divers, the northern and southern elephant seals, which have been recorded diving to 1,735 and 2,388 m, respectively (Costa et al., 2010; Costa, Robinson, et al., 2010; Robinson et al., 2012). However, close review of the published literature reveals that recorded maximum depths are often not representative of species' overall diving patterns. For example, the California sea lion has been recorded at a depth of 575 m, and yet this otariid is generally considered a moderately shallow diver (Berta et al., 2015; Costa, Kuhn, & Weise, 2007).

Why might selection favor smaller RelCP, reduced olfactory anatomy, in aquatic carnivorans in general and species performing deeper, sustained dives in particular? We present alternative evolutionary explanations. First, although odor cues play an important role in social interactions and predator defense among aquatic carnivorans above water (Lowell & Flanigan, 1980; Peterson & Bartholomew, 1967; Riedman & Estes, 1990; Ross, 1970), below water, where pinnipeds and sea otters typically forage, odor cues are no longer detectable. Although another semi-aquatic mammal, the water shrew, is known to exhale and inhale bubbles to access scent cues from food surfaces underwater (Catania, Hare, & Campbell, 2008), this behavior has been hypothesized but not tested in the

carnivoran river otter (Marriott et al., 2013). Unlike terrestrial carnivorans, which follow deposited and airborne prey scents to locate food sources (Smith, 1980; Ylönen et al., 2003), aquatic carnivorans forage with shut nostrils and locate prey without scent cues, except those detected above water upon surfacing. Utilizing scent cues at or above the water surface is a probable tool of foraging at sea, given that harbor seals (*Phoca vitulina*) have shown keen sensitivity to dimethyl sulfide (DMS), a volatile phytoplankton odorant and indicator of local marine productivity that is utilized by sea birds as well (Kowalewsky et al., 2006; Nevitt, Reid, & Trathan, 2004). However, deeper and more extended dives increase the diver's distance from these informative odor cues at the surface (Davis et al., 2001, 2003). Consequently, over time, as selective pressure for detecting prey via odorant cues was relaxed, olfactory systems among carnivorans adapting to life in water likely decreased in size. Reduced olfactory structures were further favored because olfaction is a costly sensory system made up of millions of continually self-replacing olfactory sensory neurons (Graziadei & Graziadei, 1985).

A second and related explanation for the reduction of olfactory anatomy in diving aquatic mammals focuses on the evolution of keen alternative sensory specializations adapted to underwater foraging. For example, pinnipeds and the sea otter possess a tactile

acuity exhibited in dense arrays of highly innervated vibrissae, the most prominent of which are the mystacial (mustache) whiskers (Berta et al., 2015). Such compact arrangements of whiskers in the phocid bearded seal (*Erignathus barbatus*) and the walrus (*Odobenus rosmarus*) are thought to assist in locating mollusks in the shallow benthic substrate (Marshall, Amin, Kovacs, & Lydersen, 2006). Experiments using blindfolded animals revealed that harbor seals (*Phoca vitulina*) use their vibrissae to track the hydrodynamic trails of swimming fish (Dehnhardt, Mauck, & Bleckmann, 1998). In addition to enhanced vibrissae, aquatic carnivorans rely on a visual system adapted for hunting in dark waters. Visual specializations may include spherical lenses (Berta et al., 2015), wide pupil size range (Levenson & Schusterman, 1999) a tapetum lucidum (Kröger & Katzir, 2008) as well as proportionally large eye orbits (Debey & Pyenson, 2013). Considering these enhanced sensory specializations, it seems likely that the reduction of olfactory anatomy in pinnipeds and the sea otter over time stems, in part, from relaxed selective pressures on olfactory acuity as aquatic species come to rely more heavily on alternative sensory systems for underwater foraging.

Why does selection favor a greater reduction in CP size in aquatic carnivorans performing longer and deeper average dives? There are a number of alternative hypotheses, all of which require further testing. First, it is possible that shallow, short dive patterns reflect a closer tie to the land/pack ice, while deeper and longer dive patterns represent a more pronounced separation from a terrestrial ecology. Longer separation from land, that is, a more aquatic life, likely results in increased disconnection from airborne and deposited odor cues that terrestrial animals rely on for food, predator protection, social communication, and reproduction. To further test whether deeper, more sustained diving reflects a more fully aquatic lifestyle and an increasingly remote relationship to the land, all four diving variables might be viewed in relationship to other ecological proxies for relative proximity to land/sea ice. These factors could include foraging trip duration (Kooyman & Gentry, 1986), long-distance migration patterns (Costa, Huckstadt, et al., 2010; Costa, Robinson, et al., 2010), pupping season duration (Stirling, 1983), haul-out patterns (Cunningham et al., 2009) and overall at-sea duration (Costa, Huckstadt, et al., 2010; Costa, Robinson, et al., 2010), among others.

An alternative, or complementary, interpretation for the negative relationship between diving depth/duration and RelCP suggests that volatile odor cues at the water's surface emitted by underwater prey play a role in prey detection for marine carnivorans, and that reliance on these surface odorants selects for retention of a larger olfactory system in shallow as opposed to deep divers. One such volatile, mentioned above, is dimethylsulfide (DMS), an odorant emitted by phytoplankton, particularly when grazed upon by krill and other zooplankton (Dacey & Wakeham, 1986). Concentrations of DMS at the sea-air interface are variable, and "hotspots" indicate underlying primary production, including the presence of krill and krill-feeding animals, such as fish or penguins (Barnard, Andreae, Watkins, Bingemer, & Georgii, 1982). The leopard seal (*Hydrurga leptonyx*), a shallow and short diver that feeds primarily on krill, penguins, and

crabeater seal pups (Pauly et al., 1998), likely navigates a rich landscape of scent cues at the water's surface as well as on the ice sheet. By contrast, deep divers appear to have less access to surface cues while foraging. For example, the northern elephant seal dives in a staggered stair-step pattern, reaching its prey of pelagic squid and mesopelagic fish (Pauly et al., 1998) at depths between ~300 and 1,500 m, displaced horizontally, sometimes by hundreds of meters, from the dive initiation location (Davis et al., 2001). It is notable then, that the shallow-diving leopard seal and the deep-diving elephant seal, close relatives among the pinnipeds, have the most disparate RelCP among all phocids (Figure 6a). To strengthen the argument that surface odorant cues influence foraging behavior in some aquatic carnivorans, future behavioral experiments, such as those used to test responsiveness of seabirds and whales to variable concentrations of DMS (Bouchard et al., 2019; Nevitt, Veit, & Kareiva, 1995), may be performed on pinnipeds and sea otters.

