

Preputial skin and glands in *Ceratotherium* and *Diceros*

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SYNOPSIS

The histology of the preputial skin and its appendages is described in the two African rhinoceros forms *Ceratotherium* and *Diceros*. Apocrine sweat glands occur in both. A feature of the *Ceratotherium* penis is the presence of distinctive surface papillae which are the mouths of eccrine sweat glands whose secretory tubules are embedded in a mass of subepidermal lymphoid tissue, an arrangement hitherto unrecorded for any mammal.

INTRODUCTION

During a morphological study of the rhinoceros penis (Cave, 1964a) histological examination was made of the preputial skin and its appendages in single and tolerably equal-aged specimens of the African white rhinoceros (*Ceratotherium simum*) and the African black rhinoceros (*Diceros bicornis*), the results of which are recorded below. This histological enquiry was prompted by the presence in the *Ceratotherium* specimen of certain peculiarly obtrusive preputial papillae (figs. 1, 2) to which preliminary reference has been made elsewhere (Cave, 1964b). The relevant literature contains no reference to any earlier investigation of penis skin histology in any rhinoceros form.

MATERIAL AND METHODS

The spirit-preserved pars libera penis of a three-year-old specimen of *Ceratotherium simum* (R.20) and that of a four year-old-specimen of *Diceros bicornis* (R.24) were examined both as to surface features and histological structure. From each specimen various portions of preputial skin were excised, formalin-fixed and paraffin-wax blocked: the blocks were sectioned at a thickness of 10 μ and the resultant sections stained by haematoxylin and eosin, by haematoxylin and orange G erythrosin, by haematoxylin and van Gieson, by Verhoeff and van Gieson and by alcian blue. From the *Ceratotherium* specimen (fig. 1) samples of skin were taken from the papillary and the non-papillary areas: skin from the flank and the belly wall was also studied histologically, both by way of control and for comparison with sections of the nuchal skin of a wild-killed Uganda specimen described previously (Cave & Allbrook, 1958). Serial sections were made of the *Ceratotherium* papillae and of the subepidermal glandular masses which, in this form, conferred a "goose pimple" effect upon certain areas of the preputial skin. Sections of the pedal skin

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of an adult specimen of *Rhinoceros unicornis* (Indian rhinoceros) were also available for comparison.

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BODY SKIN IN *Ceratotherium*

The first (and so far only) account of the microscopic structure of the skin of *Ceratotherium* was that given by Cave and Allbrook (1958) concerning nuchal skin taken from an adult animal wild-shot in Uganda: the histological findings recorded for this first specimen are confirmed by those obtained from other skin areas in the present and younger (Whipsnade) specimen. In this latter the epidermis is in many places finely papilliform externally (recalling the surface appearance of the felid tongue), being produced into tall, narrowly conical, spicular processes with the Malpighian layer following closely the contours of the individual external spikes. The stratum corneum, some 15 to 18 cells thick, is heavily keratinized: the stratum granulosum is but 1 to 2 cells thick: traces of a stratum lucidum appear but sporadically in the sections: the pigmented stratum Malpighii is some 8 cells thick between contiguous epidermal papillae.

