THE PROCESSŪS GLANDIS IN THE RHINOCEROTIDAE

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(With 2 plates and 5 figures in the text)

The lateral lobes (processūs glandis) of the penis are reviewed for all extant rhinoceros genera. Previous accounts of these structures are confirmed for *Rhinoceros unicornis* and for *Diceros bicornis* and a first description of them is given for *Ceratotherium simum*. The morphological nature of these external penile features (as extensions of the corpus cavernosum) is established and their taxonomic value is considered. Observations are made upon the penis constitution of *Diceros* and of *Ceratotherium*.

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INTRODUCTION

The extant Rhinocerotidae are characterized by an unusual morphological feature of the glans penis, viz. the presence thereupon of a pair of external lateral flanges or lobes (processūs glandis) attached to the glans near its base. Relatively little has been recorded concerning these peculiar penile characters. Descriptions of them are available for one specimen each of *Rhinoceros sondaicus* and *Diceros bicornis*, for two specimens of *Rhinoceros unicornis* and for three specimens of *Didermocerus sumatrensis*. Nothing relevant has been recorded hitherto for *Ceratotherium simum*. The morphological nature of these processes has been hinted at, rather than established. Since, however, they are not devoid of taxonomic significance (Grassé, 1955), it has been deemed desirable to supplement existing knowledge of them in certain rhinoceros forms (*Rhinoceros unicornis, Diceros bicornis*), to describe them for the first time in another (*Ceratotherium simum*) and to correlate such external anatomical features of the rhinoceros penis with that organ's basic constitution.

It is generally agreed that the members of the extant Rhinocerotidae comprise at least three distinct groups, viz. (1) the Indian and Javan rhinoceroses of the genus *Rhinoceros*, (2) the Sumatran rhinoceros of the genus *Didermocerus*, and (3) the black and the white African rhinoceroses.

The taxonomic status and affinities of the forms included in the first two groups are sufficiently established upon assessment of a wide range of individual characters and any particular further analysis undertaken serves but to confirm the accuracy of this assessment. The taxonomic position of

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the African rhinoceroses, however, remains still unsettled, largely because of insufficient morphological knowledge on which to base a sufficiently comprehensive and critical evaluation. The issue requiring settlement is whether both the African forms are to be included in the single genus *Diceros* (as is presently advocated by some authorities) or whether they should be regarded as two distinct genera, *Diceros* and *Ceratotherium*. In this connection the characters of the processūs glandis in the several rhinoceros forms constitute additional evidence of value in indicating generic and specific status within the Rhinocerotidae, evidence which, to date, has not been utilized.

PREVIOUS ACCOUNTS OF RHINOCEROS GLANS

The relatively scanty literature on the anatomy of the Rhinocerotidae consists principally of the reports made periodically upon single specimens of the various rhinoceros species dying in the menagerie of the Zoological Society of London. The first such (and classical) report was that of Owen in 1850 (published 1862) which reviewed the few earlier and very incomplete studies in rhinoceros anatomy made in England.

(Contemporary continental zoological literature contained no reference to rhinoceros morphology, for though Vicq D'Azyr had, in 1793, made the first dissection of a male Great Indian rhinoceros and had prepared notes and illustrations towards a monograph thereon, his untimely death in the following year prevented publication.)

Thus it is under the aegis of the Zoological Society of London that knowledge of the morphology of the Rhinocerotidae has been mainly acquired and, indeed, continues to develop.

Rhinoceros unicornis

Owen (1862) in his monograph of this species drew particular attention to the peculiarities of the "singularly complex glans": he stated that "on each side of the base of the glans, and rather towards its under part, there is a longitudinal ridge or lobe three inches and a half in length and eight lines in basal thickness". Later Owen (1868) described this lobe as "a longitudinal thick oblong ridge or lobe", adding that "the thick rounded free border of each lobe inclines downwards". His illustrations of these (dissected) glans lobes are not particularly satisfactory and a simple outline figure of one of them was therefore supplied by Forbes (1881), who also re-examined Owen's original specimen and considered the lobes to be more dorsally situate upon the glans, to "lie, in fact, on each side of the dorsum a little removed from the middle line". Forbes gave the height of each lobe as $1\frac{1}{4}$ inches at its middle, wherefrom it diminished both proximally and distally until indistinguishable from the rest of the glans.

Owen omitted any specific reference to the earlier account of the penis of *Rhinoceros unicornis* given by Leigh Thomas (1801) in that author's anatomical description of a young animal. Leigh Thomas had noted that "upon throwing some coloured wax into the corpora cavernosa of the penis, the extremity became expanded" and that "about three inches below [i.e. proximally] a second enlargement took place, though not so compleat and perfect as the first".

Freund (1930) recapitulated the literature to date of the rhinoceros penis in an ambiguous and relatively uninformative paper, for which he employed an admittedly defective specimen of the *Rhinoceros unicornis* penis. He gave original figures of the urethra in longitudinal and in transverse section and derivative figures of the penis in its entirety. On the glans penis he depicted very diagrammatically a median dorsal eminence, flanked by a pair of dorsally situate processūs glandis, but to the appearance, structure and morphological relationships of these he made no textual reference whatever.

Grassé (1955) reproduced Freund's penis figure with altered labelling but provided no new information concerning the structure of the organ.

Rhinoceros sondaicus

Beddard & Treves (1887) studied the anatomy of this species; they stated that "the penis appears to correspond closely to that of *Rhinoceros indicus*; it is hardly worth while to describe it in detail, as Prof. Owen's description would apply almost word for word to the present species; it is important, however, to record the fact that there is this similarity, since Mr Forbes has pointed out that the glans penis of *Rh. sumatrensis* is somewhat different in shape from that of *Rh. indicus*".

That such close correspondence in penile structure should obtain between *R. unicornis* and *R. sondaicus* is not unexpected: it is paralleled on numerous other morphological grounds and is further expression of their common generic kinship.

