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## Observations on rhinoceros tongue morphology

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(With 1 plate and 6 figures in the text)

The rhinoceros tongue is distinguished among perissodactyl organs by its sagittally divided intermolar eminence crowned by a dextral and a sinistral cluster of circumvallate papillae. These structures were originally noted in the Indian rhinoceros by Owen (1852) but have since remained unmentioned for this, or for any other rhinoceros form. They are here described for specimens of the Indian, African White and African Black rhinoceroses. The structural and functional nature of the intermolar eminence is established and this entity is distinguished from an hitherto unrecognized topographical component of the tongue, designated the *pars elliptica linguae*. The lingual morphology of the three rhinoceros forms is summarised and certain intergeneric differences are noted.

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### Introduction

The circumvallate papillae of perissodactyls, as of mammals generally, are the fewest, largest, most localized and most conspicuous of the lingual papillae and are situated upon an intermolar eminence of the tongue dorsum. Both the papillae and the eminence have been jointly utilized (Sonntag, 1925) as diagnostic criteria in perissodactyl taxonomy. For the Rhinocerotidae, however, information concerning these structures remains confined to their original brief mention by Owen (1852) in the Indian rhinoceros (*Rhinoceros unicornis*).

Therein Owen described the intermolar eminence as "a small protuberance on the upper surface [of the tongue] opposite the posterior grinders, divided by a longitudinal depression" and observed that "the large fossulate papillae are principally collected in a group of ten to twelve" on each moiety of the divided eminence. He left unmentioned the size, structure and precise mode of division of the eminence and much concerning the

external and internal anatomy of the tongue: his account therefore permits the erroneous inference that the intermolar eminence is an epithelial formation on the dorsum linguae. Owen's observations remained unsupplemented by subsequent report upon the lingual morphology of the Indian rhinoceros or indeed of any other rhinoceros form, so that they constituted the sole information regarding the Rhinocerotidae available to Sonntag (1922, 1925) during his taxonomic study of the perissodactyl tongue. Sonntag lacked rhinoceros study material and included all rhinoceroses under a single genus (*Rhinoceros*). His scheme of perissodactyl tongue classification was as follows:

- A. *Intermolar eminence high, medianly divided*  
 Circumvallate papillae in fields  
 Fungiform papillae absent  
 Lateral organ absent.....*Rhinoceros*
- B. *Intermolar eminence low, undivided*  
 (a) Circumvallate papillae two  
 Fungiform papillae present  
 Lateral organ absent.....*Equus*
- (b) Circumvallate papillae in V or rows  
 Fungiform papillae present  
 Lateral organ present .....*Tapirus*

This scheme is valid in its differentiation of the rhinoceros tongue from those of its congeners. Yet it uncritically attributes to all rhinoceros forms the data established for a single specimen of a single genus, fails to define one diagnostic criterion (intermolar eminence) and leaves unspecified the assessment of this structure as either "high" or "low". These defects, plus the reference to the occurrence of fungiform papillae on the intermolar eminence prompt a suspicion that Sonntag may have confused the true intermolar eminence with another obtrusive, but wholly separate, feature of the tongue dorsum. This is an hitherto unrecognized topographical component of the tongue—an elevated, marginated, indurated region of the dorsum linguae, rendered semi-discrete by a peripheral groove, and which bears the intermolar eminence proper upon its dorsum posteriorly. This specialized topographical tongue component is herein designated *pars elliptica linguae*, and the groove demarcating it superficially from the remainder of the tongue mass the *sulcus limitans*. In all rhinoceros forms this specialized *pars elliptica linguae* is exceptionally well developed and may aptly be termed "high": but its surface may manifest fungiform papillae which never occur on the smaller and topographically independent intermolar eminence. It is likely that in the ill-preserved non-rhinocerine perissodactyl tongue, wherein the intermolar eminence is less emphatically developed, tissue shrinkage and distortion may obscure the topographical distinction between intermolar eminence and *pars elliptica linguae*, occasioning confusion in their identification and consequent misinterpretation of tongue morphology.

Since in the Rhinocerotidae the nature of the intermolar eminence has remained undetermined, the topographical anatomy of the tongue undescribed and the circumvallate papillae uninvestigated, a separate study was undertaken of lingual morphology in the

Indian, the African White and the African Black rhinoceros. (Material representing the Javan and Sumatran rhinoceroses was unavailable for examination). This study involved a myological investigation of the tongue productive of evidence bearing upon the debated independence of the so-called intrinsic musculature, but dissection findings are referred to below insofar only as they confirm or explain the nature of the superficial characters and appearance of the tongue.

