



Aspects of the skin morphology in the sub-Antarctic fur seal *Arctocephalus tropicalis*

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Abstract

The present study examined whether sweat glands are present in the skin of sub-Antarctic fur seals, *Arctocephalus tropicalis*, using standard histological procedures and light microscopy. Aspects of the microanatomy and histology of skin were described to elucidate structure and function. Sweat glands were present both in the furred areas of the body trunk, as well as in naked skin areas of the flippers. The density of the apocrine sweat glands appeared higher in fur-covered areas than in naked areas, while the size of sweat glands was similar amongst naked and fur-covered skin. The superficial position of sweat glands in the dermis of naked skin areas and the large, coiled, tubular nature of the secretory portion seem to indicate sweat gland activity in contrast to the deep lying, narrow sweat glands in fur-covered areas.

Keywords Epidermis · Dermis · Hair follicles · Pinnipeds · Sweat glands · Thermoregulation

Introduction

Pinnipeds are adapted to conserve heat in their normally cold marine surroundings with its higher thermal capacity. They are, however, subjected to considerable heat loading on land (exogenous and endogenous) when they haul out to breed and moult. Behavioural (Bester and Rossouw 1994) and postural (Gentry 1973) adjustments are utilized in addition to physiological thermoregulation (Castellini 2018) to combat thermal overloading.

Postural adjustments related to the degree of exposure of the essentially naked flippers are extensively used by otariids (fur seals and sea lions) under conditions of thermal loading (Bartholomew and Wilke 1956; Gentry 1973). Fur-covered skin varies little in temperature resulting from the constant external insulation (fur), but changes in skin temperature of naked flippers allow dissipation of excessive heat (Irving et al. 1962). In naked or hairless skin, by definition, hair cannot be seen by the naked eye over the general skin surface, whether there are openings present or not (Rotherham et al. 2005). Such naked skin areas are considered the major sites

for heat dissipation (Irving et al. 1962; Whittow et al. 1972) through a combination of heat convection, radiation and cutaneous evaporation of sweat while on land (Odell 1974).

Sweat glands associated with the pelage occur over the general body surface of pinnipeds (e.g., Montagna and Harrison 1957; Sokolov 1960; Scheffer and Johnson 1963; Ling 1965a, 1968; Ling and Button 1975; Rotherham et al. 2005; Khamas et al. 2012; da Silva et al. 2020). Sokolov (1958) thought that in pinnipeds there were no sweat glands associated with naked areas of flippers, or other hairless areas of skin. Subsequently, sweat glands were reported from naked skin of both the hind and fore flippers of the northern fur seal *Callorhinus ursinus*, the hind flipper (but not the fore flipper) of the New Zealand fur seal, *Arctocephalus forsteri*, but not from the hairless part of the front flipper of the Antarctic fur seal *A. gazella* (Ling 1965a). Due to the inconsistent usage and unqualified meaning of "naked" and "hairless" skin in the literature, the interpretation of published information is difficult. In California sea lions *Zalophus californianus* sweat glands were present throughout the dermis, and the presence and distribution of sweat glands appeared to be species specific (Khamas et al. 2012). However, there is no doubt that amongst fur seals, the northern fur seal *C. ursinus* (Ling 1965a), the Cape fur seal (CFS) *A. pusillus pusillus* (Rotherham et al. 2005), and the South American fur seal (SAFS), *A. australis* (da Silva et al. 2020), possess sweat glands in both fur-covered and naked skin areas.

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The present study investigated (a) furred and (b) naked skin in the sub-Antarctic fur seal (sAFS), *A. tropicalis*, to ascertain the presence/absence of sweat glands. We briefly describe aspects of the microanatomy and histology of skin to elucidate structure and function, in terms of the thermoregulatory process, following Rotherham et al. (2005). Such information might be important to address the influence of the sub-Antarctic environment on aspects of the terrestrial phase of fur seal populations (Bester 1982).