Finally, the inverse relationship between RelCP and diving depth and duration may also indicate a structural constraint on CP size imposed by the stresses of diving. The adverse effects of diving to depth are well cited in the literature. Two notable effects are (a) the risk of increased nitrogen diffusion into the blood stream as gas tensions rise within air-filled cavities and (b) the potential deformation of tissue surrounding compressed gas-filled cavities (Kooyman & Ponganis, 1998). Adaptations to these challenges include, among others, collapsible alveoli, which minimize gas exchange (Scholander, 1940), distensible venous sinuses, which are thought to reduce external and middle ear cavity volume (Odend'hal & Poulter, 1966; Stenfors, Sadé, Hellström, & Anniko, 2001), and structural reductions in skull cavities, such as the narrowing of the external auditory canal (Kastak & Schusterman, 1999) and the loss of frontal sinuses (Curtis et al., 2015). Reductions in air-filled skull cavities, while adaptive under hydrostatic pressure, may constrain the development of the olfactory recess in the aquatic mammal skull, specifically the olfactory turbinals and attendant airway fluid dynamics necessary for robust odorant deposition (Craven, Paterson, & Settles, 2009). In terrestrial carnivorans, ethmoturbinals often extend from the nasal cavity dorsally into the frontal sinuses, increasing surface area for odorant deposition and detection (Negus, 1958) (Figure A5a). By contrast, without the doming of the skull afforded by large frontal sinuses, the space available for ethmoturbinals and the CP in pinnipeds and the sea otter is limited dorsally (Figure A5b). Moreover, a survey of snout lengths in our sample reveals that aquatic carnivorans have significantly shorter snouts than terrestrial carnivorans, further reducing the nasal air space, and thereby perhaps constraining anterior extensions of ethmoturbinals as well (Tukey, $p = .036$, Table A4). Two exceptions to this are the California sea lion (*Zalophus californianus*) and the leopard seal (*Hydrurga leptonyx*), both of which have ethmoturbinals that extend into relatively long anterior nasal cavities, and large RelCPs as well (Figure 3 Appendix A1, Figure A5b). Finally, because aquatic carnivorans possess visual specializations for underwater vision, including relatively large eyeballs and orbits (Debey & Pyenson,

2013), the posterior nasal cavity is relatively narrow in most pinniped species (Berta et al., 2015), and most markedly in the elephant seals, further limiting space for ethmoturbinals laterally as well as ventrally (Figure A6a,b). Because ethmoturbinals and CP are developmentally linked and their surface areas tightly correlated (Bird et al., 2014), we expect any structural constraints on ethmoturbinal development to be reflected in smaller CPs as well. A future comparative study of ethmoturbinal surface area and nasal cavity volume across a large sample of aquatic carnivorans would be needed to test this (Van Valkenburgh et al., 2011). Additionally, to better resolve whether diving pressures have imposed adaptive structural constraints on the ethmoturbinal development in aquatic carnivorans, Finite Element Analysis (FEA) could be used to estimate the effects of variable compressive forces on bone surrounding air-filled skull cavities, ethmoturbinal bones and the cribriform plate itself (Alam, Amini, Tadayon, Miserez, & Chinsamy, 2016).

Whereas many studies highlight the acquisition of multiple adaptations to aquatic life, we focused on a single loss, that is, reductions in the cribriform plate within two lineages that independently invaded marine environments, Pinnipedia, and Mustelidae. Among the mustelids, there were two parallel invasions of the water, one within the otters (Lutrinae) and the second within the weasels (Mustelinae) as represented by the mink. Relative to all the terrestrial arctoids in our sample except for the long-tailed weasel, the mink and both otters have reduced RelCP that likely evolved in parallel. As each group (pinnipeds, mustelids) independently evolved to forage underwater, a central function of the olfactory apparatus, prey detection, became less important to diving carnivorans. Based on our results and established olfactory losses in cetaceans, we might expect reduced CP size to be a convergent adaptation among all marine mammals. To answer this, we need to investigate the cribriform plate morphology of mammals from all the lineages that secondarily invaded the sea, including the extant Afrotherian Sirenia as well as extinct aquatic mammals, such as the Afrotherian Desmostylia, Xenarthran *Thalassocnus* sloths (Amson, Billet, & de Muizon, 2018), stem Pinnipedia (*Enaliarctos* and *Puijila*), and stem cetaceans. Because the CP is fairly well preserved in the fossil record (Amson et al., 2018; Bird et al., 2018), it allows us to work backwards in deep time and visualize the evolutionary loss of olfactory anatomy among mammals as they transition from land to water. The cribriform plate, an informative, osseous record of olfactory activity in living and extinct mammals, offers a critical look into the evolution of olfaction at depth.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

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DATA AVAILABILITY STATEMENT

Please see the Appendix for tables and figures. Within the text, we have referred readers to MorphoSource as well as Digimorph as open access repositories for computed tomography scan data as well as digital images. All files are available on Dryad: <https://orcid.org/0000-0001-8217-8985>; <https://doi.org/10.5068/D1CQ2G>

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APPENDIX

CONTACT FOR RESOURCE SHARING

Further information and requests for resources, scanning parameters, CT scan files, and 3D skull models should be directed to and will be fulfilled by the Lead Contact, Deborah Bird (dbirdseed@gmail.com).

