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In-situ observations of the sensory hairs of Antarctic minke whales (*Balaenoptera bonaerensis*)

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Abstract

The sense of touch in the largest marine mammals is poorly understood. While mysticetes possess specialized sensory hairs that are present through adulthood, descriptions of these structures are based almost entirely on examination of tissues in post-mortem individuals. Sensory hairs have rarely been observed and described in living whales. We photographed Antarctic minke whales *Balaenoptera bonaerensis* in the Western Antarctic Peninsula and used high-resolution images to describe the number, distribution, orientation, and relative size of sensory hairs in freely swimming individuals. Sensory hairs were well developed. They were distributed on the tip of the lower jaw, the margins of the upper and lower jaw, and near the blowhole. Far fewer hairs were observed than reported for other mysticete species, including the related species *Balaenoptera acutorostrata*. Placement and apparent stiffness of sensory hairs within living tissue combined with observations and images of moving whales suggest these structures aid in detecting air and ice interfaces, and possibly, the boundaries of submerged prey fields.

KEYWORDS

follicle, mysticete, somatosensory, tactile, vibrissae, vibrissal crypt, whisker

1 | INTRODUCTION

Mysticete whales remain some of the most mysterious animals on Earth. Their sensory biology is known primarily from descriptions of anatomical structures in post-mortem specimens while detailed observations of sensory structures in living animals are rare. Mysticetes have hairs that are retained throughout all life stages with characteristics that vary by species. These hairs are considered to be vibrissae with dedicated neural and circulatory investment to support sensory function (as originally described by Japha, 1912). Sensory hairs have not yet been described for all mysticetes. Descriptive data are available for fewer than half of 14 extant species (Bauer, Reep, & Marshall, 2018), with histological examinations conducted in bowhead *Balaena mysticetus*, gray *Eschrichtius robustus*, fin *Balaenoptera physalus*, blue *Balaenoptera musculus*, humpback *Megaptera novaeangliae*, and sei whales *Balaenoptera borealis* (Berta et al., 2015; Drake, Crish, George, Stimmelmayr, & Thewissen, 2015; Japha, 1912; Nakai & Shida, 1947; Springer et al., 2020; Yablokov & Klevezal, 1962).

Lunge-feeding rorquals (family *Balaenopteridae*) generally have sensory hairs on the sides of their upper and lower jaws as well as near the blowhole (Ling, 1977). Other mysticetes have additional sensory hairs

This article includes AR WOW Videos. Video 1 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=6263667019001 and Video 2 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=6263667309001 distributed more broadly over the head (Berta et al., 2015; Drake et al., 2015). In all species studied thus far, the greatest concentration of these hairs occurs near the tip of the lower jaw. There is some suggestion that hairs positioned in different areas of the head have different mechanoreceptive properties and vary anatomically (Drake et al., 2015; Japha, 1912). In all cases, sensory hairs are firmly anchored within subdermal follicles that are sometimes associated with prominent epidermal recesses (*Balaena mysticetus*; Drake et al., 2015), protuberances (*Eubalaena glacialis*, C. Marshall in Bauer et al., 2018), or tubercles on the skin surface (*Megaptera novaeangliae*; Mercado, 2014). Individual hairs are reported to vary in length from 5 to 30 mm, with maximum diameter <0.2 mm (Berta et al., 2015; Japha, 1912; Yablokov & Klevezal, 1962). Apparent differences in the number, distribution, and characteristics of sensory hairs and the surrounding skin (Ling, 1977) may reflect differences in mechanoreceptive function among mysticete species.

The sensory hairs—or vibrissae—of Antarctic minke whales *Balaenoptera bonaerensis* (Burmeister, 1867) have not yet been described (but see Benham, 1901). As these roquals regularly forage in ice-filled polar waters and are among the smallest and most maneuverable mysticetes, an initial description of these structures in living individuals will provide valuable comparative information.

2 | METHODS

Digital images of freely swimming Antarctic minke whales were obtained in 2019 and 2020 during field research in the nearshore waters around the Western Antarctic Peninsula, with associated activities including biotelemetry and biopsy sampling. Supplementary archival images were sourced from colleagues. Photographs were taken with a Nikon D4S DSLR camera with Nikkor 300 mm f/2.8 ED lens or a Nikon D610 DSLR camera with AF-S Nikkor DX 18–300 mm f/3.5–5.6G ED VR lens from a rigid hull inflatable boat (RHIB) during daylight hours. Underwater video was obtained with a GoPro HERO8 Black camera mounted to a pole and extended below the RHIB.