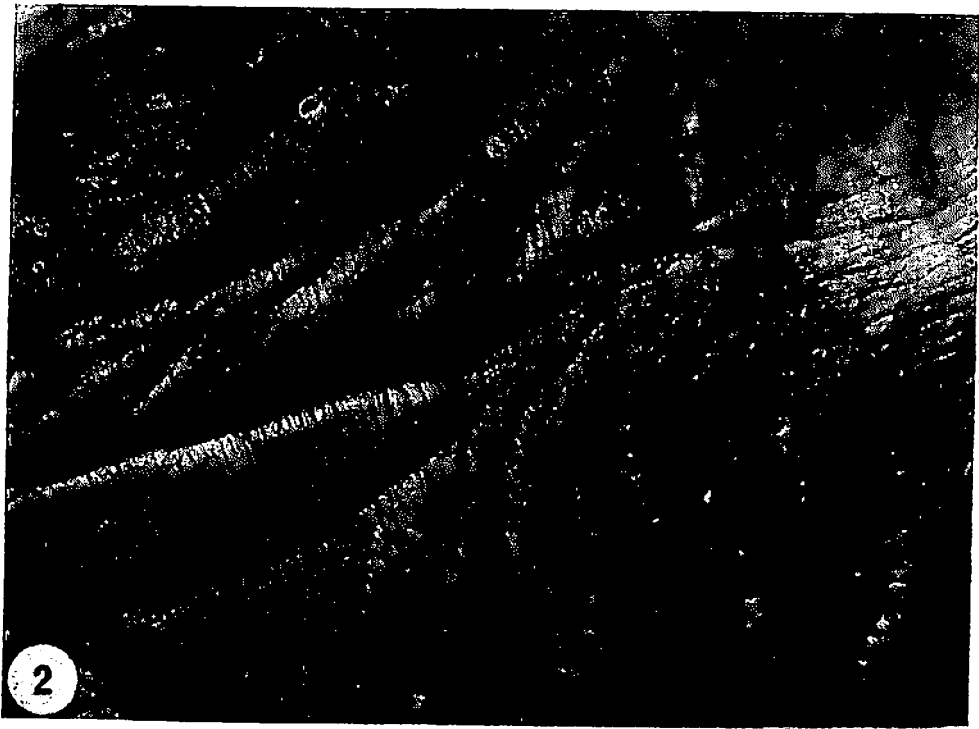
The enormously thick dermis is a densely interwoven felting of collagen fibres: the pectinate dermal papillae are tall, narrow and closely spaced and exactly similar to those in the skin of the hump in the Uganda adult specimen: hair follicles are present and contain the bulbs at least of hairs: the impressively abundant cutaneous blood-vessels pursue a fairly straight course towards the surface and the arteries among them are extremely thick-walled. Well developed sebaceous glands are associated in the usual manner with the hair follicles. Arrectores pilorum are absent. Sweat glands are unexpectedly abundant and are invariably of apocrine type: numerous large and well developed myoepithelial cells embrace the walls of their secretory portions, and their ducts, of round cross section, are lined by stratified epithelium. These ducts discharge into the pilary canal, as do those of the corresponding glands of the hump region of the Uganda specimen. The many attendant myoepithelial cells represent the anatomical machinery for a sudden and copious discharge of sweat, which is a notable phenomenon in *Ceratotherium* when the animal is physiologically hard pressed. The apocrine gland secretion contains a relatively scanty precipitate, perhaps less rich in protein than that of the corresponding preputial glands. Nerve trunks of appreciable size are numerous in the sections and testify to a degree of cutaneous sensitivity corrective of the misleading impression of insensitivity given by the gross appearance of the external skin surface.

Sections examined of the general body skin from the *Diceros* specimen differ in no essential from those of the *Ceratotherium* specimen.

Fig. 1. *Ceratotherium simum*. Left lateral aspect of glans penis and prepuce, showing preputial papillae.

Fig. 2. *Ceratotherium simum*. Preputial papillae, showing detailed appearance and disposition.

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PREPUTIAL SKIN OF *Diceros bicornis* (R.24)

The thin preputial skin of the *Diceros* specimen is of dark, clove-brown tint. Its surface presents a series of irregularly polyhedral elevations, over which the epidermis tends to be disposed in fronds or spikes, and in the centre of which occurs a pore—the ostium of a pilary canal generally, though not invariably, wanting any contained hair shaft. The preputial skin nowhere manifests any “goose pimple” appearance and it completely lacks the large, pale-coloured papillae which are so obtrusive an external characteristic of the *Ceratotherium* specimen.

Histologically the epidermis is smooth save over the elevations mentioned, where it is thrown up into a series of fine external spikes. The stratum corneum is extremely thin (frequently but 1 to 2 cells thick): the stratum granulosum is discontinuous and represented by single cells disposed at irregular intervals: the stratum Malpighii is well developed and heavily melanin-laden in its deepest portion, the melanin tending to be specially concentrated in some places.

The dermis is the expected dense felting of collagen bundles, and contains dartos elements and extremely numerous blood-vessels, the arteries among which are markedly muscular (thick-walled) and pursue an almost straight course towards the epidermis. The dermal papillae are relatively broad (broader than those seen in the general skin of the *Ceratotherium* specimen) and are frequently branched at their extremities.

Hair follicles, relatively few in number, are present, and each is associated in the usual way with a cluster of sebaceous glands (sometimes as many as 16 such glands per follicle). Mm. arrectores pilorum are wanting. The bulb of the hair follicle—which may or may not contain a hair shaft—extends deeply to make intimate contact with an underlying apocrine sweat gland (fig. 3).