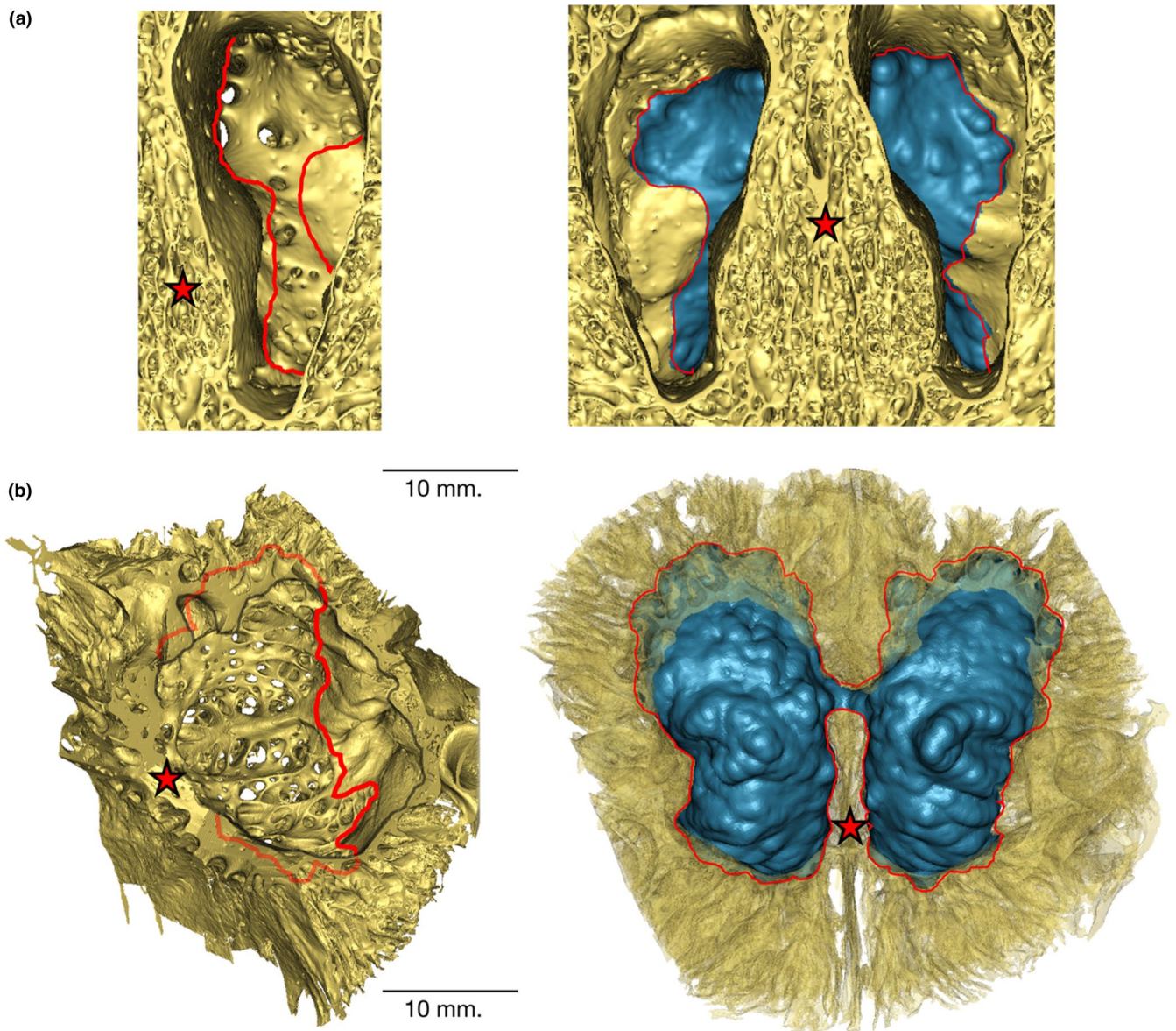


FIGURE A1 Quantifying the cribriform plate surface area. 3D digital rendering of (a), Northern elephant seal (*Mirounga angustirostris*) and (b), grizzly bear (*Ursus arctos*) cribriform plates (CP), constructed in Mimics and viewed here in posterior aspect from the brain case. Left: right half of CP viewed in oblique angle; the region perforated by olfactory foramina is delineated (red). Right: full CP, posterior view; olfactory foramina are digitally filled and the generalized surface of the perforated region (blue) is calculated in 3-matic. The full grizzly bear CP (b, right) is rendered transparent in order to better view its deep concavity. Star: crista galli (CP midline)

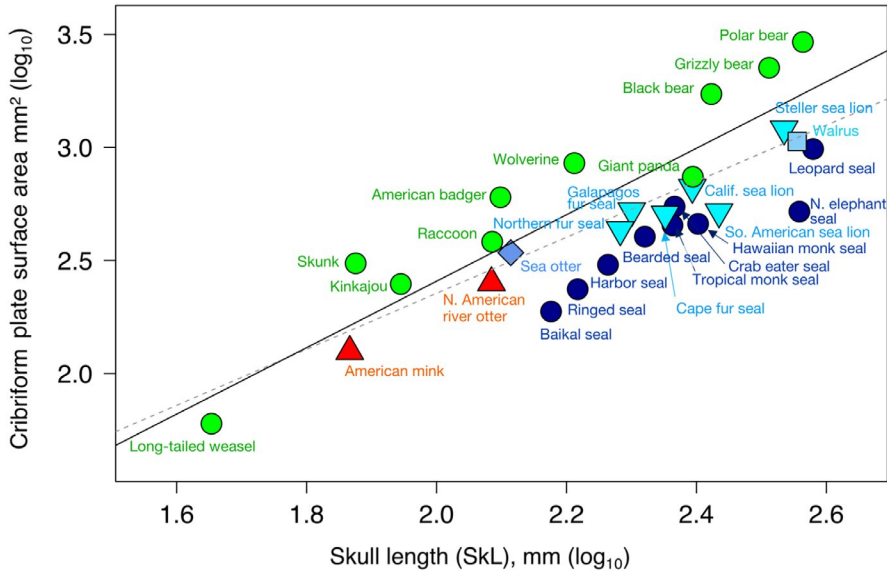


FIGURE A2 Log-Log plot of CP surface area vs. full skull length (occipital condyle to prosthion)(SkL) for three ecological groupings. Green circles, terrestrial species; red triangles, semi-aquatics; blue, aquatics; dark blue circles, Phocidae; turquoise inverted triangles, Otariidae; blue diamond, Mustelidae (sea otter, *Enhydra lutris*); light blue square, Odobenidae (walrus, *Odobenus rosmarus*); Solid line, best fit from phylogenetic generalized least squares (PGLS) regression; dotted line, best fit from generalized least squares regression (GLS)

