VIBRISSA FOLLICLES OF THE ROSS SEAL

By John K. Ling*

Abstract. *Ommatophoca rossi* has between 15 and 17 mystacial vibrissa follicles on each side of the snout. The tactile hairs are short (10–40 mm. in length), round in cross-section and smooth in outline. The follicles are up to 18 mm. deep and are lodged in the facial musculature. Their gross and microscopic anatomy is essentially similar to that of *Mirounga leonina* but they are stouter and have more extensive gland complexes. The significance of these structural similarities and differences is discussed in relation to the probable sensory role of the vibrissae.

Of all the Antarctic seals it is perhaps the Ross seal (*Ommatophoca rossi* Gray, 1844) about which least is known. This species is rarely seen and very few specimens have been collected for detailed scientific study. General descriptions have been given by Scheffer (1958) and King (1964, 1968). Polkey and Bonner (1966) described its pelage and also commented on the vibrissae. Ling's (1966) study of the facial vibrissae of the southern elephant seal (*Mirounga leonina* Linn.) appears to be the only detailed account of these structures in pinnipeds. They have, however, been alluded to by many other authors.

A female Ross seal was captured by members of the British Antarctic Survey 725 km. north of Kapp Norvegia, Dronning Maud Land (lat. 64°22′S., long. 10°00′W.) on 25 January 1963. The carcass was frozen and despatched to the British Museum (Nat. Hist.). About 2 years later a small block of tissue containing five complete or partial vibrissa follicles was excised from the right posterior mystacial region and preserved in 10 per cent formalin. It was kept for another 3 years before being examined.

One follicle was sectioned longitudinally by freezing microtome and sections were stained with oil red O to reveal neutral lipids, and Mayer's haemalum for nuclear detail. The other four follicles were dehydrated, cleared and embedded in paraffin wax or celloidin, sectioned longitudinally and transversely at 7–20 μm. on a rotary or sledge microtome, and stained by the following methods:

i. Heidenhain's iron haematoxylin and eosin.
ii. Mayer's haemalum, eosin and picric acid (Carter and Clarke, 1957).
iii. Verhoeff's haematoxylin and Van Gieson's stain (Gurr, 1952) for elastic and collagen fibres.
iv. Periodic acid–Schiff reaction with saliva-digested control sections for the removal of glycogen.

Description and Gross Anatomy

Illustrations of vibrissa follicles of rats and mice have appeared in papers by Vincent (1913), Davidson and Hardy (1952), and Melaragno and Montagna (1953). Ling (1966) figured an elephant seal vibrissa follicle.

Polkey and Bonner (1966) stated that only the mystacial vibrissa group occurs in *O. rossi*. According to a figure in their paper and a photograph by King (1968), there appear to be 15 to 17 whiskers on each side of the snout of this species. In addition, King's photograph shows what appears to be a single follicle on one side of the rhinarium, but no hair can be seen to confirm the presence of rhinal vibrissae. King (1969) counted 19 facial vibrissae including one rhinal hair on the same female Ross seal from which material for this study was obtained. No superciliary vibrissae were present. The longest vibrissa in the present material measured 40 mm., the shortest only 10 mm., beyond the follicle orifice. The vibrissae were round in cross-section, with a maximum diameter of approximately 0·5 mm.; their outline was smooth, not corrugated, and they were pale creamy-yellow in colour. The tips were rounded or abraded and the surfaces also showed signs of wear. The medulla was simple, unbroken, of medium width, and extended over about three-quarters of the length of the hair fibre. The cuticular scale