Materials and methods

Skin samples were collected immediately after death from two male sAFS, *A. tropicalis*, aged 8 (standard length [STDL] = 1.31 m, mass = 37.5 kg) and 14 years (STDL = 1.62 m, mass = 97.3 kg), respectively, that were shot, as part of another study at Gough Island (40° 20' S, 9° 54' W) during October 1978. Pieces of skin of 100 mm² were cut with a scalpel to the depth of the subcutaneous adipose tissue from a number of sites ($n = 12$) representing (a) fur-covered ($n = 6$ sites, e.g., chest and neck), (b) naked ($n = 5$ sites, e.g., leading edge of front flipper and tip of hind flipper), and (c) thick naked skin from a pressure area on the underside of a front flipper ($n =$ one site). Furred areas were clipped before sampling.

All tissue was fixed with Bouin's fluid (Disbrey and Rack 1970) for 48 h and stored in 70% ethanol. Further processing used standard histological procedures (Disbrey and Rack 1970) following Rotherham et al. (2005). Tissue sections were cut transversely and longitudinally to the long axis of the body, perpendicular to the free skin surface, at 7 μm with a sliding microtome. Sections were stained with Ehrlich's acid haematoxylin and counterstained with a 1% eosin solution, and studied under a light microscope. The sweat glands and layer thickness of the skin were measured (μm) using a calibrated eyepiece micrometer. The outside diameters (width + depth)/2 of tubules in the secretory portion of the sweat gland were taken from the first 10 tubules viewed in cross section from each sample site. The volume of individual sweat glands was estimated using the formula for determining the volume of a sphere ($4/3\pi r^3$), where the radius (r) was taken as the half of the mean of two outside diameters measured at right angles to each other. The penetration of sweat glands into the dermis relative to the free surface of the skin was measured. The numbers of common pilary canals opening on the surface of the skin per unit surface area (mm⁻²) were counted as a measure of pilosebaceous unit density.

Mean values and standard deviations (S.D.) were calculated for each parameter. But without the original data (see next paragraph), we could not test for differences within and between the fur-covered and naked skin sample sites. In the

original study, measurements were taken from fur-covered [6 sites] and naked [5 sites] skin areas. Sample sizes for each parameter measured, could therefore vary between 10 (per site) and 50 (5×10) in naked skin areas to 60 (6×10) from fur-covered sites, not distinguishing from which of the two adult males the samples were taken from. The sample sizes for the calculated parameter means and S.D. must therefore be assumed to lie between 10 and 60 (this study).

The present study of the sAFS preceded that of the CFS by 25 years, using almost the exact same sample processing and measuring procedures as for the CFS (Rotherham et al. 2005). Unfortunately, the original sAFS data which were processed to produce a BSc Zoology honours project report by one of us (MvO), was subsequently lost. All that remained was (a) the text of the report without accompanying figures, (b) two tables, and (c) colour images ($n = 7$) of cross sections through the skin (no scale available) representing (a) a furred area on the trunk of the body, (b) a naked area from the dorsum of a flipper, and (c) a pressure area from the ventral side of a flipper.

We therefore only use the numerical data contained in the surviving two tables. We also limit ourselves to a concise qualitative description of the histology of sAFS skin without elaboration beyond that which can be seen in the few (low resolution) colour images. We then compare the information with the measurements and histological descriptions of the skin in the closely related CFS (Rotherham et al. 2005) and SAFS (da Silva et al. 2020).

Results and discussion

The skin of fur seals is composed of two principal layers: the outer epidermis and the underlying dermis. Beneath the dermis a layer of loose connective tissue commences (Fig. 1a).

Epidermis

Four cell layers—the inner stratum germinativum (or stratum basale), stratum spinosum, stratum granulosum and a stratum corneum were distinguished (Fig. 1b–d). The poor resolution of the photomicrograph prevented the possible identification of a 5th layer, the stratum lucidum (Fig. 1d) which is present in the thick epidermis of flippers in SAFS (da Silva et al. 2020). In the thicker epidermis, the stratum corneum was dense and compact (Fig. 1d), making it more resistant to sloughing (da Silva et al. 2020).