Data were obtained opportunistically when curious whales approached the boat and milled near the surface or alternatively, during tagging/biopsy approaches. The handheld DSLR cameras were positioned 0.5–2.5 m above the water's surface (with the photographer sitting on the RHIB to standing on the elevated pulpit) and oriented downward toward the submerged whale or else angled towards the whale at the surface. Submerged images were obtained by the photographer sitting in the RHIB and holding the lowered extension pole with the underwater camera positioned <1 m below the surface. Ideal environmental conditions during several encounters—including glassy sea surface conditions (Beaufort Sea State 0), high ambient light, and extremely clear water—enabled fine details of the skin to be resolved in a subset of high-resolution images (>240 DPI) obtained at estimated ranges from 2 to 12 m.

We screened available images and video footage for fortuitous capture of sensory hairs and empty hair follicles or crypts, with emphasis on the head and dorsal surface of the body. When such structures were visible in an image, we sourced relevant metadata for the given whale, which included age class estimation (calf, juvenile, adult), field identification code if available, and in some cases, sex determination, which was based on subsequent genetic analysis following associated biopsy sampling. In a few images that included the blowhole region, a biologging tag with a camera lens (CATS-Cam, Queensland, Australia, www.cats.is) was visible on the whale within 0.5 m of the sensory structures. This tag provided a scaled reference for sensory hairs that were in a similar plane from the perspective of the DSLR camera. We determined approximate relevant anatomical distances by referencing focal structures to a 24 mm diameter circular marker on the tag using ImageJ2 software (Rueden et al., 2017).

The same data were reviewed to identify surfacing events. In instances that clearly showed the whole-body contour of the whale as it broke the surface of the water prior to air exchange, we used individual frame analysis to identify and describe how the skin surface typically emerged from the water at the water–air interface. We then related this information to the expected position of sensory hairs derived from fine-scale image analysis.

3 | RESULTS

The skin of the whales was smooth, taut, and well illuminated in many images, allowing sensory hairs and associated or empty follicles to be identified with confidence in the regions surrounding the jaws and on the dorsal surface extending from the front of the head to approximately 0.5 m posterior to the paired nasal openings, or blowholes. Sensory hairs were present on the tip of the lower jaw, the sides of the upper and lower jaws, and near the blowholes as illustrated in Figure 1; examination of images did not reveal vibrissae on the ventral surface of the head. The skin surrounding the follicle of a given sensory hair was not notably raised or depigmented. At the insertion point of each hair the skin appeared darker than the surrounding skin, possibly coinciding with a slight depression at