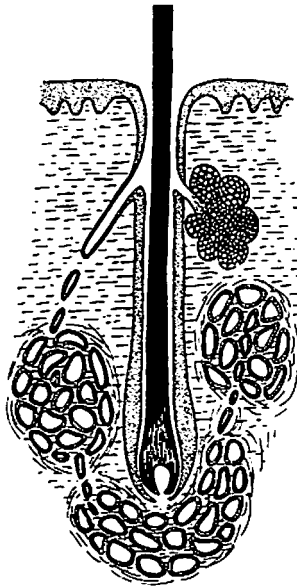


Fig. 3. *Ceratotherium simum*. Dorsal preputial skin, showing large, multi-locular apocrine sweat gland surrounding hair follicle base and with duct opening into pilary canal. (Diagrammatic).

The sweat glands present are all of apocrine type. They are concentrated very deeply in the dermis in great abundance and are so remarkably large that a single gland may extend almost the entire length of a single section. Well developed myoepithelial cells are liberally associated with these sweat glands, and are intimately disposed around their secretory tubules. The gland tubules everywhere

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contain an appreciable amount of solid (apparently protein) material, which is possibly associated with the odiferous nature of the region. This secretion is discharged into the pilary canal, whose ostium is the only recognizable interruption of the surface continuity.

The sebaceous glands contain a partly protein, partly lipid secretion, which may well be of mixed function, i.e. partly lubricant and partly sexual. The protein content of this secretion is probably higher than in the corresponding human secretion and the lipid content probably lower.

Sweat glands of eccrine type are nowhere present nor does lymphoid tissue in any form appear in any of the sections studied.

PREPUTIAL SKIN OF *Ceratotherium* (R.20)

The preputial skin of the *Ceratotherium* specimen, mauve-grey in colour, is notably thinner than the general body skin and lacks any subcutaneous adipose layer. Dorsally and laterally it is almost translucent and there displays a "goose pimple" appearance (fig. 4) due to the presence of discrete masses of subjacent apocrine

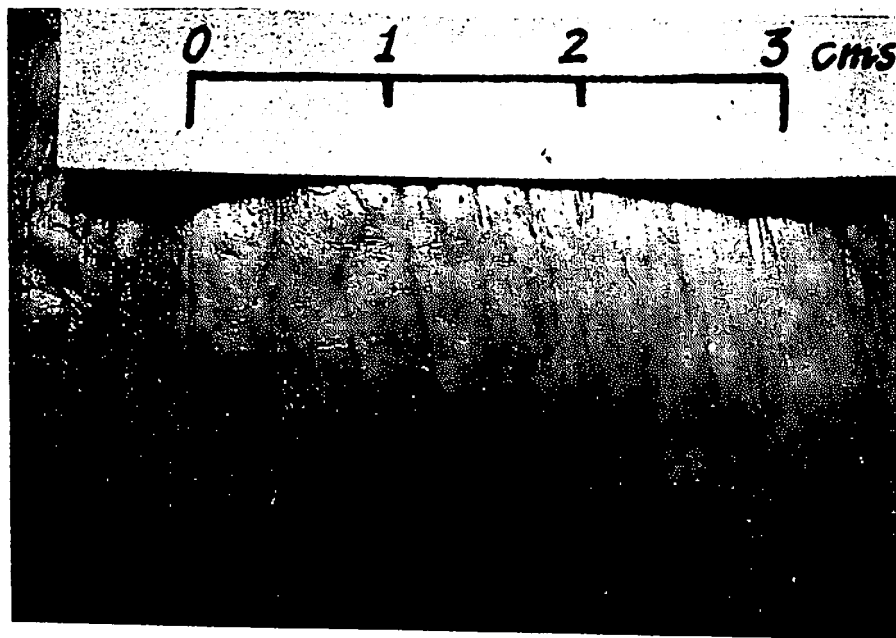


Fig. 4. *Ceratotherium simum*. Dorsal "goose pimple" area of prepuce. Apocrine sweat glands visible through translucent skin, also short hairs emerging from pilary ostia.

sweat glands. Where reflected on to the glans penis and its lateral processes it displays its most obtrusive characteristic, viz. clusters and rows of white-coloured, low papillae (fig. 2). Hair follicle ostia are generally distributed over the preputial skin and from some of these project short, dark-coloured, very fine hairs: these follicle ostia are the only skin pores present. (No corresponding "goose pimples" or white papillae are discernible in the *Dicerops* specimen).

