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#### Key to figure lettering

	Act to J.S. To Tolland							
afv	anterior filter valve	h	heart					
ba	branchial arch	1	lung					
bc	buccal cavity	lbc	lining buccal cavity					
bcp	blood capillary	mf	middle fold					
bft	branchial food trap	mmuc	main mucous cord					
cg	ciliated groove	msc	mucous secreting cell					
ch	ceratohyal	muc	mucous cord					
ctl	connective tissue layer	oef	oesophageal funnel					
dft	dorsal food trap	oeff	oesophageal funnel floor					
dmuc	dorsal mucous cord	oefr	oesophageal funnel roof					
fc	filter crevice	oep	oesophageal projection					
fcl	filter canal	pc	pressure cushion					
ff	filter fold	pfv	posterior filter valve					
fn	filter niche	pr	pharyngeal roof					
fp	filter plate	rbft	rim of branchial food trap					
fr	filter ridge	se	squamous epithelium					
fs	filter shelf	ser	secretory ridge					
ge	gill chamber	sf	side fold					
gem	gill chamber membrane	sp	secretory pit					
gf	gill filament	spl	sensory papilla					
gft	gill filter	e modelomtil äle	tongue					
gl	glottis							

J. Zool., Lond. (1969) 157, 247-257

## Hairs and vibrissae in the Rhinocerotidae

A. J. E. CAVE\*

c/o The Zoological Society of London

(Accepted 8 October 1968)

(With 2 plates and 2 figures in the text)

Evidence is reviewed and observations are submitted concerning the occurrence and distribution of body hair in rhinoceroses. Absence of externally visible hair is shown to be not necessarily indicative of absence of hair follicles and to be part of a morphological cooling mechanism necessitated by the dynamics of the large body. Eyelashes are shown to be present on the lower cyclid of three species at least. The post-natal absence of all groups of facial vibrissae is confirmed for all rhinoceros forms, but a genal vibrissa is recorded for a *Diceros* foetus. Observations are submitted upon the hitherto undescribed histology of *Diceros* skin.

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#### Introduction

The larger rhinoceros forms (*Rhinoceros unicornis*, *Diceros bicornis*, *Ceratotherium simum*) are known to lack body hairs, other than those of the ear-and tail-fringes, characteristic of the family. The smaller forms (*Rhinoceros sondaicus*, *Didermocerus sumatrensis*) are known to manifest an extremely sparse hair coat, best developed in the smallest form (*Didermocerus*), upon a particularly hirsute specimen of which, from Chittagong, Sclater (1872) erected the fallacious species *Rhinoceros lasiotis*. According to Pocock (1914) the Rhinocerotidae are characterized by the presence of eyelashes upon the upper eyelid only and by the total absence of specialized tactile hairs (facial vibrissae).

Close scrutiny of the skin for the presence of hairs in living or recently shot animals is rarely possible in the field, and captive animals are notable for a progressive loss of the

<sup>\*</sup> Morrison Watson Research Fellow.

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ear- and tail-fringes and of such other hairs as may be present originally. Even the particularly hairy Sumatran rhinoceros (Didermocerus sumatrensis) suffers such loss of body hairs, both in the wild state (Hubback, 1939) and in captivity (Thomas, 1901). The absence of observable (i.e. freely projecting) hairs does not however necessarily imply any corresponding absence of hair follicles for in the externally hairless Ceratotherium, at least, non-projectile hair stumps may be present but concealed within the depths of well developed hair follicles (Cave & Allbrook, 1959). Hence accurate assessment of the extent to which body hair may occur in any particular rhinoceros form necessitates a systematic histological exploration of the entire skin. Since so formidable a task remains unassayed precise information is wanting concerning the presence and regional distribution of hair follicles in the several rhinoceros forms. Available studies of rhinoceros skin histology are limited to those of the nuchal hump skin of Ceratotherium (Cave & Allbrook, 1959), the penile and preputial skin of Ceratotherium and Diceros (Cave, 1964, 1966) and the metatarsal skin of Rhinoceros unicornis (Cave, 1962). These restricted observations are supplemented herein by observations upon the histology of Ceratotherium flank skin, of Diceros abdominal skin and of foetal Diceros shoulder skin. A more topographically extensive histological investigation of the skin of all extant rhinoceros forms is an obvious desidera-