TABLE I

*Rhinoceros tongues: mensural data (cm) and relation of pars elliptica to whole organ expressed as a percentage of total tongue length and width. Young specimens marked with an asterisk*

Specimen	<i>R. unicornis</i>						<i>C. simum</i>				<i>D. bicornis</i>			
	R41		R45		R31		*R20		R162		R76		*R19	
Tongue, total length	55		54		54		30		58		47		27	
Tongue, posterior width	14		16		15		11		14		10		7.5	
Tongue, anterior width	10		12		12		9		12		8.5		—	
Tongue, apical width	14		14		14		—		—		—		—	
Pars elliptica, length	28		27		28		18		35		34		14.5	
Pars elliptica, posterior width	7		7		7		9		8		7		5	
Pars elliptica, anterior width	0.31		0.32		0.30		0.28		7.5		7		5	
Pars elliptica, % of tongue length	51%		50%		52%		60%		62%		72%		54%	
Pars elliptica, % of tongue width	50%		45%		47%		80%		60%		70%		70%	
Length (mm) intermolar eminence	100		105		110		110		116		90		48	
Width (mm) sagittal furrow	15		12		10		12		12		15		10	
No. circumvallate papillae	R	L	R	L	R	L	R	L	R	L	R	L	R	L
	10	11	11	10	12	11	12	17	11	12	12	12	22	21

### Material and methods

Anatomical examination was made of the tongue in the following rhinoceros specimens from the menagerie of the Zoological Society of London, excised organs being studied in the fresh and the formalinized state and appropriate measurements (Table I), photographs and drawings made: the tongue substance was dissected both to determine the myology of the organ and to account for certain of its surface features.

#### Indian rhinoceros (*Rhinoceros unicornis*)

Specimen R 41, Male, adult (20 years)	1941
Specimen R 45, Male, adult (15 years)	1945
Specimen R 21, Male, adult (18 years)	1964

#### African White rhinoceros (*Ceratotherium simum*)

Specimen R 20, Male, young (3 years)	1964
Specimen R 162, Female, adult (11–12 years)	1964
Specimen R 76, Female, adult (10 years)	1976

#### African Black rhinoceros (*Diceros bicornis*)

Specimen R 19, Female, young (2–3 years)	1960
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### Observations

For present descriptive purposes the rhinoceros tongue comprises the following topographical components:

1. pars apicalis linguae: the anterior, smaller, shorter, more mobile portion of the organ: dorso-ventrally compressed: lytta containing: anterior termination in free apex linguae: mucosa corium relatively thick.
2. corpus linguae: the larger, ventral part of the longer, thicker, posterior portion of the organ: continuous dorsally with, but demarcated from pars elliptica: mucosa laxly attached, corium unthickened.
3. pars elliptica linguae: the smaller, dorsal component of the posterior portion of the organ: elongately oval, elevated, margined: circumscribed peripherally by sulcus limitans: intermolar eminence on dorsum posteriorly: mucosa corium enormously thickened, indurated, adherent to subjacent musculature.
4. radix linguae: the fixed portion of the organ behind the circumvallate papillae: mucosa corium unthickened: submucosal lymphoid follicles sometimes present.

#### *On the Indian rhinoceros (*Rhinoceros unicornis*)*

##### *Specimen R 41*

The tongue is long (55 cm) and narrow (14 cm wide posteriorly). The pars apicalis (10 cm wide) is thin and dorso-ventrally compressed: it contains a well-developed, 130 mm long, lytta and terminates anteriorly in an expanded (14 cm wide) spatulate apex. The corpus linguae, tall, thick and laterally compressed, constitutes the posterior three-fifths or so of the tongue mass: dorsally it is continuous with a prominent semi-discrete pars elliptica but demarcated therefrom by a sulcus limitans. This pars elliptica (28 cm long, 7 cm wide) is elevated, oval in outline and covered with a thick, almost leathery mucosa, everywhere firmly adherent to the deeper tissues. On the dorsum of its posterior third stands an intermolar eminence, 100 mm long by 70 mm wide, which is remarkably hard and immovable: it is bisected by a sagittal 15 mm wide furrow, its dextral moiety being surrounded by a cluster of 10 circumvallate papillae, its sinistral moiety by a cluster of 11. Within each cluster the papillae lie in oblique convergent rows: the smallest are 3×4 mm diameter, the largest some 9×5.5 mm diameter: three are subdivided. Circumvallate papillae are confined to the eminence moieties, from which fungiform papillae are absent (Figs 1 and 2).

The mucosa on the sides and back of the corpus linguae is relatively thin and readily detachable, unlike the thick, opaque and uniformly fixed mucosa of the pars elliptica which defies ready removal. Filiform papillae form a close brush-work over most of the dorsum linguae (including the intermolar eminence): fungiform papillae occur on the forepart of the pars elliptica, on the dorsum generally and most plentifully on the tongue margins and apex: lenticular papillae are randomly distributed over the tongue dorsum: recurved conical papillae appear in parallel rows upon the radix linguae, succeeded by V-shaped rows of taller papillae occupying the epiglottic vallecula. A lingual "tonsil" is not discernible.