The general histological structure of the preputial skin is as follows: the epidermis, smooth externally and of almost polished appearance, reveals a thin stratum corneum (2 to 3 cells thick), an absence of any stratum lucidum and a discontinuous

stratum granulosum represented by isolated cells appearing here and there in the sections. The stratum Malpighii is well developed, being some 12 cells thick over the summits of the dermal papillae and some 27 cells thick between these papillae: its deepest cell layer contains a considerable amount of melanin.

The dermis, extremely dense, consists of an intimately interwoven feltwork of collagen bundles and contains dartos or retractor preputii muscle elements: it is markedly vascular and some of the arteries present are relatively very large indeed: the smaller arteries and arterioles are more or less surrounded by clumps of mesenchyme cells. On the dorsum of the prepuce the dermal papillae are relatively broad and are mutually separated by about their own width of surface epithelium: they are taller, narrower and more closely packed than elsewhere in the prepuce, save over the lymphoid nodules accompanying the eccrine sweat glands (*vide infra*) where they are somewhat rudimentary. Subcutaneous nerve trunks are liberally disposed throughout the sections.

Hair follicles are present, some containing a hair shaft, others empty, but all attended by sebaceous glands in the usual manner. Some of these follicles effect a most intimate juxtaposition (fig. 3) with the subjacent apocrine glands, which occupy the deepest part of the dermis as relatively enormous masses and are characterized by an accompaniment of well developed myoepithelial cells. These apocrine glands are so relatively huge that in a single section (15 μ m) no more than four such may be present, while occasionally a particularly large example may occupy a comparable distance. Mm. arrectores pilorum are wanting.

Thus, as might be anticipated, in its general structure the preputial skin of *Ceratotherium* differs in no histological particular from that of *Diceros*. Its distinctive features (*viz.* the "goose pimples" and the white papillae) remain to be explained. Each "goose pimple" proves on the histological examination of serial sections to be a cutaneous area overlying an enormous multilocular apocrine sweat gland, whose duct opens into or alongside a hair follicle (fig. 3). Each such apocrine gland may comprise two, three, or more discrete but interconnected masses closely surrounding the base of a hair follicle, and representing a single, continuous, but extremely long coiled tube, the terminal portion of which opens into the pilary canal. The duct itself is lined by stratified squamous epithelium for a variable (usually considerable) distance from its ostium, beyond which such epithelium is replaced by that of the cubical variety.

A given hair follicle may or may not contain a hair shaft, but is attended by a numerous cluster of well developed sebaceous glands (fig. 3).

The external skin pore (from which a hair shaft may protrude) is the ostium of the pilary canal and is thus the common exit for the hair, the sebum and the secretion of the associated apocrine gland, which last shows an abundant precipitate of a protein nature.

The peculiar pale-coloured papillae which constitute so obtrusive a topographical feature of the distal preputial skin and glans penis of *Ceratotherium* prove on histological examination to be part of a most unusual anatomical arrangement (not, apparently, recorded hitherto for any region in any mammal), namely, the raised ostia of eccrine sweat glands whose secretory mechanism is intimately embedded within an aggregation of dense lymphoid tissue.

The papillae themselves (figs. 1, 2) occur either singly or in clusters or in short rows in the regions indicated and show white against the general cutaneous background. Each papilla is a low, flat-topped surface elevation, elliptical or circular in outline, and some 2.0 mm in maximum diameter: its umbilicated centre, measuring up to 1.0 mm in diameter, is the mouth of a largish crypt within a rim of pale-coloured epidermis. Histologically each papilla is a cutaneous elevation overlying a consider-

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able subepidermal aggregation of remarkably dense lymphoid tissue associated both with crypts and with sweat glands of undoubted eccrine type (fig. 5 and fig. 9). Its epidermis is the customary stratified squamous epithelium whose relatively thin stratum corneum is very heavily infiltrated by lymphocytes. This stratum frays out at the crypt mouth, and is prolonged into the crypt as a lining, being everywhere much invaded by lymphocytes (figs. 7, 8). In the papillary region the true dermal papillae are shorter and more widely spaced than those of the surrounding preputial skin, which are strikingly tall, slender and closely packed, in pectinate fashion.

