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Comparing vibrissal morphology and infraorbital foramen area in pinnipeds

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Abstract

Pinniped vibrissae are well-adapted to sensing in an aquatic environment, by being morphologically diverse and more sensitive than those of terrestrial species. However, it is both challenging and time-consuming to measure vibrissal sensitivity in many species. In terrestrial species, the infraorbital foramen (IOF) area is associated with vibrissal sensitivity and increases with vibrissal number. While pinnipeds are thought to have large IOF areas, this has not yet been systematically measured before. We investigated vibrissal morphology, IOF area, and skull size in 16 species of pinniped and 12 terrestrial Carnivora species. Pinnipeds had significantly larger skulls and IOF areas, longer vibrissae, and fewer vibrissae than the other Carnivora species. IOF area and vibrissal number were correlated in Pinnipeds, just as they are in terrestrial mammals. However, despite pinnipeds having significantly fewer vibrissae than other Carnivora species, their IOF area was not smaller, which might be due to pinnipeds having vibrissae that are innervated more. We propose that investigating normalized IOF area per vibrissa will offer an alternative way to approximate gross individual vibrissal sensitivity in pinnipeds and other mammalian species. Our data show that many species of pinniped, and some species of felids, are likely to have strongly innervated individual vibrissae, since they have high values of normalized IOF area per vibrissa. We suggest that species that hunt moving prey items in the dark will have more sensitive and specialized vibrissae, especially as they have to integrate between individual vibrissal signals to calculate the direction of moving prey during hunting.

KEYWORDS

seal, sea lion, touch sensing, vibrissa*, walrus

1 | INTRODUCTION

The order Carnivora is an ecologically and taxonomically diverse group of mammals. Perhaps the largest ecological

transition in Carnivoran evolution was the shift from terrestrial to aquatic lifestyles (Botton-Divet, Cornette, Houssaye, Fabre, & Herrel, 2017; Goswami, Milne, & Wroe, 2011; Jones, Smaers, & Goswami, 2015;

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Radinsky, 1981; Slater, Figueirido, Louis, Yang, & Van Valkenburgh, 2010; Van Valkenburgh, 2007), which is strongly apparent in the semiaquatic pinnipeds: seals, sea lions, and walruses (Berta et al., 2015), as well as in the mustelids: otters and minks (Botton-Divet et al., 2017) and ursids (polar bears) (Slater et al., 2010). An aquatic lifestyle has driven morphological diversity in the Carnivora, especially in skeletal structures, such as the spine, limbs, digits, and skull (Botton-Divet et al., 2017; Goswami et al., 2011; Jones et al., 2015; Radinsky, 1981; Slater et al., 2010; Van Valkenburgh, 2007). While skull morphology is less divergent in the aquatic Carnivora species compared to other marine mammal groups, such as cetacean or sirenians, this does make it easy to directly compare between aquatic and terrestrial species (Jones et al., 2015). Despite similarities in Carnivora skulls, all pinnipeds, including fossil and recent taxa, can be defined by a range of morphological skull characteristics, including a large infraorbital foramen (IOF) (Figure 1, red arrow), large nasal openings, an anteriorly positioned incisive foramen, some reduction of molar teeth, and a fused or absent lacrimal (Berta, 2018; Berta, Churchill, & Boessenecker, 2018; Jones et al., 2015). These adaptations in skull morphology in pinnipeds are likely to be especially associated with feeding and sensing underwater (Botton-Divet et al., 2017; Van Valkenburgh, 2007). One such sensory specialization is the vibrotactile vibrissal sense that is particularly well-developed in pinnipeds to guide foraging and hunting underwater (Bauer, Reep, & Marshall, 2018; Dehnhardt & Hanke, 2018; Dehnhardt, Hanke, Wieskotten, Krüger, & Miersch, 2014).

Indeed, vibrissae are thought to be especially important in pinnipeds to guide navigation and hunting in dark underwater environments (Bauer et al., 2018; Dehnhardt et al., 2014; Dehnhardt & Hanke, 2018), and their vibrissae are well-adapted to their function. Pinniped vibrissae tend to be shorter, thicker, and more tapered than those of terrestrial species (Dougill et al., 2020). They also vary across species in shape, number, and arrangement. Indeed, Phocid seals are the only family to have undulating vibrissae (Ginter, Fish, & Marshall, 2009; Hanke et al., 2010), which are suggested to be an adaptation to underwater sensing by reducing signal-to-noise ratios as the animal swims through the water (Hanke et al., 2010).

As well as having morphological specializations, pinniped vibrissae are also particularly sensitive (Hyvärinen, 1989; Jones & Marshall, 2019; Marshall, Amin, Kovacs, & Lydersen, 2006; Mattson & Marshall, 2016; Smodlaka, Gale, Palmer, Borovac, & Khamas, 2017; Sprowls & Marshall, 2019), further supporting the importance of vibrissal sensing in pinnipeds. The deep vibrissal nerve, which is a branch of the infraorbital nerve (ION), contains 10 times more nerve

fibers in pinnipeds, than in terrestrial mammals (Hyvärinen, 1989; Hyvärinen, Palviainen, Strandberg, & Holopainen, 2009). In addition, pinniped vibrissal follicles are protected from cooling by having a good blood supply (Erdsack, Dehnhardt, & Hanke, 2014; Mauck, Eysel, & Dehnhardt, 2000), enabling the vibrissae to be sensitive over a wide range of air and water temperatures (Dehnhardt, Mauck, & Hyvärinen, 1998). Diversity in vibrissal shape and arrangement, and the adaptations within the follicle, are all likely to affect vibrissal mechanics as well as the distribution of innervation within the follicle (Ebara, Kumamoto, Matsuura, Mazurkiewicz, & Rice, 2002) and across the vibrissal pad (Mattson & Marshall, 2016; Sprowls & Marshall, 2019). It is, however, challenging to quantify vibrissal innervation and sensitivity. Such quantification requires precise, time-consuming measurements from anatomy (Hyvärinen, 1989; Sprowls & Marshall, 2019) or behavioral procedures (Dehnhardt, 1990; Dehnhardt et al., 1998; Dehnhardt & Dücker, 1996).