The characteristic of the glans lobe in *Rhinoceros* is its relatively long sessile antero-posterior attachment to the dorsal moiety of the glans and its relative narrowness even at the point of its maximum projection therefrom.

Didermocerus sumatrensis

Forbes (1881) paid particular attention to the penile characters of *Didermocerus* and gave a well-illustrated account of the glans and its processes. These last have the disposition of "two large oblong-ovate lobes . . . which are free for the greater part of their length and only attached to the rest of the glans at their bases. The lobes lie on the side of the dorsum of the penis, and are closely approximated at their bases". No measurements were given. Forbes's findings in his own specimen proved identical with those of a second (store) specimen in the Royal College of Surgeons Museum: his account therefore would appear to be valid for the genus *Didermocerus* and as such has been subsequently accepted.

In his description of the processūs glandis of *Didermocerus* Forbes appeared to be unaware that he had been anticipated by William Bell (1793) who first drew attention to these structures in his account of a wild-shot animal, and was the first, presumably, to appreciate their anatomical significance. For Bell wrote, "at about nine inches from the opening of the urethra are placed two bodies on the upper part of the glans, very like the nipples of a milch cow, and as large; they become turgid when the penis is erected". This last sentence presupposes that Bell had observed erection in the living animal.

The characteristics of the *Didermocerus* processus glandis are its teat-like appearance, its restricted and pedunculate mode of attachment to the glans

dorsum, its otherwise total independence thereof and its ventralward dependence.

Diceros bicornis

Little indeed is recorded concerning the anatomy of the African rhinoceroses, but fortunately the relevant literature contains an admirably illustrated account by Lönnberg (1912) of the external features of the *Diceros* penis. Herein again bilateral processūs glandis (lateral lobes) are present, but of a shape and disposition remarkably different from those of both *Rhinoceros* and *Didermocerus*. Lönnberg described each process as attached nearer the dorsal than the ventral aspect of the glans and as somewhat triangular in outline. One side of the triangle is the attached base of the lobe, some 58 mm (over 2 inches) in length ; the second is the anterior (distal) border, some 75 mm (3 inches) in extent ; the third is the superior border, convex and (with the organ flaccid) in apposition with its contralateral fellow in the median dorsal line over the glans. The free borders of the lobe average some 6–7 mm (about one-quarter inch) in thickness, the anterior border being the thinnest. (The thickness of the lobe at its basal attachment was not stated, neither was the age of the animal, presumably an adult individual.) Lönnberg's excellent illustrations of the *Diceros* glans lobes (his Pl. II, figs. 3, 4) are reproduced by Grassé (1955). The accuracy of his anatomical description of the *Diceros bicornis* glans was confirmed by the writer's examination (1962) of the pars libera penis of a four years old specimen from Whipsnade Zoological Park (vide infra).

The characteristics of the processus glandis in *Diceros* comprise its distinctive rounded-triangular outline, its vertical anterior (distal) border, its long base of attachment and its close apposition to the dorsum of the glans so as to meet its contralateral fellow mid-dorsally.

Ceratotherium simum

Nothing has been recorded hitherto concerning the morphology of the penis in this form. A plaster cast of the foetal inguinal region (Muséum National d'Histoire Naturelle, Paris : No. A 1457.1) affords no evidence as to the presence of processūs glandis. The account given below is based upon the first anatomical investigation to be made of the *Ceratotherium* penis, the material deriving from a three years old specimen from Whipsnade Zoological Park. As will be seen the characteristics of the *Ceratotherium* processus glandis are its semilunar superior border, its generally vertical disposition and the apposition of its medial surface to the lateral, but not the dorsal, aspect of the glans.

(Ottow's (1955) monograph on mammalian penis structure is notably deficient concerning earlier work on the Rhinocerotidae and adds nothing to knowledge of the rhinoceros penis.)

PRESENT OBSERVATIONS

Rhinoceros unicornis

Examination of the penis of a fifteen years old animal which died in Whipsnade Zoological Park in 1945 confirmed the accuracy of Forbes's (1881)

description of the processūs glandis in this form. The glans presented a well-marked median dorsal eminence and two lateral lobes or flanges. Each such flange was a sessile ridge, of roughly semilunar outline, thickest in its middle portion, and relatively more pronounced and rounded at its posterior (proximal) end. Its base or attached border measured some 15 mm (half an inch or more) in thickness and its free lateral border was rounded and somewhat dependent. The process sprang from the dorsal moiety of the glans and, from a maximal width (some 25 mm) in its middle portion, tapered therefrom both anteriorly and posteriorly to merge with the general surface of the glans (Fig. 1).

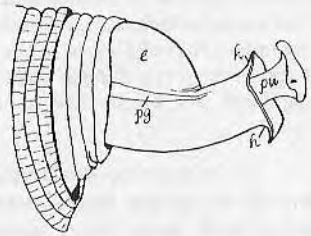

Fig. 1—*Rhinoceros unicornis*. Glans penis, lateral aspect.
e = median dorsal eminence ; h = glans hood ; pg = processus glandis ; pu = processūs urethralis.

Diceros bicornis

The features of the processus glandis in the young *Diceros bicornis* from Whipsnade agree in all morphological particulars with those described by Lönnberg (1912) for the (presumably) adult animal. Each lobe or process is an approximately triangular flange attached obliquely to the lateral aspect of the glans with its medial surface closely applied thereto. The base or attached border of the triangle measures 48 mm ; the anterior (or distal) vertical border, 37 mm ; and the convex superior border some 45 mm. The maximum height of the lobe (from base to superior border) is some 30 mm : the lobe is 10 mm thick at its basal attachment (inferior border) and 5 mm thick at its anterior (thinnest) border. The line of attachment of the processus to the glans is divergently oblique in a proximo-distal direction, so that the proximal (posterior) extremities of the lobes are 16 mm apart, but the distal (anterior) extremities 36 mm apart. The superior borders of the two processes are contiguous for the middle one-third of their length in the median dorsal line above the glans (Pl. 1, fig. 1). Each process is of firm consistency, mere palpation proclaiming it to be something more than a redundant flap of the penile skin. Its vertical sectioning reveals its true composition, viz. that it is a blunt lateral free wing of the corpus cavernosum penis, ensheathed in investing fascia and covered by the penile integument (Fig. 3 A, C). Lönnberg's speculation (vide infra) as to the nature of the glans lobe is thus substantiated upon a firm anatomical basis.