#### Observations

## Body hairs

Flower & Lydekker (1891) gave "hairy covering scanty" as characteristic of their genus Rhinoceros, which, however, included the modern genera Didermocerus, Diceros and Ceratotherium: doubtless they had in mind the condition present in Didermocerus sumatrensis and Rhinoceros sondaicus, but they did not particularize the degree of hairiness in the several rhinoceros forms. Neuville (1927) stated hairs to be observable around the horn base in Asian rhinoceroses, an observation not subsequently confirmed.

In all the extant rhinoceroses hair fringes adorn the ears and tail. The former consist of soft, dark brown or blackish hairs upon the pinna margin, longer and stiffer hairs occurring at the pinna tip: shorter hairs are commonly present within the aural cavity. The latter consists of opposing streams of stiff, black, long hairs upon the dorsal and ventral margins of the flattened distal extremity of the tail. Beyond noting the tendency of such fringes to disappear with advancing age, their further consideration here is unnecessary.

## Rhinoceros unicornis (Indian rhinoceros)

This is the form most frequently kept in captivity, whose docility facilitates close inspection of the body surface. Yet neither Owen (1852) nor any subsequent writer has recorded the presence of body hairs, nor do any such appear in the standard illustrations of the species, drawn competently from the living animal. Personal observation failed to detect the presence of body hairs in the following specimens, specifically examined: 3 21 years, London Zoo, November 1941; 3 15 years, Whipsnade, March 1945; 3 18 years, Whipsnade, March 1961; living ♀ 10–11 years and infant ♂ offspring, Whipsnade, August 1960.

Histological examination of the metatarsal skin of the 18 years old 3 (Cave, 1962) revealed a thin melanin-containing epidermis covering a highly vascular, fat-free dermis,

composed of a dense and intricate feltwork of collagen and elastic tissue. Sweat glands and hair follicles were notably absent.

The occurrence of hair follicles outside the metatarsal region remains unknown.

## Rhinoceros sondaicus (Javan rhinoceros)

The Wolf-Smit lithograph of the living young ♂ animal (Sclater (1876), Pl. 46) depicts a sparse coating of stiff, somewhat bristly, hairs over the body dorsum, extending from the anterior part of the neck to the tail root. Garrod (1877) noted the presence of brownish hairs within the intertrabecular crevices of the dorsal skin of a young ♀ animal. The Javan rhinoceros is much less hirsute than the Sumatran form, but few specimens have survived sufficiently long in captivity to permit observations being made upon the persistence or otherwise of the hairs so prominent in the young animal. Hair follicles devoid of protruding hairs may well be present in regions other than the body dorsum. Since, however, histological observations are unrecorded for any region of the skin the exact extent of body-hair development in *Rhinoceros sondaicus* remains unknown.

## Didermocerus sumatrensis (Sumatran rhinoceros)

This is the smallest and the most hirsute of all extant rhinoceroses. It is well illustrated by Sclater (1876: Pls 48, 49), the delineation from the life showing clearly the sparse hairy coat, thickest over the body dorsum but obtrusive also upon the flanks, belly and limbs. Bartlett (1873: Pl. 11) reported a newborn specimen to be "covered with short, crisp, black hairs", not clearly evident in his accompanying illustration. Hubback (1939) noted that an infant specimen in Malaya had "much hair on its body and ears" and stated further that "the young rhinoceros is hairy, but the hair disappears as the animal ages" so that in the adult "only very short hairs, almost bristles, are found on most of the exposed parts of the body".