In terrestrial mammals, the IOF area is suggested to reflect vibrissal sensitivity. The IOF is a small hole in the skull through which the ION passes (Muchlinski, 2008). The ION innervates the lower eyelid, nose, cheek (including the whiskers), and upper lip. The ION area accounts for over 85% of IOF cross-sectional area in terrestrial mammals, so IOF area can act as a proxy for ION area (Gasser & Miller, 1972; Muchlinski, 2008; Patrizi & Munger, 1966). Large IOF and ION areas are found in terrestrial mammals that have more numerous vibrissae (Kay & Cartmill, 1977; Muchlinski, 2010). In small, terrestrial mammals, IOF area is also associated with vibrissal movement abilities, and species that cyclically move their whiskers (whisk) have larger IOF areas (Muchlinski, Wible, Corfe, Sullivan, & Grant, 2020). Therefore, a large IOF area is thought to be associated with high vibrissal sensory acuity. However, the association of IOF area with vibrissal number and sensitivity is complex, and we do not yet fully understand this relationship. Certainly, it is not possible to predict vibrissal number from IOF area as this relationship is not strong enough (Muchlinski, 2010; Muchlinski et al., 2020). While the IOF area has been reported to be especially large in pinnipeds and some terrestrial, fossorial Carnivorans (Berta et al., 2018; Hafed, Koretsky, & Rahmat, 2020), this has not yet been systematically measured in pinnipeds. Although we might expect IOF area to increase with vibrissal number in a similar way to terrestrial species, and for it to also be large, due to the many nerve fibers around pinniped vibrissal follicles.

The aim of this study is to characterize vibrissal morphology (length, number, and presence of undulations), IOF area, and skull size in 16 species of pinniped and



FIGURE 1 Example vibrissal morphology of Odobenidae (a), Phocidae (b), and Otariidae (c). Individual vibrissal shape can be seen on the left, the gross vibrissal layout in the center, and the skull shapes on the right, with the infraorbital foramen (IOF) indicated by the red arrow. Representative species here include Pacific walrus (*Odobenus rosmarus*), Harbor seal (*Phoca vitulina*), and California sea lion (*Zalophus californianus*)

12 terrestrial Carnivora species. While vibrissal morphology can be measured from images (Dougill et al., 2020; Ginter, DeWitt, Fish, & Marshall, 2012; Starostin, Grant, Dougill, van der Heijden, & Goss, 2020), vibrissal sensitivity is especially challenging to quantify. Here, we discuss whether measuring the IOF area in pinnipeds could serve as an estimation of gross vibrissal sensitivity. If so,

we might expect the IOF area to be larger in pinnipeds compared to terrestrial Carnivora species, due to their increased vibrissal innervation. If we can confirm an association between whisker metrics and IOF area, then perhaps IOF area can be used to evaluate differences in maxillary mechanoreception in extinct and extant Carnivora species.

2 | METHODS

2.1 | Specimens

All data were collected from museum specimens and approved by the local ethics committee at Manchester Metropolitan University. For the pinniped specimens, skin and skull collections were examined at Liverpool World Museum (Liverpool, UK), Manchester Museum (Manchester, UK), and National Museums Scotland (Edinburgh, UK). Sixteen pinniped species were included in this study, representing ~50% of all extant pinniped species, and included 11 phocids, four otariids, and one odobenid (Supplementary Table S3). To compare pinnipeds with other terrestrial Carnivora species, available data from a previous study by Muchlinski (2010) were used, including data from 12 species: one canid, five Felids, three mustelids, and three procyonids (Supplementary Table S3). Sample sizes for all specimens can be seen in the Supplementary data table (Supplementary Table S3).

2.2 | Skull measurements

Pinniped skulls were measured if the whole skull was intact, including the IOF. Full species identification labels also had to be present. Skull length was measured as the maximum cranial length (mm), which is the linear distance between the prosthion and opisthocranium. Skull width was measured as the linear distance between the most lateral points on the zygomatic arches. The geometric mean (GM) was approximated by using these two measurements as a proxy of skull size by taking the square root of the skull width multiplied by skull length (Muchlinski, 2010). The IOF width and length were also measured using digital calipers and could be identified as the shortest and longest diameter measurement of the IOF, respectively. In order to compare to other studies and datasets, the IOF area was calculated from our length measurements. Since pinniped IOFs were relatively regular in shape (Supplementary Figure S1), IOF area (in mm^2) could be approximated well as an oval ($\pi \times \text{length}/2 \times \text{width}/2$), with a maximum error of 7 mm^2 (Supplementary Table S1).

For the other Carnivora species, data were used from Muchlinski (2010). GM was obtained in the same way as above. IOF area was approximated by taking a mold of the IOF area. These molds were sectioned and photographed with a scale under a stereomicroscope, and IOF area was obtained by tracing around the mold using Scion Image[®] software (for details see Muchlinski, 2010). This approach is especially important when species have

irregularly shaped IOFs and is equivalent to measuring the IOF area using other techniques, such as manually tracing around the IOF from images (Muchlinski et al., 2020, Supplementary Table S1).

