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# Diversity of vibrissal follicle anatomy in cetaceans

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## Abstract

Most cetaceans are born with vibrissae but they can be lost or reduced in adulthood, especially in odontocetes. Despite this, some species of odontocetes have been found to have functioning vibrissal follicles (including the follicle itself and any remaining vibrissal hair shaft) that play a role in mechanoreception, proprioception and electroreception. This reveals a greater diversity of vibrissal function in odontocetes than in any other mammalian group. However, we know very little about vibrissal follicle form and function across the Cetacea. Here, we qualitatively describe the gross vibrissal follicle anatomy of fetuses of three species of cetaceans, including two odontocetes: Atlantic white-sided dolphin (*Lagenorhynchus acutus*), harbour porpoise (*Phocoena phocoena*), and one mysticete: minke whale (*Balaenoptera acutorostrata*), and compared our findings to previous anatomical descriptions. All three species had few, short vibrissae contained within a relatively simple, single-part follicle, lacking in muscles. However, we observed differences in vibrissal number, follicle size and shape, and innervation distribution between the species. While all three species had nerve fibers around the follicles, the vibrissal follicles of *Balaenoptera acutorostrata* were innervated by a deep vibrissal nerve, and the nerve fibers of the odontocetes studied were looser and more branched. For example, in *Lagenorhynchus acutus*, branches of nerve fibers travelled parallel to the follicle, and innervated more superficial areas, rather than just the base. Our anatomical descriptions lend support to the observation that vibrissal morphology is diverse in cetaceans, and is worth further investigation to fully explore links between form and function.

## KEYWORDS

delphinid, electrosensing, mechanosensation, touch sensing, whisker

## 1 | INTRODUCTION

Vibrissae, or whiskers, are present on the faces of most mammals (Ahl, 1986; Grant & Goss, 2021). They are slender, keratinized, tactile hairs that can vary across species in terms of their size, shape, number, and arrangement,

as well as their degree of innervation and musculature (Muchlinski, Wible, Corfe, Sullivan, & Grant, 2020; Grant & Goss 2021). Vibrissal specialists, such as rodents and pinnipeds, actively use their vibrissae to guide foraging and locomotion in dark, underwater environments (Grant et al., 2018; Grant & Arkley, 2015; Grant,

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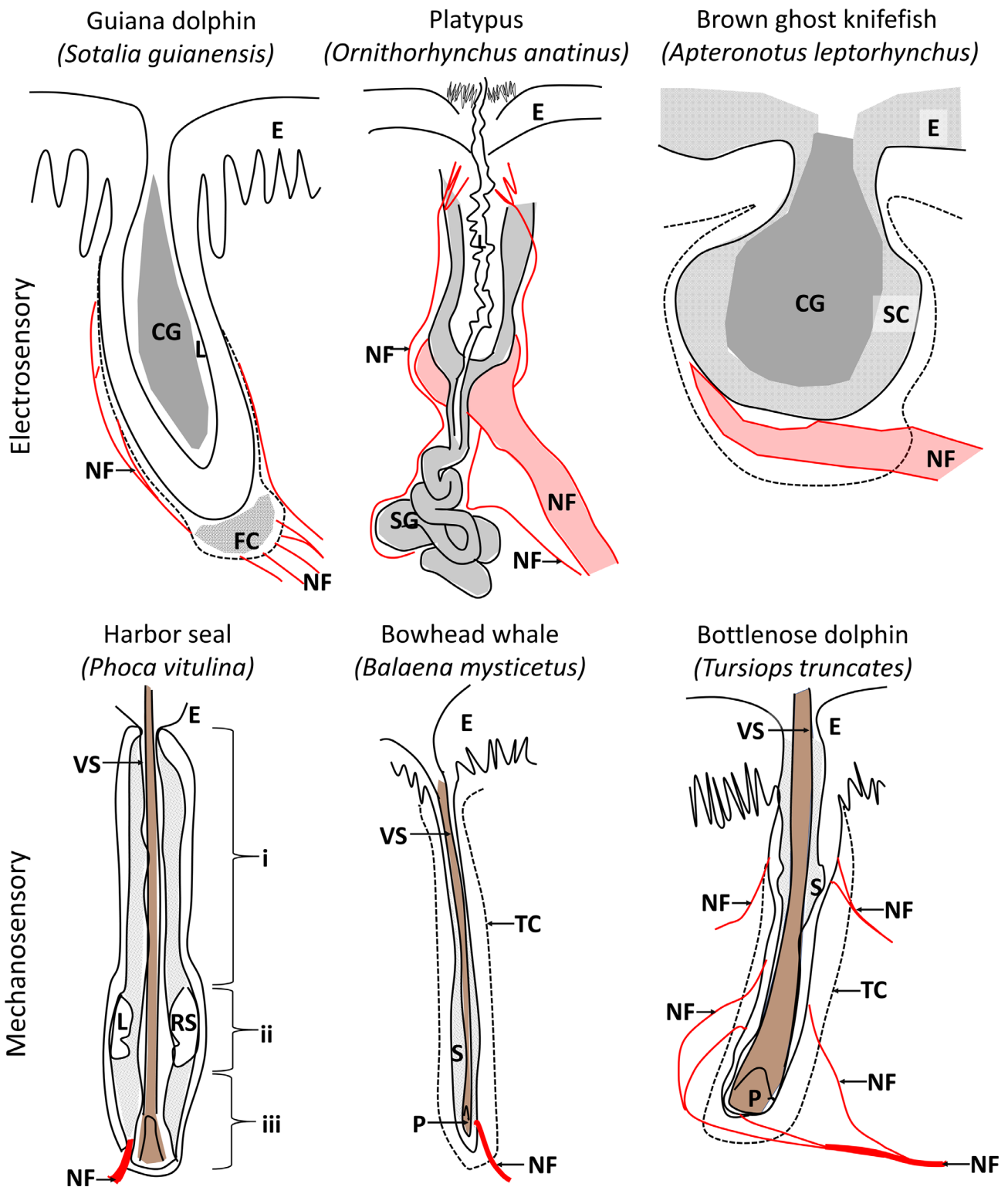
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Mitchinson, Fox, & Prescott, 2009; Milne, Smith, Orton, Sullivan, & Grant, 2020; Prescott, Diamond, & Wing, 2011). Terrestrial and aquatic vibrissal specialists have long, prominent vibrissae (Dougill et al., 2020; Muchlinski et al., 2020) that are well-innervated and regularly organized with intrinsic muscles around each vibrissal follicle (Dörfl, 1982; Muchlinski et al., 2020). Being aquatic is likely to be an important driver in vibrissal specialization in mammals (Dougill et al., 2020). Perhaps the most diverse vibrissae can be seen in the pinnipeds, which have huge variation in layout, lengths, numbers and shapes (Ginter, Fish, & Marshall, 2009; Ginter, DeWitt, Fish, & Marshall, 2012; Dougill et al., 2020; Milne et al. 2021), and their vibrissae are also extremely well-innervated (Hyvärinen, 1989; Jones & Marshall, 2019; Marshall, Amin, Kovacs, & Lydersen, 2006; Mattson & Marshall, 2016; Smodlaka, Galex, Palmer, Borovac, & Khamas, 2017; Sprowls & Marshall, 2019). Cetaceans are an especially interesting group since many are born with vibrissae on their rostrum or upper jaw, as well as around the blowhole (Bauer, Reep, & Marshall, 2018; Drake, Crish, George, Stimmelmayer, & Thewissen, 2015; Ling, 1977). However, while mysticetes retain their vibrissae into adulthood (Berta et al., 2015; Drake et al., 2015; Ogawa & Shida, 1950), many odontocetes lose their vibrissae altogether within the first few weeks of life (Bauer et al., 2018; Czech-Damal et al., 2012). Indeed, both beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) do not develop vibrissal hairs at all (Yablokov, Bel'kovich, & Borisov, 1972). Subsequently, cetacean vibrissae—especially those of odontocetes—were often thought to be vestigial (Yablokov & Klevezal, 1969). Sensory adaptations in toothed whales were mainly associated with improved hearing abilities (Johnson, 1966) as well as the use of active echolocation for long-range prey detection (Au, 1980, 1993), rather than vibrissal sensing. However, there is an emerging realization that cetacean vibrissal follicles are likely to be functional in many species (Berta et al., 2015; Czech-Damal et al., 2012; Drake et al., 2015; Gerussi et al., 2020).