Ceratotherium simum

In its general form and appearance, the glans penis of *Ceratotherium*, herein described for the first time, closely resembles the comparable structure in *R. unicornis* and *Diceros bicornis*. It presents a dorsal median eminence, flanked by a pair of processūs glandis of characteristic shape. Each process has a fairly horizontal attached border, some 49 mm long and 9 mm thick, situate about two-thirds up the side of the glans, and a free, superior border of evenly curvilinear outline, which does not encroach upon the glans dorsum, thus left completely uncovered. Proximally the two processes are 20 mm apart. The median aspect of each is adpressed to the side of the glans and shows a scattering of large, flattened papillae : the lateral aspect shows many such papillae, disposed both singly and in clusters.

Thus the processus glandis of *Ceratotherium* resembles that of *Rhinoceros* in its relatively horizontal attachment, its limited height and its evenly curved free border : it resembles that of *Diceros* in the application of its medial surface to the glans. It differs from the *Diceros* structure, however, in being less tall, in lacking an angulated free border and in not encroaching upon the glans dorsum (Pl. 2).

TAXONOMIC CONSIDERATIONS

The taxonomy of the extant Rhinocerotidae presents no problem with regard to the component Asian forms, since *Rhinoceros* and *Didermocerus* are recognized universally as distinct genera. Matters are otherwise, however, concerning the two African forms, viz. the black (hook-lipped) rhinoceros and the white (square-lipped) rhinoceros. The first of these has long been accorded generic status as *Diceros*, but the second has undergone a remarkably variant assessment by taxonomists. Known simply as *Rhinoceros simus* by its discoverer (Burchell, 1817), it was given by Gray (1867) the generic name of *Ceratotherium*, which was accepted by Heller (1913), Pocock (1944), Simpson (1945) and others. Grassé (1955) adopted the generic name of *Ceratorhinus*. Contrariwise Oldfield Thomas (1900, 1901), Roosevelt (1910) and Lydekker (1916) regarded the white rhinoceros as only specifically distinct (as *Diceros simus*) from the black rhinoceros (*Diceros bicornis*) ; while Ellerman, Morrison-Scott & Hayman (1953) considered these forms as subgenerically distinct. Since the morphology of both African rhinoceros forms remains largely unknown, it is not always apparent what criteria have served as the basis for the differing taxonomic assessments made. Some of the known morphological differences between these two forms have been marshalled (Cave, 1962) in favour of the ascription of generic status to the white rhinoceros (as *Ceratotherium*). Since the processūs glandis serve a common purpose in all living rhinoceroses and since these structures are obviously uninfluenced by external environmental factors, any differences they may manifest may reasonably be assumed to be of genetical rather than physiological significance. The additional morphological evidence so provided indicates that *Ceratotherium* shows a closer affinity to *Diceros* than to any Asian rhinoceros form.

A review of the morphological characters of the processūs glandis throughout the Rhinocerotidae demonstrates differences strongly indicative (at least) of

differences at generic level. Thus the type of process occurring in *Rhinoceros* is identical in each of the two species thereof, viz. *R. unicornis*, *R. sondaicus*. The type of process in the admittedly separate genus *Didermocerus* is of a wholly distinctive character. The two African rhinoceros forms manifest a certain similarity of processūs glandis morphology which immediately distinguishes either of them from any Asian rhinoceros form and indicates their relatively close genetic relationship. The processes are upstanding flanges attached to the side of the glans with their medial aspects closely applied in greater or lesser degree to the glans dorsal moiety. Nevertheless (and perhaps surprisingly if these forms are considered to be species of a single genus) distinct differences occur between the *Diceros* and the *Ceratotherium* processes. Thus in *Diceros* the process is relatively large, with an angled superior free border (=anterior and superior borders) and in the resting state the two processes so completely cover the dorsal moiety of the glans as to become mutually contiguous upon its dorsum. In *Ceratotherium* the process is relatively small, with an evenly curvilinear superior free border and its medial aspect closely applied to the side only of the glans, the dorsum of which it leaves wholly uncovered.

The morphological differences so curiously manifested by the processūs glandis in the several rhinoceros forms are summarized in Table 1 and are represented schematically in Pl. 2 and Fig. 5.

ANATOMICAL CONSIDERATIONS

Of all (Bell, 1793 ; Leigh Thomas, 1801 ; Owen, 1862 ; Beddard & Treves, 1887 ; Forbes, 1881 ; Lönnberg, 1912 ; Freund, 1930) who have recorded observations upon the glans processes in the Rhinocerotidae, Leigh Thomas, Owen and Freund alone appear to have anatomized the penis and its adnexa to any extent ; the others have treated the processes exclusively as highly distinctive external characters without seeking to determine their structure or to correlate this with the intrinsic constitution of the penis.

In *Rhinoceros unicornis* Owen (1862) had observed that the processūs glandis " consist chiefly of erectile tissue ". He did not associate these lateral processes with the median dorsal eminence (a " narrow ridge " increasing distally in elevation to subside short of the rim of the terminal fossa of the glans) nor did he establish by dissection their continuity with the corpus cavernosum. Owen's statement concerning the erectile nature of the processūs glandis in *Rhinoceros* may therefore depend partly upon Leigh Thomas's (1801) findings following injection of the corpus cavernosum.