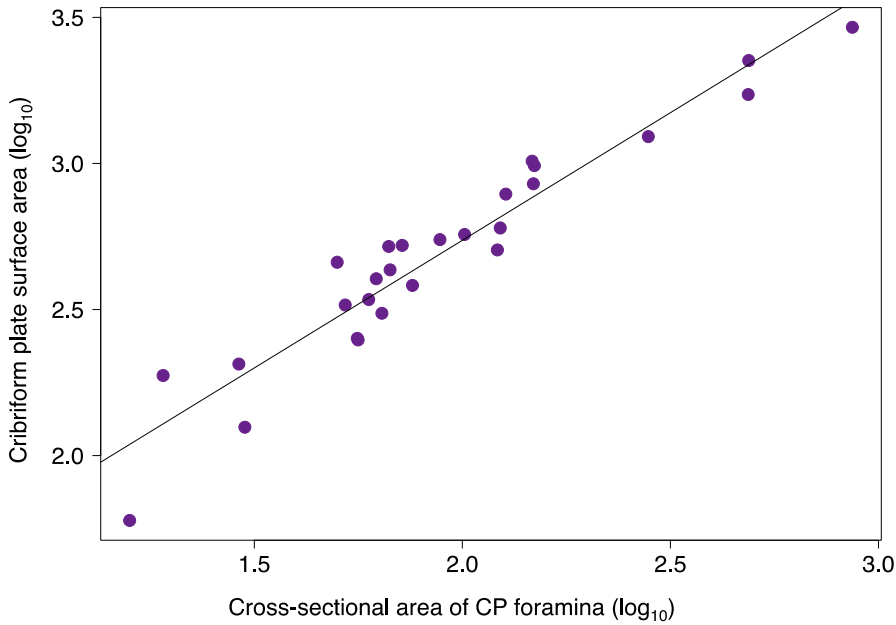
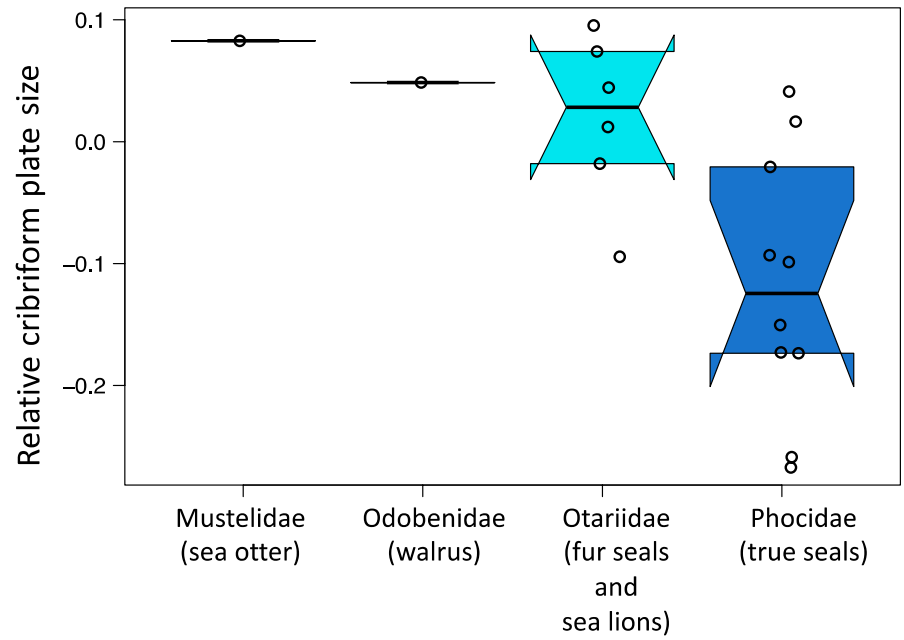


FIGURE A3 Log-log regression plot of CP surface area vs. cumulative cross-sectional area of CP foramina (mm^2) for 26 arctoid species, ($r^2 = .92$, $\text{pgls-}r^2 = .9$, $p < .001$).

FIGURE A4 The influence of phylogeny on relative cribriform plate size among aquatic carnivorans. While there is overlap across all four families, the phocids tend to have, on average, smaller cribriform plates than the otariids, as well as the odobenid and mustelid. See Table S3 Summary Statistics.



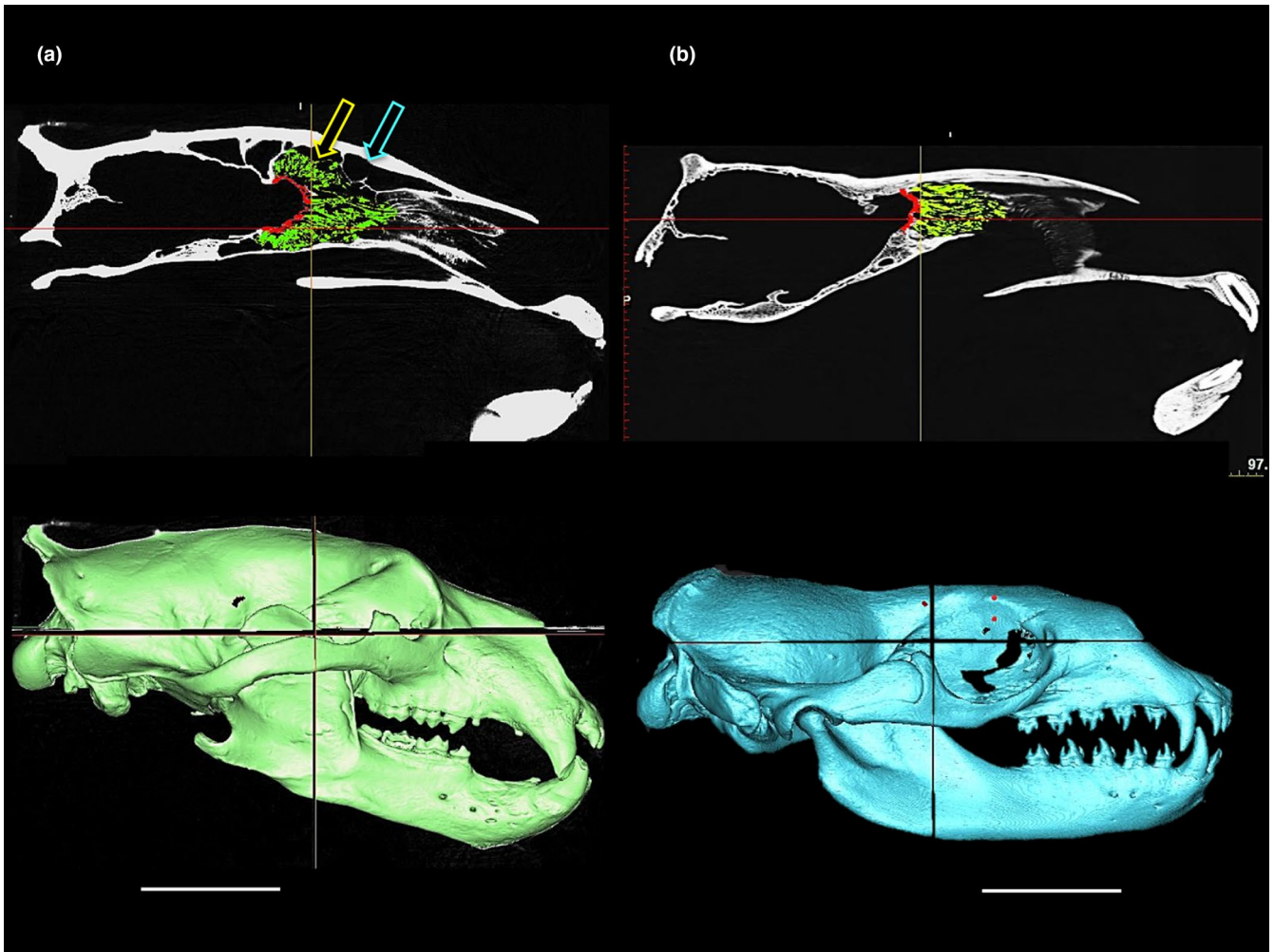


FIGURE A5 Dorsal distribution of olfactory turbinals in terrestrial and aquatic carnivorans. (a) Terrestrial carnivoran, polar bear (*Ursus maritimus*) skull in lateral aspect. Top, sagittal section at skull midline from CT scan. Green, olfactory ethmoturbinals. Red, cribriform plate. Blue open arrow, frontal sinus with no turbinals. Yellow open arrow, ethmoturbinals that have invaded the frontal sinus. Bottom, 3D digital model (b), Aquatic carnivoran, leopard seal (*Hydrurga leptonyx*) skull. Top, sagittal section of skull from CT scan. Where turbinals extend dorsally into the frontal sinus in the polar bear, there is no frontal sinus in the leopard seal skull and no dorsal projection of the olfactory turbinals (green). Scale bars, 100 mm.