Vibrissal follicle anatomy has already been described for several mysticete species including in grey whale (*Eschrichtius robustus*; Berta et al., 2015), bowhead whale (*Balaena mysticetus*; Drake et al., 2015), fin whale (*Balaenoptera physalus*; Ogawa & Shida, 1950) and sei whale (*Balaenoptera borealis*; Ogawa & Shida, 1950), among others (Japha, 1912). While vibrissal number and arrangement is variable in the mysticetes (Ling, 1977), vibrissal follicle anatomy is relatively conserved—they are simple, single-part capsules that contain the hair shaft, and lack any intrinsic muscles (Drake et al., 2015).

At the base of each follicle is a deep vibrissal nerve (Drake et al., 2015; Figure 1 bottom, NF label), similar to that of pinnipeds (Dehnhardt et al., 1998; Figure 1, bottom, NF label) and those of terrestrial mammals (Ebara, Kumamoto, Matsuura, Mazurkiewicz, & Rice, 2002; Rice, 1993). Hairs can also be found enclosed within the tubercles of humpback whales (*Megaptera novaeangliae*), which are thought to play a similar vibrotactile role (Mercado, 2014). To date, only preliminary assumptions have been made about the function of mysticete vibrissae, but they are likely to be tactile (Nakai & Shida, 1948; Ogawa & Shida, 1950) and could aid in foraging (Bauer et al., 2018), prey detection (Berta et al., 2015) and providing the animal with information about water movement and body position within their environment (Bauer et al., 2018). A better understanding of the form and function of vibrissae in mysticetes is therefore needed.

In odontocetes, vibrissal follicle anatomy is more diverse than in mysticetes. Several species of river dolphins maintain vibrissal hair shafts throughout adulthood (Bauer et al., 2018). However, many species of odontocetes have been observed to possess only hairless follicle pits as adults, including common (*Delphinus delphis*), bottlenose (*Tursiops truncatus*; Palmer & Weddell, 2009; Bauer et al., 2018) and Guiana dolphins (*Sotalia guianensis*; Czech-Damal et al., 2012). In adult *Sotalia guianensis* (Czech-Damal et al., 2012; Figure 1, top) and *Tursiops truncatus* (Czech, 2007), the hair shaft was found to be entirely absent from the follicle, although the follicles were still innervated. Therefore, these vibrissal follicles are often described as “vibrissal crypts” (Czech-Damal et al., 2012, 2013), since characteristic features such as a hair shaft, blood sinus, hair papilla and root sheaths are absent (Czech-Damal et al., 2012; Dehnhardt, Miersch, Marshall, von Fersen, & Hüttner, 2020). However, recently, Gerussi et al. (2020) found hair shafts still present within the follicles of adult *Tursiops truncatus*, although they were not protruding external to the skin. They also found the follicles to be well-innervated (Figure 1, bottom) and concluded that the vibrissal follicles were still functional, despite not having external hair shafts, and could play a proprioceptive role. Yablokov et al. (1972) also suggested that short vibrissal hair shafts could move within the follicle to provide information about water movement and the speed of angular head movements. If so, a distributed network of nerve fibers along the follicle length could help detect these vibrissal shaft movements, as well as potentially providing a thermoregulatory capacity (Gerussi et al., 2020). Indeed, branching nerve fibers along the vibrissal shaft have been observed in the delphinid species *Sotalia guianensis* and *Tursiops truncatus* (Czech-Damal et al., 2012; Gerussi et al., 2020).



**FIGURE 1** Anatomy of electrosensory and mechanosensory structures. A summary of common anatomical structures. Top row shows electrosensory structures, including vibrissal crypt in Guiana dolphin (*Sotalia guianensis*) adapted from figure 2 in Czech-Damal, Dehnhardt, Manger, and Hanke (2013); mucous glands in Platypus (*Ornithorhynchus anatinus*) adapted from figure 1 in Czech-Damal et al. (2013); and tuberous sensory organ in Brown ghost knifefish (*Apteronotus leptorhynchus*) adapted from figure 2a in Zakon et al. (1998). Bottom row shows mechanosensory vibrissal follicles in Harbor seal (*Phoca vitulina*) adapted from figure 1 in Dehnhardt, Mauck, and Hyvärinen (1998); bowhead whale (*Balaena mysticetus*) adapted from figure 3a, b in Drake et al. (2015); and bottlenose dolphin (*Tursiops truncatus*) adapted from Gerussi et al. (2020). E: Epidermis; L: Lumen; S: Sinus; RS: Ring Epidermis; CG: Conductive gel; FC: Fat cells; SC: Secreting cells; SG: Secreting gland; NF: Nerve fibers; VS: Vibrissal shaft; TC: Tissue complex; P: Dermal papilla; *Phoca vitulina* has three sections to the follicle (i, ii, iii), whereas all the other species have one section to the follicle. *Tursiops truncatus* represent juvenile specimens; adult specimens are represented in all other species