Freund (1930) figured the processes very sketchily. He neither detailed them in his own specimen nor established their anatomical nature. He interpreted a statement by Hofmann (1924) anent the erectile nature and continuity with the glans of the processūs glandis of *Tapirus americanus* as meaning that these processes in Perissodactyla pertain to the corpus spongiosum penis and not, as Lönnberg (1912) had correctly surmised, to the corpus cavernosum. (Hofmann (1924) did not, in fact, assign the processūs glandis to either penile component : his illustration of the tapir glans in

Table 1

Processus glandis	*RHINOCEROS* *R. unicornis* *R. sondaicus*	*DIDERMOCERUS* *D. sumatrensis*	*DICEROS* *D. bicornis*	*CERATOTHERIUM* *C. simum*
Form	Elongate semilunar ridge	Pedunculated tapering ovoid mass	High triangular flap	Low semilunar flap
Attachment to glans	By medial border	By restricted paramedian base	By inferior border obliquely	By inferior border
Location on glans	Dorso-laterally	Paramedially dorsal	Laterally	Dorso-laterally
Free borders	Lateral only	Superior, anterior and inferior	Anterior and superior	Superior only
General disposition	Lateral to glans	Divergent from contralateral fellow	Applied to glans dorsum and to contralateral fellow	Applied to glans side

transverse section (*op. cit.* Taf. 10, fig. 8), however, renders it obvious that the processes must be continuous with the corpus cavernosum).

In *Didermocerus sumatrensis* Bell (1793) had observed the processes to become turgid during penis erection, which implies their erectile tissue composition.

In *Diceros bicornis* Lönnberg (1912) illustrated a triad of surface elevations comparable to those recorded by Owen for *Rhinoceros unicornis* (viz. a convex median dorsal eminence and two lateral lobes or flanges). He suggested, in the absence of any direct supportive anatomical evidence, that the processūs glandis of the rhinoceros correspond to the two lateral of the three terminal "apices" of the equid corpus cavernosum, and evidence for the validity of this morphological interpretation is given, for the first time, below.

Grassé (1955) accepted Lönnberg's identification of the processūs glandis as lateral portions of the corpus cavernosum and remarked that these two "lobes erectiles" varied in form in the different rhinoceros species. He added nothing, however, to knowledge of these structures.

Thus, in the absence of direct anatomical proof by dissection, it had been sufficiently implied previously that the processūs glandis in the Rhinocerotidae are but lateral superficial prolongations of the erectile tissue of the penis. Since however both the corpus cavernosum and the corpus spongiosum are erectile tissue bodies, it remained to show, by dissection evidence, that the rhinoceros processūs glandis are directly continuous with the corpus cavernosum. Such evidence is submitted below for both *Diceros* and *Ceratotherium*.

PENIS STRUCTURE IN *DICEROS*

Detailed examination of the radix penis of the young Whipsnade *Diceros* specimen proved impracticable but the pars libera penis was dissected completely. This agrees in general form and constitution with that of *Rhinoceros unicornis* as described by Owen (1862) and Freund (1930) and in its external characters with that of *Diceros bicornis* as described by Lönnberg (1912).

Proximal to the prepuce the corpus penis is of oval cross-section ; distal thereto the glans, of sinuous outline and ovoid cross-section, proceeds to its termination in an obliquely disposed cup-like arrangement, having thin crenated margins and enclosing a fossa terminalis (Pl. 1, fig. 1 and Fig. 2). Dorsally the glans presents a tapering ovoid median eminence, most prominent immediately distal to the processūs glandis and fading distally to disappear proximal to the terminal fossa rim (Pl. 1, fig. 1). This eminence is flanked by a pair of upstanding lateral flanges or lobes (processūs glandis) of rounded triangular outline, so applied to the dorsal moiety of the glans as to be partly contiguous mid-dorsally. (The dimensions and features of these lateral processes are detailed above.) A distinct lateral groove on the glans forms a ventral border to the dorsal eminence and most anterior portion of the lateral lobe. Section of the processūs glandis reveals each to be composed of a basic core of erectile tissue, enveloped in a dense fibrous sheath and covered by the glans skin (Fig. 3 A, C).

The cup-like distal extremity of the glans encloses the fossa terminalis and forms a kind of hood around the emergent processus urethralis. The thin, slightly crenated fossa margin is produced ventrally into an inferior lip ; the inner surface of the fossa is continuous at its fundus with the external surface of the processus urethralis, and mid-dorsally a short, stout frenum unites the two. A distinct median raphé begins mid-ventrally on the discoid terminal extremity of the processus urethralis, extends the whole length of that process and is reflected on to the inner aspect of the ventral portion of the fossa terminalis. From the somewhat exaggerated ventral lip thereof the raphé continues exteriorly and proximally along the mid-ventral aspect of the glans proper to the commencement of the prepuce itself, forming upon glans and prepuce a low but distinct fold.

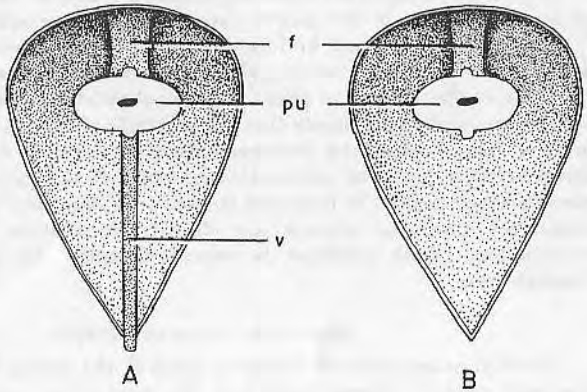

Fig. 2—Diagrammatic representation of processus urethralis (sectioned) within glans hood of (A) *Diceros*, (B) *Ceratotherium*.
f=frenum ; pu=processus urethralis ; v=ventral raphé.

The trumpet-like processus urethralis projects from the fossa terminalis of the glans (Pl. 1, fig. 1 and Fig. 2). Its cylindrical body has an oval, obliquely truncated, discoid extremity, 26 mm high by 15 mm broad, with thin, somewhat scalloped, everted edges. Nearer the ventral than the dorsal edge of this disc appears the external urethral orifice, some 4 mm wide and 3 mm high.

