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THE PEDAL GLANDS OF OWEN

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SIR RICHARD OWEN (1804-1892), the most distinguished of the scientific sons of Bart's, was a student under John Abernethy (1764-1831), whose greatest claim to the gratitude of later generations lay perhaps in his recognition of Owen's extraordinary talents as a morphologist and his singular fitness to be the custodian of John Hunter's unique Museum. Largely through Abernethy's influence, Owen abandoned clinical work to become Assistant Conservator (1827), under William Clift, and later Conservator (1852) of the Hunterian Museum at the Royal College of Surgeons of England. The routine checking, re-examination, cataloguing and augmentation of the extensive comparative series in that Museum, conducted for the most part under considerable difficulties, compelled Owen to undertake an increasingly wide and detailed exploration of the comparative morphological field, both vertebrate and invertebrate, work resulting in a phenomenal output of memoirs, catalogues and papers which were to remain classics of their kind.

As an anatomist Owen displayed an acute observational faculty and a promptitude of attention to detail. Since his avowed and constant practice was "to describe with accuracy and to delineate with fidelity", it is small wonder that his copious and varied monographs were exemplars of their kind, that numerous discoveries in palaeontology and morphology stand to his name, and that his findings were, and are still, accepted almost unreservedly.

To some of these findings attention has been previously drawn (Cave[1, 2]) in these columns, as much for their moral as their scientific value, since the observant eye and the accurate pen are not devoid of exhortatory influence in any department of medical or biological science. In similar fashion, and in a spirit of filial piety, attention is hereby drawn to another of Owen's minor, but not insignificant, discoveries—that of the pedal glands of the Great Indian Rhinoceros (*Rhinoceros unicornis* Linn.), and corroborative evidence is given (seemingly for the first time) of the accuracy of Owen's original observations.

In 1834 Owen had persuaded the Council of the Zoological Society of London to purchase for £1,000 a male Indian rhinoceros, the first of its kind to be acquired by the Society. This animal died in 1849 and was immediately anatomised by Owen[3], whose subsequent monograph (1862), with its 14 lithographic plates, remains the classic account of the anatomy of this species and by chance the first such to be published. (By chance, because another male animal of this species had lived in the Royal Menagerie at Versailles from 1772 to 1793. At death it was dissected by Vicq D'Azyr and Mertrud and its skeleton is still preserved (No. A7974) in the Musée d'Anatomie Comparée in Paris. Vicq D'Azyr also wrote an account of its anatomy, illustrated by some 31 plates prepared by Maréchal and by P. J. Redouté *père et fils*, but this account and the accompanying plates have remained unpublished in the Archives of the Muséum National d'Histoire Naturelle.) It may be argued that the establishment of the descriptive anatomy of any large mammal requires no particular acumen or knowledge—but merely industry, prosectorial assistance and a sufficiency of time. This contention is but partially true, for the known gross anatomy of man is necessarily based upon a vast number of meticulous dissections, and, where the dissection of large mammals is concerned, certain adverse factors inevitably complicate procedure. The material under examination is both bulky and unwieldy: its injection or embalmment is usually impracticable: the physical labour of manipulation is considerable, and investigation tends quickly to become a race against advancing putrefaction. Not surprisingly, therefore, an accurate and complete picture of the morphology of any very large animal is unlikely to be obtained from the examination of a single carcase, while the necessary specimens themselves become available but sporadically. Consequently, knowledge remains wanting of the gross structure of a wide variety of undomesticated mammals. Though much is known, much more requires elucidation.

It is ever a tribute to the original recorder of morphological data that subsequent investigation should but confirm the accuracy of his findings. And in this present matter

of the pedal glands it is a tribute to Owen that his original description requires merely the slightest emendation.

Examining the external characters of his rhinoceros specimen in 1849, Owen[3] noted a feature missed by Daubenton, F. Cuvier and other earlier and excellent observers, namely the presence of an " orifice behind each carpus and tarsus, which forms the termination of the duct of a pretty large subdermal glandular pouch ". In the thick and tuberculated skin of this species this orifice is easily enough overlooked, particularly since all four orifices " are concealed from cursory observation in the middle of the transverse fold that runs parallel to the interspace between the carpus and metacarpus, and between the tarsus and metatarsus "[3]. Even when their existence is known beforehand, these gland orifices are by no means obtrusive, so that their original discovery reflects great credit upon their finder's observational acuity. The authors of subsequent zoological treatises have been content to accept the existence of these pedal glands solely on Owen's great authority, without, apparently, any re-investigation of their presence and nature, but taking due notice of these structures in connexion with the niceties of rhinoceros taxonomy.

The present writer has, however, confirmed the presence of these pedal glands in three specimens of the Great Indian Rhinoceros from the menagerie of the Zoological Society of London, viz. in a male (" Felix ") of 20 years in 1941: in a younger male (" Hush ") of some 15 years in 1945, and in an adult male (" Mohan ") aged 18 years at least, in 1961. From the last of these specimens the glands were dissected and are illustrated in the accompanying figure.