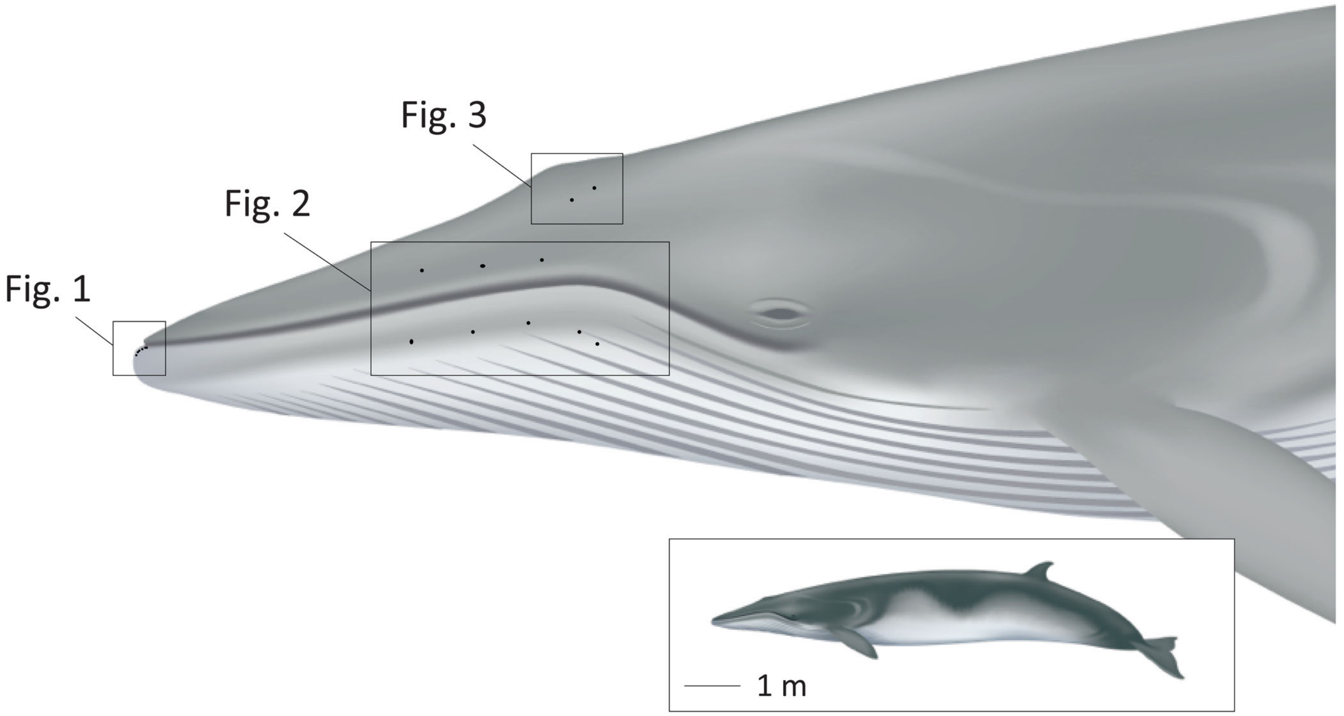

FIGURE 1 Placement of sensory hairs observed on free swimming Antarctic minke whales. Body regions with sensory hairs (black-filled circles) are referenced to corresponding figures in this manuscript. Illustration provided courtesy of the artist, Uko Gorter

the opening of the follicle. Vibrissae were transparent (uncolored) but readily visible in images obtained when the whale's skin was above the water's surface. When the skin was submerged, vibrissae were sometimes visible in the water while hair follicles were nearly always visible, except on the dark skin near the blowholes.

On the tip of the lower jaw at the mandibular symphysis, two tightly spaced columns of sensory hairs were present, separated by a narrow margin. These columns were equidistant to the dorsal midline (Figure 2a–d). The sensory hairs and/or follicle openings in this region were evident in 11 images obtained from at least five different adult individuals. In most cases, the skin at the tip of the lower jaw was pale and appeared thickened, with a dark focal spot marking each hair follicle (Figure 2e–f). There were 7–8 visible hairs in the column on the right side, and 6–7 hairs present in the corresponding column on the left. The columns extended anteriorly from the inner margin of the lower jaw with 1–3 hairs spaced over the curve of the jaw tip where the two columns converged. In most cases, these sensory hairs appeared stiff (relatively straight) and erect (>45° elevation from the skin surface). The follicles were regularly spaced within each column, with separation between aligned follicles approximately the length of an individual hair. The right column always contained more follicles and extended further anteriorly than the left column; thus, there was consistent lateral asymmetry in placement of sensory hairs in the individuals photographed. Observations of surfacing kinematics in transiting whales perfectly matched the placement of sensory hairs in this region; review of images and video data showed that whales consistently initially broke the tension of the water–air interface with the vibrissae-covered tip of the lower jaw during surfacing events (Figure 2g–h, Video S1). The sensory hairs appeared to be flattened or compressed when pushing against the cohesive force (surface tension) of the water (Figure 2i–j). Other images showed these vibrissae to be erect when completely above the water's surface (Figure 2a–f).

There were few sensory hairs visible on the sides of the upper and lower jaw extending to the jaw flange, or gape. There were three readily identifiable hairs that were widely and equally spaced along the anteroposterior axis on the upper jaw, and 4–5 hairs similarly distributed along the parallel axis of the lower jaw (Figure 3a,b). The most anterior of these hairs on the upper and lower jaw were positioned near but not at the margin of the closed mouth, proximal to the downward curve of the mouth (Figure 3c). These were similarly spaced above and below the opening of the mouth and slightly offset from upper to lower jaw, with the sensory hairs on the lower jaw shifted slightly anteriorly (Figure 1). On the upper jaw, the first hair was positioned ~60% along the axis extending from the symphysis towards the gape. The third hair was positioned about 80% of the distance from symphysis to gape. On the lower jaw, there were one or two additional hairs that were caudal to the preceding three hairs. The fourth-most posterior hair was spaced similarly to the three preceding hairs, but lower on the head (further below the opening of the mouth); this hair was aligned vertically with the downward curve of the mouth opening and on horizontal axis with the forward-facing eye of the whale (Figure 1). If a fifth hair