2.3 | Vibrissal measurements

Vibrissal number was obtained for the pinniped species from counting all the vibrissal follicles (macro and micro-vibrissae) present on skin collections. Skins were included in the study if there were no rips or tears on either side of the face, vibrissae were present on both sides of the muzzle, and full species identification labels were present. The availability and quality of skins were more variable than skulls, therefore, only 12 species of pinniped could be examined (including 16 individual skins). For the other four species, including the Ribbon seal (*Histriophoca fasciata*), the Harp seal (*Pagophilus groenlandicus*), the Ross seal (*Ommatophoca rossii*), and the Southern Elephant seal (*Mirounga leonina*), vibrissae were counted from suitable photographs via a Google Image search (recorded in Supplementary Table S2). Photographs were selected of adult pinnipeds with their faces in focus to count vibrissal follicles. Three photographs (of three different individuals) were selected for each species to give an average number for each of the species. Vibrissae were counted on each side of the face in the skin specimens and one side of the face from photographs. Median per-side vibrissal counts were calculated for each species. Vibrissal number was obtained for other Carnivora species from the Muchlinski (2010) dataset, which were calculated as median vibrissal counts for each species, also from one side of the face.

For the 12 pinniped species with intact skins, vibrissal length was also approximated. This was done by measuring the three longest vibrissae on each side of the face, and an average was recorded. Vibrissal length of the three longest vibrissae was also compiled for the other Carnivora species from Muchlinski (unpublished). It was also recorded whether the vibrissae were smooth (0) or undulating (1), indicated by the presence of waves or bumps along the profile of the vibrissa that was identified by touch and by eye.

2.4 | Statistical analysis

A carnivoran consensus tree and posterior distribution of 1,000 trees were downloaded from the 10kTrees website (<https://10kTrees.nunn-lab.org/>). We investigated the phylogenetic signal of our vibrissal and skull morphology measures, which is the tendency of related species to

resemble each other more than species drawn at random from the same tree. The strength of phylogenetic signal present was calculated across the 1,000 trees as Pagel's lambda (λ), using the "phylosig" function of phytools. We assume the measures all follow the expectations of Brownian motion modeling ($0 < \lambda < 1$). A likelihood ratio test evaluated whether λ was significantly different from zero. A strong phylogenetic signal, indicating that the trait is evolving by Brownian motion, is indicated by a λ -value close to 1 and a p -value $< .05$. Previous studies have found that skull morphology does not have a strong phylogenetic signal, being better associated with life history and ecological traits (Jones & Goswami, 2010); however, vibrissal morphology has been found to be similar in related otariid or phocid species (Ginter et al., 2012). Therefore, we may also expect vibrissal morphology variables to have a phylogenetic signal but not skull morphology.

All variables were analyzed using per-species mean values. All variables were correlated against the skull size (GM) to identify which needed to be normalized [as per the recommendations of Jungers, Falsetti, & Wall, 1995]. Only IOF area was correlated to GM ($p < .05$), therefore, a normalized ratio measure was calculated by dividing IOF area by the GM, termed here *normalized IOF area*. However, both raw and normalized values will be presented throughout for transparency. Since sample numbers were low and data were not normally distributed, nonparametric tests were used. Spearman's rank correlations were used to correlate IOF area, GM, normalized IOF area, normalized vibrissal length, and vibrissal number in all the Carnivora species and pinnipeds. GM, normalized IOF area, normalized vibrissal length, and vibrissal number were compared between pinnipeds and other Carnivora species using Mann-Whitney U tests, and between families using Kruskal-Wallis tests.

3 | RESULTS

3.1 | Vibrissal and skull morphology descriptions in pinnipeds

All measured vibrissae-related variables had highly significant phylogenetic signals within the pinnipeds (within the black box in Figure 2, Table 1), indicated by λ -values of around 1 and p -values $< .05$, including IOF area, normalized IOF area, vibrissal length, vibrissal number, and undulations. However, GM did not have a significant phylogenetic signal (within the black box in Figure 2, Table 1). This indicates that more related species had similar vibrissal lengths, numbers, undulations, and IOF areas (within the black box in Figure 2, Table 1). However, statistically comparing these measures between the families

(Phocidae, Otariidae, and Odobenidae) indicated that there were no significant differences in vibrissal and skull variables between the different pinniped families, apart from normalized IOF area, which was larger in otariids than phocids [Figure 3(e), Supplementary Table S4].

Although not significant, there were gross vibrissal morphology patterns between the pinniped families, which probably accounted for the significant phylogenetic signals. Otariids had the longest vibrissae and largest IOF areas overall, Odobenidae had the highest number of vibrissae, and phocids were the only family to have undulating vibrissae (Figures 1 and 3, Supplementary Table S3). Vibrissal number for the majority of the otariids was relatively low in comparison to most other pinnipeds (phocids 22–53 vibrissae, otariids 20–32 vibrissae, Odobenidae 149 vibrissae, Figure 3c). Phocid vibrissae varied in length from a few centimeters (3.7 in the Leopard seal, *Hydrurga leptonyx*) to 12 cm in the Grey seal, *Halichoerus grypus* (Supplementary Table S3). The longest vibrissae were found in the otariids with all species studied having vibrissae longer than 9 cm (9–20 cm). California sea lions (*Zalophus californianus*) and Stellar sea lions (*Eumetopias jubatus*) had the longest vibrissae (Supplementary Table S3). The odobenids had slightly shorter vibrissae than both otariids and phocids, measuring 5–8 cm (Figures 1 and 3d, Supplementary Table S3). The phocids had a variety of different sized IOF areas, ranging from 0.2 to 0.9 cm², while the otariids had slightly larger IOF areas (and normalized IOF areas) than the phocids, ranging from 0.4 to 2.0 cm² (Supplementary Table S3, Figure 3a,e).

