THE PEDAL SCENT GLAND IN *RHINOCEROS*

BY

A. J. E. CAVE

University of London

[Accepted 12th December, 1961]

(With 2 plates)

Pedal scent glands, common in Artiodactyla, are shown to be confined to the genus *Rhinoceros* among Perissodactyla. Owen's original account of these glands in *R. unicornis* is reviewed. The histology of the glands and of the pedal skin of this species is described for the first time.

CONTENTS

INTRODUCTION

Included among the numerous and varied appendages of the multipotential mammalian skin are a variety of cutaneous glands, some of known, others of unknown, function. Such structures may be developed upon almost any region of the body surface, as witness the facial gland of *Phacochoerus*, the antorbital glands of the Cervidae, the postcornual gland of *Rupicapra*, the temporal gland of *Elephas* and *Loxodonta*, the occipital gland of *Camelus*, the mid-dorsal lumbar gland of *Dicotyles* and *Dendrohyrax*, the caudal gland of *Capra*, the peri-anal and perineal glands of many carnivores and rodents, the preputial glands of *Orycteropus*, *Moschus*, *Sus* and *Nototragus*, the inguinal glands of numerous ungulates, the metatarsal glands of *Llama*, the digital glands of *Sus*, the unguiculate glands of *Tetraceros*, the sternal glands of many marsupials, of *Hylobates* and of *Ateles*, the gular gland of *Pithecia* and the epigastric glands of *Tarsius*.

A special category of such cutaneous glands is comprised by the pedal glands of ruminants and of some other forms, which were extensively studied by Pocock (1910, 1916). Whatever the specific function of these structures, all (save perhaps those occurring in primates) appear essentially to be localized sacciform infoldings of the skin, characterised by a concentration of specialized sebaceous glands which produce the particular glandular secretion. With the exception of the elephant temporal gland, none of these cutaneous derivatives seems to have been subjected to microscopical investigation, and illustrations given in the relatively scanty literature depict no more than their naked eye anatomy, and that somewhat diagrammatically.

Pocock's (1910, 1916) studies demonstrated the almost universal occurrence of pedal glands throughout the Artiodactyla and their function as scent organs for the manufacture of a secretion characterised by an odour probably specific for each mammalian form.

On the contrary, among the Perissodactyla (not studied by Pocock) such glands would appear to be wanting in the Equidae and Tapiridae and to be confined to a single genus (*Rhinoceros*) among the Rhinocerotidae.

PEDAL GLANDS IN THE RHINOCEROTIDAE

The pedal gland in the Rhinocerotidae appears to be confined exclusively to *Rhinoceros*. First noted by Owen (1862) for *Rhinoceros unicornis*, it was later observed by Beddard & Treves (1887) in *Rhinoceros sondaicus*. According to Garrod (1873) this structure is wanting in *Didermocerus sumatrensis*, which herein would seem to agree with the African rhinoceroses. For careful inspection of captive specimens shows no glandular ostium to be present in either the fore- or hindlimb of *Ceratotherium simum*, and the gland was plainly wanting in three specimens of *Diceros bicornis* (a two-year-old female, a year-old male and a female foetus) specially dissected by the writer.

In the remaining perissodactyl families the pedal gland is unknown in the Equidae and would appear to be equally wanting in the Tapiridae, for it is not recorded for *Tapirus indicus* by Murie (1872) or by Beddard (1909), nor for *Tapirus terrestris* by Beddard (1889) or Bressou (1950). In a very young specimen of the American species, the writer found no trace of any such organ.

So far, therefore, as present knowledge goes, specialized pedal glands among the Perissodactyla are restricted to a single genus (*Rhinoceros*), whilst among the many families of the Artiodactyla such organs are widely distributed (Pocock 1910).

These rhinoceros pedal glands are undoubtedly scent glands, which express their thickish secretion fairly continuously during the animal's peregrinations and so lay an olfactory trail for the guidence of mate or offspring or other members of the species. Hence their restriction to the two species of a single genus among the extant Rhinocerotidae is somewhat puzzling. Clearly an olfactory trail is most successfully laid in a firm and fairly dry terrain and must prove much less effective if laid in a predominantly swampy or watery terrain. *A priori*, therefore, well developed pedal scent glands might be expected to occur in *Ceratotherium* and *Diceros*, inhabiting the relatively dry African bush and savannah, whilst their absence in *Rhinoceros* and *Didermocerus*, dwellers in wet or swampy jungles, would not be surprising. The morphological facts are, however, directly contrariwise, and this apparently anomalous distribution of scent glands requires explanation.