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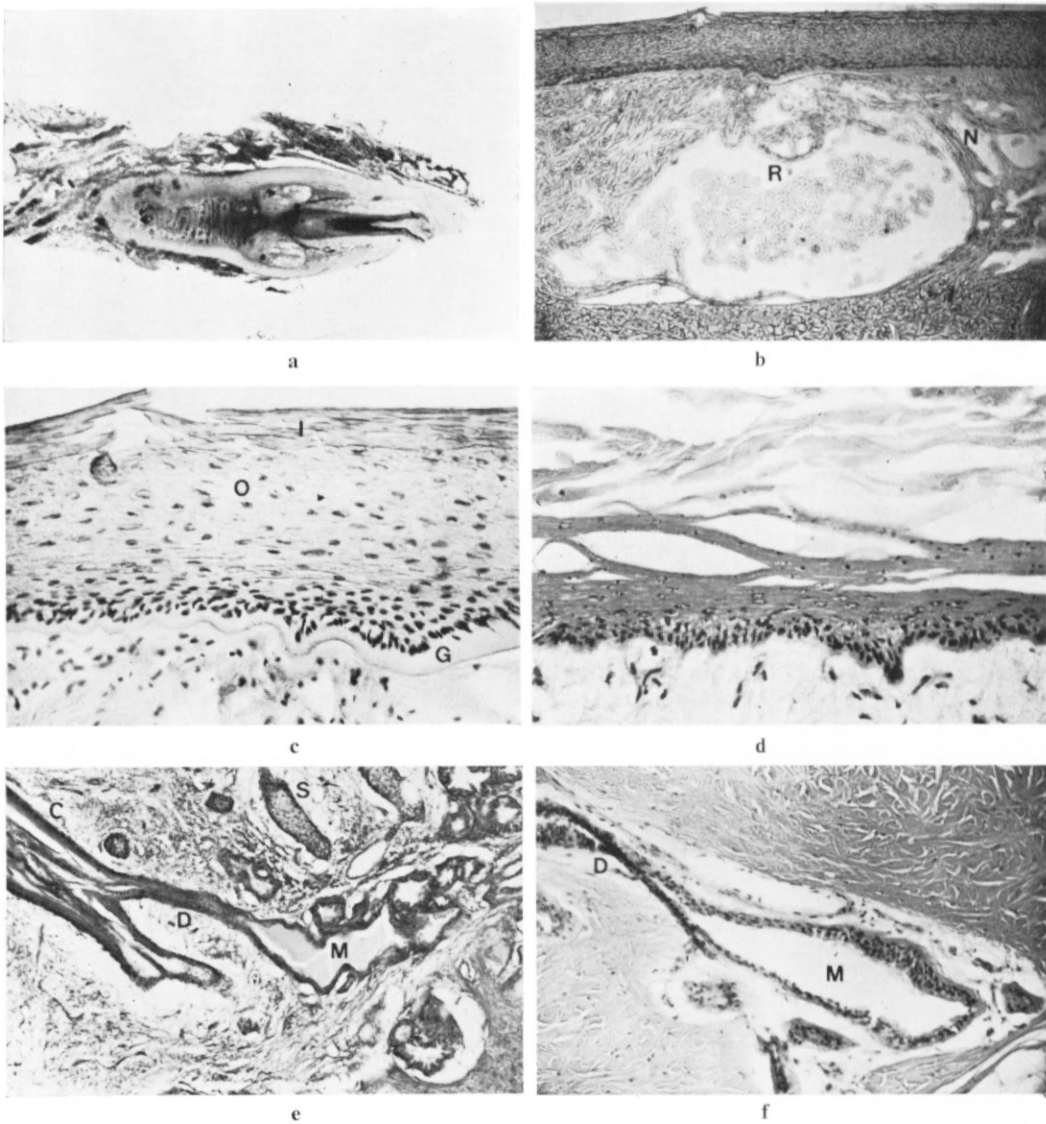

Fig. 1. a. Longitudinal section of mystacial vibrissa follicle at active (anagen) stage of hair growth. Stained with oil red O and haemalum (Mayer's); × 4·1.

b. Longitudinal section of follicle showing one-half of the ring sinus. Observe the ringwulst (R) and nerve fibres (N) (see also Fig. 1c). Haematoxylin (Heidenhain's) and eosin; × 47·5.

c. Longitudinal section of inner (canal) region of follicle (an enlargement of part of Fig. 1b). Note the wide inner root sheath (I), three obvious cell zones of the outer root sheath (O) and insinuating tongues of glassy membrane (G) among outer root sheath cells. Haematoxylin (Heidenhain's) and eosin; × 167.

d. Epidermal activity within the vibrissa canal. Note the nuclei in the desquamating cornified epidermis. Periodic acid–Schiff and haematoxylin (Harris'); × 225.

e. Gland complex comprising sebaceous (S) and (sweat-type) merocrine glands (M), ducts (D) and common canal (C) opening into distal region of vibrissa canal. Periodic acid–Schiff and haematoxylin (Harris'); × 22.

f. Secretory portion (M) and duct (D) of merocrine glands. Periodic acid–Schiff and haematoxylin (Harris'); × 122.

All figures are orientated so that the distal end of the follicle lies to the left of the page.

pattern was not discernible but Polkey and Bonner (1966) stated that it is similar to the mosaic type characteristic of the pelage hairs.