3.2 | Vibrissal and skull morphology comparisons

Looking at the measured variables across the Carnivora species (including the pinnipeds), GM, normalized IOF area, vibrissal length, and undulations all had significant phylogenetic signals (Table 1, indicated by λ -values of around 1 and p -values $< .05$). GM, IOF area, and vibrissal length were all significantly larger in pinnipeds compared to other Carnivora species, while vibrissal number was significantly lower (all p -values $< .05$, Figure 3; Supplementary Table S4). There were no significant differences in GM, normalized IOF area, IOF area, vibrissal length, or vibrissal number between families of other Carnivora species that did not include the pinnipeds (Figure 3, $p > .05$, Supplementary Table S4).

While the IOF area was significantly larger in pinnipeds compared to other Carnivora species, it was also well-correlated to GM, so species with larger skulls had larger IOF areas ($r = .697$, $p < .001$, Figure 4a). Once IOF was normalized to skull size, it was not significantly larger in pinnipeds compared to other Carnivora

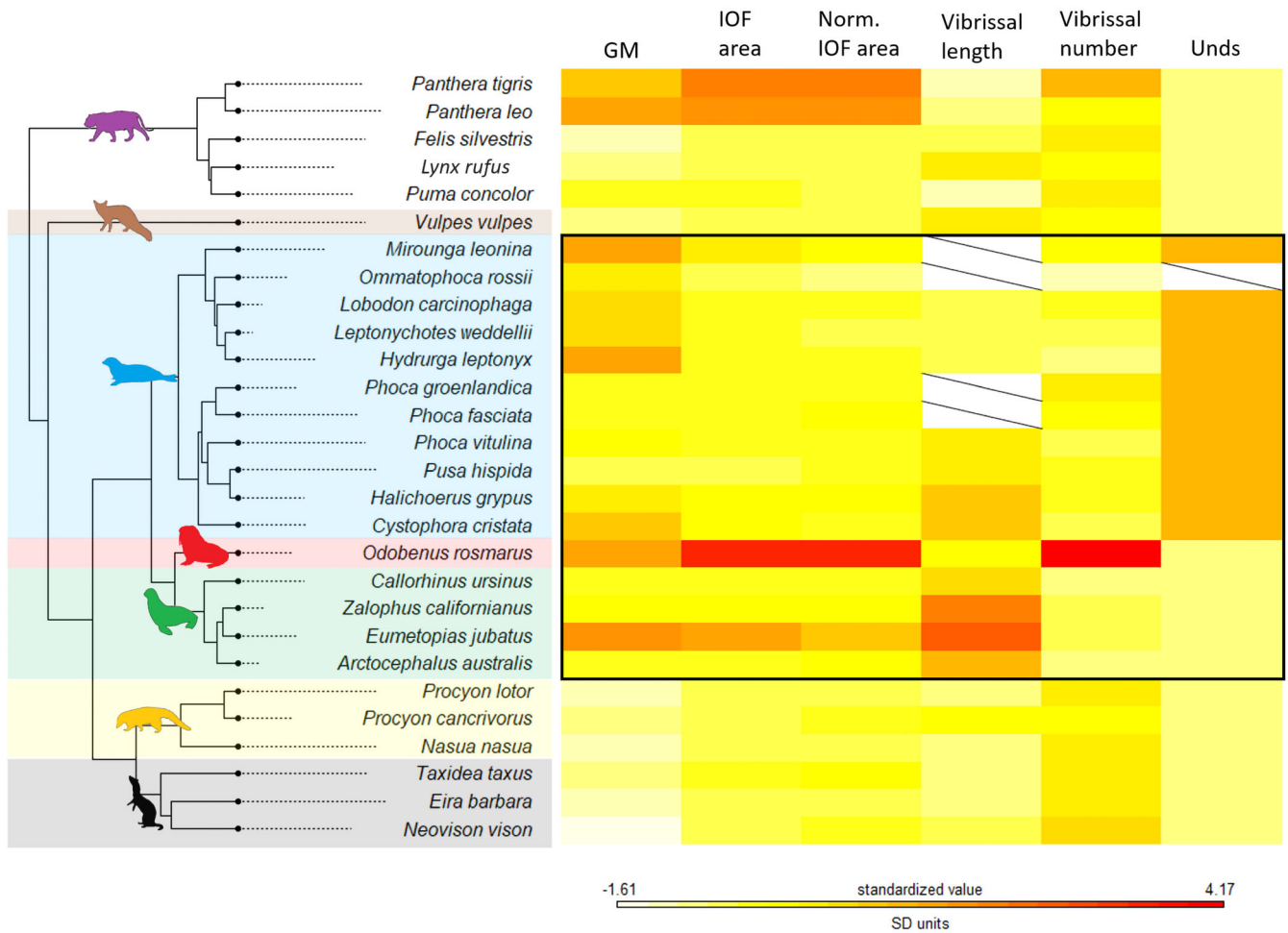


FIGURE 2 Phylogeny of the Carnivorans and heatmap of vibrissal and skull variables. Values in each column of the heatmap have been standardized to have the same mean and variance to facilitate the use of a shared colormap. Colors correspond to the families Felidae (purple), Canidae (brown), Phocidae (blue), Odobenidae (red), Otariidae (green), Procyonidae (yellow), and Mustelidae (black). Pinnipeds are all contained by the black box. White boxes with black strike-through correspond to absent data

| Variable | Pinnipeds only | | Carnivora (including pinnipeds) | |
|---------------------|----------------|--------|---------------------------------|--------|
| | λ | p | λ | p |
| GM | <0.001 | 1 | 0.68 | .024* |
| IOF area | 1.00 | .029* | 1.00 | .074 |
| Normalized IOF area | 1.00 | .005* | 1.00 | .023* |
| Vibrissal length | 0.99 | .011* | 0.91 | <.001* |
| Vibrissal number | 1.00 | .004* | 0.03 | .073 |
| Undulations | 1.00 | <.001* | 1.00 | <.001* |

TABLE 1 Skull and vibrissal morphology phylogenetic signal

species ($U = 58, z = -1.764, p = .082$; Figure 3e). The odobenid walrus (*Odobenus rosmarus*), otariid Stellar sea lion (*Eumetopias jubatus*), and felids lion (*Panthera leo*) and tiger (*Panthera tigris*) all had large IOF areas and normalized IOF areas (Figures 2 and 4, Supplementary Table S3).