THE PEDAL GLAND OF *RHINOCEROS UNICORNIS*

To Owen belongs the credit for the discovery of the pedal glands in *Rhinoceros* during his anatomization in 1849 of the first specimen of the Great Indian rhinoceros (*R. unicornis* L.) to be acquired by the Zoological Society of London. This animal, a male, was purchased on Owen's recommendation in May 1834 for one thousand guineas. It engaged his particular interest

while alive in the menagerie, and when, in November 1849, his " ponderous and respectable old friend and client " died from thoracic trauma Owen predicted, in a private letter (Owen, 1894), that " his anatomy will furnish forth an immortal Monograph "—a jocular prophecy which was duly fulfilled by the subsequent publication (March 2, 1850) of his classic memoir on the rhinoceros (Owen 1862), which remains the authoritative treatise on the morphology of this species.

Therein Owen described and figured the pedal glands which had escaped the notice of such earlier observers as Daubenton and F. Cuvier. Subsequent writers accepted his findings so unreservedly that no record appears of any attempted confirmation by independent dissection of the presence of pedal glands in this species.

The writer has, however, verified the presence and disposition of the pedal glands in three male specimens of Great Indian rhinoceros from the Society's menagerie, viz. :—

(1) Adult c.20 years (" Felix ") died 1941
(2) Subadult c.15 years (" Hush ") died 1945
(3) Adult c.18 years (" Mohan ") died 1961

The glands from the last of these specimens were preserved and histologised and are noticed below.

(It is perhaps remarkable that the pedal glands should have passed unnoticed by Vicq d'Azyr and Mertrud, whose dissection of a male Great Indian rhinoceros antedated Owen's by over half a century. Their specimen was the animal which had lived in the Royal Menagerie at Versailles from 1772 to 1793, and whose skeleton is preserved (No. A7974) in the Musée d'Anatomie Comparée, Paris. Vicq d'Azyr wrote a descriptive account of the visceral anatomy of this specimen, to illustrate which some 31 plates (listed by Gervais & Gervais, 1875) were prepared by Maréchal and by P. J. Redouté *père et fils*. Vicq d'Azyr died prematurely in 1794 : his account, which would have constituted the earliest authoritative monograph on the morphology of the species, was never published but is preserved in the archives of the Muséum National d'Histoire Naturelle).

GROSS ANATOMY OF *R. UNICORNIS* GLAND

Owen's original account (1862) described the pedal gland of *Rhinoceros unicornis* as a " pretty large subdermal pouch " whose distensible external orifice, situate some 2½ inches to 3 inches above the sole pad, was " concealed from cursory observation in the middle of the transverse fold " opposite the carpo-metacarpal (or tarso-metatarsal) articulation. The gland itself (Owen, *op. cit.*, Pl. IX, fig. 1), of a " compressed ovate figure ", measured 1½ inches long by 1 inch broad and its wall was " two or three lines " (i.e. about ¼ inch) in thickness. Its parietes were said to " consist of a compact congeries of follicles, surrounded externally by a muscular and tendinous coat " and the fully distended ostium had a diameter of " about eight lines " (i.e. 2/3 inch). No mention was made of the obtrusively abundant vasculature of the gland, nor of the fascial retention bands which anchor it in place (Pl. 2, fig. 3).

The general accuracy of this description is confirmed by personal examination of the pedal glands from the animal " Mohan ", a male of approximately the same age as Owen's specimen. The formalin-preserved forefoot gland (Pl. 1, fig. 1) of " Mohan " measures 1-4/5 inch (46 mm.) in length by 1-1/10 inch (29 mm.) in breadth : the similarly preserved hindfoot gland (Pl. 1, fig. 2) measures 1-9/10 inch (48 mm.) in length by 9/10 inch (22 mm.) in breadth The transversely elliptical neck of each gland in the fresh state is readily distensible up to a diameter of 3/4 inch (18 mm.) : the gland wall is about 3/10 inch (8 mm.) thick and the undistended round ostium (Pl. 2, fig. 4) is some 3 mm. in diameter. The shape of either gland is apparent from the accompanying illustrations, which also show the considerable fundal vasculature, the enclosing " ligaments " and the shortness of the sac neck. Compression of the gland in the fresh state causes the exudation of a thick grumous secretion.