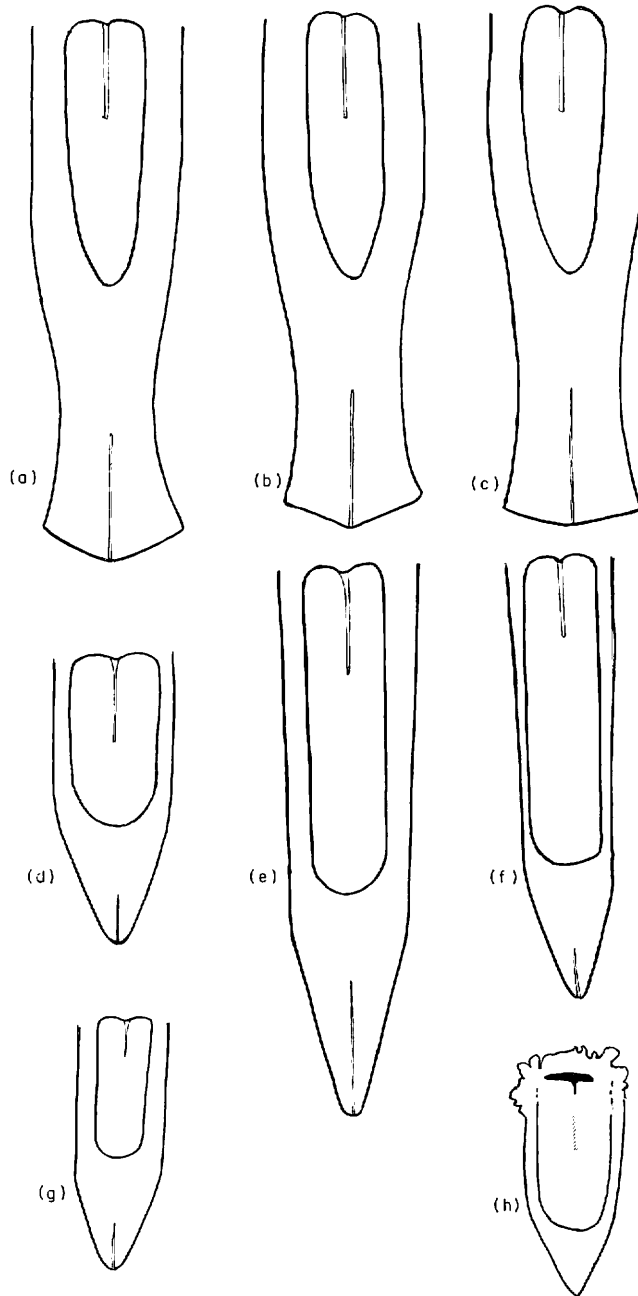


FIG. 1. Rhinoceros tongues in norma dorsalis: to indicate shape and relative proportions of lingual mass, pars elliptica, intermolar eminence and lytta. Explanation in text. Outlines (a), (b), (c), Indian rhinoceros specimens R41, R45, R21; (d), (e), (f), White rhinoceros specimens R20, R162, R76; (g), Black rhinoceros specimen R19; (h), Black rhinoceros tongue from Gordon Atlas, Rijksmuseum.