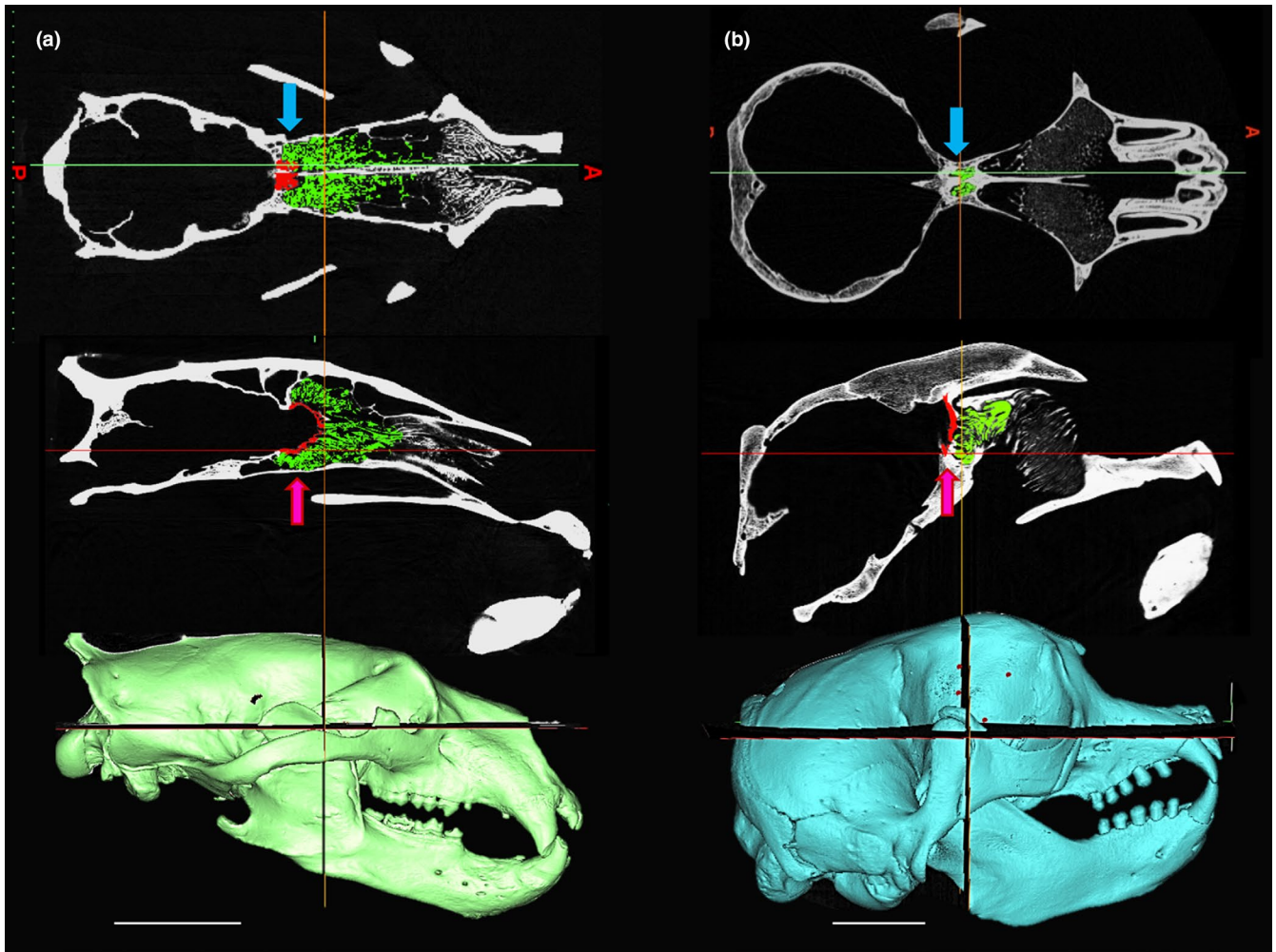


FIGURE A6 Lateral distribution of olfactory turbinals in terrestrial and aquatic carnivorans. (a) The terrestrial polar bear (*Ursus maritimus*) skull. Top, dorsal view of CT scan; middle, sagittal section at skull midline. Green, olfactory ethmoturbinals. Red, cribriform plate. Bottom, 3D digital model in lateral view. Scale bar, 100 mm. (b) Aquatic female northern elephant seal (*Hydrurga leptonyx*) skull. Top, dorsal view of CT scan; middle, sagittal section of skull from CT scan; bottom, 3D digital model in lateral view. Scale bar, 50 mm. The elephant seal skull is laterally (blue arrow) and ventrally (pink arrow) constricted in the ethmoid turbinal region relative to the polar bear.