Vibrissa follicles, like all hair follicles, are epidermal derivatives, lodged at varying depths within the dermis and muscles of the face. The outermost zone of connective tissue surrounding them is modified to a greater or less extent to form a thick fibrous capsule or dermal sheath. A characteristic feature is the expansion of this dermal tissue to form blood sinuses, usually three in number: a proximal cavernous sinus, a central ring sinus and a distal sinus. The latter is much more extensive in Pinnipedia than, for example, in rodents where it merely forms a roof to the ring sinus.

Vibrissa follicles of *O. rossi* (Fig. 1a) measure up to 18 mm. in length and 3 mm. in diameter. Pelage hair follicles are lodged in the skin surrounding the orifice of each vibrissa follicle but none actually opens into the tactile hair canal. Sebaceous glands and other tubular glands enter common canals which in turn open into the distal region of the vibrissa canal. An anterior and a posterior nerve enter the base of the follicle through apertures in the dermal sheath. Although the origins of these nerves were not traced, they are presumed to be branches of cranial nerves V and VII. There is no erector muscle attached to the follicle, which is accommodated and moved by the general snout musculature (Ling, 1966).

Histology

The tough dermal sheath consists of densely packed collagen, short elastic fibres and a few fibrocytes. This sheath varies in thickness along its length and is also thicker on the posterior side of the follicle. Here it measures from 156 to 484 μm. and, anteriorly, from 156 to 328 μm. in width. It tends to be thinner in the region of the ring sinus.

The connective tissue is arranged more openly within the dermal sheath and contains three large blood sinuses. The cavernous sinus, which surrounds the proximal two-fifths of the follicle, is transected by trabeculae and nerves. The latter enter at the base of the follicle, where the dermal sheath is less compact, and send small branches ramifying through the proximal sinus and to the ringwulst or annulus in the ring sinus (Fig. 1b). The trabeculae have more elastic fibres and fibrocytes than the connective tissue of the dermal sheath. The cavernous sinus can become gorged with blood and many of the spaces contain clumps of red blood cells. The ring sinus extends over the middle fifth of the follicle's length. In longitudinal section it is almost oval in shape, tapering slightly in its distal region. A ringwulst forms a circular bulge around the inner wall of the ring sinus but there are no other tissue inclusions such as nerves and trabeculae. The distal sinus extends through the rest of the vibrissa follicle beyond the ring sinus. It consists of fairly densely packed connective tissue in the form of horizontal trabeculae and many ovoid blood vessels, especially in more distal zones. Sebaceous and tubular glands, to be described below, also occur in this part of the follicle.

The tissue of the dermal sheath becomes less compact around the follicle base, where it also extends into the invaginated follicle bulb in the form of a papilla containing blood vessels. These are important for nutrition during development and growth of the hair. Three of the vibrissa follicles described here were in a resting (telogen) stage, with dermal papillae and vascularization reduced, and the base of the capsules themselves somewhat constricted. One follicle was in an active (anagen) stage of hair proliferation. The fifth follicle was incomplete and the stage of hair growth was not observed.

The dermal and epidermal components of the follicle are separated from each other by the glassy or vitreous membrane. This is a hyaline, non-cellular structure of variable thickness throughout its length. It appears to be two-layered and thickest just proximal to the ring sinus, but one-layered and tapering on either side of this zone. Sometimes it becomes indiscernible around the dermal papilla and the distal parts of the follicle. Adjacent to the distal sinus the glassy membrane has a folded wavy outline, but below this region it follows the smooth curve of the follicle. The outer border of this membrane is generally smooth, but the inner margin is irregular and sends tongue-like projections between the cells of the outer root sheath (Fig. 1c). In some sections the glassy membrane can be seen to continue around the base of the follicle within the dermal papilla and enter the medulla of the hair fibre. Further insight into its nature could not be gained, due to the prolonged and less than satisfactory preservation of the material.

In the deeper part of the follicle, the outer root sheath becomes thicker than the Malpighian layer of the surface epidermis with which it is continuous. In median longitudinal sections of a follicle the maximum thickness of the outer root sheath is 590 μm. at the level of the ring sinus and cavernous sinus. This thickening is not uniform; anteriorly, the outer root sheath widens abruptly in the superficial region of the follicle, whereas posteriorly it tapers more gradually. An outer, middle and inner layer of cells is recognizable in the outer root sheath. The outer zone is one cell thick, the middle zone up to three cells thick and the inner layer has six or more cells. In telogen follicles the tactile hairs appear to have lost all connection with the bulb except for a thin strand of dedifferentiated outer root sheath cells. Cellular activity in the anagen follicle could not be reliably interpreted in the present material and differentiation of the inner root sheath cells into their respective layers could not be observed. Remnants of inner root sheath within the hair canal did indicate that this structure attains a considerable thickness around the base of the tactile hair (Fig. 1c). Glycogen and other PAS-reactive substances in the outer root sheath were not revealed by the PAS test.