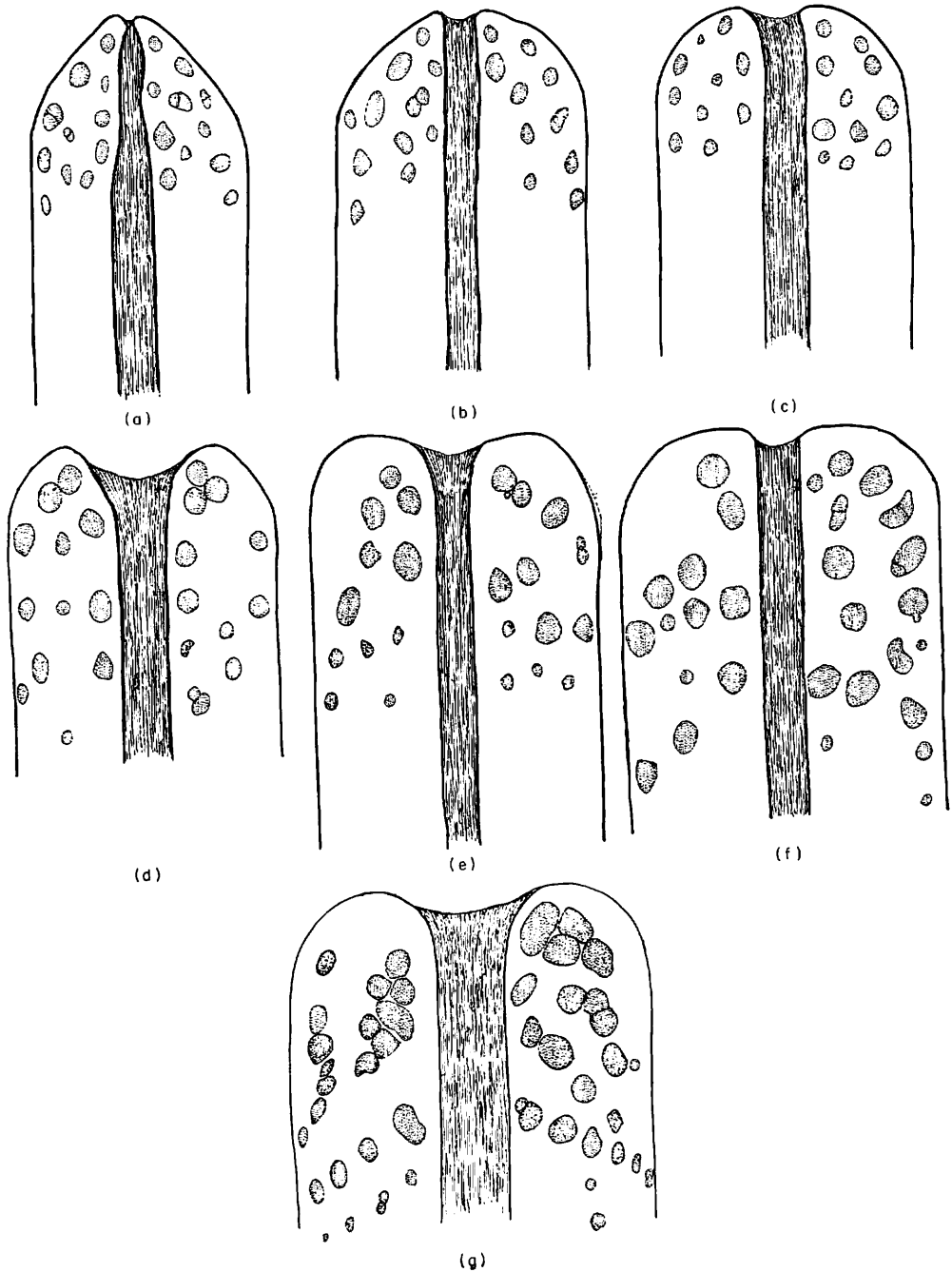


FIG. 2. Rhinoceros tongues showing distribution of circumvallate papillae on intermolar eminence. Semi-diagrammatic. (a), (b), (c), Indian rhinoceros; (d), (e), (f), White rhinoceros; (g) Black rhinoceros.

*Specimen R 45*

The tongue is long (54 cm) and narrow (16 cm wide posteriorly) and much like the preceding specimen in general features and proportions. The pars apicalis (12 cm wide) is relatively short and dorso-ventrally compressed: it contains a 150 mm long lytta and terminates anteriorly in an expanded (14 cm wide) spatulate apex (Fig. 1). The relatively longer, thicker, more bulky corpus linguae is laterally compressed and high standing: dorsally it is continuous with a prominent pars elliptica but is superficially demarcated therefrom by a sulcus limitans: its mucosa is unthickened and easily detachable and laterally renders visible a continuous submucosal layer of macroscopic mucous glands.

The pars elliptica, some 27 cm long and 7 cm wide is half the total length and width of the tongue: of oval outline, it is clothed with a thick, leathery, opaque mucosa, everywhere firmly attached to subjacent tissues and necessitating laborious dissection for its removal: posteriorly its dorsum presents an intermolar eminence, 105 mm long by some 70 mm wide, bisected sagittally by a 10–12 mm wide furrow. Each eminence moiety is surmounted by a cluster of circumvallate papillae, numbering 10 dextrally, 11 sinistrally: the papillae lie in irregularly longitudinal, convergent rows: the smallest are 4×4 mm diameter, the largest 9×5 mm diameter: one papilla is subdivided (Fig. 2).

Filiform papillae carpet the dorsum linguae (including the eminence): fungiform papillae occur somewhat sparsely on the anterior part of the pars elliptica and more numerous upon the pars apicalis and the tongue margins: conical papillae appear initially behind the intermolar eminence and spread thence into the vallecule.

*Specimen R 21*

The tongue is long (54 cm) and narrow (15 cm wide posteriorly) and closely resembles the foregoing specimens in features and configuration. The pars apicalis, 12 cm wide, and dorso-ventrally compressed, contains a 150 mm long lytta and terminates in an expanded (14 cm wide) spatulate apex (Fig. 1). The corpus linguae, thick and laterally compressed, is half the length of the whole tongue: dorsally it is continuous with, but superficially demarcated from, an oval, prominent pars elliptica, 28 cm long and 7 cm wide, that is, half as long and as wide as the entire tongue. Unlike the mucosa clothing the rest of the tongue that of the pars elliptica is tough, thick, opaque, uniformly adherent to the underlying substance of the tongue and removable with some difficulty only. Upon the posterior third of the pars elliptica dorsum stands a prominent intermolar eminence, 110 mm long by some 65 mm wide, an extremely hard, fixed protuberance, divided sagittally by a 10 mm wide furrow. Each eminence moiety is surmounted by a cluster of circumvallate papillae, numbering 12 dextrally, 11 sinistrally. These papillae lie in convergent longitudinal rows and vary in diameter between 3×3.5 mm and 9×5.5 mm; three show subdivision; circumvallate papillae do not occur elsewhere on the tongue.