Owen[3] described the pedal glands, which he duly figured, as " of a compressed ovate figure, measuring one and a half inches in length and one inch in breadth " with parietes " two to three lines " thick (i.e. about one quarter inch), and consisting of " a compact congeries of follicles, surrounded externally by a muscular and tendinous coat ". The duct orifice could stretch to some three quarters of an inch. Personal observations are largely confirmative of this original description. The formalin-preserved forefoot gland of specimen " Mohan " (Fig. 1, A) measures 44 mm. long by 29 mm. wide; the similarly preserved hindfoot gland (Fig. 1, B) measures 48 mm. long by 22 mm. wide. The transversely elliptical neck of each gland when fresh was readily distensible up to 20 mm.: The gland wall is some 8 mm. in thickness; the undisturbed ostium is a round orifice, some 3 mm. across. The shape of either gland is apparent in the accompanying illustration, which shows also the substantial fundal vasculature, the anchoring " ligaments ", and the short neck of the sac: in the fresh state, compression of the gland causes the exudation of a thick grumous secretion.

The pedal gland in *Rhinoceros unicornis* is essentially a local invagination of the entire skin supported by a circumscribing condensation of the dense collagen tissue of the subcutaneous fascia: this dermal invagination is associated with a localised augmentation of modified sebaceous glands which are strikingly absent from other areas of the skin of the foot. Histologically the wall of the invagination shows successive dermal, capsular and fascial layers. The epidermis lining the sac is a thick, excessively cornified, stratified squamous epithelium. In its stratum corneum " ghost " cells are discernible and one particularly obvious layer of such cells represents a stratum lucidum. The stratum granulosum, which in places is 8 cells thick, shows basophilic granules of varying size, some of the granules being relatively large. In the cells of the basal layer of the stratum Malpighii (i.e., next to the basement membrane) considerable patches of melanin are present. The dermal papillae are long, narrow and close-set, and penetrate so far into the epidermis as to reach the stratum granulosum: dermis and epidermis are thus very tightly keyed together. Outside the dermal layer lies the capsular component of the sac wall, a thick, dense, felting of collagen fibres liberally supplied with blood vessels, some of which possess extremely muscular walls. This tough, thick, collagen layer is a condensation of the local subcutaneous fascia from which it is easily separable and by local " ligamentous " thickenings of which the whole sac is anchored in position.

Deep in the dermal layer of the sac wall lie numerous, large, apocrine glands, the acini of which manifest recognisable myoepithelial cells. The mouths of these specialised 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, sug-