Normalized IOF area was not significantly correlated to vibrissal length ($r = -.077, p = .719$), and vibrissal length was not correlated to vibrissal number in any of the species ($r = -.320, p = .127$). Normalized IOF area was, however, correlated to vibrissal number ($r = .674, p < .001$, Figure 4b) in all Carnivora species and was

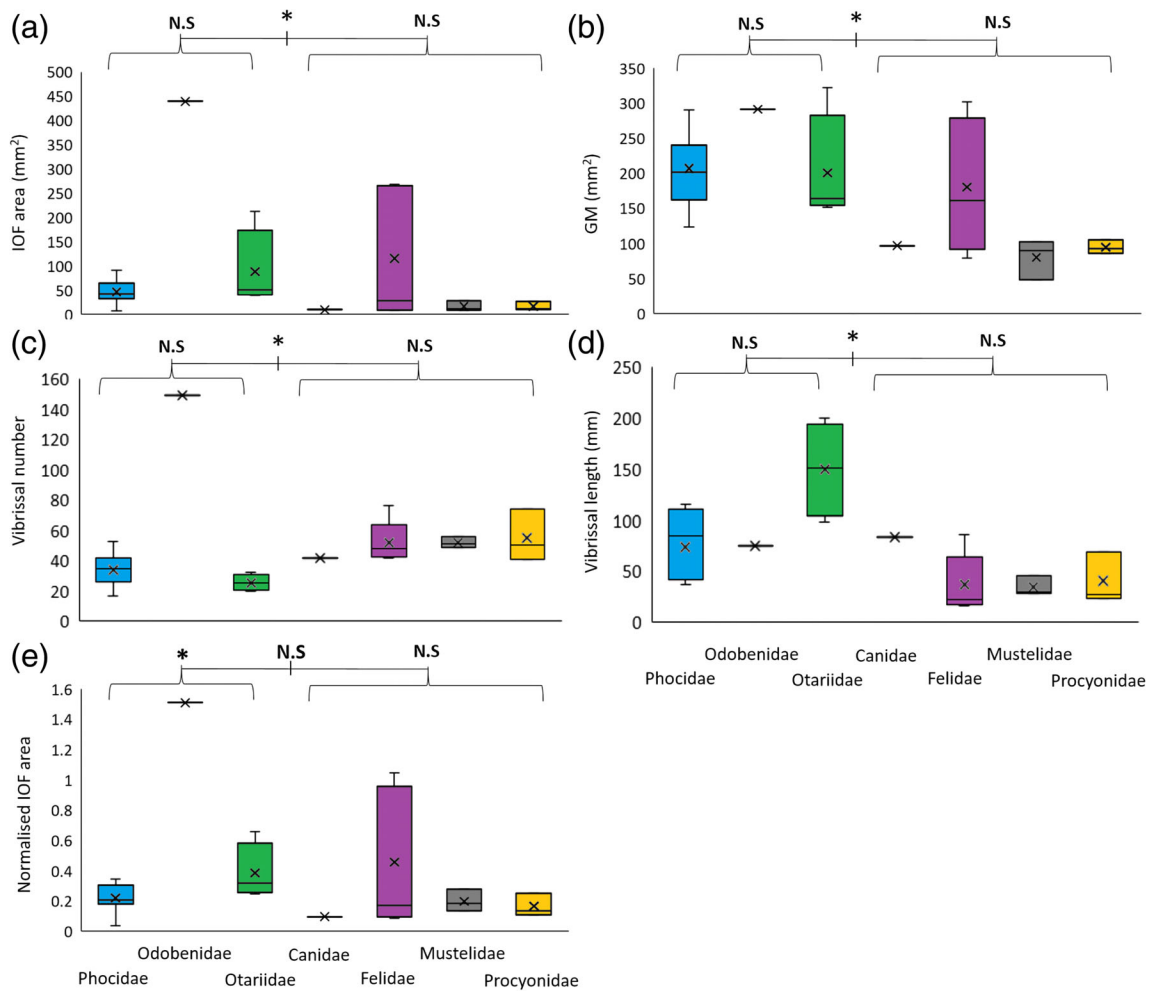


FIGURE 3 Summary vibrissal and skull morphology measures in boxplots. Statistical comparisons are conducted between pinniped species (Phocidae, Odobenidae, Otariidae) and between other Carnivora species (Canidae, Felidae, Mustelidae, Procyonidae); and also between pinnipeds and non-pinnipeds. N.S.: Nonsignificant results, $p < .05$. Colors correspond to the families Felidae (purple), Canidae (brown), Phocidae (blue), Odobenidae (red), Otariidae (green), Procyonidae (yellow), and Mustelidae (black)