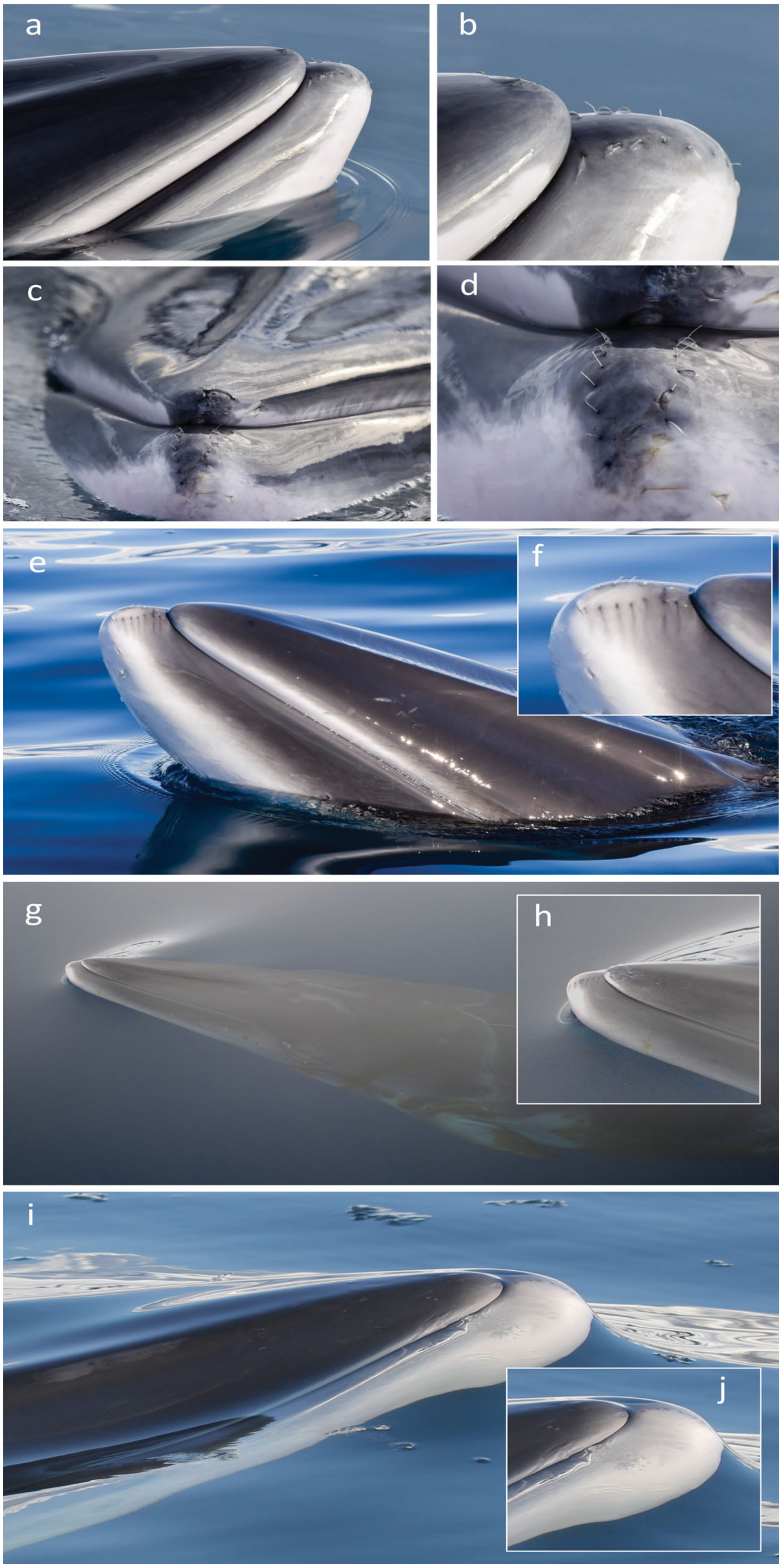

FIGURE 2 Several views of "chin" hairs and follicles on Antarctic minke whales. (a,c) Adult female identified as Bb19_055b, shown with enlarged views (b, d) of the same images. (e,f) Individual of unknown age and sex with enlarged inset. (g,h) Surfacing whales of unknown age and sex, with enlarged views (h,j) of the same images. Images a–h were taken in Andvord Bay during February 2019 by A. Friedlaender. Images i–j were taken in Fornier Bay in March 2013 by J. Goldbogen