Thus, findings in the Whipsnade specimen confirm the accuracy of Lönnberg's (1912) earlier observations on *Diceros*, particularly with respect to the uniquely disposed processūs glandis and to the presence of a well-marked median raphé (absent, according to Owen (1862), in *Rhinoceros unicornis*). Lönnberg's speculation that the processūs glandis pertained to the corpus cavernosum is shown to be justified, for dissection (vide infra) reveals that these processes are essentially the laterally projecting portions of that structure and are devoid of any connection with the corpus spongiosum as implied by Freund (1930).

The corpus penis presents the following anatomical features. The clove-coloured skin up to the prepuce shows the typical surface pattern of contiguous rosettes, each composed of a number of triangular elevations. It is sparsely beset with 3 mm long stiff black hairs, most abundant ventrally where the common integument joins the non-cornified skin of the prepuce. This last is thinly studded circumferentially with stiff black hairs, from 3 to 7 mm long, and with the orifices of hair follicles lacking any projecting hairs.

The superficial fascia is the usual felting of lax and very vascular connective tissue, which accommodates the penile superficial nerves and blood vessels. Relatively thin dorsally, it increases in thickness ventralwards where, below the retractor muscles, it constitutes a 35 mm thick layer, considerably admixed with elastic tissue, and lodging the M. retractor preputii, whose fibres attach to the preputial skin. It is condensed around the corpora cavernosa and spongiosum, thinly disposed in the glans region and wanting upon the processus urethralis. The corpora cavernosa remain separated by a median septum, but virtually form a single corpus cavernosum by their common enclosure within an exceedingly tough tunica albuginea, some 10 mm thick dorsally. Their larger cavernous spaces are situate dorsally. Distally the corpus cavernosum terminates in the midline below the proximal portion of the dorsal eminence of the glans ; from this it receives an accession of fibres and thereafter expands bilaterally into wing-like flanges, the processūs glandis. Apart from the ligamentous connection mentioned, the corpus cavernosum is demonstrably independent of the glans eminence (Fig. 4).

The arteria dorsalis penis superficialis divides into a larger dorsal and a smaller ventral branch, each accompanied by large and numerous veins. The former lies lateral to the fibrous tunnel enclosing the levator tendon and supplies distally a series of twigs to the medial aspect of the ipsilateral processus glandis, reinforcing the essential supply thereto from the a. profunda penis : the latter branch descends into the groove between corpus cavernosum and corpus spongiosum, and supplies the superficial tissues and the skin.

The corpus spongiosum is the expected cylindrical mass of erectile tissue, bound by dense fibrous tissue to a shallow sulcus urethralis on the under aspect of the tunica albuginea and traversed by the penile urethra (Fig. 4). The relatively large venous spaces of its erectile tissue are visible to the naked eye. Histologically these are seen to be separated by thick fibrous septa containing a certain admixture of unstriped muscle and elastin. The " muscular " and extremely thick-walled arteries are distributed directly to the erectile tissue, but a series of smaller vessels is disposed in very close proximity to the urethral epithelium.

A m. bulbo-cavernosus is wanting in this portion of the urethra, being confined (as in *Rhinoceros*) to the proximal portion of that channel within the radix penis.

Distal to the division of the superjacent corpus cavernosum into the processūs glandis (i.e. below the eminence of the levator tendon) the corpus spongiosum receives some fibres from that tendon and proceeds distally to the glans hood to become continuous with the emergent processus urethralis

In the inactive state the capacious penile urethra appears on section as a transverse slit, some 8 mm in diameter : its longitudinally plicated mucosa bears throughout a stratified squamous epithelium. Urethral glands of the Littre variety are wanting.

The two mm. levatores penis insert into a strong, thumb-thick, rounded tendon, situate in an accommodating groove upon the corpus cavernosum dorsum and enclosed within a long tunnel of dense fibrous tissue. Between tendon and tunnel wall loose areolar tissue facilitates tendon play (Fig. 4). Distally on the glans, where the corpus cavernosum ends by branching into the two processūs glandis, the tendon enlarges in ovoid fashion to constitute the median dorsal eminence of the penis (Fig. 3). The ventral aspect of this enlarged portion of the tendon is firmly adherent to the distal extremity of the undivided corpus cavernosum, beyond which it fuses with the penultimate portion of the corpus spongiosum. The lateral surface groove on the glans indicates the line of demarcation between the tendon's terminal portion and the subjacent spongiosum.

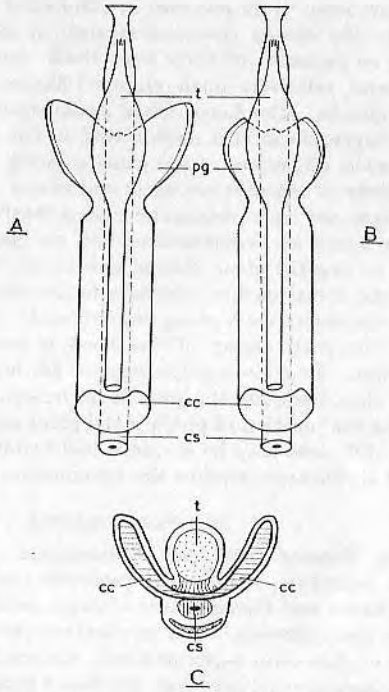

Fig. 3—Glans penis constitution (diagrammatic) in *Diceros* and *Ceratotherium*. A and B represent dorsal views of glans in *Diceros* and *Ceratotherium* respectively ; C represents either glans in transverse section to show cavernosal nature of processūs glandis.
cc = corpus cavernosum ; cs = corpus spongiosum ; pg = processūs glandis ; t = levator penis tendon enlargement.