Upon a young and particularly hairy Q specimen from Chittagong in 1869 Sclater (1872) erected his now discredited *Rhinoceros lasiotis*. Examination of this animal in 1870 by Anderson (1872) showed the pre-orbital facial region to be hairless (save for scattered upper lip bristles), the ear-fringes to be exceptionally (almost five inches) long and the body to be uniformly coated with inch-long bristles, those on the head and neck and upon the flanks being somewhat shorter: over the wrists and heels the hairs tended to curliness: the tail was bristle-clad on its proximal two-thirds and terminally fringed by stiff hairs, almost six inches long at the tip. (The hair colour varied somewhat regionally, from almost black over the head, neck and body venter, to dark brown dorsally anterior to the shoulder fold and rufous posterior thereto.)

This animal died in the London Zoo in 1901, aged some 32–33 years. Examined then by Oldfield Thomas (1901) it was found that the originally obtrusive hairy coat had disappeared completely and that the originally exaggerated ear-fringes had become reduced to mere apical bristle-tufts.

Hubback (1939) regarded the progressive loss of body hair in the wild Sumatran rhinoceros as due to friction imposed by the dense thorny jungle terrain: Thomas's (1901) findings in the captive animal would suggest however that hair-loss in this form is not the result of environmental friction but a natural age-change.

The skin of the Sumatran rhinoceros appears never to have been studied histologically.

RHINOCEROS HAIRS AND VIBRISSAE

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Nevertheless recorded observations upon the hair-coat of the young living animal render certain a liberal and general distribution of hair follicles throughout the skin.

# Diceros bicornis (African black, hook-lipped rhinoceros)

The extraordinarily scanty anatomical literature relating to this most familiar and most hunted of all rhinoceroses contains no record of visible body hairs, and authoritative delineations of the living animal depict no hairs other than those of the ear and tail-fringes. Hairs were not detected upon personal examination of the following specimens: Q advanced foetus; 2 2 years, Whipsnade, 1960; 3 4 years, Whipsnade, 1962; 2 18-20 years, London Zoo, 1964; living 3 8 years and living 9 6-7 years, London Zoo, 1968.

Closer examination of the genital skin of the 4 years of specimen showed however the presence of minute hairs. The penile skin showed a trabeculated surface pattern of contiguous rosettes, each compounded of several triangular elevations: it was sparsely beset by stiff black hairs, some 3 mm long. The non-cornified preputial skin was circumferentially studded by stiff black hairs (ranging in length from 3 to 7 mm) and by the ostia of hair follicles devoid of projecting hairs (Cave, 1964).

Histological examination was made of the shoulder skin of the  $\mathcal{P}$  foetal Diceros. The remarkably thin epidermis was but slightly cornified (not more so than the human gum epithelium), the Malpighian layer contained pigment and no distinct stratum lucidum was demonstrable. The extremely thick dermis was composed of very stout collagen fibres disposed in every direction, and was wholly devoid of elastic tissue. Micro-sections 24 mm long were stained by haematoxylin and eosin and by van Gieson stain. These sections showed an abundance of apocrine type sweat glands provided with myoepithelial cells, whose ostia opened into the bottoms of the crevices separating the surface elevations of the skin. In all the sections hair follicles were strikingly absent.

Histological examination was also made of the abdominal skin of the 2 years 2. The externally mammillated thin epidermis showed good cornification and extreme vascularity, with a 100  $\mu$  thick stratum corneum and an 18.5  $\mu$  thick stratum Malpighii. The dermal papillae were large, abundant and riddled with capillary blood-vessels. The dermis was a dense, closely woven feltwork of large collagen fibres, disposed in bundles running in all directions. Elastic fibres were virtually non-existent-special staining with Weigert's resorcin-fuchsin and neutral red revealed a very few such, extremely tenuous and confined principally to the subepithelial zone. The dermis was permeated throughout its thickness by small, arteriolar-type blood-vessels, extremely numerous and provided with perivascular sheaths of undifferentiated mesenchyme cells, the average diameter of a single vessel and sheath being some 5  $\mu$ . Sweat glands were abundantly present as spherical masses (each some  $0.5 \times 0.2$  mm) of coiled tubes situated relative superficially (i.e. some 0.37 mm below the free surface of the skin). Each mass was associated with a discrete capillary plexus, and the sweat gland tube was surrounded, in all its convolutions, by myoepithelial cells. From every section examined hair follicles (and sebaceous glands) were absent.