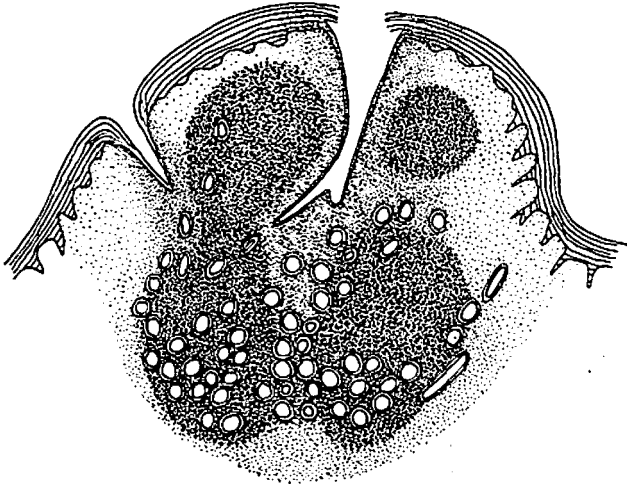


Fig. 5. *Ceratotherium simum*. Preputial papilla, sectioned, to show crypts in relation to eccrine sweat glands and surrounding lymphoid tissue (stippled) containing secondary nodules. (Diagrammatic).

At least one (central) crypt is associated with each preputial papilla, its orifice accounting for the umbilicated external appearance thereof: additional crypts however may be present, opening on the flattish shoulders of the papilla. Each crypt is surrounded by a large and conspicuous mass of extremely dense lymphoid tissue, in which secondary nodules occur, so that the general histological arrangement is reminiscent of the disposition and association of the crypts within the faucial tonsil (fig. 6). This lymphoid tissue extends surfacewards to the papillary epidermis, which its lymphocytes invade, and it is densely packed around the intrapapillary crypts. Embedded within its mass are somewhat diffusely disposed sweat glands of typical eccrine type attended by small myoepithelial cells: these glands open, some into the crypt lumina, others upon the free surface of the papilla. Special staining methods confirm the total absence of mucin from their secretion and establish their true sudiparous nature.

Subjacent to the lymphoid tissue occur scattered bundles of striped muscle representing the terminal fascicules of the *m. retractor preputii*.

DISCUSSION

Whereas the external appearance of the thick, apparently hairless, hide of *Ceratotherium* and *Diceros* might well suggest an overkeratinized and relatively inert type

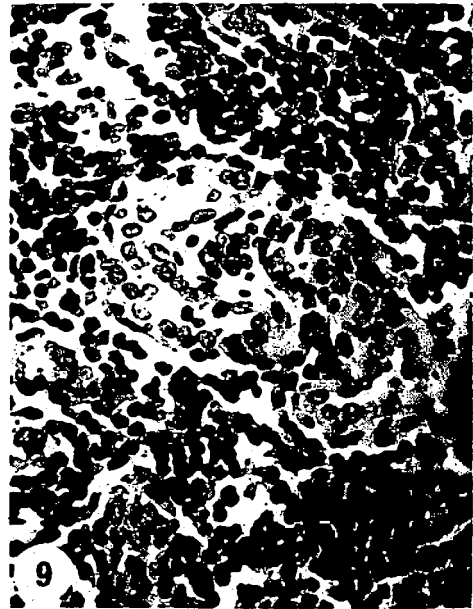
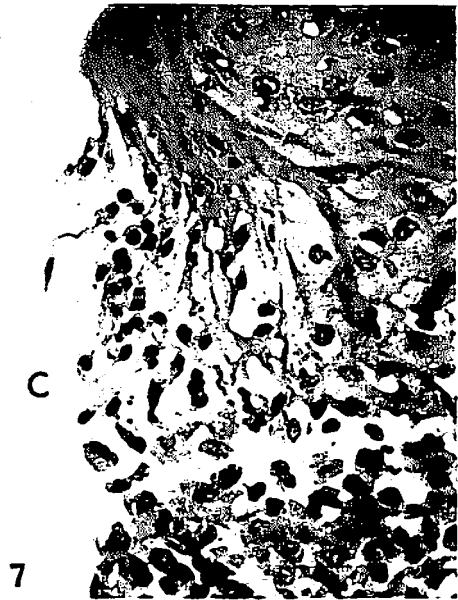


Fig. 6. *Ceratotherium simum*. Transverse section of a preputial papilla, showing central crypt and associated lymphoid tissue. $\times 50$. Haematoxylin and eosin.

Fig. 7. *Ceratotherium simum*. Frayed epithelium at mouth of central crypt (c) and intra-epidermal lymphocytes. $\times 500$. Haematoxylin and eosin.