The epidermis (Fig. 1d) lining the upper part of the vibrissa canal consists of only three recognizable layers: germinal, spinous and horny. In the present material mitotic activity in the germinal layer and superficial keratinization were proceeding. The outermost horny layer is composed of thick lamellae in varying stages of desquamation. Although many nuclei present in the germinal cells disappear in the course of epidermal proliferation, a number are carried over into the horny lamellae, where they remain clearly visible, even into quite late stages of sloughing. This condition was observed in all five follicles. The skin surface epidermis around the orifice of each vibrissa follicle was very thin, there were few mitoses and no desquamation was occurring; all are indicative of relative inactivity. What appeared to be a granular zone was clearly visible in the superficial strata of the skin surface epidermis, but it was absent from the epidermis of the vibrissa canal. The few pelage hair follicles in the region of the vibrissae were reduced in size and active hair proliferation was not in progress.

Two types of gland, holocrine and merocrine, were associated with each of the five vibrissa follicles examined. They are located in the outer region of the distal sinus and some parts even extend into the connective tissue sheath which is reduced to accommodate them. There appear to be four gland complexes each consisting of paired sebaceous glands and three sets of tubular glands in the nature of apocrine sweat glands. Each of the glands has a separate duct into a large common canal which then opens into the vibrissa canal (Fig. 1e).

This common secretory canal is lined with epidermal tissue continuous with that of the skin surface and the follicle wall in which it probably forms as an outgrowth of cells in typical fashion during ontogeny. The skin surface epidermis is densely pigmented with brown dendritic melanocytes and these are carried over into the vibrissa canal, along the walls of the secretory canal, around the outer cellular zone of the sebaceous glands and even into the secretory epithelium of two of the three sets of tubular glands. The outer root sheath of the follicle is pigmented only beyond the level of the orifice of the canal serving the gland complex. From the top of this canal to the deepest secretory tubule measures approximately 2 mm.

The sebaceous glands are of the usual holocrine type in the large cells of which oil droplets are discernible. In their greatest extent the sebaceous glands measure 240 μm. across and 31[illegible] μm. deep. They open by way of short ducts into the base of the common canal. The tubular merocrine glands consist of a thin-walled (1 or 2 cells thick) expanded secretory portion and a thicker-walled (2 or 3 cells thick) duct (Fig. 1f). Sets of tubular glands measure up to 435 μm. in depth and 210 μm. in width. Myoepithelial cells surround the secretory portions of the glands which are not as coiled as typical sweat glands. A substance occupying the secretory tubules stained readily with eosin.

Lipids abound in the tissues surrounding the capsule and many fat droplets invade the vibrissa follicle from this source. However, some lipids had obviously spread during preservation and preparation of the sections. The only unequivocal lipid deposits occur as droplets in the sebaceous glands, within the secretory product of the tubular glands, and between the trabeculae of the distal blood sinus. Here the lipid has a gel-like appearance and completely fills the spaces. The nerve fibres also colour slightly with oil red O, but oil droplets were not noted, in contrast to their presence along with pale oil red O-staining material in the dermal papilla. It is deemed that lipids have not been reliably demonstrated at these two sites.

Discussion

The vibrissa follicles of the Ross seal are essentially similar in structure to those of the southern elephant seal. The tactile hairs of *O. rossi* are much shorter than those reported for any other seal and the follicles, if anything, are relatively stouter. The function of the vibrissae and their follicles in the Ross seal, as in other aquatic mammals, is still largely unknown. Reduction in hair size does not appear to be accompanied by any diminution in size or structural complexity of the follicles in so far as can be judged on the basis of studies of only two pinniped species. Even the sensory pits on the snout of the bottle-nose dolphin, *Tursiops truncatus*, with only vestigial hairs, are still clearly recognizable sinus hair follicles (Palmer and Weddell, 1964). Thus it appears likely that the follicles themselves are the more important components of the vibrissae complex and have a probable sensory role.