It may well be that histological examination of other Diceros skin areas will yet reveal the presence of hair follicles but so far their occurrence has been established in the male genital skin only, associated sometimes with extremely short projecting hairs.

The relative abundance of large apocrine sweat glands in Diceros, as in Ceratotherium, their heavy investment with myoepithelial cells and the great vascularity of the whole skin, indicate unmistakably the paramount importance of copious sweat discharge as a means of effecting loss of body heat in these two large-bodied forms.

## Ceratotherium simum (African white, square-lipped rhinoceros)

Apart from those of the ear- and tail-fringes, body hairs are not visible in the white rhinoceros, which is as "naked" as the Indian and the black forms. Yet hair follicles abound in some, if not in all, regions of the skin, and these may conceal in their depths the roots

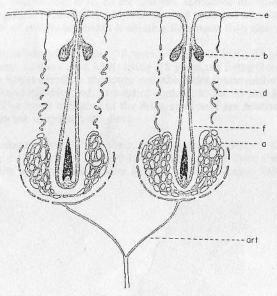


Fig. 1. Ceratotherium (ad. 3). Nuchal skin showing presence of hair follicles containing the roots and shaftstumps of non-projecting hairs (diagrammatic).

a, Apocrine sweat gland; art, arteriole; b, small sebaceous gland; d, duct of sweat gland; e, epidermis; f, hair follicle with contained hair root.

and basal stumps of hairs whose shafts do not project beyond—or even attain—the epidermis (Cave & Allbrook, 1959). Histological examination of the skin is so far restricted to observations upon that of the nuchal hump (Cave & Allbrook, 1959) and of the male genital organ (Cave, 1964, 1966).

Heller (1913) states that "the young at birth are no more hairy than the adults, possessing only the ear and tail fringes of coarse hair". However, Bigalke, Steyn, de Vos & de Waard (1950), describing the phases of epidermis moulting in a 3¼ months old ♀ animal, reported a sparse distribution of short, black hairs over "practically the whole of the body". the hairs being most noticeable "at the base of the toes and on the lower front sides of the limbs". One year later the same animal, viewed in full sunlight, exhibited hairs "on the back and sides of the body", indicating an interim reduction of projecting hairs in number or size or both.

Visible body hairs were undetectable upon personal examination of the following specimens: living  $2\frac{1}{2}$  years, Paraa, Uganda, 1962; 3 years, Whipsnade, 1964; 2 10 years, London Zoo, 1964; living 3 c. 18 years and living 2 10–11 years, London Zoo, 1968.