Fig. 8. *Ceratotherium simum*. Crypt of preputial papilla (c), showing epidermal lining and, on left, portions of eccrine sweat gland embedded in lymphoid tissue. $\times 300$. Haematoxylin and eosin.

Fig. 9. *Ceratotherium simum*. Preputial eccrine sweat gland and surrounding lymphoid tissue. $\times 300$. Haematoxylin and eosin.

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of integument, its histological examination corrects such an impression. It demonstrates such skin to be of typically mammalian constitution, and to be remarkably vascular, sensitive and secretory, in a word, to be well designed to subserve effectively the multiple functions of the mammalian integument. Its individual histological features are readily seen to have their physiological expression in the habits and behaviour of the living animal.

Save for the well developed hairs of the ear- and tail-fringes and the eyelashes, recognizable projecting hairs are generally wanting in both young and adult *Ceratotherium* and *Dicerops* specimens: nevertheless, in each form well developed hair follicles are abundant in the general skin and lodge hair shafts which are either broken off at the mouth of the pilary canal or project but a trifling distance beyond.

This reduction of individual hair length and the consequent absence of any external hairy coat is part of the physiological machinery devised to regulate the necessary balance between heat production and heat loss in so large an animal body, the temperature maintenance of which at the requisite level dictates the animal's habits, e.g. its restriction of physical activity to the cool conditions of early morning and evening, its retreat into shade during bright sunshine periods and its repeated wallowing in mud or water. Correlated with this reduction of hair length in *Ceratotherium*, *Dicerops* and *Rhinoceros unicornis* is the absence of mm. arrectores pilorum.

It is obvious that were the present tropical climates to become arctic in nature, the extant rhinoceroses could respond successfully to the altered external environment and, by developing from their hair follicles hairs sufficiently long to provide a body covering, reproduce the adaptive conditions which characterized the Pleistocene woolly rhinoceros (*Tichorhinus*).

Sebaceous glands are well developed in both *Ceratotherium* and *Dicerops* and are often relatively numerous in relation to a single hair follicle. Apocrine sweat glands, discharging into the pilary canal and intimately associated with large numbers of well developed myoepithelial cells, occur in all parts so far examined of the skin of *Ceratotherium* and *Dicerops*, a not unexpected finding since the apocrine gland is the dominant (often sole) type of sweat gland present in the hair-bearing skin of non-Primate mammals. The presence of numerous and vigorous myoepithelial cells in close proximity to the secretory tubules of these glands represents an anatomical mechanism for the sudden "let down" of sweat in large quantities. For, though the living animal manifests a slow gait and avoids both intense sunshine and sudden exertion, and appears not to sweat unduly, when physically hard pressed it has been observed to become suddenly drenched in sweat as though doused with water.

In *Ceratotherium* the semitranslucent, less deeply pigmented dorsal skin of the prepuce (and its lack of a subcutaneous fatty layer) renders the large local apocrine glands observable by the naked eye as the "goose pimples" described above.

Eccrine sweat glands in mammals appear to be confined to areas of non-hairy skin, e.g. the rhinarium, the foot pads and the genital region, though they may, in some forms, be elaborated as localized special organs (e.g. the metacarpal glands of some pigs). They are not concerned so much with thermal regulation as with the production of a (watery) secretion which has an olfactory significance for other members of the same species, and it would seem that the specialized eccrine glands described herein for the *Ceratotherium* penis fall into this same category.

These particular *Ceratotherium* glands possess the usual raised ostium, though somewhat exaggerated and rendered the more conspicuous by virtue of a pale coloration. Their totally unexpected characteristic is their intimate association with a surrounding mass of dense lymphoid tissue. Such an association of a sweat gland

with lymphoid tissue appears to be unrecorded for any region of the mammalian body, and in the present material distinguishes *Ceratotherium* very markedly from *Diceros*.

Accepting these *Ceratotherium* eccrine glands as scent glands of a sexual nature, it is difficult to account for the presence of the lymphoid tissue in which each gland is buried. An association of lymphoid tissue with mucus-secreting crypts is familiar enough (e.g. in fauces, radix linguae, oropharynx), the lymphoid tissue there being generally regarded as a necessary local defensive mechanism against infection. It is difficult however to imagine what analogous risk of infection attends the preputial eccrine glands of *Ceratotherium*, or otherwise to account for the presence of lymphoid tissue in association with a manifestly serous mechanism.

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