Using behavioral and anatomical evidence, Czech-Damal et al. (2012) demonstrated that, rather than being mechanosensory or proprioceptive, the vibrissal crypts of *Sotalia guianensis* are transformed postnatally into passive electroreceptors. They are filled with a gel-like mixture of corneocytes and keratinous fibers that possibly facilitate electric signal conduction (Czech-Damal et al., 2012, 2013), playing a similar function to the conductive gel found in electrosensory follicles within the Platypus (*Ornithorhynchus anatinus*; Czech-Damal et al., 2013; Figure 1, top) and some fish, i.e. Brown ghost knifefish (*Apteronotus leptorhynchus*; Zakon, Lu, & Weisleder, 1998; Figure 1, top). *Sotalia guianensis* are known to forage on bottom-dwelling prey (Rossi-Santos & Wedekin, 2006), and the detection of bioelectric fields might, therefore, function as a supplementary sensory modality to vision and echolocation, to aid in prey localization during benthic feeding (Czech-Damal et al., 2012; Dehnhardt et al., 2020). *Tursiops truncatus* is another promising candidate to possess passive electroreception based on behavioral observations of benthic feeding activities (Roszbach & Herzing, 1997), and preliminary data suggests a similar vibrissal follicle function as that of *Sotalia guianensis* (Dehnhardt et al., 2020), but further research is needed.

This study will qualitatively describe the gross follicle anatomy of fetal specimens of three cetacean species, including two odontocetes: Atlantic white-sided dolphin (*Lagenorhynchus acutus*), harbour porpoise (*Phocoena phocoena*), and one mysticete: minke whale (*Balaenoptera acutorostrata*). Previous work has noted the vibrissal counts of these species as 5–6, 1–3, and 8–10, respectively (Ling, 1977); therefore, we may expect variation in vibrissal numbers between the species. *Phocoena phocoena* vibrissal follicles have previously been described in Japha (1912) as being similar to those of mysticetes (Balaenopterid), but with a notable reduction in size and complexity (Japha, 1912; Ling, 1977). Therefore, we may also expect *Phocoena phocoena* and *Balaenoptera acutorostrata* follicles to be relatively similar. *Lagenorhynchus acutus* may have more branched nerve fibers along the vibrissal shaft, similar to those of other delphinid species. We will compare our findings to the follicle anatomy of other well-described species in the literature, including *Tursiops truncatus*, *Sotalia guianensis*, and *Balaena mysticetus*.

## 2 | METHODS

### 2.1 | Samples

Samples were obtained from three species of cetaceans: Atlantic white-sided dolphin (*Lagenorhynchus acutus*),

harbour porpoise (*Phocoena phocoena*) and minke whale (*Balaenoptera acutorostrata*). All samples were donated from Edinburgh's National Museum of Scotland from fetuses that had died due to natural causes and washed up on Scottish beaches. As usual for museum specimens, the specimens were kept in freezer conditions and occasionally went through freeze–thaw, which affected the quality of the samples somewhat, especially by making ice crystals within the sample. Ice crystal freezer damage can especially be seen in the *Balaenoptera acutorostrata* samples (Figure 2f). This damage meant it was not possible to collect quantitative data, such as nerve fiber counts, from our samples. One individual per species was used in this study, with three to four vibrissal follicles investigated per individual (three *Lagenorhynchus acutus*, four *Phocoena phocoena* and four *Balaenoptera acutorostrata*). A whole row of vibrissal follicles was dissected from each side of the whole fetal specimen (in red shading in Figures 2a, 3a, and 4a). An area around each vibrissal follicle was then dissected, leaving an 8 cm<sup>3</sup> tissue sample cube with the vibrissal hair shaft intact.

### 2.2 | Histology

Once dissected, the samples were prepared for slicing and staining with Masson's Trichrome (as per Barbera, Delaunay, Dougill, & Grant, 2019). All samples were flattened in histology cassettes with foam and left in 4% paraformaldehyde (PFA) overnight. Samples were then dehydrated through a graded series of ethanol (70%, 80%, 90%, and 100%) and xylene baths and infiltrated with paraffin wax, in a process lasting approximately 20 hr. Tissue was then embedded in solid blocks of paraffin that were sliced at 15 µm on a rotary microtome (Thermo Scientific Microm HM355S) with water bath (37°C), and mounted on to slides, which were stained with standard Masson's Trichrome staining (Trichrome Stain Kit, Sigma–Aldrich) and cover-slipped with Distyrene Plasticizer Xylene mountant (DPX; Sigma–Aldrich). Masson's Trichrome stains muscles and keratin as red, cytoplasm as light red/pink, nerves as red/purple and connective tissue, such as collagen, as blue. It is a commonly used stain, and allows for easy comparison with other cetacean follicle anatomy papers (Czech-Damal et al., 2012; Drake et al., 2015; Gerussi et al., 2020). A selection of slides were also stained with Luxol fast blue solution, which stains myelinated fibers blue. Microscope images were taken on a Zeiss Axioimager M1 light microscope, using Zen Pro 3.1 (blue edition). Maximum follicle length and width measurements were taken from each follicle, and a mean was presented per species. Only adjustments in exposure and white balance were made to the images.