Histological examination of the flank skin of the 3 years & animal revealed a complete absence of hair follicles. In contradistinction, histological examination of the nuchal hump skin of an adult & (Cave & Allbrook, 1959) demonstrated an abundance of well formed hair follicles. Each such follicle was implanted within a basketwork of apocrinetype sweat glands. Freely projecting hairs were restricted to a solitary slender tuft upon the hump summit. But the vast majority of the hair follicles contained in their fundi the well formed roots and shaft stumps of abbreviated hairs (Fig. 1). None of these hairs occupied the follicle for any great distance from the fundus. Sweat glands of customary type were wanting, being replaced by particularly large apocrine-type sweat glands, situated superficially in the dermis and disposed as basketworks of coiled tubing around the bases of the hair follicles. Their spiral ducts narrowed somewhat in their passage through the epidermis. Both glands and ducts were liberally provided with numerous and strikingly large myoepithelial cells, disposed both between the basement membrane and secretory cells of the glands and helicoidally around the ducts. Each apocrine sweat gland was supplied directly by an independent arteriole derived from a more deeply situate dermal artery. Whether other regions of the Ceratotherium skin manifest a comparable pattern of hair follicles containing non-projecting hairs is not known. But the histological findings in nuchal hump skin establish the significant fact that, in this species at least, absence of projecting (i.e. visible) body hairs is not necessarily indicative of a corresponding topographical absence of hair follicles and hair roots. Moreover the abundance of large myoepithelial cells in association with the apocrine sweat glands indicates the physiological necessity for sudden and copious sweat discharge and the cells themselves represent the anatomical machinery effecting such discharge. In its suppression of hair development, in its elaboration of its sweat gland apparatus and in its intense vascularity Ceratotherium skin is obstrusively designed to function actively in the elimination of fluid, and thereby of heat, from the body.

The penis skin of the young Ceratotherium (Plate I(a)) is patterned by raised cuneiform areas, each a rosette of smaller, pseudo-triangular elevations bearing centrally the ostium of a hair follicle: very fine, very short hairs are scattered sparsely over this skin (Cave, 1964). Hair follicles, together with sebaceous glands and sweat glands, are present also in the skin of the prepuce (Cave, 1966).

#### Evelashes

Pocock (1914) considered eyelashes in the Rhinocerotidae to be confined to the upper eyelid. How far this opinion was based upon examination of living specimens and how far upon preserved skins does not appear. Certainly in all rhinoceros species the upper eyelid is heavily fringed with a mat or awning of long, upcurving, very prominent eyelashes. When the upper lid droops this thick fringe obscures the lower eyelid, completely so when the eye is closed. Its component hairs, in both wild and captive animals, survive the loss of the ear- and tail-hairs. Equally certainly, however, eyelashes occur in the rhinoceros lower eyelid: observable in *Rhinoceros unicornis*, *Diceros bicornis* and *Ceratotherium simum*,

they are doubtless present also in the now rare and unavailable Sumatran and Javan rhinoceroses. Whereas the upper eyelashes form a continuous series of exceptionally long, stiff, black (or reddish black) hairs, the lower eyelashes are an irregular, much sparser, arrangement of very much shorter, finer, and less obtrusive hairs. In the prepared skin they may be unrecognizable. Such lower lid eyelashes have been personally observed in the following specimens:

Rhinoceros unicornis: Living  $\bigcirc$  10½ years, Whipsnade, 1960; living 3 infant, Whipsnade, 1960; 3 18 years, Whipsnade, 1961. In the first two specimens the lower lashes are discernible in photographs (Plate I(b),(c),(d)): in the last specimen they were reduced to a discontinuous row of stubby elevations containing little more than their roots.

Diceros bicornis: advanced  $\[ \varphi \]$  foetus;  $\[ \varnothing \]$  2 years, Whipsnade, 1960;  $\[ \varnothing \]$  4 years, Whipsnade, 1962;  $\[ \varphi \]$  18–20 years, London Zoo, 1964; living  $\[ \varnothing \]$  8 years and living  $\[ \varphi \]$  6–7 years, London Zoo, 1968. In the foetal specimen the lower eyelashes were sparse and stumpy (some 2–3 mm long) and irregularly disposed, in marked contrast to the 15 mm long overhanging upper eyelashes. The lower eyelashes of the living specimens are relatively fine, but very short hairs, somewhat irregularly disposed.