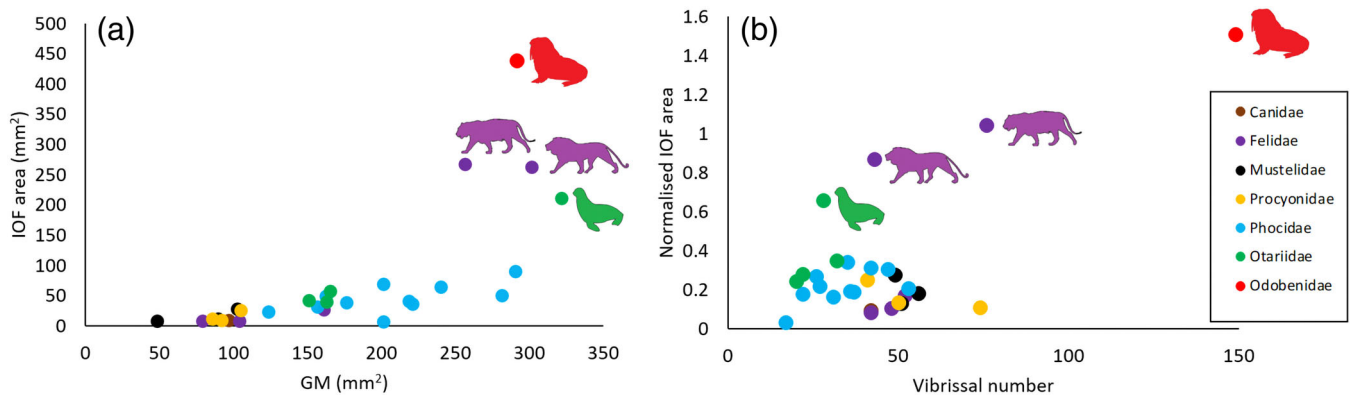


FIGURE 4 Vibrissal and skull morphology scattergrams for (a) IOF area and skull geometric mean (mm^2). IOF area and skull geometric mean (GM) were well-correlated ($p < .001$); (b) Normalized IOF area was correlated to vibrissal number ($p < .0001$). Colors correspond to the families Felidae (purple), Canidae (brown), Phocidae (blue), Odobenidae (red), Otariidae (green), Procyonidae (yellow), and Mustelidae (black). Species with the largest IOF areas and normalized IOF areas are indicated on the graph by the species silhouette images and include *Odobenus rosmarus*, *Eumetopias jubatus*, *Panthera leo*, and *Panthera tigris*

maintained when only the pinniped species were tested ($r = .889, p < .001$) (Figure 4b). IOF area was also correlated to vibrissal number in all the Carnivora species ($r = .637, p < .001$), and this correlation was also maintained when only the pinniped species were tested ($r = .858, p < .001$).

4 | DISCUSSION

Pinnipeds had significantly larger skulls and IOF areas, longer vibrissae, and fewer vibrissae than the other Carnivora species measured here (Figure 3). However, when IOF area was normalized against skull size, pinniped normalized IOF areas were not significantly larger than the terrestrial Carnivora species (Figure 3e). While pinnipeds do appear to have diverse and specialized vibrissae, the significant, positive correlation between IOF area and vibrissal number holds true, as it does in terrestrial mammals.

All the terrestrial mammal species that we observed had smooth, circular vibrissae that lacked the morphological diversity, such as undulations, that we observed in pinniped vibrissae. Indeed, our data show that many of the terrestrial Carnivora species within the same family had similar vibrissal lengths, skull sizes, and IOF areas and that these did not significantly differ between families (Figure 3). The only exception to this was in the Felidae, specifically the lions (*Panthera leo*) and tigers (*Panthera tigris*), which had large IOF areas, normalized IOF areas, and skull sizes (GM), which led to variation in these measures in the felids. Our data agree with previous observations that the most diverse vibrissae can be observed in the pinnipeds (Supplementary Table S3) (Dougill et al., 2020; Ginter et al., 2009, 2012). Indeed, pinnipeds included species with the most (walrus, *Odobenus rosmarus*) and least (Northern fur seal, *Callorhinus ursinus*) vibrissal numbers in our dataset (Supplementary Table S3). General patterns could also be observed between the pinniped families; the phocids had vibrissae in greater numbers than the otariids, otariids had the longest vibrissae, and odobenids the most vibrissae (Figure 2). Phocids were also the only group to have vibrissae with undulations. The diversity of vibrissal morphology across the pinnipeds suggests that this is an excellent group to further explore associations in vibrissal and skull morphology.

4.1 | Vibrissal length and number

Vibrissal length was significantly longer in the pinnipeds, compared to the other Carnivora species. Recent studies,

normalizing for body length, have found that aquatic mammals have shorter vibrissae than terrestrial mammals (Dougill et al., 2020). We did not normalize the vibrissal length values, as they did not significantly vary with skull size (GM), as per the recommendation of Jungers et al. (1995). However, normalizing against body length would certainly cause the vibrissal length to be smaller in pinnipeds. We need to further investigate the association of vibrissal length with body or skull size, to explore the best way to normalize this variable for between-species comparisons. Shorter vibrissae have previously been suggested to have less underwater drag than longer vibrissae in aquatic mammals (Dougill et al., 2020). Although not significant, phocids tended to have shorter vibrissae than otariids (Figures 2 and 3d), and they were also undulated. Perhaps phocid vibrissae are especially adapted to underwater sensing by reducing drag with their undulated shape and reduced length (Dougill et al., 2020; Hanke et al., 2010).

Pinnipeds also had significantly fewer vibrissae than the other Carnivora species, with otariids having the fewest vibrissae of all the pinnipeds and odobenids having the most (Figure 3c). Perhaps having vibrissae will affect drag as the animal swims through the water—with less vibrissae having less drag overall. To our knowledge, the hydrodynamics of a full vibrissal field has not yet been explored, although it would be interesting to investigate how the number and arrangement of vibrissae affect flow around the animal. Having fewer vibrissae might reduce drag around the face in the fast swimming, actively hunting phocids and otariids, in comparison to odobenids who forage on the seafloor, using their vibrissae like a brush.