Filiform papillae constitute a "pile" over the general tongue dorsum: fungiform papillae are most numerous upon the tongue margins and apex but occur also, though sparsely, upon the pars elliptica: lenticular papillae have a random distribution over the tongue dorsum: conical papillae are restricted to the radix linguae, whence they invade the vallecule in greater numbers and size. No recognizable lingual "tonsil" is developed.

*On the African White rhinoceros (Ceratotherium simum)*

*Specimen R 20*

The tongue is long (30 cm) and narrow (11 cm wide posteriorly). The shorter anterior portion (pars apicalis) is dorso-ventrally compressed, triangular in outline and narrows to a sharply rounded apex: it contains a short, slender lytta. The larger posterior portion (corpus linguae) is thick and laterally compressed; it is well demarcated by a sulcus limitans from a prominent pars elliptica, whose length (18 cm) and width (9 cm) are about half the respective dimensions of the whole tongue. The mucosa of the corpus and radix linguae is soft, relatively thin and easily detachable, that of the pars elliptica however is obtrusively hard, thick, opaque and everywhere firmly adherent to the subjacent tissues. On the posterior third of the pars elliptica rests a hard, immovable intermolar eminence, 110 mm long by 92 mm wide, which is divided by a 12 mm wide sagittal furrow into moieties surmounted by circumvallate papillae. These papillae are restricted to the eminence dorsum in a dextral cluster of 12 and a sinistral cluster of 17 (Plate I(a)), wherein they form convergent, discontinuous longitudinal rows: the smallest are some 3 × 3 mm diameter, the majority some 4 × 5 mm, the largest 6 × 6 mm: three show subdivision.

Closely packed filiform papillae render the general mucosa of the dorsum linguae hairy in appearance and silky of texture: fungiform papillae, absent from the intermolar eminence, are somewhat randomly distributed, most abundantly upon the tongue margins and apex: scattered simple (lenticular) papillae are encountered: conical papillae are restricted to the radix linguae, being small at first but increasing in size and number towards the vallecule.

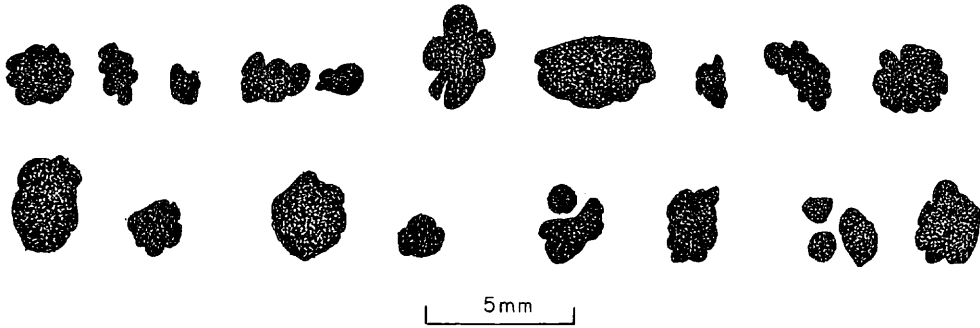
*Specimen R 162*

The tongue is long (58 cm) and narrow (14 cm wide posteriorly). The pars apicalis constitutes the anterior third of the organ, is dorso-ventrally compressed and contains a well-developed lytta: its triangular outline narrows rapidly anteriorly and terminates in an acuminate apex (Fig. 1). The corpus linguae is thick and laterally compressed: its almost vertical sides are clothed with an unthickened, laxly attached mucosa, through which, posteriorly, a submucosal layer of macroscopic glands is visible to the naked eye: dorsally it is continuous with, but externally demarcated from, an obtrusive pars elliptica. This last, 35 cm long and 8 cm in posterior width is half the length and width of the entire tongue: broadly oval in outline, it displays a distinct margin, most pronounced anteriorly and upon its posterior third an intermolar eminence. This eminence, some 115 mm long and 80 mm wide, is an extremely hard, fixed elevation, divided sagittally by a furrow 12 mm wide by 3 mm deep. The dorsum of each eminence moiety is crowned by a cluster of circumvallate papillae, 11 dextrally, 12 sinistrally, disposed in discontinuous longitudinal rows (Fig. 2): such papillae are confined to the eminence, whence fungiform papillae are absent.