Ceratotherium simum: living  $\,^{\circ}$ ,  $\,^{\circ}$ 2½ years, Paraa, Uganda, 1962;  $\,^{\circ}$ 2 10 years, London Zoo, 1964; living  $\,^{\circ}$ 3 18 years and living  $\,^{\circ}$ 10–11 years, London Zoo, 1968. In the first of these specimens the upper eyelashes were in three continuous rows, that containing the

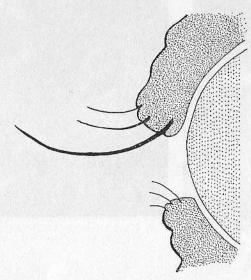


Fig. 2. Ceratotherium (juv. 9). Vertical section through eyelids showing arrangement of upper and lower eyelashes (diagrammatic).

longest and coarsest hairs being attached nearest to the conjunctival aspect of the lid, the two other rows, of shorter hairs, being attached more superficially (Fig. 2). The lower eyelashes were arranged in three irregular, discontinuous rows: short, and of equal size, they much resembled the bristles of a worn toothbrush. In the living specimens the lower eyelashes are very short and irregularly spaced hairs, recognizable on close naked eye inspection and exhibiting in some lights a rufous tint.

These admittedly limited observations suffice to refute Pocock's (1914) implication.

#### Facial vibrissae

The Rhinocerotidae lack all the canonical groups of facial vibrissae, a morphological specialization, which, coupled with the lack of a rhinarium, renders them the most specialized of the extant Perissodactyla (Pocock, 1914). Vibrissae were absent in the following specimens personally examined:

Rhinoceros unicornis: living ♂, 3 months; living ♀ 10-11 years; ♂ 15 years; ♂ 18 years; ♂ 21 years

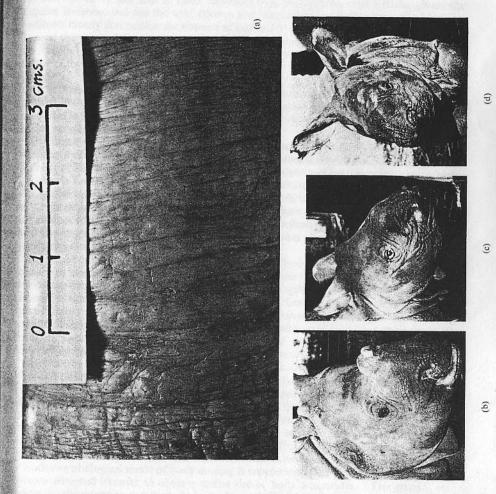
Diceros bicornis:  $\bigcirc 2$  years;  $\bigcirc 3$  years;  $\bigcirc 4$  years; living  $\bigcirc 8$  years; living  $\bigcirc 6-7$  years;  $\bigcirc 18-20$  years.

Ceratotherium simum: living  $\ \ 2\frac{1}{2}$  years;  $\ \ 3$  years;  $\ \ 3$  years;  $\ \ 3$  years;  $\ \ 10$  years. However, in the advanced  $\ \ 2$  Diceros foetus previously mentioned, the genal group of vibrissae was bilaterally represented by a single, relatively long vibrissa, lying against the local hairless skin and easily overlooked (Plate II(a),(b)). No other groups of facial vibrissae were so represented. Whether this genal vibrissa represented a sporadic atavism or the norm for the developing Diceros is indeterminable for want of information concerning other Diceros foetuses. No study of facial vibrissae in foetal rhinoceroses appears to have been made. It is possible that a genal dimple in Frechkop's (1951) photograph of a Rhinoceros sondaicus foetus represents the site of a lost vibrissa; but long preserved foetuses are apt to undergo considerable epidermal desquamation, so that neither they, nor photographs of them, provide very reliable evidence. Further examination of fresh, well preserved foetal material, representing all rhinoceros forms, in respect of vibrissa incidence is most desirable.