4.2 | IOF area and vibrissal sensitivity

IOF area was significantly positively correlated to vibrissal number in all the species tested here (Figure 4b), including the pinnipeds. This agrees with previous research that found vibrissal number to be correlated with IOF area in primates and other terrestrial mammals (Kay & Cartmill, 1977; Muchlinski, 2010). Indeed, the walrus (*Odobenus rosmarus*) had over a hundred vibrissae on each side of the muzzle and the largest IOF area (Supplementary Table S3). Therefore, despite pinnipeds having diverse and specialized vibrissae, the simple association between IOF area and vibrissal number still holds true in these species. However, the IOF area was not particularly well-correlated with vibrissal number in our data ($r^2 = 0.64$), which is consistent with other studies, which have also advised not to use the IOF area to approximate vibrissal number (Muchlinski, 2010;

Muchlinski et al., 2020). Therefore, we recommend not to solely use IOF area to evaluate differences in maxillary mechanoreception in extinct and extant Carnivora species.

While previous studies have associated large IOF areas with pinniped species (Berta et al., 2018; Hafed et al., 2020), this might actually be due to their large skulls overall, and not necessarily indicative of enhanced tactile sensitivity of the whole muzzle area. Indeed, we observed that while the IOF area was significantly larger in pinnipeds compared to other Carnivora species, once IOF was normalized to skull size, there was no significant difference. Pinnipeds did, however, have significantly fewer vibrissae (Figure 3c). This could suggest that each individual pinniped vibrissa may be more sensitive with more numerous nerve fibers in their surroundings, compared to other Carnivora species. Our data suggest that this would be especially true in otariids—that had larger IOF areas and lower vibrissal numbers than the other pinniped families. We investigated this further here, using the measure: *normalized IOF area per vibrissa* (Figure 5a), which was significantly higher in pinnipeds, compared to the other species of Carnivora, and significantly higher in the otariids than the phocids (Figure 5a, Supplementary Table S4).

If the normalized IOF area is associated with sensory acuity [as suggested by Muchlinski, 2010], we may expect an association with our normalized IOF area per vibrissa and a measure of vibrissal innervation, such as the mean number of nerve fibers per vibrissal follicle. Previous studies have found that pinniped vibrissae are well-innervated, with 10 times more nerve fibers around the vibrissal follicles in pinnipeds than in terrestrial mammals (Hyvärinen, 1989; Hyvärinen et al., 2009). Indeed, in the Ringed seal (*Phoca hispida*) the mean number of nerve fibers per follicle is 1,350, compared to 110 in Polecat (*Mustela putorius*) and 300 in Otter (*Lutra lutra*) (Hyvärinen et al., 2009). We extracted mean number of nerve fibers per follicle from the literature, including studies of the same species that we had also measured (Hyvärinen, 1989; Jones & Marshall, 2019; Mattson & Marshall, 2016; Smodlaka et al., 2017; Sprowls & Marshall, 2019). In agreement, we observed a positive relationship between normalized IOF area per vibrissa and mean number of nerve fibers per follicle (Figure 5b) in the phocids. The otariid, *Zalophus californianus*, did not fit well with the phocid examples (Figure 5b). Indeed, while we would predict from our data that otariids would have more nerve fibers around their vibrissal follicles than the phocids; previous anatomy work suggests they have similar numbers to phocids (Sprowls & Marshall, 2019) (Figure 5b). More otariid samples are needed to see if they do fit with this pattern, or why they

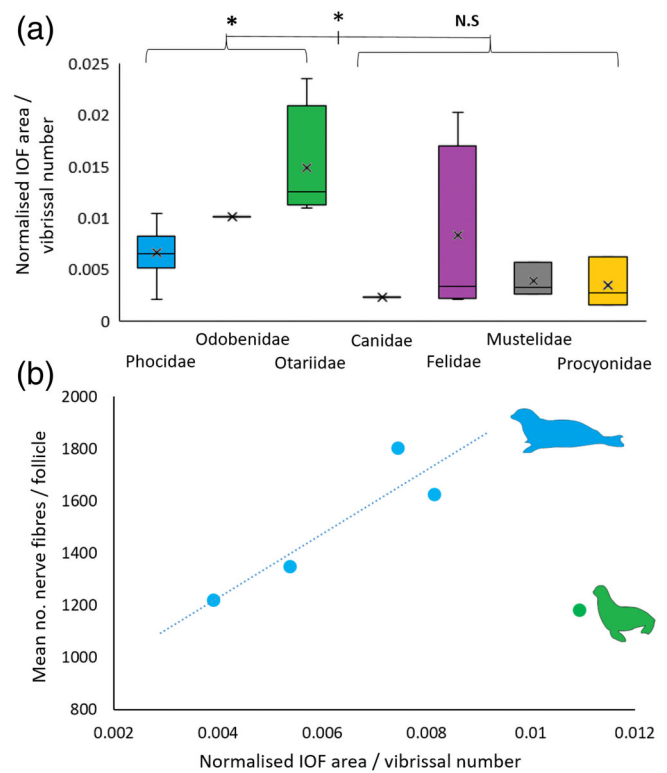


FIGURE 5 Normalized IOF area per vibrissa. (a) Normalized IOF area/vibrissal number, for each family. Pinnipeds had a significantly higher normalized IOF area/vibrissal number than other Carnivora species, and within the pinnipeds, otariids had larger normalized IOF area/vibrissal number than phocids. (b) Mean number of nerve fibers per vibrissal follicle for phocids: (1) *Pagophilus groenlandicus* (Mattson & Marshall, 2016), (2) *Phoca hispida* (Hyvärinen, 1989), (3) *Mirounga* sp. (Smodlaka et al., 2017), (4) *Phoca vitulina* (Jones & Marshall, 2019), and otariid (5) *Zalophus californianus* (Sprowls & Marshall, 2019). Colors correspond to the families Felidae (purple), Canidae (brown), Phocidae (blue), Odobenidae (red), Otariidae (green), Procyonidae (yellow), and Mustelidae (black)