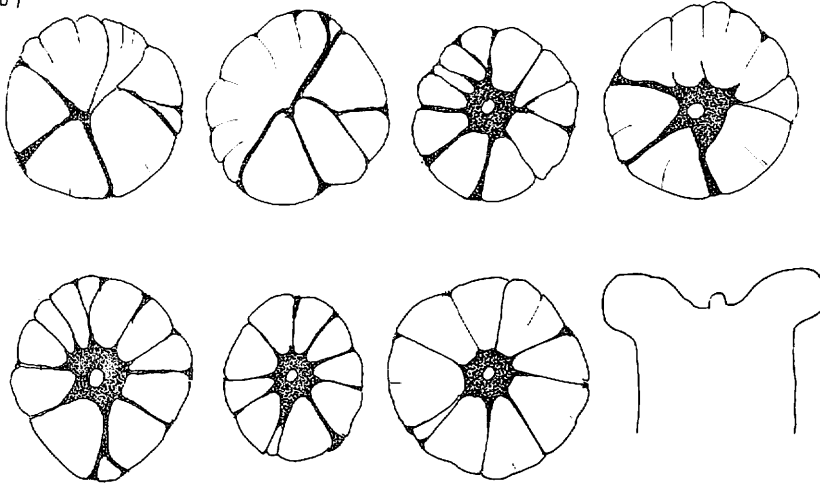
The general mucosa of the dorsum linguae is densely matted by filiform papillae: it presents scattered lenticular papillae and randomly distributed fungiform papillae, concentrated particularly upon the tongue margins and the pars apicalis: behind the intermolar eminence small conical papillae appear in parallel rows and taller, recurved, papillae of the same variety cover the radix linguae and the parieties of the epiglottic vallecule in serried rows. There is no development of submucosal lymphoid follicles in the radix region.



(a)



(b)



(c)

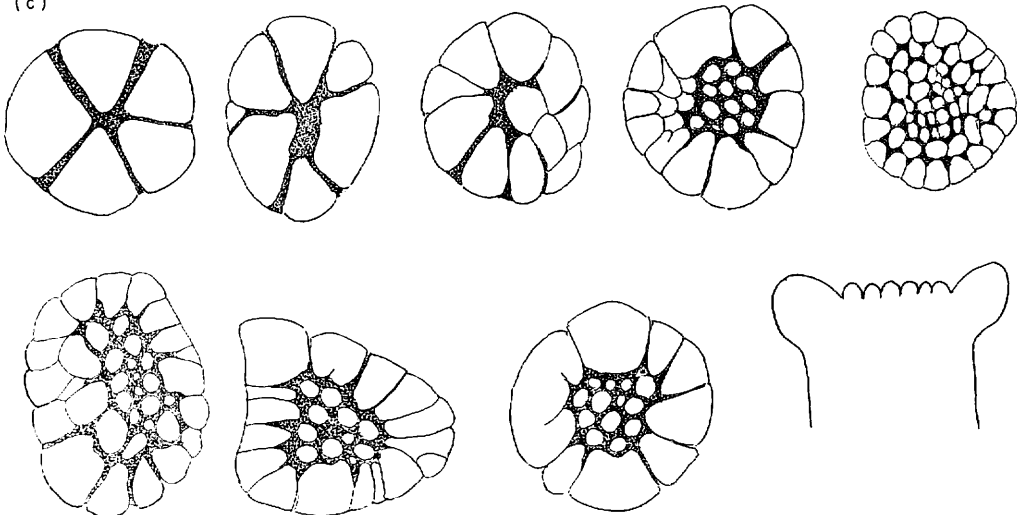


FIG. 3. Rhinoceros circumvallate papillae. Showing (a) variation in papilla size and outline, (b) capitular surface features in *Ceratotherium* papillae, (c) capitular surface features in *Diceros* papillae. Description in text.

*Specimen R 76*

The tongue is long (47.5 cm) and narrow, five times as long as wide. The pars apicalis (13.5 cm long) constitutes its anterior third: of dorso-ventrally compressed subconical shape and triangular outline it contains an 80 mm long lytta and tapers rapidly to an acuminate apex (Fig. 1). The corpus linguae (34 cm long), tall, thick and laterally compressed, constitutes the ventral posterior two-thirds of the tongue mass and continues dorsally into a prominent, well demarcated subdistrict, the pars elliptica, some three-quarters the total length and width of the organ. This elliptical region is of almost parallelogram outline, with prominent margin and extremities, is markedly convex and projects notably above the adjacent tongue mass, demarcated therefrom by an emphatic sulcus limitans, which undercuts its anterior end: on its posterior third stands a sagittally divided intermolar eminence.

This last is a hard, sessile protuberance, 90 mm long and 75 mm wide, divided into symmetrical moieties by a 12–15 mm wide median longitudinal furrow: each of the moieties is surmounted by a cluster of 12 circumvallate papillae, arranged in convergent discontinuous longitudinal rows (Fig. 2), and conspicuous against the filiform papillary "pile" of the eminence mucosa. The circumvallate papillae are confined to the eminence: the smallest are 4 × 4 mm diameter, the largest 7 × 5 mm: their free flattish surfaces display a typical central dimpling, radial grooving and marginal crenation (Fig. 3).