The two mm. retractores penis lie side by side, a muscular ribbon running the entire length of the pars libera penis immediately ventral to the corpus spongiosum, and terminate by insertion into the ventral aspect of that body's penultimate portion, immediately proximal to the fossa terminalis glandis. These muscles are separated from the ventral penile skin by an enormously thick layer of loosely knit superficial fascia (Fig. 4).

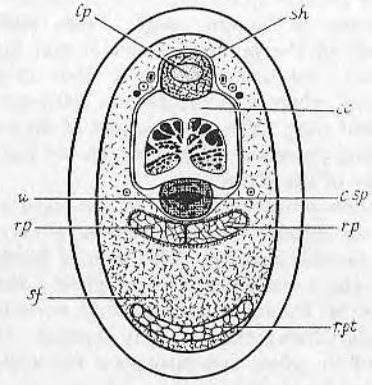

Fig. 4—Transverse section of glans penis of *Ceratotherium* (and, ignoring the retractor preputii, of *Diceros*).
cc = corpus cavernosum ; c.sp = corpus spongiosum ; lp = levator penis tendon within sheath (sh) ; rp = retractor penis ; r.pt = retractor preputii ; sf = fascia ; u = urethra.

The median dorsal eminence of the *Diceros* penis is obviously no part of the corpus cavernosum, as Lönnberg (1912) supposed, but a mere terminal thickening of the levator penis tendon, firmly attached ventrally to the median undivided portion of the corpus cavernosum and beyond this to the corpus spongiosum. The processūs glandis, on the other hand, are the bilaterally-expanded portion of the corpus cavernosum. The processus urethralis is simply the free terminal portion of the corpus spongiosum.

This anatomical summary reveals the pars libera penis of *Diceros* to be essentially comparable with that of *Rhinoceros unicornis*, save only in the detailed morphology of the processūs glandis.

PENIS STRUCTURE IN *CERATOTHERIUM*

The external genital region of the *Ceratotherium* specimen closely resembles that of the *Diceros* specimen, i.e. the relatively large and conical mammillae are prepenially situate, a true scrotum is wanting, the processūs vaginales are widely patent, and the testes lie below the parapenial skin between mammillae and prepuce. The pars libera penis agrees morphologically with that of the comparably aged *Diceros* specimen, save in respect of the configuration and relative size of its processūs glandis. The genital skin is of lighter colour (pale grey with a mauve undertone) than in *Diceros* but shows a similar surface pattern of raised, cuneiform areas, comprising a rosette of smaller,

mostly triangular, elevations, each bearing a central hair follicle Scattered sparsely over the genital region are hairs, usually short and fine, though one para-mammillary hair attains a length of 16 mm. Large pale-coloured, flattish papillae occur singly or in clusters or in rows upon the glans and prepuce and upon both aspects of each processus glandis : a few smaller papillae beset the sides of the dorsal median eminence.

The glans penis is much like that of the *Diceros* specimen. The median dorsal eminence is 95 mm long, 21 mm wide proximally (between the proximal ends of the processūs) and 32 mm maximum width (immediately distal thereto) : its distal extremity ends 12 mm proximal to the rim of the glans hood (whereas in the *Diceros* specimen, as in Lönnberg's specimen, it attained that rim). The dorsal aspect of the eminence is entirely uncovered by the flanking processūs glandis, which are restricted to direct contact with the sides only of the glans.

Each of these processes is a low (8 mm high) semilunate, vertically disposed flange, with an oblique inferior border, an evenly curved superior border, and medial and lateral surfaces. The inferior border, 49 mm long, is attached obliquely to the dorsal moiety of the glans : the superior border is free, not angulated as in *Diceros*, but uniformly curvilinear, and falls short of the dorsum glandis which is thus left fully exposed : the medial surface is adpressed to the side of the glans and displays a few scattered papillae : the external surface is beset by numerous large, conspicuous, centrally-depressed papillae, some 2 mm in diameter, and disposed either singly or in rows or clusters. The entire process is notably smaller than that of *Diceros* and of a different and characteristic shape (Pl. 1, fig. 2 and Pl. 2).

The distal extremity of the glans expands hood-wise to enclose the fossa terminalis glandis and partly to surround the emergent processus urethralis. The hood margin is strongly crenated and its inferior moiety is prolonged ventralwards as a distinctly recurved, pointed lip, the upper (internal) aspect of which, unlike its *Diceros* counterpart, is devoid of any median raphé (Fig. 2 B). The *Ceratotherium* ventral median raphé begins on the external aspect of the hood's ventral lip, whence it proceeds proximally along the glans and prepuce, without the formation of any projectile fold.

The trumpet-like processus urethralis projects freely from the fundus of the fossa terminalis glandis : its obliquely truncated cylindrical body (23 mm long) terminates in the usual discoidal extremity (28 mm high by 17 mm broad) whose thinnish, faintly crenated, elliptical periphery is somewhat pointed inferiorly. The external urethral orifice, some 4 mm in diameter, opens nearer the ventral than the dorsal edge of the discoidal surface. As in the *Diceros* specimen, the processus urethralis manifests a prominent dorsal median raphé, continuous proximally with a short, wide frenum connecting it to the deep (inner) aspect of the glans hood, and a ventral median raphé confined to the process itself (Fig. 2).

The pars libera penis of the *Ceratotherium* specimen agrees in basic constitution with that of the *Diceros* specimen. Thus the corpora cavernosa are fused into virtually a single body enclosed within a tough, thick tunica albuginea and the major spaces of the cavernous tissue are relatively enormous.