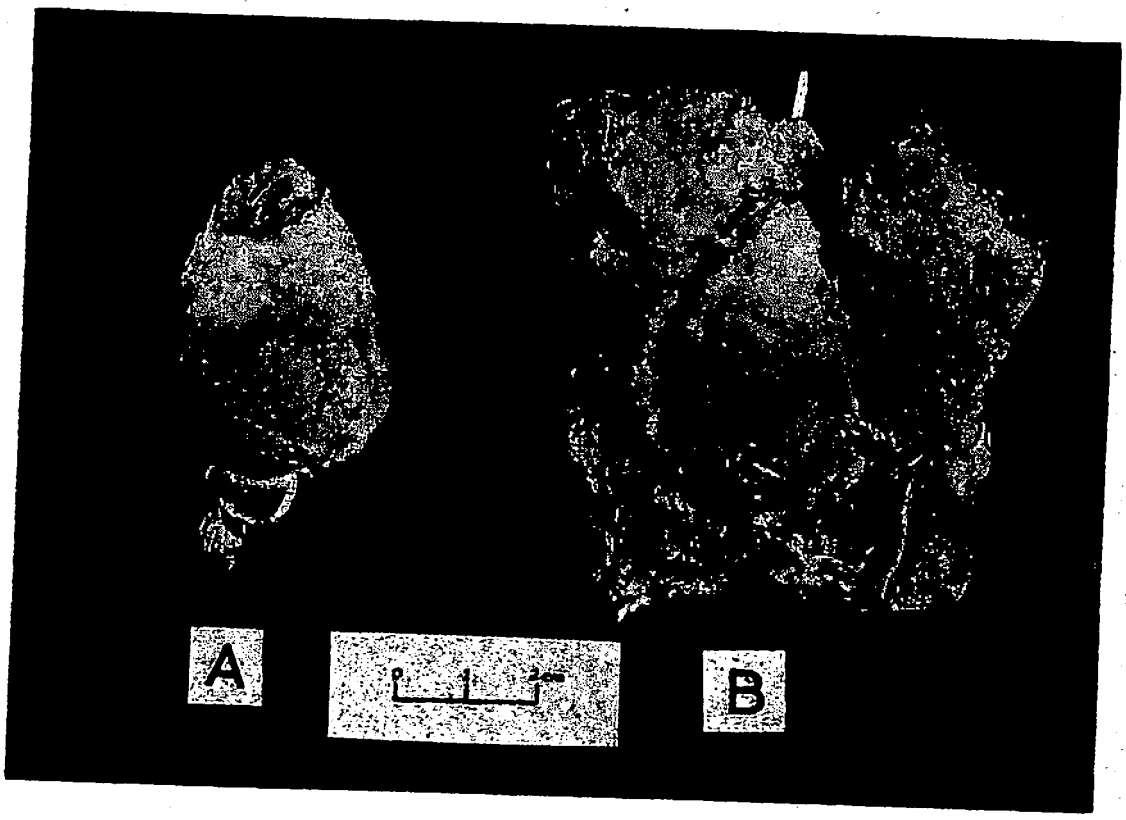

Fig. 1 Pedal scent gland of Great Indian Rhinoceros (*R. unicornis* L.). Adult male animal.
(a) Isolated gland of left manus, showing ostium and fundal vasculature.
(b) Gland of left pes, dissected *in situ*, showing vasculature, retention "ligaments", and introduced rod.
Cm. scale

gests that secretion is a fairly continuous process, and that the lumen of the sac is never wholly devoid of content. Apart from the smooth muscle in the walls of the local blood vessels, no muscle tissue whatsoever is present in the sac wall, contrary to Owen's original statement. This discrepancy of description doubtless arises from Owen's omission to make a microscopical preparation of the wall of his pedal gland and hence to realise that the pinkish colour of the sac parietes is due, not to the presence of muscle, but to an extremely elaborate vasculature.

The presence or absence of the pedal gland is helpful in connexion with the taxonomy of the extant Rhinocerotidae. This family comprises two Asian genera (*Rhinoceros, Didermoceros*) and two African genera (*Diceros, Ceratotherium*). The genus *Rhinoceros* has two species, viz. *R. unicornis* (Great Indian Rhinoceros) and *R. sondaicus* (Javan Rhinoceros). The exact relationships of *Diceros* (Black African Rhinoceros) and *Ceratotherium* (White Rhinoceros) remain unsettled, largely for want of sufficient morphological knowledge concerning these two forms. Certain it is, however, that the living rhinoceroses represent the products of three distinct phylogenetic lines, one leading to the Great Indian and Javan species, a second to the two African species and a third to the Sumatran species.

In certain of its anatomical characters this last form (*Didermoceros sumatrensis*) agrees with its Asian congeners, but in other characters it agrees with the African forms. In a

particular character (e.g. the separation or confluence of the foramina lacerum et ovale) different specimens may show variant affinities.

The pedal gland is confined to the genus *Rhinoceros*. Noted first by Owen[3] for *R. unicornis*, it was later observed by Beddard and Treves[4] in *R. sondaicus*. According to Garrod[5] it is absent in *Didermoceros*, which herein would seem to agree with the African rhinoceroses. The gland was also wanting in three specimens (a 2-year-old female, a 1-year-old male and a late foetal female) of *Diceros* examined by the writer and, so far as observation is possible of captive animals, it is wanting also in *Ceratotherium*.

In the remaining Perissodactyla the gland is unknown in the Equidae and appears to be equally wanting in the Tapiridae, for it is not recorded for the Malayan Tapir by Murie[6] or Beddard[7], nor for the American Tapir by Beddard[8] or Bressou[9]. The writer found no trace of any pedal gland in a very young specimen of the American species. So far, therefore, as present knowledge goes, specialised pedal glands among the Perissodactyla are confined to the genus *Rhinoceros*, whilst among the many families of the Artiodactyla such organs are widely distributed (Pocock[10]).

Since the pedal glands are undoubtedly scent glands, expressing their secretion pretty continuously during the animal's peregrinations and so blazing an olfactory trail for the benefit of its mate, young or fellows, their restriction to a single genus among extant rhinoceroses is puzzling. An olfactory trail is obviously most successfully laid in a firm, dry terrain (e.g. grassland, low bush, savannah) and can scarcely prove successful in a marshy or swampy habitat. Thus, a priori, well-developed pedal scent glands might be expected to occur in *Diceros* and *Ceratotherium*, which frequent the dry African bush, and their absence in *Rhinoceros* and *Didermoceros*, inhabiting swampy jungle, would not be surprising. As indicated, however, the facts are obstinately otherwise and the answer to this apparently anomalous distribution has yet to be sought.

It may be added that problems of function and distribution are not confined to the pedal glands, which are but one among the many forms of specialised cutaneous appendage which the multi-potential mammalian skin is capable of producing. Other intriguing cutaneous glands include those of the face (Wart Hog), the preorbital region (Cervidae), the temporal region (Elephant), the occipital region (Camels), post-cornual region (Chamois), dorsal mid-lumbar region (Peccary, Tree-Hyrax), the tail (Goats), the perianal region (many Carnivores and Rodents), the prepuce (Aard-Vark, Pig, Musk Deer, Grysbok), the inguinal region (many Ungulates), the metatarsus (Llamas, Deer), the digits (Pig), the nails (Four-horned Antelope), the sternum (most Marsupials, Gibbon, Spider Monkey), the gular region (Saki Monkey) and the epigastrium (Tarsier).

The function of some of these glands is extremely obscure, so that a wide and rewarding field of exploration still awaits the attention of both the histologist and the animal ecologist.

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