was visible on the lower jaw it was just posterior to and below the fourth hair. Sensory hairs positioned on the sides of the jaw were documented in at least seven images obtained from three individuals. These hairs appeared longer and more pliable than those on the rostrum tip. They extended outward from the skin of the whales, especially when photographed on submerged individuals (Figure 3b,d). In most cases, whether above

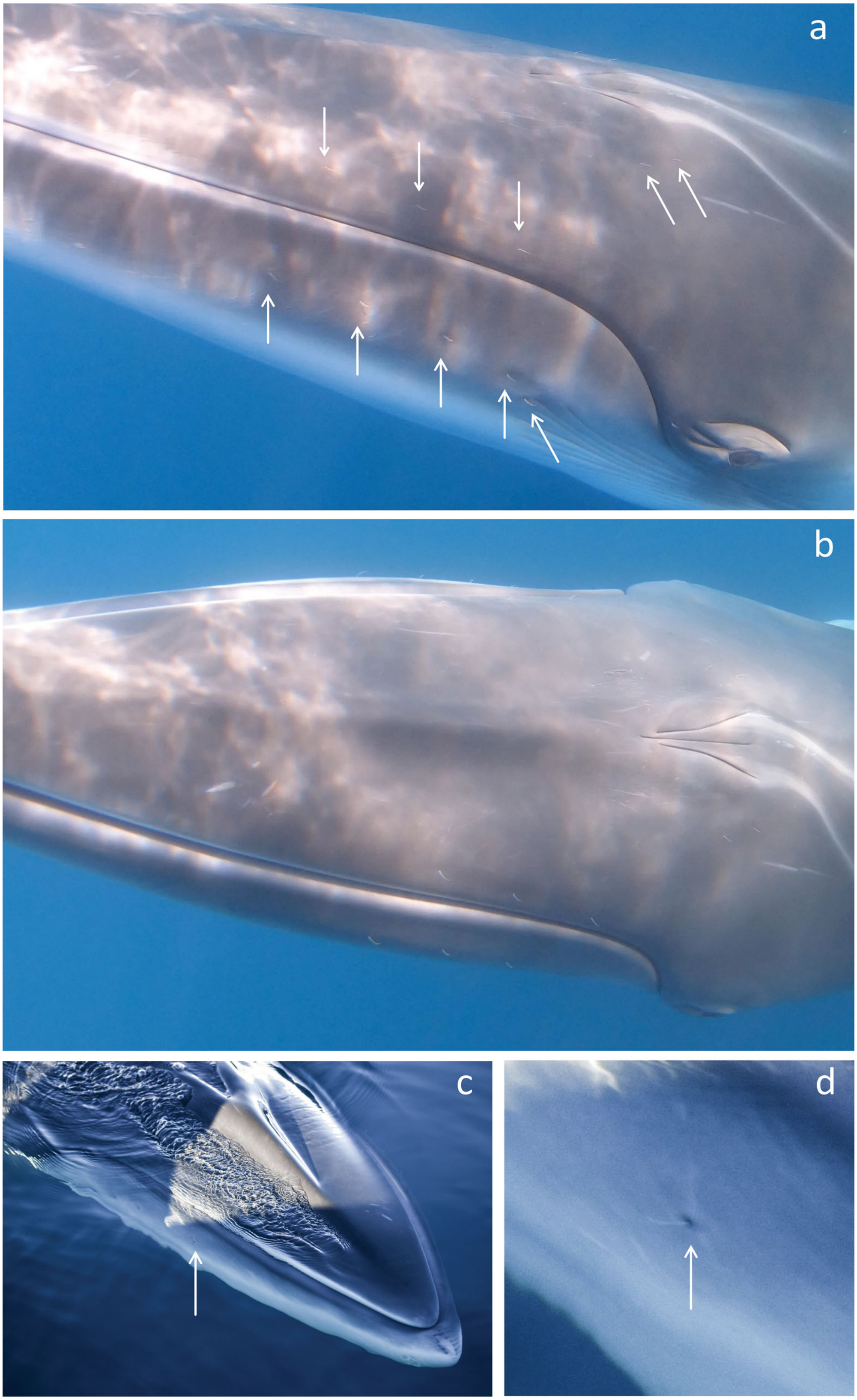

FIGURE 3 Several views of hairs on the sides of the upper and lower jaws of Antarctic minke whales. (a,b) Images of a submerged adult of unknown sex extracted from Video S2. (a) There are three sensory hairs associated with the upper jaw, five hairs associated with the lower jaw, and two hairs visible on each side of the paired blowholes; all are indicated by arrows. (b) Another view of the same individual shows the same sensory hairs as well as four hairs extending from the lower jaw on the right side of the individual at the top of the frame. (c) A whale of unknown age and sex photographed by J. Goldbogen in March 2019 in Paradise Bay showing the follicles of the chin as well as the four most anterior follicles on the lower jaw; the arrow points to the most anterior follicle. (d) Enlarged image from panel d showing the follicle and associated erect hair

or below the water's surface, these sensory hairs were aligned along a diagonal caudal-ventral plane, orientated back and down relative to the direction of typical body movement (Figure 3a, Video S2).

There were two obvious sensory hairs positioned reliably and symmetrically medial to each blowhole (Figure 4a,b). Examination of the smooth, dark skin on the dorsal surface of the whales both anterior and posterior to the blowholes