TABLE A1 Study specimens, morphological data and scan data sources

Species	Common name	Sex	ID number	CP (mm ²)	OOL (mm)	SkL (mm)	SnL (mm)	Habitat
<i>Mephitis mephitis</i>	Striped skunk	M	USNM147553	334.65	56.49	79.78	23.29	T
<i>Mephitis mephitis</i>	Striped skunk	F	UCLAJXS001	279.35	50.05	70.35	20.3	T
<i>Enhydra lutris</i>	Sea otter	M	SO2951	363.13	113.93	133.2	19.27	A
<i>Enhydra lutris</i>	Sea otter	F	SO2853-97	321.03	106.29	126.94	20.65	A
<i>Gulo gulo</i>	Wolverine	M	USNM314885	889.6	103.6	173.36	69.76	T
<i>Gulo gulo</i>	Wolverine	F	USNM157327	813.88	100.78	152.5	51.72	T
<i>Lontra canadensis</i>	No. Amer. river otter	M	UCLA15275	223.29	87.14	121.93	34.79	SA
<i>Lontra canadensis</i>	No. Amer. river otter	F	UCLA18958	280.77	89.24	121.02	31.78	SA
<i>Mustela frenata</i>	Long tailed weasel	M	USNM52702	70.43	38.54	49.78	11.24	T
<i>Mustela frenata</i>	Long tailed weasel	F	USNM95054	49.5	31.55	40.27	8.72	T
<i>Neovison vison</i>	American mink	M	UCLA8488	125.09	59.96	73.51	13.55	SA
<i>Taxidea taxus</i>	American badger	M	UCLA14841	558.62	78	121.79	43.79	T
<i>Taxidea taxus</i>	American badger	F	LACM45012	644.17	86.3	128.99	42.69	T
<i>Potos flavus</i>	Kinkajou	M	USNM291066	268.54	66.76	88.71	21.95	T
<i>Potos flavus</i>	Kinkajou	F	LACM07241	228.84	64.56	87.45	22.89	T
<i>Procyon lotor</i>	Raccoon	M	LACM52261	353.08	75.53	120.95	45.42	T
<i>Procyon lotor</i>	Raccoon	F	LACM07241	412	77.94	122.62	44.68	T
<i>Ailuropda melanoleuca</i>	Giant panda	U	CAS6072	741.58	170.52	247.93	77.41	T
<i>Ursus americanus</i>	American black bear	M	USNM22070	2218.1	178.74	231.46	52.72	T
<i>Ursus americanus</i>	American black bear	F	USNM211397	1339.4	129.79	261.7	131.91	T
<i>Ursus americanus</i>	American black bear	M	MVZ162985	1607.4	196.6	301.2	104.6	T
<i>Ursus arctos</i>	Grizzly bear	M	USNM82003	2964.9	237.14	371.24	134.1	T
<i>Ursus arctos</i>	Grizzly bear	F	USNM98062	2317.9	205.65	325.7	120.05	T
<i>Ursus arctos</i>	Grizzly bear	U	MFWP113	1467.8	194.8	277.88	83.08	T
<i>Ursus maritimus</i>	Polar bear	F	MVZ123991	2453.6	232.1	329.2	97.1	T
<i>Ursus maritimus</i>	Polar bear	M	H001_51	2800.1	266.74	374.41	107.67	T
<i>Ursus maritimus</i>	Polar bear	U	USNM275072	3523.5	279.7	395.22	115.52	T
<i>Erignathus barbatus</i>	Bearded seal	M	LACM072575	337.6	139.56	195.57	56.01	A
<i>Erignathus barbatus</i>	Bearded seal	F	LACM072576	468.15	155.01	222.8	67.79	A
<i>Hydrurga leptonyx</i>	Leopard seal	M	USNM270326	992.41	254.23	374.49	120.26	A
<i>Hydrurga leptonyx</i>	Leopard seal	F	USNM269533	973.3	273.88	385.05	111.17	A
<i>Leptonychotes weddellii</i>	Weddell seal	F	MVZ127755	548.55	214.5	NA	NA	A
<i>Lobodon carcinophagus</i>	Crabeater seal	U	MVZ127751	552.23	175.53	246.13	70.6	A
<i>Lobodon carcinophagus</i>	Crabeater seal	F	MVZ127754	541.97	156.11	218.79	62.68	A
<i>Mirounga angustirostris</i>	No. elephant seal	F	MVZ 184140	310.62	181.51	241.74	60.23	A
<i>Mirounga angustirostris</i>	No. elephant seal	M	LACM054394	729	352.92	481.74	128.82	A
<i>Mirounga leonina</i>	So. elephant seal	M	LACM084290	755.24	365	NA	NA	A
<i>Mirounga leonina</i>	So. elephant seal	F	LACM084245	575	264.93	NA	NA	A
<i>Neomonachus schauinslandi</i>	Hawaiian monk seal	U	LACM54438	453.85	184.95	NA	NA	A
<i>Neomonachus schauinslandi</i>	Hawaiian monk seal	U	LACM53325	451.18	176.64	230.72	54.08	A
<i>Neomonachus tropicalis</i>	Tropical monk seal	M	USNM100358	510.89	187.09	268.61	81.52	A
<i>Neomonachus tropicalis</i>	Tropical monk seal	F	USNM102527	407	170.38	236.7	66.32	A
<i>Pusa sibirica</i>	Baikal seal	U	LACM52337	187.99	109.44	150.04	40.6	A
<i>Phoca vitulina</i>	Harbor seal	U	UCLA1408	339.3	156.9	NA	NA	A

(Continues)

TABLE A1 (Continued)

Species	Common name	Sex	ID number	CP (mm ²)	OOL (mm)	SkL (mm)	SnL (mm)	Habitat
<i>Phoca vitulina</i>	Harbor seal	M	LACM095963	295	125.21	167.61	42.4	A
<i>Phoca vitulina</i>	Harbor seal	F	LACM31462	348.67	139.04	199.53	60.49	A
<i>Pusa hispida</i>	Ringed seal	M	LACM54781	216.29	132.37	177.75	45.38	A
<i>Pusa hispida</i>	Ringed seal	F	LACM22949	195.35	115.75	152.01	36.26	A
<i>Arctocephalus galapagoensis</i>	Galapagos fur seal	M	LACM031309	524.4	152.22	199.69	47.47	A
<i>Arctocephalus pusillus</i>	Cape fur seal	M	LACM052358	614.92	190.35	252.9	62.55	A
<i>Arctocephalus pusillus</i>	Cape fur seal	F	LACM052359	396.92	155.49	196.77	41.28	A
<i>Callorhinus ursinus</i>	Northern fur seal	M	LACM052343	453.18	144.56	194.96	50.4	A
<i>Callorhinus ursinus</i>	Northern fur seal	F	LACM054630	411.63	149.01	188.51	39.5	A
<i>Eumetopias jubatus</i>	Steller sea lion	M	LACM052314	1475.2	295.39	374.75	79.36	A
<i>Eumetopias jubatus</i>	Steller sea lion	F	LACM052316	996.41	241.81	310.61	68.8	A
<i>Otaria flavescens</i>	So. Amer. sea lion	M	LACM095756	681.19	237.95	335.19	97.24	A
<i>Otaria flavescens</i>	So. Amer. sea lion	F	LACM095771	461.62	161.96	208.94	46.98	A
<i>Zalophus californianus</i>	California sea lion	M	UCLA252	868.25	214.3	291.75	77.45	A
<i>Zalophus californianus</i>	California sea lion	F	LACM95730	599.49	155.72	203.29	47.57	A
<i>Zalophus californianus</i>	California sea lion	M	UCLA1118	888.52	200.39	NA	NA	A
<i>Odobenus rosmarus</i>	Walrus	F	UCLA2471	1018.2	258.82	350.42	91.6	A
<i>Odobenus rosmarus</i>	Walrus	M	UCLA15306	1104.7	270.46	367.47	97.01	A
High resolution CT scanner			Scanning facility					
GE Phoenix nanotom s			Molecular Imaging Center, University of Southern California					
Nikon Metrology XT H 225 ST			Molecular Imaging Center, University of Southern California					
North Star Imaging ACTIS			The Univ. of Texas High-Resolution X-ray Computed Tomography Facility					
Xradia microXCT			The Univ. of Texas High-Resolution X-ray Computed Tomography Facility					
Siemens SOMATOM definition AS64			Ronald Reagan Medical Center UCLA					
Imaging software								
Mimics v. 15.0-21.0			Materialise; Leuven, Belgium					
3-Matics v. 7.0.1-13.0			Materialise; Leuven, Belgium					
Rhinceros v. 4			Robert McNeel and Associates					