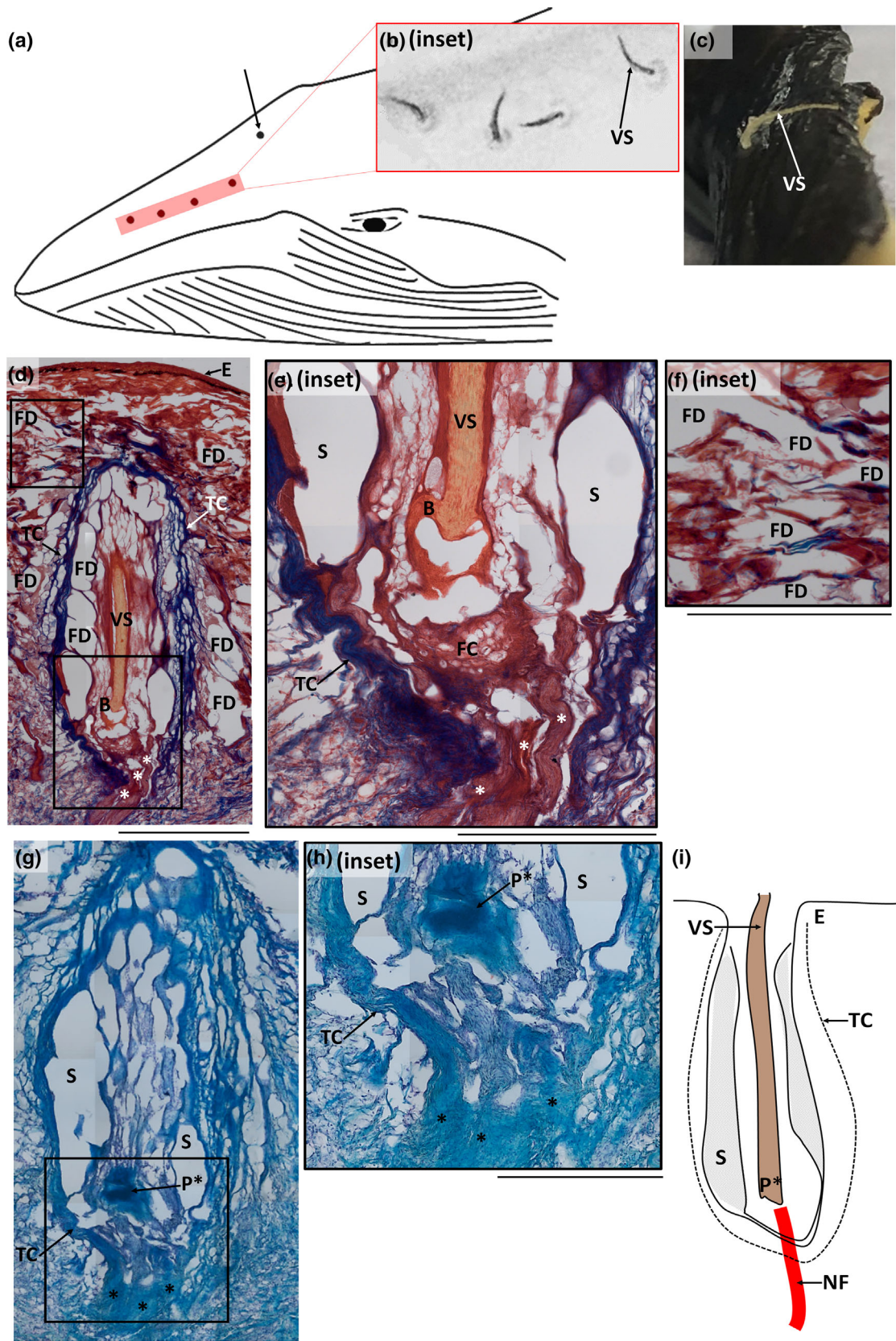


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### 3 | RESULTS

#### 3.1 | Minke whale (*Balaenoptera acutorostrata*)

In *Balaenoptera acutorostrata*, the vibrissae were arranged in a single row of four vibrissal follicles on each side of the rostrum (shown as four red dots in Figure 2a, also shown in Figure 2b). The follicles each contained a short, pale hair—the vibrissal shaft—that projected externally around 10 mm from the follicle. These vibrissal shafts had large intrinsic curvatures that caused the hairs to emerge out of the skin and then curve over, so that most of the vibrissal tips contacted the skin of the specimen (Figure 2b,c). Other hairs could also be found on the head of the *Balaenoptera acutorostrata* specimen, but these did not sit within the row of follicles and therefore were not included for histology (an example hair is indicated in Figure 2a as a black dot with arrow). The vibrissal follicles were elongated in shape (3 mm in length and 1.2 mm wide), but were the widest and shortest of the species studied here (compare Figure 2d,g to Figures 3b and 4f). The hair bulb could clearly be seen (Figure 2d, e); however, the dermal papillae were less clear. Figure 2g and h show a possible dermal papilla at the base of the bulb. Figure 2e also shows some fatty cells at the base of the bulb too.

The follicles contained both epidermal and dermal parts (Figure 2d). The epidermal layer was thin (Figure 2d). Within the dermis, the follicles were simple—lacking a ring wulst and musculature in their surroundings. All follicles were contained by a tissue capsule (Figure 2d,e, g), with a thin follicle wall that was slightly thicker on one side of the follicle than the other, i.e. in Figure 2d the blue wall of the follicle was slightly thicker on the right hand side than the left. The hair shafts were surrounded by a sinus (Figure 2e,h). The follicle sinus was large in the *Balaenoptera acutorostrata* specimen, compared to the other specimens (Figures 3 and 4), although this could be exaggerated by the ice crystals that formed from freezer damage in this specimen. *Balaenoptera acutorostrata* had a tight bundle of

nerve fibers at the base of each follicle that appeared to only have one insertion point, entering into the follicle capsule almost vertically from below (Figure 2d,e,g, h).