In naked areas (Fig. 1b–d) the mean epidermal thickness (μm) appeared thicker than in the fur-covered areas (Fig. 1a; Online Resource 1a), especially the stratum spinosum and the stratum granulosum. Significant differences in the thickness of skin layers between fur-covered areas and naked skin areas, as well as the thickness of skin layers amongst naked

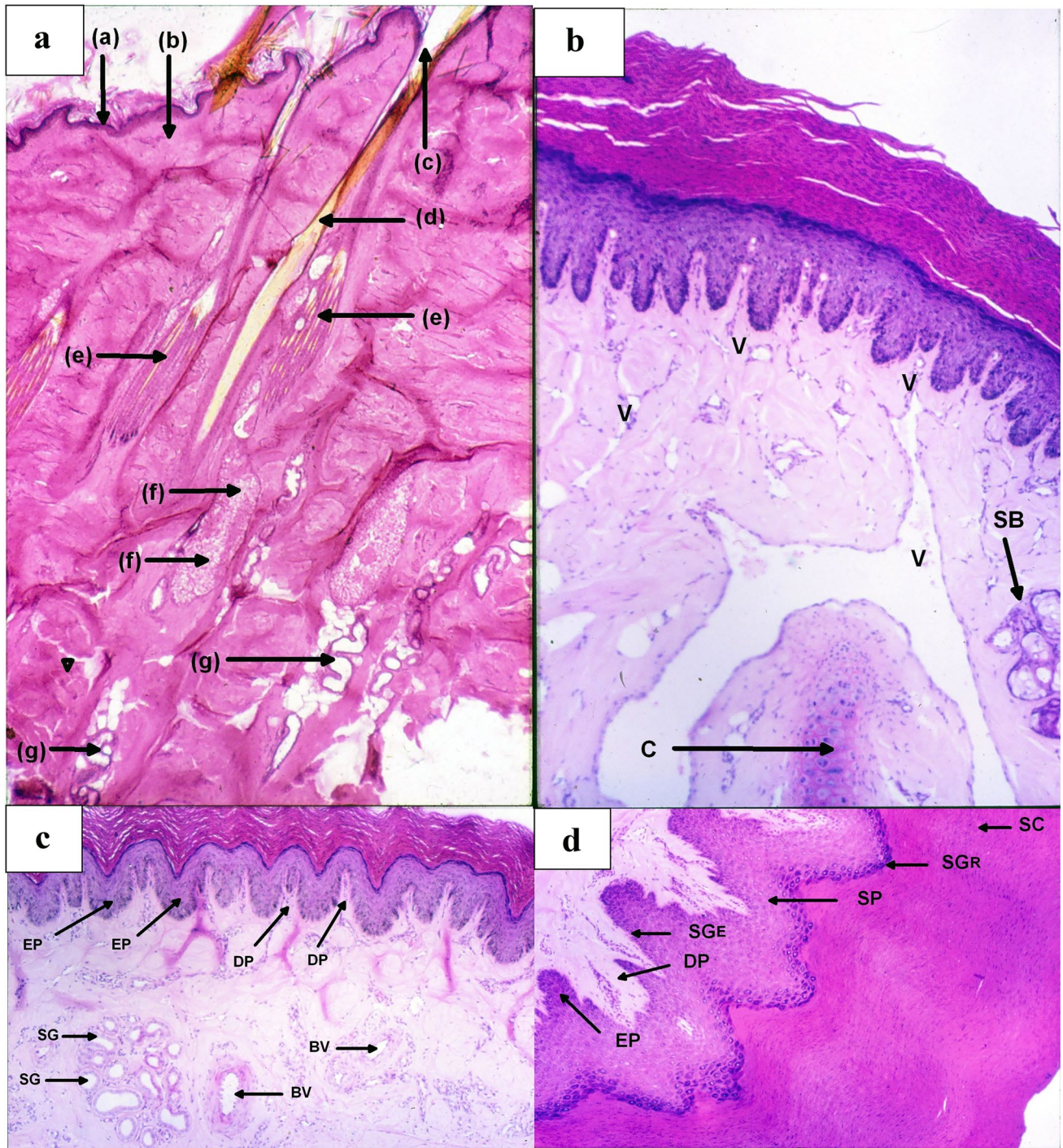


Fig. 1 **a** Photomicrograph (no scale available) of an oblique cross section through the furred skin of a sub-Antarctic fur seal showing the two principal layers of the skin, **(a)** the outer epidermis, and **(b)** the underlying dermis, and a pilose sebaceous unit comprising **(c)** a common pilary canal, **(d)** a guard hair, **(e)** associated under hairs, **(f)** sebaceous gland, and **(g)** sweat glands. **b** Photomicrograph (no scale available) of a cross section through the naked skin of a flipper tip in a sub-Antarctic fur seal showing the **(a)** vascularization (V), **(b)** a sebaceous gland (SB) and **(c)** the cartilaginous extension of a digit. **c** Photomicrograph (no scale available) of a cross section through the naked skin of a sub-Antarctic fur seal showing the **(a)** layered epider-