The little organ is essentially a local invagination of the entire thickness of the skin, supported by a circumscribent condensation of the stout collagen tissue of the subcutaneous fascia and associated with a localized augmentation of slightly modified sebaceous glands which are so strikingly absent from other areas of the pedal skin.

HISTOLOGY OF THE GLAND

Histologically the wall of the invagination shows successive dermal, capsular and fascial layers. The lining epidermis is a thick, excessively cornified, stratified squamous epithelium. Ghost cells are discernible in its stratum corneum, and a stratum lucidum is present. The stratum granulosum, which in some places is eight cells thick, contains basophilic granules of different sizes, some of the granules being relatively large. The cells of the basal layer of the stratum Malpighii (i.e. those next to the basement membrane) contain considerable patches of melanin.

The dermal papillae are very notably long, narrow and close-set and they penetrate into the epidermis so far as to reach the stratum granulosum, so that dermis and epidermis are thus very tightly " keyed " together.

Outside the dermal layer lies the capsular component of the sac wall, composed of a thick, dense felting of collagen fibres, and liberally supplied with blood-vessels, some of which manifest extremely muscular walls. This tough, thick collagen layer is a condensation of the local subcutaneous fascia, from which, however, it is readily separable and which also provides a number of " ligamentous " thickenings serving to maintain the entire sac in position.

Deep within the dermal layer of the sac wall appear numerous large apocrine glands, the acini of which display recognisable myoepithelial cells. The mouths of these specialized mucous glands open at intervals through the epidermal lining of the sac to discharge their thick secretion into its lumen. The abundance of these apocrine glands in conjunction with the extreme vascularity of the sac wall suggests that secretion is a fairly continuous process and that the lumen of the sac is never wholly devoid of content.

Apart from the unstriped muscle in the relatively thick-walled blood-vessels of the glandular sac, muscle tissue is completely absent from its parietes. Owen's statement that a periglandular muscular coat is present is demonstrably

while alive in the menagerie, and when, in November 1849, his " ponderous and respectable old friend and client " died from thoracic trauma Owen predicted, in a private letter (Owen, 1894), that " his anatomy will furnish forth an immortal Monograph "—a jocular prophecy which was duly fulfilled by the subsequent publication (March 2, 1850) of his classic memoir on the rhinoceros (Owen 1862), which remains the authoritative treatise on the morphology of this species.

Therein Owen described and figured the pedal glands which had escaped the notice of such earlier observers as Daubenton and F. Cuvier. Subsequent writers accepted his findings so unreservedly that no record appears of any attempted confirmation by independent dissection of the presence of pedal glands in this species.

The writer has, however, verified the presence and disposition of the pedal glands in three male specimens of Great Indian rhinoceros from the Society's menagerie, viz. :—

(1) Adult c.20 years (" Felix ") died 1941
(2) Subadult c.15 years (" Hush ") died 1945
(3) Adult c.18 years (" Mohan ") died 1961

The glands from the last of these specimens were preserved and histologised and are noticed below.

(It is perhaps remarkable that the pedal glands should have passed unnoticed by Vicq d'Azyr and Mertrud, whose dissection of a male Great Indian rhinoceros antedated Owen's by over half a century. Their specimen was the animal which had lived in the Royal Menagerie at Versailles from 1772 to 1793, and whose skeleton is preserved (No. A7974) in the Musée d'Anatomie Comparée, Paris. Vicq d'Azyr wrote a descriptive account of the visceral anatomy of this specimen, to illustrate which some 31 plates (listed by Gervais & Gervais, 1875) were prepared by Maréchal and by P. J. Redouté *père et fils*. Vicq d'Azyr died prematurely in 1794 : his account, which would have constituted the earliest authoritative monograph on the morphology of the species, was never published but is preserved in the archives of the Muséum National d'Histoire Naturelle).