#### 3.2 | Harbour porpoise (*Phocoena phocoena*)

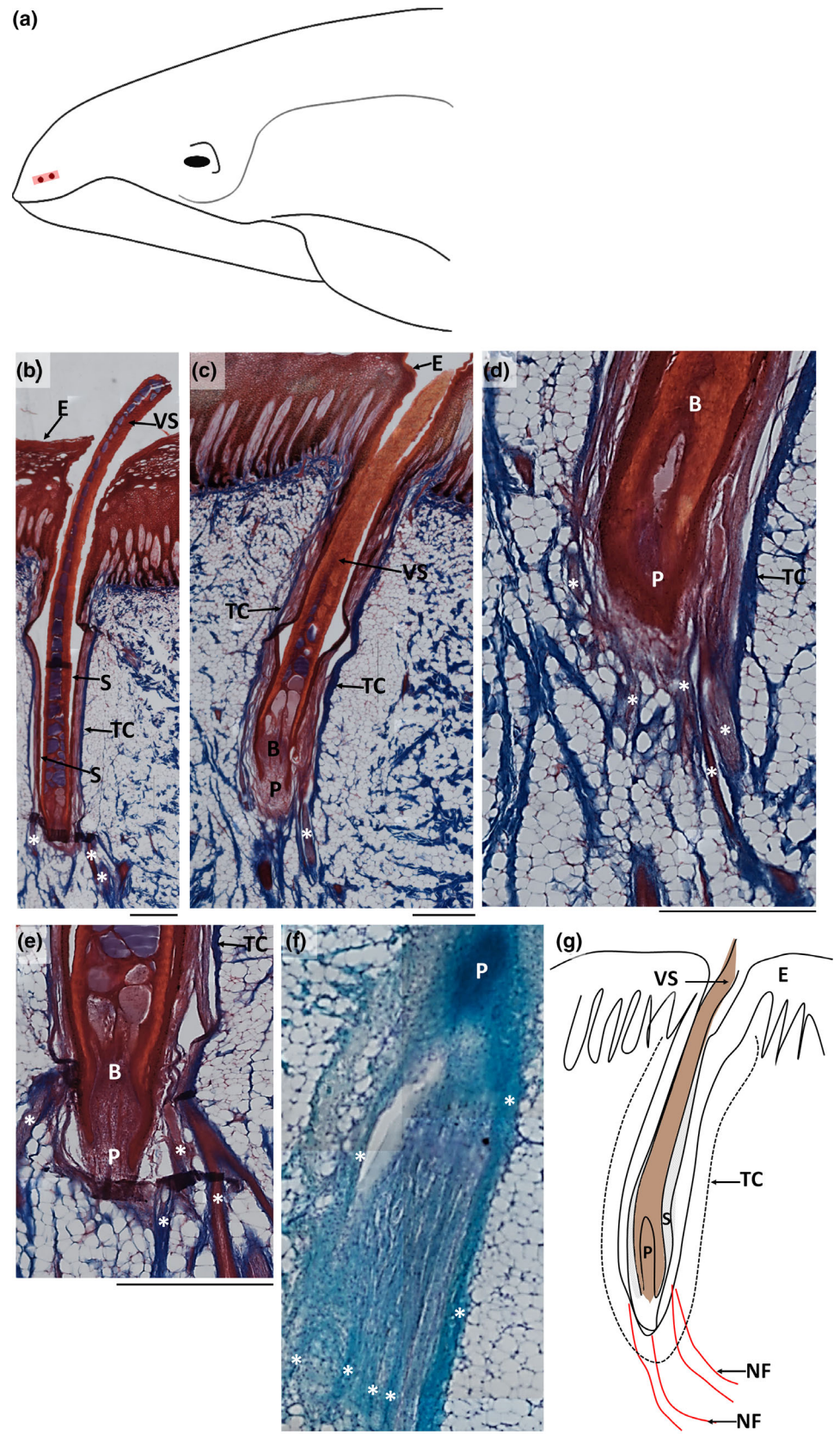
In *Phocoena phocoena*, there were only two vibrissae in a single row on each side of the rostrum (Figure 3a). The follicles each contained a short, pale hair that all projected externally from the follicle <10 mm. These vibrissal shafts had large intrinsic curvatures, similar to that of *Balaenoptera acutorostrata*. The vibrissal follicles were slender, and were the thinnest of the three specimens, with a width of 0.6 mm and length of 3.4 mm (Figure 3b, c). The hair bulb and dermal papilla could clearly be seen in most follicles (Figure 3c–e). The follicles contained both epidermal and dermal parts (Figure 3b,c), and the epidermal layer was thicker in *Phocoena phocoena* than in the other specimens (Figure 3b,c). Within the dermis, the follicles were simple and lacked a ring wulst and musculature. All follicles were contained by a tissue capsule, with a thin follicle wall of uniform thickness (Figure 3b,c). A follicle sinus was also present (Figure 3b). The nerve bundles were slightly different from those of *Balaenoptera acutorostrata*; they were looser, with about four to six branches (Figure 3d–f) that penetrated into the base of the follicle. Figure 3d, f show that some nerve fibers may also penetrate into the dermal papilla directly.

#### 3.3 | Atlantic white-sided dolphin (*Lagenorhynchus acutus*)

The *Lagenorhynchus acutus* specimen had four vibrissae in a single row on each side of the rostrum (Figure 4a). The follicles each contained a short, dark, curving hair that all projected <10 mm from the follicle. The vibrissal follicles were long and slender; indeed, they were the longest of the three specimens, with a length of 3.7 mm, and

**FIGURE 2** Vibrissal follicle anatomy of minke whale (*Balaenoptera acutorostrata*). (a) A diagram of the vibrissal hairs on the fetal specimen; the highlighted area in red was dissected. The arrow indicates an additional vibrissal hair on the head that was outside of the row of dissected vibrissae (in red). (b) An illustration of the four vibrissal hairs; (c) a photograph of one of the vibrissal hairs; (d) a full vibrissal follicle view, with insets shown in panels e and f; (g) a full vibrissal follicle view, with inset shown in panel h. Panels d and f also demonstrate freezer damage (FD), which causes ice crystals within the tissue, defined by open spaces within the slices; (i) a summary diagram of a *Balaenoptera acutorostrata* vibrissal follicle. Panels d–g show Masson's Trichrome staining, panels h and i show Luxol fast blue staining. B: Hair bulb; E: Epidermis; FC: Fat cells; FD: Freezer damage; P\*: possible dermal papilla; S: Sinus; TC: Tissue capsule; NF: Nerve fibers; VS: Vibrissal shaft; Asterisks (\*) also correspond to Nerve fibers. Scale bars are 1 mm in panels d and g, and 0.5 mm in panels e, f, and h

**FIGURE 3** Vibrissal follicle anatomy of harbour porpoise (*Phocoena phocoena*). (a) A diagram of the vibrissal hairs on the fetal specimen; the highlighted area in red was dissected. Panels b and c show A full vibrissal follicle view. Panels d–f show close-ups of a follicle base; (g) is a summary diagram of a *Phocoena phocoena* vibrissal follicle. Panels b–e show Masson's Trichrome staining, panel f shows Luxol fast blue staining. B: Hair bulb; E: Epidermis; FD\*: Possible freezer damage; NF: Nerve fibers; S: Sinus; P: Dermal papilla; TC: Tissue capsule; VS: Vibrissal shaft; Asterisks (\*) also correspond to Nerve fibers. Scale bars are 0.5 mm



width of 0.8 mm (Figure 4f,h). The hair bulb and dermal papilla could clearly be seen in all follicles (Figure 4f–h). The follicles contained both epidermal and dermal parts

(Figure 4b,d,f,h), and the epidermal layer was thinner than that of *Phocoena phocoena* (Figure 4b,d,f,h). As in the other species, the follicles of *Lagenorhynchus acutus*