Dorsally a groove accommodates the rounded tendon of m. levator penis, which plays within a special fibrous tunnel containing delicate areolar tissue : distally the tendon enlarges in ovoid fashion to produce the dorsal median eminence of the glans. The subjacent corpus spongiosum is accommodated partly in a shallow sulcus urethralis and is secured to the cavernosum by a condensation of connective tissue. The spongy urethra presents a vertically T-shaped lumen whose surrounding vascular spaces are visible to the naked eye. The longitudinally plicated urethral mucosa bears a transitional epithelium. (The m. bulbo-cavernosus is again restricted to the proximal part of the urethra.) Ventral and contiguous to the corpus spongiosum lie the two mm. retractores penis in mutual midline juxtaposition : they insert into the distal portion of the glans. Immediately subjacent to the ventral skin of the part lies a well-developed m. retractor preputii. This muscular ribbon (4 cm broad and 0·5 cm thick) arises in the pre-anal region and inserts more or less circumferentially into the greater portion of the preputial skin. (In the *Diceros* specimen no corresponding muscle was observed nor did Owen (1962) refer to its presence in *Rhinoceros unicornis*.)

Distally the corpus cavernosum ends in an ill-defined median process (receiving an accession of fibres from the levator tendon's enlargement) and in two lateral, relatively small, elliptical flanges, which form the core of the processūs glandis. The dense, felted penile superficial fascia has a disposition exactly comparable to that encountered in the *Diceros* specimen.

Anatomical differences of the penis anatomy of *Diceros* and *Ceratotherium* consist chiefly of the different form and extent of the processūs glandis : in *Diceros* these are large, triangular and mutually contiguous over the glans dorsum, whereas in *Ceratotherium* they are small, elliptical and vertically disposed, leaving the glans dorsum uncovered. Further (as Lönnberg (1912) showed), the dorsal median eminence in *Diceros* attains the rim of the glans hood : in *Ceratotherium* it stops short thereof. A ventral median raphé upon the deep (internal) aspect of the hood is present in *Diceros* but not in *Ceratotherium*. In *Diceros* penile papillae are few and confined to the ventral preputial skin alongside the prominent frenum : in *Ceratotherium* they are plentiful at the junction of prepuce and glans and upon the processūs glandis. (This last difference may be an individual variation only : the determination of its full significance requires the examination of further material.)

THE PERISSODACTYL PENIS

Among Perissodactyla the Rhinocerotidae are characterized by the invariable possession of obtrusive processūs glandis, structures which, as the present *Diceros* and *Ceratotherium* evidence establishes for the first time, are essentially the projecting lateral terminal extremities of the corpus cavernosum. A review of rhinoceros penis structure renders it apparent that in all genera the penile components, save one, manifest a comparably uniform morphology. The exception is the corpus cavernosum, whose mode of distal termination varies in the different genera and thus accounts for the several varieties of processūs glandis. In all rhinoceros forms the distal end of the corpus cavernosum is trifid, comprising a single blunt median process and two

projectile lateral processes, which constitute the core of the processūs glandis. These cavernosal processes in *Rhinoceros* are long, narrow and horizontal, in *Didermocerus* elongate, pedunculate and teat-like, in *Diceros* large, triangular and dorsally directed, in *Ceratotherium* short, elliptical and vertically disposed (Fig. 5).

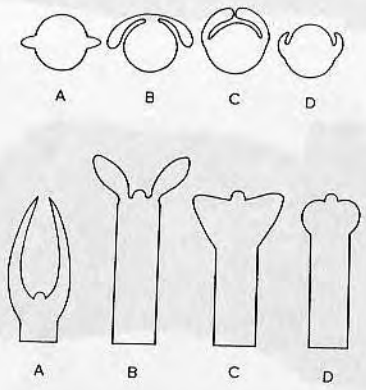

Fig. 5—Schema of (above) glans penis in cross-section to show relation to glans of the processūs glandis and (below) of mode of termination of corpus cavernosum in (A) *Rhinoceros*, (B) *Didermocerus*, (C) *Diceros*, (D) *Ceratotherium*.

External lateral lobes (processūs glandis) are absent from the penis of the Equidae. (Owen's (1868) statement that the glans of *Equus* possesses " two lateral semilunar lobes " as well as " a certain pyramidal process on which the urethra opens " is misleading, as not distinguishing between the cavernous and the spongy components of the penis. In *Equus* it is the corpus cavernosum which ends distally as three (a single median and two blunt lateral) processes). Processūs glandis proper occur in the Tapiridae (probably throughout the family), having been recorded for the Malayan tapir (*T. indicus*) by Poelman (1853), Owen (1868) and Grimpe (1931), and for the Brazilian tapir (*T. terrestris*) by Hofmann (1924). Owen reported *T. indicus* as possessing three external penile lobes (viz. " an upper lobe as well as one on each side ") and Poelman mentioned the occurrence of " trois espèces de crêtes ou de bourrelets aplatis ". Grimpe (1931) demonstrated the processūs in *T. indicus* by intravascular injection. In *T. terrestris* Hofmann noted a median dorsal eminence on the glans having flattish bilateral extensions. Parker (1882) however could distinguish no lateral lobes on the glans of a young Malayan tapir. Lönnberg (1912) spoke of having clearly observed such structures " in the living tapir " (species unnamed), wherein they were " well developed ".

The correspondence between the processūs glandis of the rhinoceros and of the tapir was clearly recognized by Owen (1868). Lönnberg (1912) suggested that the two lateral " apices " of the terminally trifid equid corpus cavernosum penis correspond morphologically to the two external lobes (processūs glandis)

of the rhinoceros penis and, as the present anatomical evidence indicates, was justified in this assumption. He erred, however, in regarding the median dorsal eminence of the rhinoceros glans as the equivalent of the median prong of the equid structure. Freund (1930) erroneously interpreted Hofmann's (1924) description of the tapir processūs glandis to mean that these were continuous with the corpus spongiosum and so considered a similar arrangement to obtain in the Rhinocerotidae. Lönnberg further suggested that the lateral apices of the corpus penis of *Equus* may formerly have been associated with external lateral lobes and that the common perissodactyl ancestor of the Tapiridae, Equidae and Rhinocerotidae possessed such penile features. These suggestions appear plausible and consistent with what is known concerning perissodactyl morphology, but it remains unclear by what means the Equidae came to lose any ancestral processūs glandis. Freund also postulated the presence of glans processes in the common perissodactyl ancestor, subsequently elaborated in the Tapiridae, and, still more so, in the Rhinocerotidae. The origin of such processes in the remote perissodactyl ancestor remains obscure as does also the function these processes subserve in the modern tapirs and rhinoceroses.