GROSS ANATOMY OF *R. UNICORNIS* GLAND

Owen's original account (1862) described the pedal gland of *Rhinoceros unicornis* as a " pretty large subdermal pouch " whose distensible external orifice, situate some $2\frac{1}{2}$ inches to 3 inches above the sole pad, was " concealed from cursory observation in the middle of the transverse fold " opposite the carpo-metacarpal (or tarso-metatarsal) articulation. The gland itself (Owen, *op. cit.*, Pl. IX. fig. 1), of a " compressed ovate figure ", measured $1\frac{1}{2}$ inches long by 1 inch broad and its wall was " two or three lines " (i.e. about $\frac{1}{4}$ inch) in thickness. Its parietes were said to " consist of a compact congeries of follicles, surrounded externally by a muscular and tendinous coat " and the fully distended ostium had a diameter of " about eight lines " (i.e. 2/3 inch). No mention was made of the obtrusively abundant vasculature of the gland, nor of the fascial retention bands which anchor it in place (Pl. 2, fig. 3).

The general accuracy of this description is confirmed by personal examination of the pedal glands from the animal " Mohan ", a male of approximately the same age as Owen's specimen. The formalin-preserved forefoot gland (Pl. 1, fig. 1) of " Mohan " measures 1-4/5 inch (46 mm.) in length by 1-1/10 inch (29 mm.) in breadth : the similarly preserved hindfoot gland (Pl. 1, fig. 2) measures 1-9/10 inch (48 mm.) in length by 9/10 inch (22 mm.) in breadth The transversely elliptical neck of each gland in the fresh state is readily distensible up to a diameter of 3/4 inch (18 mm.) : the gland wall is about 3/10 inch (8 mm.) thick and the undistended round ostium (Pl. 2, fig. 4) is some 3 mm. in diameter. The shape of either gland is apparent from the accompanying illustrations, which also show the considerable fundal vasculature, the enclosing " ligaments " and the shortness of the sac neck. Compression of the gland in the fresh state causes the exudation of a thick grumous secretion.

The little organ is essentially a local invagination of the entire thickness of the skin, supported by a circumscribent condensation of the stout collagen tissue of the subcutaneous fascia and associated with a localized augmentation of slightly modified sebaceous glands which are so strikingly absent from other areas of the pedal skin.

HISTOLOGY OF THE GLAND

Histologically the wall of the invagination shows successive dermal, capsular and fascial layers. The lining epidermis is a thick, excessively cornified, stratified squamous epithelium. Ghost cells are discernible in its stratum corneum, and a stratum lucidum is present. The stratum granulosum, which in some places is eight cells thick, contains basophilic granules of different sizes, some of the granules being relatively large. The cells of the basal layer of the stratum Malpighii (i.e. those next to the basement membrane) contain considerable patches of melanin.

The dermal papillae are very notably long, narrow and close-set and they penetrate into the epidermis so far as to reach the stratum granulosum, so that dermis and epidermis are thus very tightly " keyed " together.

Outside the dermal layer lies the capsular component of the sac wall, composed of a thick, dense felting of collagen fibres, and liberally supplied with blood-vessels, some of which manifest extremely muscular walls. This tough, thick collagen layer is a condensation of the local subcutaneous fascia, from which, however, it is readily separable and which also provides a number of " ligamentous " thickenings serving to maintain the entire sac in position.

Deep within the dermal layer of the sac wall appear numerous large apocrine glands, the acini of which display recognisable myoepithelial cells. The mouths of these specialized mucous glands open at intervals through the epidermal lining of the sac to discharge their thick secretion into its lumen. The abundance of these apocrine glands in conjunction with the extreme vascularity of the sac wall suggests that secretion is a fairly continuous process and that the lumen of the sac is never wholly devoid of content.

Apart from the unstriped muscle in the relatively thick-walled blood-vessels of the glandular sac, muscle tissue is completely absent from its parietes. Owen's statement that a periglandular muscular coat is present is demonstrably

erroneous and would seem to have been due to reliance upon naked eye observation only and a resultant failure to realise that the pinkish colour of the sac parietes is due solely to the presence of an extremely elaborate vasculature.

HISTOLOGY OF THE PEDAL SKIN

On microscopical examination the non-glandular areas of the pedal skin of *Rhinoceros unicornis* show the deepest epidermal layers to contain melanin granules, the distribution of which ceases somewhat abruptly about the fourth cell layer from the basement membrane. Neither sweat glands nor hair follicles are apparent.