mis which forms epidermal papillae (EP), **(b)** the dermis with dermal papillae (DP), **(c)** a tightly coiled sweat gland (SG), and **(d)** blood vessels (BV). **d** Photomicrograph of a cross section through the naked skin in a pressure area of a sub-Antarctic fur seal. Although no scale can be provided, the emphasis is on the relative thicknesses of the **(a)** thick, compact outer stratum corneum (SC), **(b)** stratum granulosum (SGR), **(c)** stratum spinosum (SP), **(d)** the inner stratum germinativum (SGE), **(e)** a dermal papilla (DP), and **(f)** an epidermal papilla (EP). The poor resolution of the photomicrograph defies the identification of a 5th epidermal layer, the stratum lucidum

skin areas, were also described for the CFS (Rotherham et al. 2005). The epidermis of the sAFS formed ridges and furrows as it abuts the contours of the underlying dermis in fur-covered areas, with clear-cut interlocking epidermal and dermal papillae in thick epidermis of the naked flipper sections (Fig. 1b–d) as in SAFS (da Silva et al. 2020).

Although the thickness of individual epidermal layers, and total epidermal thickness, varied considerably between sample sites in the different body regions, the apparently greater layer thicknesses of naked areas are undoubtedly related to the absence of a protective fur coat. This finds maximum expression in areas which are more prone to abrasion and pressure such as the ventral side of the flippers (Fig. 1d) as in SAFS (da Silva et al. 2020).

Dermis

The dermis consisted of a thin outer pilary layer, and a reticular layer. The papillary layer had dermal papillae which projected into the epidermis as described above, and extended only slightly below the base of the papillae where it merged more or less gradually with the thicker reticular layer (Fig. 1b–c; Online Resource 1a).

The abovementioned information for the epidermis specifically (da Silva et al. 2020; this study), and both principal layers of skin in CFS (Rotherham et al. 2005) conforms to observations that the thickness of the epidermis plus dermis is inversely related to the development of the pelage in pinnipeds (Sokolov 1960).

Pilosebaceous units

Each pilosebaceous unit extended into the dermis and contained a guard hair, an underfur fibre bundle, a sweat gland and sebaceous glands, all sharing a common pilary canal which opens through the epidermis to the exterior (Fig. 1a; Online Resource 1a, c). The underfur fibres were grouped posteriorly to the guard hair with which they were associated, and the follicles of the underfur fibres were clustered together to form a bundle (Online Resource 1c) in sAFS (Condy and Green 1980; this study) as in all fur seals (Yochem and Stewart 2018). The epidermal matrices of the underfur (secondary) follicles were closer to the skin surface than those of the guard hair (primary) follicle (Fig. 1a; Online Resource 1a) and both the primary and associated secondary follicles occur in all the fur-covered body areas examined (Rotherham et al. 2005; da Silva et al. 2020; this study).

No emergent hairs were found in the naked area, only primary follicles as shown by da Silva et al. (2020). The pressure area was devoid of hair follicles (Fig. 1d), most likely because of the limited material (one photomicrograph) available, as hair follicles were found in the ventral flipper

regions in SAFS, but in lower numbers (da Silva et al. 2020). The density of pilosebaceous units as measured by the density of common pilary canals (Online Resource 2-Table 1) appeared higher in fur-covered areas than in naked areas. Pilosebaceous units disperse as a seal increases in age and body surface area (Scheffer and Johnson 1963); this has also been observed in *A. tropicalis* (Condy and Green 1980). The seal body and appendages grow at different rates, resulting in elongate and thin flippers, with long cartilaginous extensions to the digits, especially in otariids (Cooper 2018). Therefore, the relatively sparse pilosebaceous population of the naked skin of the flippers compared to the furred skin of the torso, may ontogenically have resulted from a stretching effect, the flippers in particular having a high surface area to volume ratio (Odell 1974).