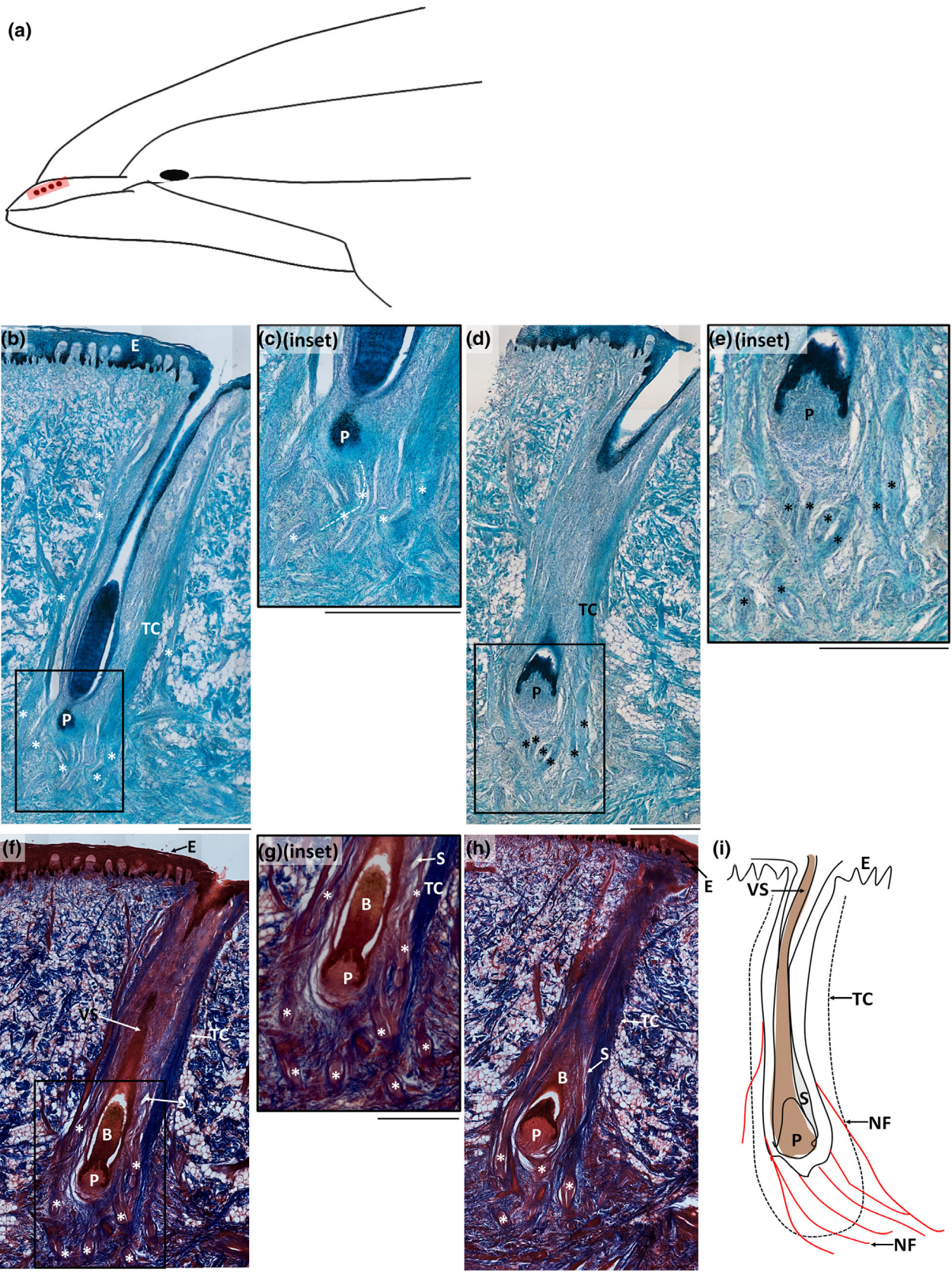


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were also simple, and lacked a ring wulst and any musculature. All follicles were contained by a tissue capsule with a follicle wall (Figure 4f–h). A small follicle sinus was also present, but was not especially clear in our samples (Figure 4f–h). The nerve bundles were slightly different again from those of *Balaenoptera acutorostrata* and *Phocoena phocoena*. Like *Phocoena phocoena*, the nerve bundles of *Lagenorhynchus acutus* were loose. However, in *Lagenorhynchus acutus* numerous branches surrounded the base of the follicle (Figure 4c,e,g) and also ran parallel to the vibrissal shaft, entering at more superficial levels of the follicle (Figure 4b,f,g). At the follicle base, some thin nerve fibers appeared to also enter the papilla directly (Figure 4c,e,h).

#### 4 | DISCUSSION

All the cetaceans studied here had simple, single-part vibrissal follicles that lacked any musculature in their surroundings. However, there were some differences between them that we will discuss further below. Perhaps the most obvious difference could be seen in the nerve fiber arrangements around the follicles. While nerve fibers were present in all species, they varied in position and distribution. *Balaenoptera acutorostrata* had one large group of nerves innervating the base of the follicle, likely to be the deep vibrissal nerve (Figure 2i). This is similar to *Balaena mysticetus* (Figure 1, bottom; Drake et al., 2015) and other (non-cetacean) mammals, such as *Phoca vitulina* (Figure 1, bottom; Rice, 1993; Dehnhardt et al., 1998; Ebara et al., 2002). In *Phocoena phocoena*, we found the deep vibrissal nerve branched to innervate a few points at the base of the follicle (Figure 3g), which is in agreement with the description of *Phocoena phocoena* follicles in Ling (1977) and Japha (1912) (see especially figure B in Japha, 1912). In *Lagenorhynchus acutus*, the deep vibrissal nerve branched even more, with bundles of nerve fibers travelling parallel to the follicle. These bundles innervated more superficial areas of the follicle than those of *Balaena mysticetus* and *Phocoena phocoena*, which only really innervated the base of the follicle (Figure 4i). The nerve fiber arrangement of *Lagenorhynchus acutus* was similar to those of the delphinids *Tursiops truncatus* (Gerussi et al., 2020; Figure 1,

bottom) and *Sotalia guianensis* (Czech-Damal et al., 2012, 2013; Figure 1, top), which also innervated more superficial areas of the follicle. It would be interesting to explore if this trait is indicative of having a reduced or absent vibrissal shaft in adulthood. Indeed, it is not yet known how differences in the distribution of follicle innervation may relate to vibrissal function in cetaceans.