The dermis is composed basically of a dense and intricate arrangement of collagen fibres, disposed in every direction, and admixed with a fair proportion of elastic fibres. These elastic fibres are of general distribution throughout the dermis ; they penetrate into the dermal papillae and are detectable up to the epidermal basement membrane. Adipose tissue is notably absent. Nerve branches of relatively substantial size are present in all the sections studied.

The dermal papillae are characteristically long, narrow and closely-packed, "keying" together dermis and epidermis in the tightest possible fashion.

Blood-vessels are everywhere abundant. They tend to occur in distinctive vascular bundles which course surfacewards from the deepest part of the dermis into the dermal papillae. Each such bundle consists of a relatively large single artery intimately surrounded by a pampiniform venous plexus comprising as many as a dozen or more parallel venae comitantes. The arteries manifest relatively thick muscular walls and elastic tissue is present in abundance between and around the accompanying veins. So striking a specialized anatomical arrangement of peripheral blood-vessels is doubtless to be correlated with facilitation of heat loss from the extensive body surface and hence with the regulation of the internal body temperature.

The overall histological picture is that of a thick, elastic and highly sensitive pedal skin, abundantly and elaborately vascularized, but devoid of sweat glands, hair follicles and subcutaneous fat.

ACKNOWLEDGMENTS

Grateful acknowledgment is made to the Zoological Society of London for providing the material forming the basis of this notice, to Mr E. H. Tong, Mr R. N. Fiennes and Mr Martin Senior for valued assistance in its collection, to Dr F. J. Aumonier for the benefit of his authoritative opinion on the histological findings and to Miss Marian Dorr for the preparation of the sections.

REFERENCES

BEDDARD, F. E. (1889). Some notes on the anatomy of the American tapir (*Tapirus terrestris*). *Proc. zool. Soc. Lond.* **1889** : 252–258.

BEDDARD, F. E. (1909). Contributions to the anatomy of certain Ungulata, including *Tapirus*, *Hyrax* and *Antilocapra*. *Proc. zool. Soc. Lond.* **1909** : 160–197.

BEDDARD, F. E. & TREVES, F. (1887). On the anatomy of the Sondaic rhinoceros. *Trans. zool. Soc. Lond.* **12** : 183–198.

BRESSOU, C. (1950). Le pied des tapirides. *Mammalia*, 140–149.

GARROD, A. H. (1873). On the visceral anatomy of the Sumatran rhinoceros *Ceratorhinus sumatrensis*. *Proc. zool. Soc. Lond.* **1873** : 92–104.

GERVAIS, P. & GERVAIS, H. (1875). Structure de l'intestin grêle chez le rhinocéros. *J. zool., Paris* **4** : 465.