Sweat glands

Each apocrine sweat gland consists of a secretory part and an excretory duct (Rotherham et al. 2005). The secretory part was situated in the dermis and extended well below the bases of the hair follicles (Fig. 1a; Online Resource 1a). The secretory part of the tubule was coiled and twisted on itself; hence, in sections it appeared as a small cluster of cross and oblique sections of tubules (Fig. 1a; Online Resource 1a, c). The excretory duct followed a somewhat spiral course through the dermis to finally open in the pilary canal (Rotherham et al. 2005). Rotherham et al. (2005) also described, for the first time in pinnipeds, eccrine sweat glands, the excretory ducts of which opened up directly on the skin surface. Da Silva et al. (2020) described the same sweat gland structure for thick epidermis, but identified it as merocrine sweat glands. In *Z. californianus*, sweat glands occupied most of the dermis in the skin of the flippers, and a few scattered sweat glands were found to be merocrine in nature (Khamas et al. 2012).

Only deep-lying sweat glands were present in fur-covered areas (Fig. 1a) that appeared to penetrate to a greater depth than the shallow-lying sweat glands of the naked areas (Fig. 1c), as in CFS and SAFS. On the other hand, a wide range of mean volume of sweat glands in fur-covered (chest and neck) and naked skin areas (hind flipper tip and anterior dorsal edge of front flipper) exists (Online Resource 2-Table 2). Neither did the volume fraction of sweat glands, whether associated with hairs (i.e., apocrine) or not (i.e., eccrine/merocrine) differ significantly amongst body regions of SAFS in both the superficial and deep dermis (da Silva et al. 2020), despite the observation that in the thick epidermis the sweat glands that opened directly at the surface of the skin were larger in size and had larger lumens. By contrast, in CFS, the mean diameters of the secretory portion of apocrine sweat glands were significantly larger (around 6–7 times larger) in the naked skin areas than in furred areas,

while the secretory portion of the eccrine sweat glands did not differ between such areas (Fig. 2, Table 1 [the 6th line entry being in error and should be ‘apocrine secretory gland diameter’] in Rotherham et al. 2005).

The density of common pilary canals (Online Resource 2-Table 1), each of which represents a pilosebaceous unit with its associated apocrine sweat gland (Fig. 1a; Online Resource 1a), was higher, on average, in fur-covered areas than in naked areas (this study). However, no significant differences in sweat gland density were found between such areas in CFS and SAFS (Rotherham et al. 2005; da Silva et al. 2020). This is the probable result of (a) our using the density of pilosebaceous units as a proxy for apocrine sweat gland density; (b) our inability to clearly separate eccrine sweat glands from apocrine sweat glands based on the differences in secretory ducts openings (directly at the skin surface or into the common pilary canal); and (c) the differences in the relative ages (and sizes) of the fur seals used in the comparison (adult male sAFS, adult female CFS, and SAFS pups). The latter consideration is likely in view of the increased dispersal of pilosebaceous units as seals increase in age and body surface area (Scheffer and Johnson 1963; Condry and Green 1980).

The role of sweat glands, and therefore cutaneous evaporation in the absence of free water to dissipate heat, is unclear. The superficial position of sweat glands in the dermis of naked skin areas (Fig. 1c) as compared to fur-covered areas (Fig. 1a), and the apparently large, coiled, tubular nature of the secretory portion (Online Resource 1b) seem to indicate sweat gland activity in contrast to the deep lying, narrow ones in fur-covered areas. In CFS the apocrine sweat glands were considerably larger in naked skin areas (Rotherham et al. 2005), and "large abundant" sweat glands were found in the flippers of *C. ursinus* (Bartholomew and Wilke 1956). Such size differences in sweat glands were, however, not significant amongst naked and fur-covered skin in SAFS pups (da Silva et al. 2020), and apparently not in sAFS adult males (this study). Also, in otariids, skin of the entire body has a tendency to be emissive during both hot and cold weather (Khamas et al. 2012). Nevertheless, what was assumed to be sweat appeared on the naked flippers of *Z. californianus* (Whittow et al. 1975), *C. ursinus* (Scheffer 1962) and *A. tropicalis* (this study). Considering that an estimated 15–22% of the heat production of *Z. californianus* was lost through cutaneous evaporation, the naked flipper areas and its array of sweat glands seem to be suited to facilitate such a process.