might not; for example, perhaps they have an interesting IOF or ION morphology. Unfortunately, our sample size is too small for statistical analyses and to make any firm conclusions here. However, investigating the relationship between IOF area, vibrissal number, and vibrissal innervation seems like a promising new area of research. Anatomical studies counting follicle nerve fibers are very precise, technical, and time-consuming. Therefore, accessing museum osteological collections to measure IOF areas and skin collections to measure vibrissal counts might offer an alternative way to quickly approximate comparative measures of vibrissal sensitivity in pinnipeds and other mammalian species. However, it is not possible to truly test this idea until we can compare it with quantitative measures of vibrissal innervation from more species.

While normalized IOF area per vibrissa may be able to quickly capture gross vibrissal sensitivity in many species, it is not able to characterize the distribution of innervation that can be obtained from the anatomical studies. It has been found that the more caudal vibrissae of pinnipeds are more innervated than the rostral vibrissae (Mattson & Marshall, 2016; Sprowls & Marshall, 2019). Sprowls and Marshall (2019) have suggested that the sensitive caudal vibrissae may detect and localize signals, while the numerous and densely packed rostral vibrissae act as a tactile fovea—a higher resolution sampling area to aid in detailed tactile investigation. In support of this, we have previously observed that following a vibrissal contact on their more caudal vibrissae, pinnipeds tend to orient toward the stimuli with their head and then place their rostral vibrissae (or microvibrissae) toward the stimuli (Grant, Wieskotten, Wengst, Prescott, & Dehnhardt, 2013; Milne, Smith, Orton, Sullivan, & Grant, 2020). Therefore, individual caudal vibrissae are likely to be more sensitive as the animal will use information from multiple vibrissae to calculate the stimulus direction of a moving prey item from these caudal vibrissal contacts. This has also previously been suggested by Krüger, Hanke, Miersch, and Dehnhardt (2018) as a likely way that Harbour seals (*Phoca vitulina*) can detect the direction of moving hydrodynamic stimuli. However, this idea relies on individual vibrissae being represented in the brain of pinnipeds, which has only been found in California sea lions (*Zalophus californianus*) so far (Sawyer, Turner, & Kaas, 2016).

4.3 | Implications for whisker use

With an elongated snout and fewer vibrissae, the distribution of vibrissae might look superficially more similar in pinnipeds and canids. However, the normalized IOF area was more similar in felids and pinnipeds (especially lion, *Panthera leo* and tiger, *Panthera tigris* Figures 3 and 4), despite them being more distantly related. Therefore, even though many of our vibrissal morphology measures had strong phylogenetic signals across the Carnivora, they might also be associated with ecological factors, such as foraging and hunting.

Pinnipeds use their vibrissae for navigation and hunting (Bauer et al., 2018; Dehnhardt & Hanke, 2018; Hyvärinen, 1989). Feeding methods of pinnipeds are diverse with four major styles: pierce, grip and tear, suction, and filter-feeding (Berta et al., 2018). Several studies have associated skull shape and jaw structure with feeding methods (Berta et al., 2018; Franco-Moreno et al., 2020; Jones, Ruff, & Goswami, 2013; Marshall,

Rosen, & Trites, 2015), but none have made associations with vibrissal touch sensing. Supplementary Table S3 shows that Stella sea lion (*Eumetopias jubatus*), California sea lion (*Zalophus californianus*), Grey Seal (*Halichoerus grypus*), Hooded seal (*Cystophora cristata*), and South American fur seal (*Arctocephalus australis*) all have large IOF areas and actively hunt fish and cephalopods; therefore, perhaps more sensitive individual vibrissae are required for active hunting. A recent article has shown that pinniped species that hunt moving prey also move their vibrissae more (Milne et al., 2020). As vibrissal movements are also associated with larger IOF areas (Muchlinski et al., 2020), it is likely that pinnipeds that hunt moving prey in dark underwater environments will have larger IOF areas. This might even be applicable more generally across the Carnivora, where species that actively hunt moving prey at night also have larger IOF areas, which would account for the large relative IOF areas of lions (*Panthera leo*) (Courbin et al., 2019) and tigers (*Panthera tigris*) (Krishnamurthy & Gayathri, 2018) (Figure 2). Indeed, we suggest that species that hunt moving prey items in the dark are likely to have more sensitive and specialized vibrissae, especially as they have to integrate between individual vibrissal signals to calculate the direction of the prey movement during hunting. Many species of pinniped and some species of felids are likely to have strongly innervated individual vibrissae, and these might be good species to focus on in future anatomical studies.

Pinniped vibrissae are diverse, and vary in shape, length, number, and innervation; however, we do not yet fully understand the association between form and function in these structures. Characterizing vibrissal interactions during natural behavior in pinnipeds and other Carnivora species is necessary to allow us to better understand vibrissal function. It would be especially interesting to investigate this by capturing vibrissal interactions during foraging, prey hunting, and capture.

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AUTHOR CONTRIBUTIONS

Alyx Milne: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing-original draft. **Magdalena Muchlinski:** Conceptualization; data curation; formal analysis; validation; writing-review & editing. **Llwyd Orton:** Formal analysis; funding acquisition; project administration; supervision; writing-review & editing. **Matthew Sullivan:** Formal analysis; funding acquisition; supervision; writing-review & editing. **Robyn Grant:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review & editing.

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