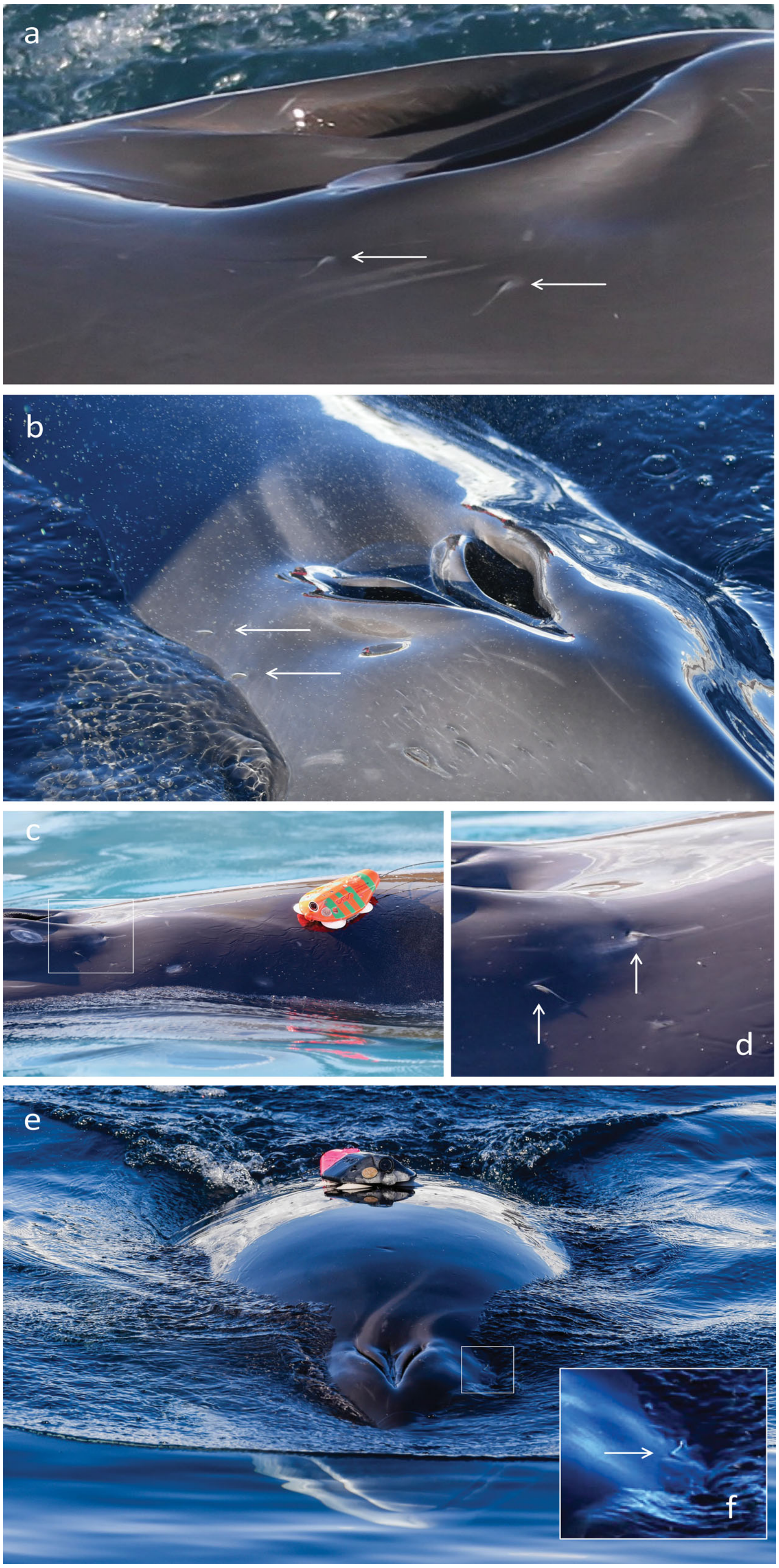

FIGURE 4 Several views of hairs associated with the paired blowholes of Antarctic minke whales. (a,b) Images of two individuals showing smooth skin surrounding the right (a) and left (b) blowhole, with the paired hairs on each side indicated by arrows. The whale shown in (a) was photographed by J. Goldbogen in Fornier Bay in March 2013 and is the same individual shown in Figure 2i,j. The whale shown in (b) was photographed by J. Goldbogen in Paradise Bay in March 2019 and is the same individual shown in Figure 3c,d. (c,e) Images of two individuals showing placement of a CATS biologging tag for size reference; there is a circular coin (24.3 mm diameter) mounted on the front of each tag. Image (c) shows the left side of an adult whale of unknown sex while at the surface, with an enlarged image (d) of the sensory hairs associated with the left blowhole; the tag is the same horizontal plane of the sensory hairs. Image (e) shows an adult whale of unknown sex diving below the surface following a breath; the inset (f) is digitally altered to reveal a sensory hair at the base of the left side of the ridge surrounding the closed nasal openings. Images c–f were taken by A. Friedlaender in Andvord Bay on different days in February 2019 and presumably show different individuals

did not confirm the presence of other hairs or vibrissal crypts. The paired hairs associated with each blowhole were located at the outer base of the ridges rimming the nasal openings. Considered topographically, these hairs were placed in tissue that would be at or above the water's surface only when the blowholes were securely raised into the air. The most anterior hair on each side was positioned medial and just caudal to the center of the nasal opening, while the posterior hair was aligned with the terminal crease on the nasal opening. These vibrissae appeared to be the longest and most pliable on the animals. Similar to those on the sides of the mouth, these structures were oriented along the anteroposterior axis of the body with the whisker tip oriented back and down relative to the direction of forward movement (Figure 4c,d). The existence and relative placement of the paired sensory hairs associated with each blowhole were photographically confirmed on six