Sebaceous glands

The sebaceous glands are located in the dermis and associated with hair follicles (Fig. 1a; Online Resource 1a). Sebaceous glands were found both in fur-covered (Fig. 1a) and naked skin areas (Fig. 1b) but were absent in pressure areas on the underside of the fore flippers (Fig. 1d). An apparent increased size of the sebaceous glands in naked skin areas compared to fur-covered skin was established for the less hairy parts of otariids (Ling 1965a). The dense fur and secretions from the sebaceous glands may help water-proof and prevent water-to-skin contact, but with the progressive loss of hair in naked areas such a need is met by enlarged lipid secreting sebaceous glands (Ling 1968).

Vascularization

Vascularization was conspicuous in those areas of the dermis that were close to the epidermal layer in naked skin areas (Fig. 1b, c). Vascularization was also conspicuous in the dermal papillary ridges in the fur-covered areas in SAFS (da Silva et al. 2020). The relatively large size of the blood vessels coupled with the reduced insulation and predominance of papillary and interpapillary pegs that would increase the dermal/epidermal interface in naked skin, promotes thermoregulation (da Silva et al. 2020).

Conclusions

The microanatomy of the skin of *A. tropicalis* suggests that naked skin areas possess functional sweat glands which may be implicated in thermoregulation through cutaneous evaporation of sweat. The presence of fine hairs with associated cutaneous glands in naked (hairless) skin was also detected in the fur seals *C. ursinus*, *A. forsteri*, *A. p. pusillus* and *A. australis*. The absence of fine hairs in the fore flippers of both *A. forsteri* and *A. gazella* (Ling 1965b) is curious and probably reflects less extensive searching or inadequate material. Although eccrine (merocrine) secretory ducts opening at the skin surface were not detected in *A. tropicalis*, eccrine sweat glands are no doubt present as in CFS and SAFS (Rotherham et al. 2005; da Silva et al. 2020). The circulatory system in naked skin areas of the (hind) flippers especially appeared conducive to heat transfer to the environment (da Silva et al. 2020).

The function of sweat glands in *A. tropicalis* is likely to play an inferior role in thermoregulation. The temperature of the flippers in pinnipeds in and out of water (Irving et al. 1962; Whittow et al. 1972; Ohata et al. 1977; Gallivan and Ronald 1979) fluctuates dynamically. The possible

precedence of consideration of water economy over the regulation of body temperature (Whittow et al. 1972) also comes into play, as does the renal efficiency of the fur seal (Bester 1975; Ortiz 2001) which can only be considered adequate when judged against the normally cool and moist marine (oceanic) environment (Bester 1975).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00435-023-00619-2>.

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Author contributions MNB planned the study, killed the sAFS and collected the skin samples. MNB and MVO sourced relevant scientific literature. MVO prepared the skin samples for histological examination, executed micro-anatomical measurements, and summarised the findings in a report in 1980. MNB prepared, read, edited and approved the final manuscript.

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Data availability The original database no longer exists. The photomicrographs on which the histological descriptions and parameter definitions are based will be available upon request.

Declarations

Conflict of interest MNB declares no conflict of interest. The whereabouts of MVO currently is unknown but she had no conflict of interest at the time of the original study (1980).

Ethical approval Field procedures in 1977/1978 were approved by the Director-General, SADT, under advice from the South African Scientific Committee for Antarctic Research, pursuant to the provisions of the South African Sea Bird and Seals Protection Act, 1973 (Act 46 of 1973), and the Convention for the Conservation of Antarctic Seals of 1972. No formal animal ethics committee existed at the University of Pretoria in 1977.