#### Discussion

Descriptively the extant rhinoceroses comprise (a) large bodied, hairless forms (Indian, African black, African white rhinoceroses) and smaller bodied, sparsely haired forms (Javan and Sumatran rhinoceroses). Anatomically, however, the extremely hairless forms may possess well developed hair follicles containing the roots and reduced shafts of genuine hairs: this has been demonstrated (Cave & Allbrook, 1959) for *Ceratotherium* and may well prove true for *Rhinoceros unicornis* and *Diceros bicornis*. No histological exploration of the entire skin has yet been undertaken for any rhinoceros species, so that the precise extent of hair follicle development and distribution throughout the Rhinocerotidae remains unknown. All that can be reasonably assumed is that in the smaller bodied Javan and Sumatran rhinoceroses the sparse hairy coat implies a fairly general distribution of such follicles.

The rapid post-natal disappearance of even the sparse hair coat of these smaller and



[To face page 254





PLATE II. Diceros bicornis (2 foctus), showing (a) genal vibrissa emerging from skin dimple, (b) the same vibrissa against a white card background.

more active forms is noteworthy. It has been attributed to external friction (Hubback, 1939) and to mere age (Thomas, 1901), but neither explanation is satisfactory. The friction allegedly imposed on the wild *Didermocerus* by an impenetrable thorny habitat produces no corresponding hair loss in other habitants (e.g. pig) and no such friction affects the captive *Didermocerus* nor the wild *Diceros* and *Ceratotherium*. Rhinoceros skin histology indicates clearly that neither the absence of external hairs in the larger forms, nor the rapid loss of the sparse hair coat in the smaller forms, results from trauma or senile change. Rather the suppression of a permanent hair coat is seen to be a morphological modification of the dermal apparatus essential to the all-important function of the skin as an excretory organ.

In rhinoceroses, as in all mammals, the maintenance of the body temperature within normal limits is vital and therein the skin plays a thermo-regulatory role: in the Rhinocerotidae it is modified to meet the physical requirements of large-bodied animals living under tropical environmental conditions.

Mammalian skin may undergo modification to function as either a conservator or an eliminator of body heat. Skin subserving heat conservation is characterized by (a) the development of hairs into an external coat, (b) the accumulation of an insulating layer of subcutaneous fat (panniculus adiposus) and (c) a quantitative or qualitative depression of sweat gland activity. (Elaboration of the hair coat tends to vary inversely with the degree of development of the panniculus.) Skin subserving heat elimination is characterized by (a) absence of an external hair coat, (b) absence of panniculus adiposus, and (c) numerical increase and/or morphological specialization of the sweat glands. Just such characteristics typify rhinoceros skin.

In large-bodied animals the surface area, whence body heat is lost mechanically, increases as merely the square of the body length, whereas body-volume, directly related to body-heat production, increases as the cube of that length. The larger-bodied the animal, therefore, the greater the proportionate increase of heat-producing body-volume over heat-eliminating body-surface and hence (as in the Rhinocerotidae) the necessity of augmenting mechanical surface heat loss by the active discharge of heat from the body in the form of sweat. Hence, therefore, the modification of the skin into an important heat-eliminating mechanism, whilst retaining its basic protective and sensorial functions.

Rhinoceros skin illustrates admirably such modification. The epidermis is extremely thin and delicate; hairs are confined to roots within the bottoms of the hair follicles, an external hair coat being inhibited; no panniculus adiposus is developed; ordinary sweat glands are replaced by very large and vascular apocrine type sweat glands, lavishly provided with large myoepithelial cells. The skin is thus structurally designed to facilitate heat loss from the body, not only by passive radiation from the naked external surface, but also by the active and copious discharge of warm fluid (sweat) from that surface itself. It is because of its heat-eliminating function that rhinoceros skin is rendered maximally hairless.

Such morphological mode of body cooling is supplemented by a distinctive behavioural pattern designed likewise to obviate undue rise of body temperature. This pattern embraces (a) the adoption (particularly in the larger-bodied forms) of an unhurried, ambling gait, (b) the avoidance of strong sunshine by lying up in thick shade, (c) the restriction of feeding to the cool periods of dusk and early morning, (d) the restriction of travel to such periods or to dull, cloudy periods and (e) the periodic cooling of the body surface itself by mud- or water-wallowing.