individuals, with either the left, right, or both sides of the animal visible. In images where the biologging tag was visible as a scaled reference (Figure 4c), the length of these hairs was conservatively estimated to be ~25 mm. The images we reviewed in which the nasal openings were above the water's surface showed these openings were closed to slits when the sensory hairs were submerged (Figure 4e,f) and open only when they were above the water line (Figure 4b).

4 | CONCLUSIONS

The number of hairs (33–35) observed in Antarctic minke whales appears to be a derived feature, as they are the fewest reported among mysticete whales. However, those hairs that are present appear to be well-developed structures that are positioned on regions of the body involved with foraging, surfacing, and respiration–suggesting these are biologically significant features.

Other mysticetes studied thus far have more than 70 hairs and up to several hundred in some species (Ling, 1977). Japha (1912, figure A) describes the related common minke whale *Balaenoptera acutorostrata* as having ~73 vibrissae (30 on the tip of the lower jaw in two columns, 8–10 hairs on each side of the upper jaw, and 12–13 hairs on each margin on the lower jaw), although only one fetal specimen was examined. One other neonatal description from Benham (1901) provides data for a species identified as *Balaenoptera rostrata* as having far fewer vibrissae, similar to our finding for *Balaenoptera bonaerensis*; that is, a vertical row of seven and eight hairs on the tip of the lower jaw, four hairs on each margin of the upper jaw, and five on each side of the corresponding margin of the lower jaw. Given the description and location of the specimen examined by Benham, it is likely that this was in fact *Balaenoptera bonaerensis*, as this species was not well differentiated within *Balaenoptera* until relatively recently (Rice, 1998). Thus, there is supporting evidence from a post-mortem evaluation for the in-situ observations of sensory hairs that we describe here (13–15 on the tip of the lower jaw in two columns, three hairs on each side of the upper jaw, five hairs on each side margin of the lower jaw). To our knowledge, the paired sensory hairs associated with each blowhole have not been previously described for minke whales.