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References

- Bartholomew GA, Wilke F (1956) Body temperature in the northern fur seal, *Callorhinus ursinus*. *J Mammal* 37:327–337
- Bester MN (1975) The functional morphology of the kidney of the Cape fur seal, *Arctocephalus pusillus* (Schreber). *Madoqua Ser II* 4:69–92
- Bester MN (1982) The effect of the subantarctic environment on aspects of the terrestrial phase of fur seal populations. *Com Nat Jr Rech Antarct* 51:469–478
- Bester MN, Rossouw GJ (1994) Time budgets and activity patterns of sub-antarctic fur seals at Gough Island. *S Afr J Zool* 29:168–174
- Castellini M (2018) Thermoregulation. In: Würsig B, Thewissen JGM, Kovacs KM (eds) *Encyclopedia of marine mammals*, 3rd edn, Elsevier Inc. pp 990–994
- Condy PR, Green ED (1980) The fur coat of the Amsterdam Island fur seal *Arctocephalus tropicalis*. *J Zool Lond* 191:85–96
- Cooper LN (2018). Forelimb anatomy. In: Würsig B, Thewissen JGM, Kovacs KM (eds) *Encyclopedia of marine mammals*, 3rd edn, Elsevier Inc. pp 385–388
- Da Silva AP, Mashado ASD, Le Bas AD et al (2020) The skin structures and their role in the thermoregulation of the South American fur seal (*Arctocephalus australis*). *Anat Rec* 303:3155–3167. <https://doi.org/10.1002/ar.24357>
- Disbrey BD, Rack JH (1970) *Histological laboratory methods*. Longman, London
- Gallivan GJ, Ronald K (1979) Temperature regulation in freely diving harp seals (*Phoca groenlandica*). *Can J Zool* 57:2256–2263
- Gentry RL (1973) Thermoregulatory behaviour of eared seals. *Behav* 46:73–93
- Irving L, Peyton LJ, Bahn CH, Peterson RS (1962) Regulation of temperature in fur seals. *Physiol Zool* 35:275–284
- Khamas WA, Smoldaka H, Leach-Robinson J, Palmer L (2012) Skin histology and its role in heat dissipation in three pinniped species. *Acta Vet Scand* 54:46 <http://www.actavetscand.com/content/54/1/46>
- Ling JK (1965a) Functional significance of sweat glands and sebaceous glands in seals. *Nature* 208:560–562
- Ling JK (1965b) Hair growth and moulting in the southern elephant seal, *Mirounga leonina* (Linn). In: Lyne AG, Short BF (eds) *Biology of the skin and hair growth*. Angus and Robertson, Sydney, pp 525–544
- Ling JK (1968) The skin and hair of the southern elephant seal, *Mirounga leonina* (L.). III. Morphology of the adult integument. *Austr J Zool* 16:629–645
- Ling JK, Button CE (1975) The skin and pelage of grey seal pups (*Halichoerus grypus* Fabricius): with a comparative study of foetal and neonatal moulting in the Pinnipedia. *Rapp P-V Reun Cons Int Explor Mer* 169:112–132
- Montagna W, Harrison RJ (1957) Specialization in the skin of the seal (*Phoca vitulina*). *Am J Anat* 100:81–113
- Odell DK (1974) Behavioural thermoregulation in the California sea lion. *Behav Biol* 10:231–237
- Ohata CA, Miller LK, Kajimura H (1977) Northern fur seal thermoregulation: thermal responses to pelagic conditions. *J Thermal Biol* 2:141–143
- Ortiz RM (2001) Osmoregulation in marine mammals. *J Exp Biol* 204:1831–1844
- Rotherham LS, Van der Merwe M, Bester MN, Oosthuizen WH (2005) Morphology and distribution of sweat glands in the Cape fur seal, *Arctocephalus pusillus pusillus* (Carnivora, Otariidae). *Aust J Zool* 53:295–300
- Scheffer VB (1962) Pelage and surface topography of the northern fur seal. *North Am Fauna* 64:1–206
- Scheffer VB, Johnson AM (1963) Moults in the northern fur seal. *US Fish Wildl Serv, Spec Sci Rep Fish Ser* 450:1–34
- Sokolov W (1958) The mechanism of heat dissipation in sea mammals. *Byull Mosk Obschch Ispyy Prir* 63:5–12
- Sokolov W (1960) The skin structure in pinnipedia of the U.S.S.R. fauna. *J Morph* 107:285–296

- Whittow GC, Matsuura DT, Lin YC (1972) Temperature regulation in the California sea lion (*Zalophus californianus*). *Physiol Zool* 45:68–77
- Whittow GC, Matsuura DT, Ohata CA (1975) Physiological and behavioural temperature regulation in the California sea lion (*Zalophus californianus*). *Rapp P-V Reun Cons Int Explor Mer* 169:479–480
- Yochem PK, Stewart BS (2018) Hair and fur. In: Würsig B, Thewissen JGM, Kovacs KM (eds) *Encyclopedia of marine mammals*, 3rd edn, Elsevier Inc. pp 447–448

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