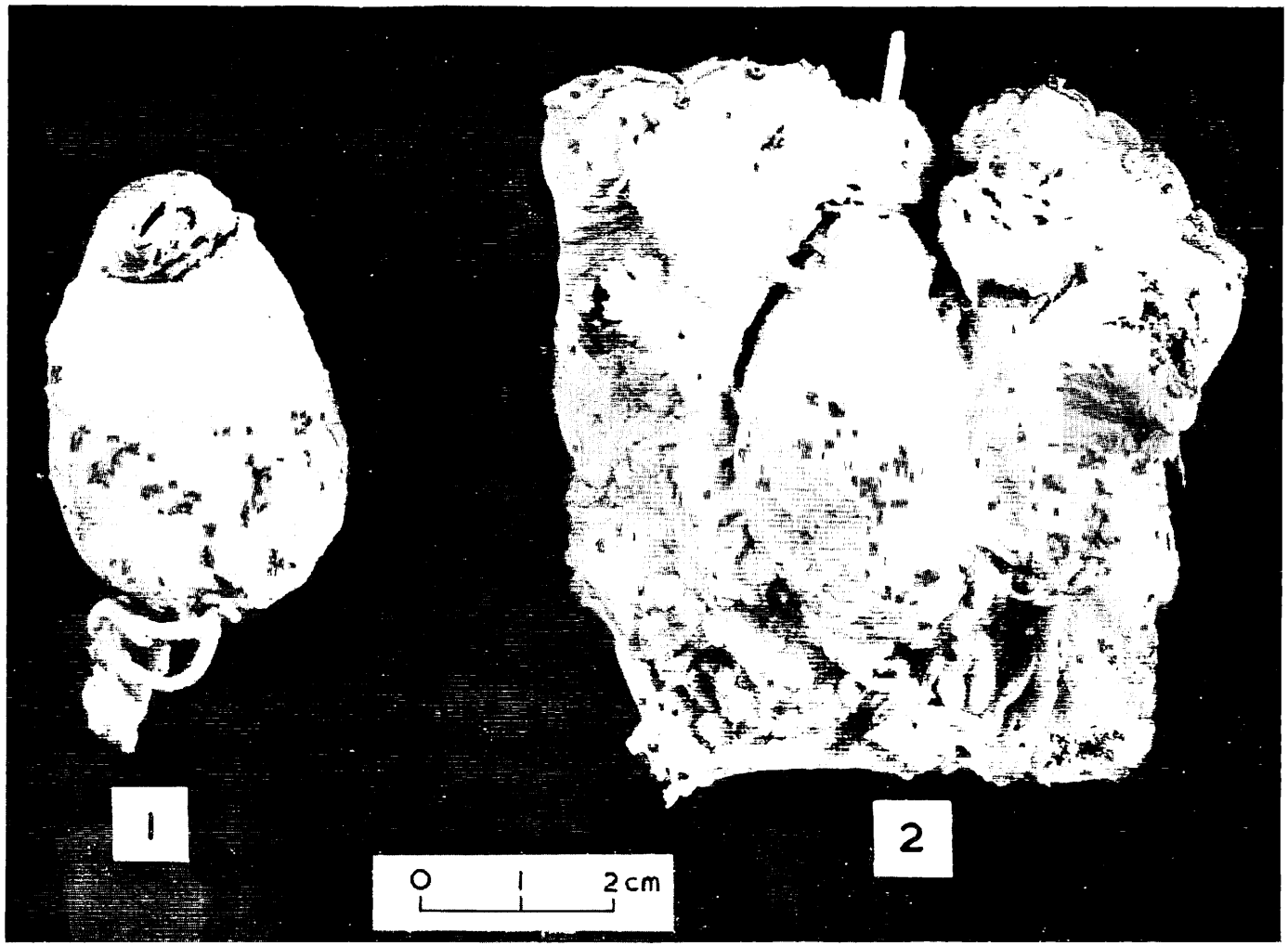
MURIE, J. (1872). On the Malayan tapir *Rhinocoerus sumatranus* (Gray). *J. Anat. Physiol., Lond.* **6** : 131–169.

OWEN, R. (1862). On the anatomy of the Indian rhinoceros (*Rh. unicornis*). *Trans. zool. Soc. Lond.* **4** : 31–58 (Art. 3 published 2 March 1850).

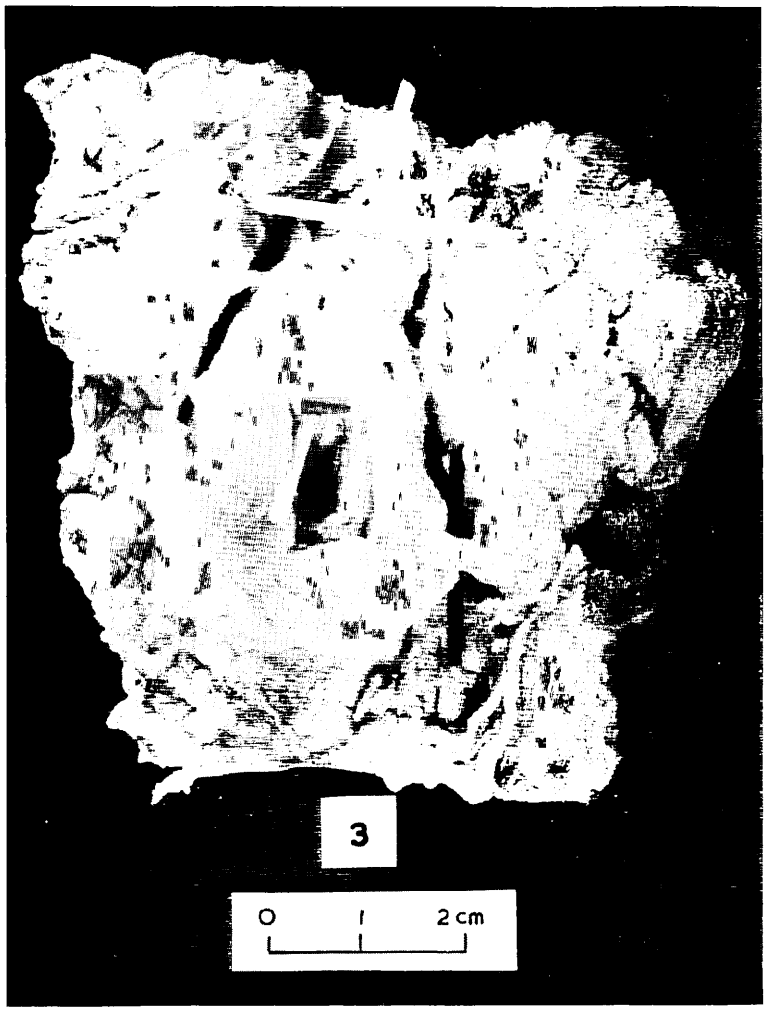
OWEN, Rev. R. (1894). *The life of Richard Owen* **1** : 347. London : Murray.