All the vibrissal follicles of the cetaceans in this study were elongated structures contained within a capsule (Figures 2–4). There was only one part to the follicle, unlike terrestrial mammals that have a bipartite follicle (Rice, 1993) and seals that have a tripartite vibrissal follicle (Ling, 1977; Hyvärinen, 1989; Marshall et al., 2006; Figure 1, bottom), the latter thought to be an adaptation to conserve heat within the follicle and maintain vibrissal sensitivity in cold water temperatures (Dehnhardt et al., 1998; Erdsack, Dehnhardt, & Hanke, 2014). A single-part follicle could imply a reduced sensitivity of cetacean vibrissae in colder waters. However, nerve fibers around the follicle, especially at more superficial follicle depths, can also play a role in regulating the blood flow and thermoregulation (Fundin, Pfaller, & Rice, 1997; Gerussi et al., 2020). Therefore, the presence of nerve fibers in cetacean follicles may indicate an ability to thermoregulate and protect the vibrissal follicles from the cold. This may be especially true in the delphinids that have vibrissal nerve fibers at more superficial locations than other cetacean species (Figures 1 and 4b,f). Indeed, Mauck, Eysel, and Dehnhardt (2000) found Guiana dolphins (*Sotalia guianensis*) to emit thermal radiation from their vibrissal follicles in a similar way to the pinniped *Phoca vitulina*, suggesting that heat is conserved in the follicles of this species.

The vibrissal follicles of each species varied in size. *Lagenorhynchus acutus* had larger follicles than *Phocoena phocoena*, and *Balaenoptera acutorostrata* had shorter and wider follicles than both of the other species. All the species studied here had smaller vibrissal follicles than *Sotalia guianensis* (LxW: 4.1–7.1 x 1.2–4.3 mm; Czech-Damal et al., 2012), but this might be because *Sotalia guianensis* was an adult specimen. The absence of a vibrissal shaft in *Sotalia guianensis* is also likely to affect the rigidity of the follicle, and probably explains why the vibrissal follicles of *Sotalia guianensis* are much wider and lanceolate (Figure 1, top) compared to our study

**FIGURE 4** Vibrissal follicle anatomy of Atlantic white-sided dolphin (*Lagenorhynchus acutus*). (a) A diagram of the vibrissal hairs on the fetal specimen; the highlighted area in red was dissected. Panels b–e show Luxol fast blue staining. Panels b and d show full follicle views, with c and e as insets, respectively. Panel c traces a bundle of nerve fibers (\*) towards the base of the follicle, indicated by the dotted white line. Panels f–h show Masson's Trichrome staining. (f) A full vibrissal follicle view, with inset shown in panel g. A full follicle view can also be seen in panel h. (j) a summary diagram of a *Lagenorhynchus acutus* vibrissal follicle. B: Hair bulb; E: Epidermis; NF: Nerve fibers; P: Dermal papilla; S: Sinus; TC: Tissue capsule; VS: Vibrissal shaft; Asterisks (\*) also correspond to Nerve fibers. Scale bars are 0.5 mm

species. Gerussi et al. (2020) characterized the follicles of juvenile and adult *Tursiops truncatus*. Although they did not explicitly state follicle lengths, examination of their figures suggests that newborns had a follicle length of around 6 mm (figures 2a and 4a in Gerussi et al., 2020) and adults of a little more than 7 mm (figure 7a in Gerussi et al., 2020); both these values are larger than the follicle lengths of our specimens, and suggests that follicles may grow somewhat with age.

Dermal papillae could clearly be seen in *Lagenorhynchus acutus* and *Phocoena phocoena*, similar to those of the juvenile and adult *Tursiops truncatus* (Gerussi et al., 2020) and *Balaena mysticetus* (Drake et al., 2015). Adult *Sotalia guianensis* lack vibrissal shafts, and hence dermal papillae (Czech-Damal et al., 2012). Since the papillae produce the components of the vibrissal shaft, they are likely to be present in any mammalian species with intact vibrissal shafts, including *Balaenoptera acutorostrata*, but the quality of the tissue made it hard to observe papillae in our specimen.

The cetacean species investigated here all had relatively few (2–4) and short vibrissae, extending around 10 mm from the follicle. These are comparable to the numbers and sizes of vibrissae in other cetacean species, including *Tursiops truncatus* (Gerussi et al., 2020) and *Delphinus delphis* (Ling, 1977; Yablokov et al., 1972). Ling (1977) recorded the number and size of vibrissae in many species of cetacean, and observed them to vary between individuals of different ages, sex, and species. They also found the vibrissae of mysticetes to be more numerous and longer than those of odontocetes. They recorded 8–10 vibrissae in their sample of *Balaenoptera acutorostrata* compared to our four; however, Ling (1977) counted all hairs on the upper jaw, whereas we only included those in the row of vibrissal follicles. We also observed other hairs on the head that were more medial than the vibrissae we included and that did not sit within the regular row arrangement. One example of an additional follicle is illustrated in Figure 2a (by a black dot and arrow). This was in agreement with observations of Japha (1912) who also observed a row of four hairs, as well as others present (see figure A in Japha, 1912). It is not yet known whether there are any anatomical or functional differences between these different groups of hairs, and a detailed classification of the arrangement and numbers of cetacean hairs would be useful.

Examining fetal specimens made the localization of the vibrissae and conducting the anatomy much easier. Gerussi et al. (2020) found that most structures of the follicle did not really change with maturity; therefore, our specimens are likely to be representative of the adult species too. However, while the gross anatomy of the follicle

is unlikely to change much from birth to adulthood (Gerussi et al., 2020), as some species of odontocetes mature, their vibrissal hair shafts become reduced or absent. The relative size of the vibrissal hair shaft in adulthood may give more clues about vibrissal function, which is not possible to achieve with our specimens.