(Didermocerus is said (Hubback, 1939) to require to wallow at least six times daily: observations on wallowing-frequency in other rhinoceroses are wanting, but the largebodied Rhinoceros unicornis, essentially a swamp and grassland dweller, spends much of its time immersed in water. Longevity records of captive animals show that the cooler climates of non-tropical countries are conducive to the good health of such animals, which, in reasonably hot weather, require nevertheless frequent and copious hosing with water.)

Thus the external hairlessness, the skin structure and the habits of the Rhinocerotidae are seen to stem directly from the dynamics of a large body sustained by a vegetarian diet

in a tropical environment.

In connection with the abolition of a permanent hair coat, as a prerequisite in rendering the skin a heat-eliminating mechanism, it is significant that only the smaller-bodied, more physically agile rhinoceroses (Didermocerus, R. sondaicus) are at any stage even sparsely haired, whilst the larger bodied, slowly moving forms (Ceratotherium, Diceros, R. unicornis) lack even this minimal and temporary hairiness.

That, sporadically, projecting (visible) hairs should occur in these larger forms is not surprising, since the formative hair follicles are retained, certainly in Ceratotherium, most probably in Diceros and R. unicornis. Such follicles contain the roots and the shaft bases of hairs which, under tropical environmental conditions, do not project beyond (or even attain) the skin surface. But any change from tropical or arctic conditions would undoubtedly witness a maximal development of hairs and the establishment of an external

hair coat akin to that of the woolly rhinoceros (R. antiquitatis).

Essentially eyelashes protect against rain and strong sunlight, coming usually from above: hence the lashes fringing the upper and mobile eyelid are maximally developed throughout the Rhinocerotidae and persist throughout life. The lashes of the immobile lower eyelid, being functionally of small importance, are but minimally developed and so easily overlooked. They are, however, clearly apparent upon close inspection of the living or the recently dead animal, but may be lost from, or unrecognizable in, prepared skins or mounted specimens. They occur in all rhinoceros species as a somewhat irregular arrangement of extremely short, dark hairs, of rufous tint in certain lights.

Personal observation confirms Pocock's (1914) recognition of the absence in all groups of facial vibrissae in the Rhinocerotidae. Such absence (not confined to this mammalian group) is a morphological specialization of undetermined significance, but correlated, presumably, with the mode of life. The representation of the genal group by a single vibrissa in a foetus of Diceros is reported herein for the first time, but evaluation of this finding must be deferred until examination shall have been made of additional foetal material in

this and in other rhinoceros forms.

## Summary

Absence of a hair coat in the Rhinocerotidae implies no corresponding absence of hair follicles. In externally hairless forms (e.g. Ceratotherium) such follicles may occur containing the roots and shaft bases of non-projecting hairs. The suppression of a hair coat is a physiological response to the dynamics of the large body under tropical environmental conditions, permitting the skin to function maximally as an eliminator of body heat. Rhinoceros sweat glands are large, numerous and of apocrine type, liberally provided with myoepithelial cells, and designed to effect the copious discharge of sweat.

Lower eyelashes are present in Ceratotherium, Diceros and R. unicornis and almost certainly in Didermocerus and R. sondaicus.

Facial vibrissae are wanting in postnatal specimens of all species examined and are doubtless absent throughout the family: such absence is not readily explicable. A genal vibrissa is reported in a foetus of Diceros. Limited observations are submitted upon the histology of Diceros skin.

Grateful acknowledgment is made of the continued generosity of the Council of the Zoological Society of London in the provision of prosectorial material, of the kind assistance of Mr V. J. A. Manton and Mr Martin Senior in its collection at Whipsnade Park, and of the help rendered by Head Keeper W. G. Crompton in the examination of rhinoceroses in his charge in the London Z00.

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