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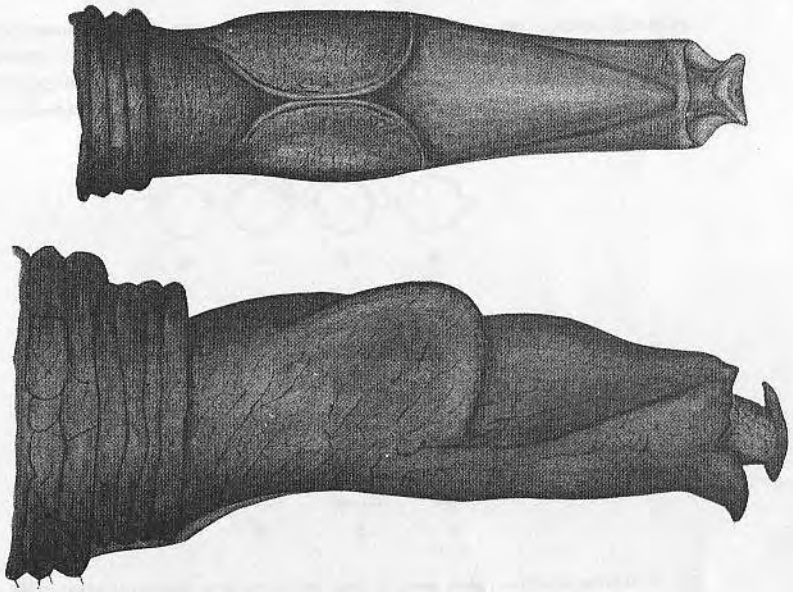
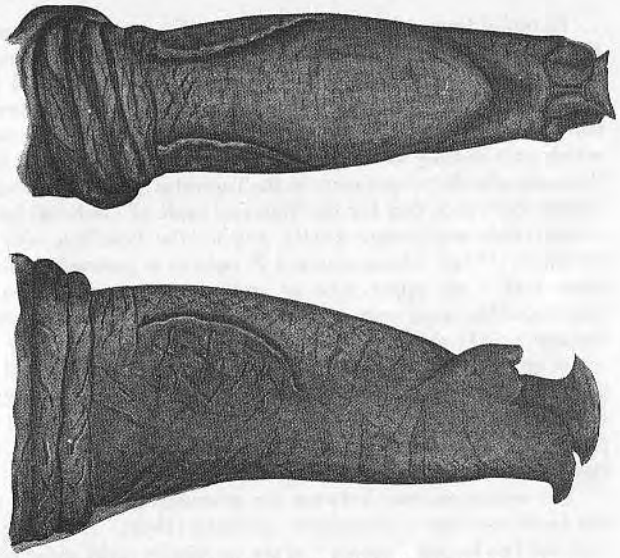
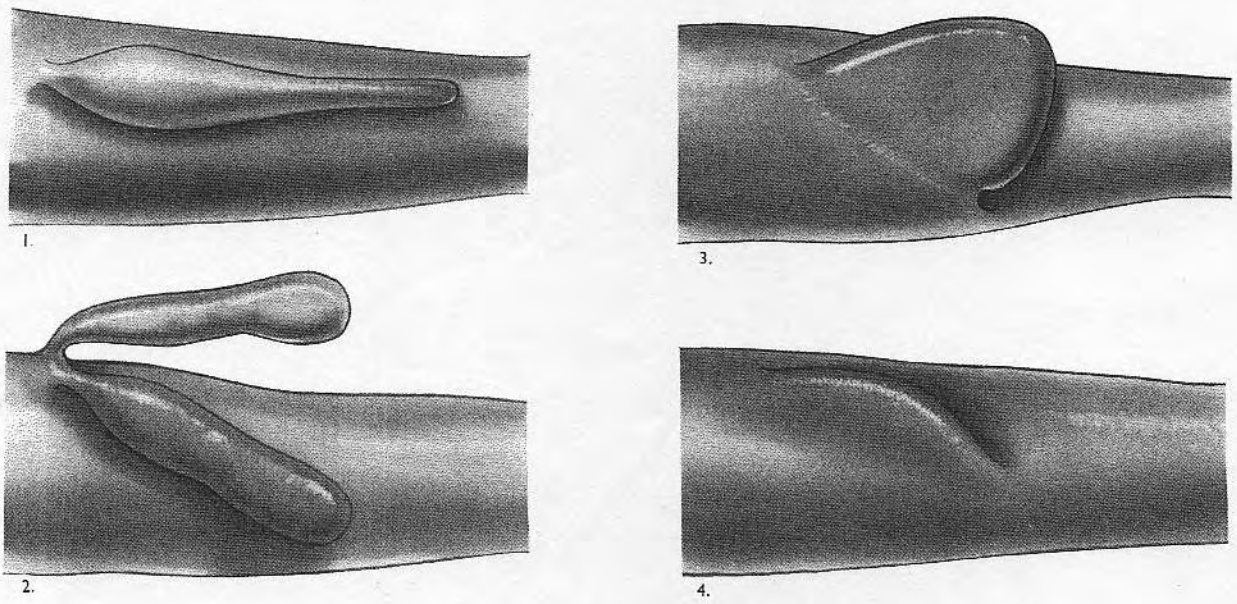


1. *Diceros bicornis*, juv. Dorsal and lateral aspects of glans penis.



2. *Ceratotherium simum*, juv. Dorsal and lateral aspects of glans penis.



The processus glandis in (1) *Rhinoceros*, (2) *Didermocerus*, (3) *Diceros*, (4) *Ceratotherium*.