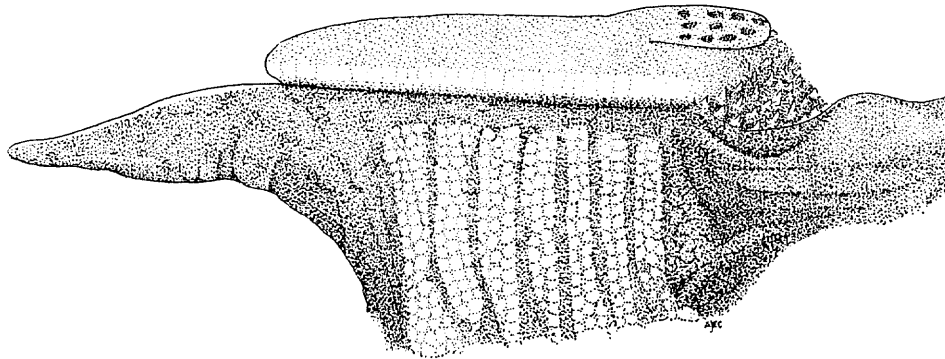
The mucous membrane clothing the radix and corpus linguae is relatively thin, un-wrinkled, readily detachable and semitransparent: over the pars elliptica it is obtrusively thick, opaque and leather-like in consistency and is everywhere inseparable from the subjacent musculature. Filiform papillae form a dense matting over most of the dorsum linguae: fungiform papillae occur on the tongue margins and apex and more sparsely elsewhere: conical papillae form low parallel rows upon the radix linguae and their larger-sized fellows abound throughout the retrolingual region.

*On the African Black rhinoceros (Diceros bicornis)**Specimen R 19*

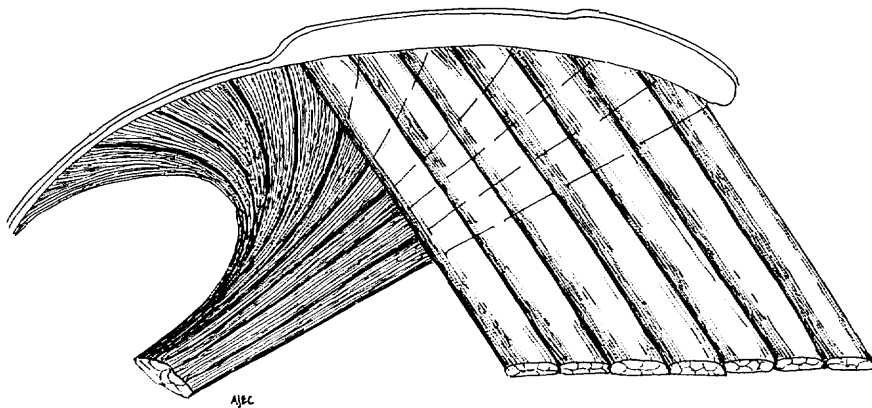
This young specimen is exceptional in the present series of tongues for its unusually large complement of circumvallate papillae: in all other respects it conforms to the canon of rhinoceros lingual morphology (Fig. 1). The tongue is long (27 cm) and narrow (7.5 cm wide posteriorly). The pars apicalis, 11 cm long and 5 cm wide posteriorly, is dorso-ventrally compressed and contains a lytta: its triangular outline narrows rapidly to an acuminate apex: its mucosa, moderately thick and firmly adherent, shows a dense dorsal covering of filiform papillae and an irregular marginal arrangement of fungiform papillae. The corpus linguae, 16 cm long and 7.5 cm wide, is thick, laterally compressed and clothed with a thin mucosa, rendered cobblestone in appearance by a submucosal layer of macroscopic mucous glands: dorsally the corpus is continuous with an emphatic pars elliptica but demarcated superficially therefrom by a pronounced sulcus limitans. The pars elliptica, 14.5 cm long and 5 cm wide, is half the tongue length and three-quarters the tongue width: of elongated oval outline, it is everywhere convex and elevated above the remainder of the tongue mass: its peripheral margin is particularly prominent anteriorly, where undercut by the sulcus limitans (Fig. 4): its mucosa is thick, indurated

and leather-like in consistency, firmly adherent to the subjacent musculature and presenting posteriorly a prominent intermolar eminence.

This last is an extremely hard, fixed mass, some 48 mm long and 50 mm wide, divided sagittally by a furrow 8–10 mm wide into moieties individually surmounted by a cluster



(a)



(b)

FIG. 4. Rhinoceros tongue (a) in norma lateralis showing pars elliptica, sulcus limitans, intermolar eminence, submucosal gland layer (b) dissected to show insertion of genioglossus and hyoglossus fasciculi into corium of pars elliptica mucosa.

of circumvallate papillae. The dextral cluster comprises 22 papillae, the sinistral cluster 21: the papillae, disposed in oblique rows, range in diameter from  $3 \times 2$  mm to  $6 \times 4.5$  mm: round or oval or polygonal in outline (Plate 1(b)) they display the central dimpling, radial sulcation and marginal crenation observable in other rhinoceros forms.