#### 4.1 | Vibrissal function

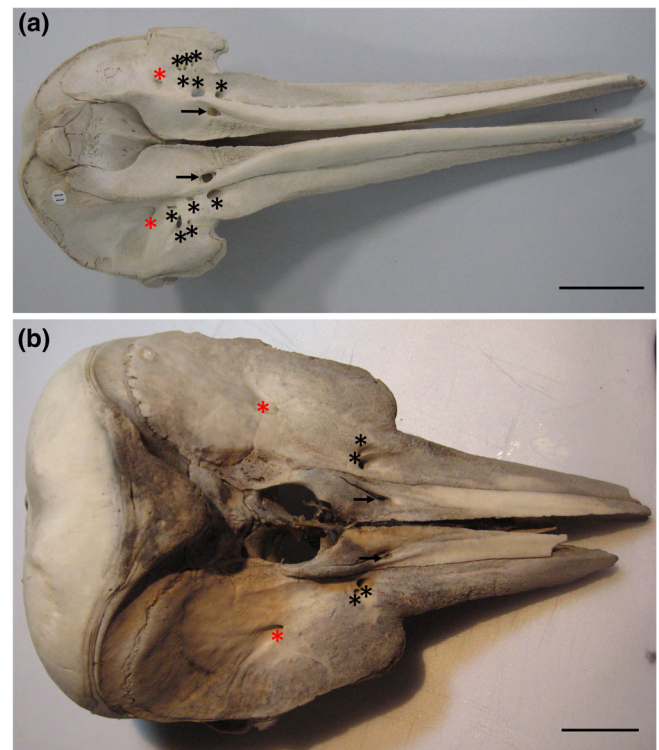
The specimens we used in this study were all fetal, with their vibrissal shafts intact. The fact that all these cetacean species retain innervated vibrissal hairs at birth suggests that they may play a functional role in neonates. This could include maintaining close contact with their mother, individual recognition and locating the nipple for feeding (Gerussi et al., 2020). Indeed, Yablokov et al. (1972) also support this idea. They suggest that in nursing specimens, the vibrissae could provide information about the animal's mouth and the mother's nipple, as well as stimulating ejection of milk by touching the papilla mammae.

Previous studies have suggested that when the vibrissal hair shaft is intact and projects external to the follicle, that the vibrissae are likely to be mechanosensory (Bauer et al., 2018; Berta et al., 2015; Ling, 1977), which includes adult mysticetes and two species of river dolphins (*Inia geoffrensis* and *Platanista* spp.; Ling, 1977). Most odontocetes possess reduced hair shafts as adults, including having only small hairs within the follicle (i.e., *Tursiops truncatus*; Gerussi et al., 2020), or having no hair shafts whatsoever (*Sotalia guianensis*; Czech-Damal et al., 2012). If the hair shaft is still present within the follicle, it could play a proprioceptive role, and provide information about water movements and head rotations (Gerussi et al., 2020; Ling, 1977). Despite hair still being visible (e.g., *Platanista*) or only present within the follicles as in *Tursiops*, it is not possible to discount the possibility that these vibrissal follicles may also be used as electroreceptors (Gerussi et al., 2020; Kelkar et al., 2018). Indeed, recent evidence from an anatomical and behavioral study with three female bottlenose dolphins provides clear evidence for electroreception in *Tursiops truncatus* (Huettner et al., *this issue*), as has already been demonstrated in *Sotalia guianensis* (Czech-Damal et al., 2012; Dehnhardt et al., 2020). Certainly, the delphinids appear to be an interesting group to further explore the mechanoreceptive, proprioceptive and electroreceptive function of vibrissae. Since mysticete vibrissal shafts are present in adults, they are likely to play a mechanoreceptive role, and their vibrissal follicle anatomy appears to be largely conserved across species too.

## 4.2 | Suggestions for future study

In the three species examined here, we observed differences in vibrissal number, follicle size and shape, and innervation distribution. A useful first step to further examine the diversity of cetacean vibrissae would be to systematically examine vibrissal shafts and follicles across more species of cetaceans, and especially in the delphinids. This was first started by Japha in 1912, who described the vibrissae of five species of mysticetes and six species of odontocetes. However, more detailed, quantitative anatomical analyses can now be carried out, incorporating more species. It is now even possible to measure the conductivity of material within the follicle to judge possible electroreceptive capabilities. In addition, the presence, position and amount of innervation should also be examined in order to estimate vibrissal sensitivity. However, quantifying the amount of innervation around the follicle is time-consuming, difficult to measure and requires good-quality anatomical samples (Hyvärinen, 1989; Marshall et al., 2006), which can be hard to come by using cetacean samples from museums or beach strandings. In terrestrial mammals, the infraorbital foramen (IOF; a branch of the trigeminal nerve) has been found to be closely associated with both vibrissal sensitivity and number (Muchlinski, 2010a), and large datasets can compare vibrissal sensitivity across species using this metric (Muchlinski, 2010b; Muchlinski et al., 2020). However, in cetaceans, and especially odontocetes, their skull contains multiple infraorbital foramina (Figure 5; Huggenberger, Oelschläger, & Cozzi, 2019; Rommel, 1990), and the infraorbital nerves run in to the melon as well as the vibrissal region (Cozzi, Huggenberger, & Oelschläger, 2017; Yamagiwa et al., 1999). Therefore, it is not possible to separate the foramina associated with vibrissal sensing and those associated with echolocation, by just looking at skull measurements of the IOF. Consequently, it is only possible to examine the follicles themselves, using histology. However, even with comprehensive anatomical descriptions of more cetacean species vibrissal follicles, it would still be impossible to truly predict their function. Detailed behavioral and psychophysical tests are necessary to further explore vibrissal function and sensitivity to electrical and mechanical stimuli, such as those developed by Czech-Damal et al. (2012); however, this is also an extremely time-consuming process. Moreover, studies in this area may be limited to species that are most common in captivity, such as *Tursiops truncatus* and *Orcinus orca*.

While it is certainly challenging to study cetacean sensory anatomy, behavior and function, we show here that cetacean vibrissal follicle anatomy is diverse, and therefore worthy of further investigation. We suggest an aquatic lifestyle is an important driver of vibrissal



**FIGURE 5** Cetacean skull foramina. (a) Skull foramina on the dorsal surface of a delphinid skull (*Delphinus delphis*) and (b) Phocoenid skull (*Phocoena phocoena*). Arrows correspond to premaxillary foramen, black asterisks identify anterior infraorbital foramina, red asterisks identify the posterior infraorbital foramen. Scale bar is 50 mm

morphology, and that differences in follicle anatomy are likely to be associated with function. However, further anatomical and behavioral studies are needed in order to better understand the associations between vibrissal form and function in cetaceans.

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## AUTHOR CONTRIBUTIONS

**Natasha Mynett:** Data curation; formal analysis; funding acquisition; methodology; project administration; visualization;

writing - original draft. **Hannah Mossman:** Conceptualization; formal analysis; investigation; project administration; supervision; visualization; writing - original draft; writing-review & editing. **Tim Huettner:** Conceptualization; supervision; writing-review & editing. **Robyn Grant:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; supervision; validation; visualization; writing - original draft; writing-review & editing.

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