Abbreviations: A, Aquatic; CP, cribriform plate surface area; F, female; M, male; OOL, occiput-orbit length (occipital condyle to prosthion); SA, Semi-aquatic; SkL, Skull length (occipital condyle to prosthion); SnL, Snout length (anterior orbit border to prosthion); T, Terrestrial; U, unknown sex.

TABLE A2 Dive data for all aquatic species, and sources. Maximum dive depth and duration values were sourced from single studies. Mean dive depth and duration were sourced and averaged from multiple studies where available. In calculating an overall average, individual study averages were weighted by sample size.

Species	Mean depth (m)	N	References	Mean duration (min)	N	References	Max. depth (m)	References	Max. duration (min)	References	
Phocidae											
<i>Erignathus barbatus</i>	20.98	11	Krafft, Lydersen, Kovacs, Gjertz, and Haug (2000), Hamilton, Kovacs, and Lydersen (2018)	3.73	11	Krafft et al. (2000) and Hamilton et al. (2018)	472	Gjertz, Kovacs, Lydersen, and Wiig (2000)	24	Hamilton et al. (2018)	
<i>Hydrurga leptonyx</i>	17.12	29	Kuhn et al. (2006), Krause, Goebel, Marshall, and Abernathy (2015) and Krause, Goebel, Marshall, and Abernathy (2016)	2.19	22	Kuhn et al. (2006) and Krause et al. (2016)	424.5	Kuhn et al. (2006)	15	Nordøy and Blix (2008)	
<i>Leptonychotes weddellii</i>	163.21	43	Schreer and Testa (1996), Costa, Huckstadt, et al. (2010), Costa, Robinson, et al. (2010), Heerah et al. (2013) and Shero, Goetz, Costa, and Burns (2018)	13.24	43	Schreer and Testa (1996), Costa, Robinson, et al. (2010), Costa, Huckstadt, et al. (2010), Heerah et al. (2013) and Shero, Goetz, Costa, and Burns (2018)	904	Heerah et al. (2013)	96	Heerah et al. (2013)	
<i>Lobodon carcinophagus</i>	47.97	80	Costa, Huckstadt, et al. (2010), Bengtson and Stewart (1992), Nordøy, Folkow, and Blix (1995), Burns et al. (2004) and Wall, Bradshaw, Southwell, Gales, and Hindell (2007)	3.02	74	Costa, Huckstadt, et al. (2010), Burns et al. (2004), Wall et al. (2007) and Nordøy et al. (1995)	712.5	Burns et al. (2004)	23.6	Burns et al. (2004)	
<i>Mirounga angustirostris</i>	504.76	353	LeBoeuf, Costa, Huntley, and Feldkamp (1989), Delong and Stewart (1991), Stewart and Delong (1995), Robinson et al. (2012) and Naito et al. (2013)	22.997	353	LeBoeuf et al. (1989), Delong and Stewart (1991), Stewart and Delong (1995), Robinson et al. (2012) and Naito et al. (2013)	1735	Robinson et al. (2012)	119	Stewart & Delong, 1995)	
<i>Mirounga leonina</i>	443.9	136	Costa, Huckstadt, et al. (2010), Hindell, Slip, and Burton (1991), Campagna, Le Boeuf, Blackwell, Crocker, and Quintana (1995), Bennett (2001), McIntyre et al. (2010), Thums, Bradshaw, Sumner, Horsburgh, and Hindell (2013) and Muelbert, de Souza, Lewis, and Hindell (2013)	28.424	136	Costa, Huckstadt, et al. (2010), Hindell et al. (1991), Campagna et al. (1995), Bennett (2001), McIntyre et al. (2010), Thums et al. (2013), and Muelbert et al. (2013)	2388	Costa, Robinson, et al., 2010; Costa, Huckstadt, et al., 2010)	120	Hindell et al. (1991)	

(Continues)

TABLE A2 (Continued)

Species	Mean depth (m)	N	References	Mean duration (min)	N	References	Max. depth (m)	References	Max. duration (min)	References
<i>Neomonachus schauinslandi</i>	33.822	48	Parrish, Abernathy, Marshall, and Buhleier (2002) pers. comm.	8	24	Parrish, Craig, Ragen, Marshall, and Buhleier (2000)	500	Parrish, Abernathy, Marshall, and Buhleier (2002)	20	Parrish et al. (2002)
<i>Pusa sibirica</i>	83.356	9	Watanabe, Baranov, Sato, Naito, and Miyazaki (2004), Watanabe (2006) and Watanabe, Baranov, and Miyazaki (2015)	7.81	9	Watanabe (2006), Watanabe et al. (2015) and Watanabe et al. (2004)	324	Watanabe (2006)	>40	Stewart, Petrov, Baranov, Timonin, and Ivanov (1996)
<i>Phoca vitulina</i>	56.81	56	Gjertz, Lydersen, and Wiig (2001), Eguchi, Harvey, and Harvey (2005) and Blanchet, Lydersen, Ims, and Kovacs (2015)	4.57	56	Gjertz et al. (2001), Blanchet et al. (2015) and Eguchi and Harvey (2005)	558	Kolb and Norris (1982)	37	Blanchet et al. (2015)
<i>Pusa hispida</i>	80.195	61	Gjertz, Kovacs, Lydersen, and Wiig (2000), Benoit, Simard, Gagné, Geoffroy, and Fortier, (2010) pers. comm., Harwood, Smith, Auld, Melling, and Yurkowski et al. (2016) pers. comm.	5.208	52	Gjertz et al. (2000)	542	Harwood et al. (2015)	>50	Gjertz et al. (2000)
Otariidae										
<i>Arctocephalus galapagoensis</i>	29.66	40	Kooyman and Trillimich (1986); Villegas-Amtmann, Jeglinski, Costa, Robinson, and Trillimich, (2013) and Jeglinski, Goetz, Werner, Costa, and Trillimich (2013)	1.7	36	Villegas-Amtmann et al. (2013) and Jeglinski et al. (2013)	131	Villegas-Amtmann et al. (2013)	7.7	Kooyman and Trillimich (1986) (2014)
<i>Arctocephalus pusillus</i>	45	2	Kooyman and Gentry (1986)	2.1	2	Kooyman et al. (1986)	204	Kooyman et al. (1986)	7.5	Kooyman et al. (1986)
<i>Callorhinus ursinus</i>	26.383	111	Goebel, Bengtson, Delong, Gentry, and Loughlin, (1991), Sterling and Ream (2004), Kuhn (2011) and Skinner, Burkanov, and Andrews (2012)	1.291	61	Sterling and Ream (2004), Kuhn (2011) and Skinner et al. (2012)	256	Gentry, Kooyman, and Goebel (1986)	9.92	Sterling and Ream (2004)
<i>Eumetopias jubatus</i>	35.522	18	Merrick, Loughlin, Antonellis, and Hill (1994), Merrick and Loughlin (1997) and Loughlin, Perlov, Baker, Blokhin, and Makhnyr (1998)	1.786	18	Merrick et al. (1994), Merrick and Loughlin (1997) and Loughlin et al. (1998)	328	Loughlin, Sterling, Merrick, Sease, and York (2003)	14	Loughlin et al. (2003)