Polkey and Bonner (1966) stated that the stratum corneum of the surface epidermis is thin and seems to be persistent, since mitoses were not observed. This is borne out by the present study but it is not true of the epidermis lining the vibrissa canal, where active cell proliferation and sloughing of cornified epidermis were taking place. Moreover, there were signs of a granular layer in the surface epidermis which, in Pinnipedia, apparently is characteristic only when the epidermis is active (Montagna and Harrison, 1957).

The relationship between surface epidermal activity, pelage cycles and growth of the tactile hairs cannot therefore be resolved on the basis of the present material. That each vibrissa may follow an independent schedule of growth is suggested by the fact that both active and resting follicles occurred together at a time when the pelage follicles and the surface epidermis appeared to be quiescent. Ling (1966) concluded that the cycles of vibrissa growth are not related to the pelage cycle in the southern elephant seal. It seems that these two organ systems, in fulfilling totally different functions, follow quite independent cycles of growth which may well correlate with different (external and internal) environmental conditions. This aspect requires considerable further study.

The gland complex is more extensive in the Ross seal than similar structures in the southern elephant seal, the only other mammal in which merocrine glands have been reported in association with vibrissa follicles (Ling, 1966). The common secretory canal draining each gland complex into the tactile hair canal is apparently a unique feature of *O. rossi*. That there may be two kinds of merocrine glands is indicated by the fact that two of the three sets have pigment cells in their epithelium, while the third lacks pigment. The significance of this apparent distinction cannot be deduced at present, but these features should be studied further in the Ross seal and other pinnipeds, care being taken to obtain well-fixed, absolutely fresh material. It is interesting to observe, moreover, that these merocrine glands occur in two pinniped species in which sweat glands associated with pelage hair follicles are reduced (as is the probable importance of the pelage itself in phocid thermoregulation) (Ling, 1965). Perhaps, then, merocrine secretion in association with elaborate pilary development is important, whether or not the fibres have a sensory or other function. Until the nature of these glands and their secretions can be more reliably established, their function must remain a matter of conjecture. At this stage it is tentatively suggested that the secretory product of possibly three kinds of gland is involved in a sort of maintenance of the tactile hair and/or hair canal and the enhancement, thereby, of the vibrissae as important sensory perceptors.

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REFERENCES

Carter, H. B. *and* W. C. Clarke. 1957. The hair follicle group and skin follicle population of Australian Merino sheep. *Aust. J. agric. Res.*, **8**, No. 1, 91–108.

Davidson, P. *and* M. H. Hardy. 1952. The development of mouse vibrissae *in vivo* and *in vitro*. *J. Anat.*, **86**, No. 4, 342–56.

GURR, G. T. 1952. *Biological staining methods*. London, George T. Gurr Ltd.
KING, J. E. 1964. *Seals of the world*. London, British Museum (Nat. Hist.).
———. 1968. The Ross and other Antarctic seals. *Aust. Nat. Hist.*, **16**, No. 1, 29–32.
———. 1969. Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia : Phocidae). *British Antarctic Survey Scientific Reports*, No. 63, 54 pp.
LING, J. K. 1965. Functional significance of sweat glands and sebaceous glands in seals. *Nature, Lond.*, **208**, No. 5010, 560–62.
———. 1966. The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.). I. The facial vibrissae. *Aust. J. Zool.*, **14**, No. 5, 855–66.
MELARAGNO, H. P. *and* W. MONTAGNA. 1953. The tactile hair follicles in the mouse. *Anat. Rec.*, **115**, No. 1, 29–50.
MONTAGNA, W. *and* R. J. HARRISON. 1957. Specializations in the skin of the seal (*Phoca vitulina*). *Am. J. Anat.*, **100**, No. 1, 81–114.
PALMER, E. *and* G. WEDDELL. 1964. The relationship between structure, innervation and function of the skin of the bottle nose dolphin (*Tursiops truncatus*). *Proc. zool. Soc. Lond.*, **143**, Pt. 4, 553–68.
POLKEY, W. *and* W. N. BONNER. 1966. The pelage of the Ross seal. *British Antarctic Survey Bulletin*, No. 8, 93–96.
SCHEFFER, V. B. 1958. *Seals, sea lions, and walruses: a review of the Pinnipedia*. London, Oxford University Press; Stanford, University Press.
VINCENT, S. B. 1913. The tactile hair of the white rat. *J. comp. Neurol.*, **23**, No. 1, 1–36.