POCOCK, R. I. (1910). On the specialised cutaneous glands of ruminants. *Proc. zool. Soc. Lond.* **1910** : 840–986.

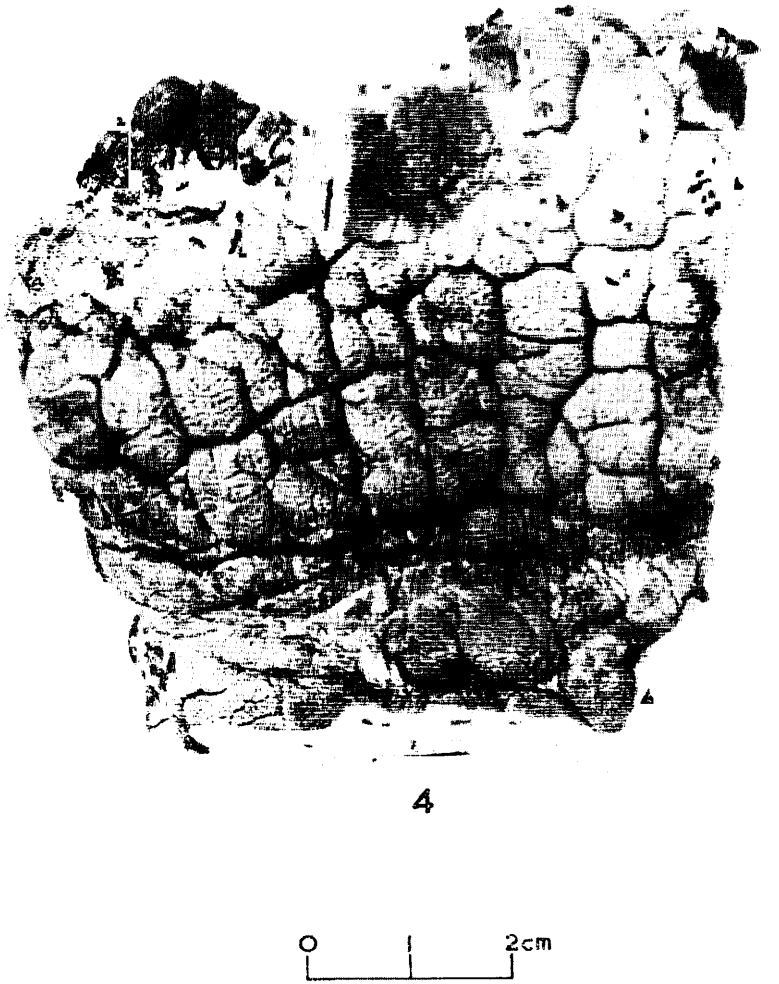
POCOCK, R. I. (1916). Scent glands in mammals. *Proc. zool. Soc. Lond.* **1916** : 742–755.



1. Pedal gland of left manus of adult male *Rhinoceros unicornis* (" Mohan "), isolated, to show gross features and fundal vasculature.
2. Pedal gland of left pes of same specimen, dissected *in situ*, to show bloodvessels and retention bands. A white rod is introduced through the ostium.



3. Pedal gland of left pes, dissected *in situ*. The sac wall has been opened; a white rod is introduced through the ostium; dark rods underly certain of the retaining ligaments.



4. Exterior view of hind foot skin, to show the small ostium of the same gland.