(Continues)

TABLE A2 (Continued)

Species	Mean depth (m)	N	References	Mean duration (min)	N	References	Max. depth (m)	References	Max. duration (min)	References
<i>Otaria flavescens</i>	42.207	67	Werner & Campagna (1995), Thompson et al. (1998), Baylis et al. (2015), Hückstädt et al. (2016)	1.95	67	Werner & Campagna (1995), Thompson et al. (1998), Baylis et al. (2015), Hückstädt et al. (2016)	325	Hückstädt et al. (2016)	12.07	Hückstädt et al. (2016)
<i>Zalophus californianus</i>	44.28	127	Costa et al. (2007) and Thomas, Harvey, Goldstein, Barakos, and Gulland (2010)	1.71	127	Costa et al. (2007), Thomas et al. (2010)	575	Costa et al. (2007)	20.1	Costa et al. (2007)
Odobenidae										
<i>Odobenus rosmarus</i>	15.4	8	Gjertz, Griffiths, Krafft, Lydersen & Wiig (2001), Wiig, Gjertz, Griffiths, and Lydersen (1993) and Nyholm (1975)	5.1	16	Nyholm, 1975; Gjertz et al. 2001; Born & Knutsen, 1997	100	Fay and Burns (1988)	24	Gjertz et al. (2001)
Mustelidae										
<i>Enhydra lutris</i>	12.07	27	Bodkin et al. (2004) and Tinker et al. (2007)	1.28	27	Bodkin et al., 2004; Tinker et al., 2007; Ralls, Hatfield, & Siniff, 1995	100	Bodkin et al. (2004)	4.1	Ralls et al. (1995)

TABLE A3 Summary statistics

Abbreviations: CP, cribriform plate; OOL, occipital condyle to orbit length; PGLS, phylogenetic generalized least squares regression; RelCP, relative cribriform plate size; SkL, skull length (occipital condyle to prosthion).

Regression	Species <i>N</i>	r^2	<i>P</i> value	PGLS r^2	<i>P</i> value	PGLS equation
CP metrics						
CP surface area (log10) vs. CP foramina cross-sectional area (log10), all habitats	26	0.92	<0.001	0.9	NA	$y = 0.88x + 0.9427$
CP vs. body size proxy OOL						
CP surface area (log10) vs. OOL (log10) in all species	31	0.55	< 0.001	0.7	< 0.001	$y = 1.37x - 0.1097$
CP surface area (log10) vs. OOL (log10) in terrestrial species only	10	0.9	< 0.001	0.84	< 0.001	$y = 1.712x - 0.654$
CP surface area (log10) vs. OOL (log10) in aquatic species only	19	0.71	< 0.001	0.69	< 0.001	$y = 1.327x - 0.2397$
CP surface area (log10) vs. OOL (log10) in phocid species only	10	0.77	< 0.001	0.64	0.006	$y = 1.285x - 0.253$
CP surface area (log10) vs. SkL (log10) in all species with complete skulls	29	0.66	< 0.001	0.75	< 0.001	$y = 1.4488x - 0.4885$
Relative CP size vs. diving metrics						
Maximum dive depth						
RelCP vs. Max Depth (log10); all aquatics	18	0.55	< 0.001	0.22	0.051	$y = -0.1747x + 0.406$
RelCP vs. Max Depth (log10); phocids only	10	0.3	0.1	0.22	0.17	$y = -0.2016x + 0.565$
Mean dive depth						
RelCP vs. Mean Depth (log10); all aquatics	18	0.75	< 0.001	0.65	< 0.001	$y = -0.206x + 0.287$
RelCP vs. Mean Depth (log10); phocids only	10	0.75	0.001	0.82	< 0.001	$y = -0.197x + 0.3499$
Maximum dive duration						
RelCP vs. Max Duration (log10); all aquatics	18	0.66	< 0.001	0.48	0.001	$y = -0.221x + 0.238$
RelCP vs. Max Duration (log10); phocids only	10	0.76	< 0.001	0.78	< 0.001	$y = -0.260x + 0.4057$
Mean dive duration						
RelCP vs. Mean Duration (log10); all aquatics	18	0.76	< 0.001	0.61	< 0.001	$y = -0.251x + 0.104$
RelCP vs. Mean Duration (log10); phocids only	10	0.79	< 0.001	0.88	< 0.001	$y = -0.260x + 0.2097$
Pair-wise ANOVA						
	<i>N</i>	Tukey HSD post-hoc test <i>P</i> value	One-way ANOVA <i>P</i> value			
Habitat and RelCP among all species						
Mean RelCP, all three habitat groupings	31		<0.0001			
Mean RelCP, Aquatics vs. Terrestrials	29	< 0.0001				
Mean RelCP, Aquatics vs. Semi-aquatics	21	1				
Mean RelCP, Terrestrials vs. Semi-aquatics	12	0.014				
Habit and RelCP among Musteloidea only						
Mean RelCP, Aquatics plus Semi-aquatics vs. Terrestrials	9	0.007				
Phylogeny and RelCP						
Mean RelCP, Phocids vs. Otariids	16	0.015				
Mean RelCP, Phocids vs. Otariids plus Odobenid	17	0.019				
Habitat and snout length						
Mean snout length, Aquatics vs. Terrestrials	27	0.036				