Aspects of life history in this species may be relevant to the low number of sensory hairs observed. During the Austral summer, *Balaenoptera bonaerensis* range in latitude from 60°S to near and within the pack ice up to 80°S where they feed primarily on euphausiids (Perrin, Mallette, & Brownell, 2018). While most Antarctic minke whales retreat seasonally to breeding grounds at mid-latitudes, some individuals apparently overwinter in polar seas (Perrin et al., 2018), where sea surface temperatures remain near 0°C year round. These relatively small (<9 m, <10 tons), highly maneuverable whales have a smooth, lean, fusiform body shape (Kahane-Rapport et al., 2020). They often forage beneath heavy pack ice, lunging repeatedly for clustered prey on every dive (Friedlaender et al., 2014). Individuals seek out and remain within gaps in the sea ice which may provide refuge from sympatric predatory killer whales *Orcinus orca* (Konishi, Isoda, Bando, Minamikawa, & Kleivane, 2020). The reduction in sensory hairs in this species may be related to increased thermoregulatory constraints on skin perfusion in a small species inhabiting productive but very cold polar habitats, while their persistence and distribution may be related to essential function.

The regional placement of sensory hairs on the body of Antarctic minke whales is similar to that reported for other mysticetes. The high density of these hairs at the symphysis of the lower jaw is consistent with presumed tactile enhancement at this site. While fewer in number than in other species, these tightly spaced, frontally oriented vibrissae—together with the few strategically positioned sensory hairs at the margins of the posterior upper and lower jaws—may function within a dispersed mechanoreceptive system related to lunge feeding as has been described for another rorqual, the fin whale (Pyenson et al., 2012). Based on our photographic and video footage, it is apparent that the skin and hairs in this anterior-most region of the body are the first tissues to contact the boundary layer of ice or air as these whales come to the surface. These sturdy hairs are obviously displaced by shear forces that are released as whales break through the surface tension of the water, providing information about the air–water interface. Interestingly, while the characteristic "chin" first surfacing behavior of this species might exploit this enhanced sensory region, few other cetacean species seem to use their lower jaw in this manner (A. Friedlaender, unpublished data).

Some sensory hairs seem positioned to ensure that the superficial mechanics of air exchange occur above the water's surface. Based on their placement and the observed opening and closing of the nares, it is likely that the paired hairs bounding the dorsal blowhole region are used to confirm regional body placement above the air–water interface prior to respiration in typical swimming posture. Further, as Antarctic minke whales often surface vertically (rostrum up) in ice-choked areas (A. Friedlaender, unpublished data), these posterior-most hairs, and possibly the posterior-most hairs of the jaws, might serve a similar purpose in determining when the head is sufficiently extended above the water for respiration to safely occur.

The sensory hairs of whales are presumed to function as displacement detectors that are "closest range receptors" when other sensory streams are unavailable (Drake et al., 2015; Yablokov & Klevezal, 1962). We suggest that in-situ observations such as those reported here can add to the scant anatomical information available for cetacean species. These data also contribute to an improved understanding of why these structures show such notable variability among species, and how they may function to provide mysticete whales with meaningful information about the surrounding environment.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Colleen Reichmuth: Conceptualization; data curation; formal analysis; investigation; methodology; writing - original draft; writing-review & editing. **Caroline Casey:** Conceptualization; data curation; investigation; writing-review & editing. **Ari Friedlaender:** Data curation; funding acquisition; investigation; project administration; resources; writing-review & editing.

ETHICS STATEMENT

Research was conducted without animal contact in accordance with the laws of the United States. Animals were photographed in the field with authorization from the National Marine Fisheries Service of the United States under NMFS permit 14809 and the Antarctic Conservation Act under ACA permit 2015-011. Animal research protocols were approved by the Institutional Animal Care and Use Committee at the University of California Santa Cruz.

DATA AVAILABILITY STATEMENT

Primary data are presented within this manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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