Lenticular papillae occur sporadically over the dorsum and margins of the tongue; filiform papilla form a dense matting over the dorsum; fungiform papillae appear upon the tongue apex and margins and are relatively large and numerous upon the pars elliptica

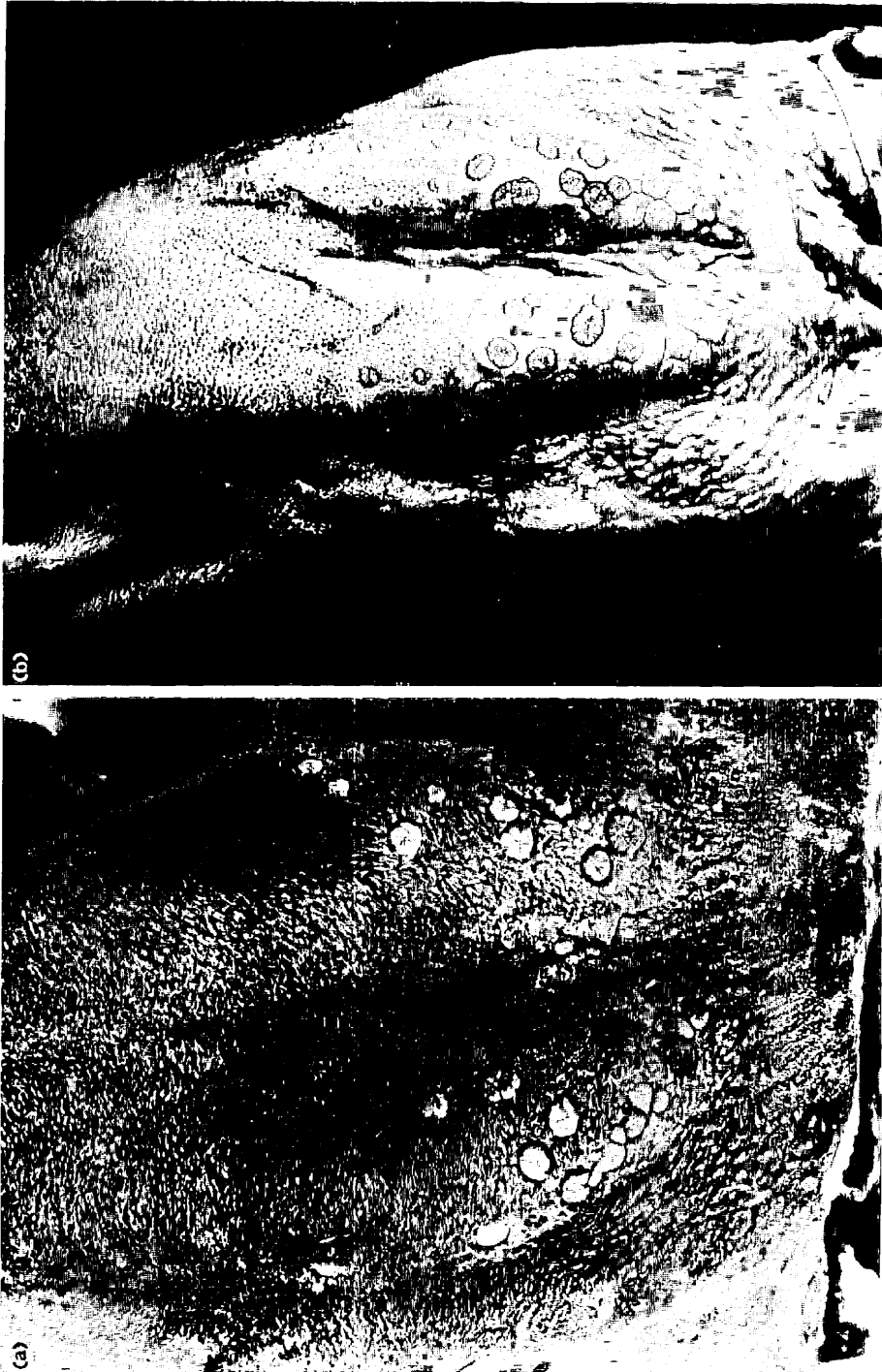


PLATE I. Rhinoceros circumvallate papillae *in situ*. (a) *Ceratotherium simum* (specimen R20). (b) *Diceros bicornis* (specimen R19).

immediately anterior to the intermolar eminence; small conical papillae form parallel rows upon the radix linguae, and larger papillae of the same variety clothe the walls of the vallecule. A lingual "tonsil" is not present, owing doubtless to the relatively large size of the faucial tonsil which extends caudally from the vallecular region into the sinus pyriformis. In the absence both of additional *Diceros* material and of any published account of *Diceros* splanchnology, reference may be pertinent to certain unpublished figures of the tongue of this rhinoceros form which are embodied in the 18th century Gordon Atlas preserved in the Rijksmuseum, Amsterdam. This Atlas contains an illustrated manuscript account, by Robert Jacob Gordon, of the external features and of certain of the viscera of an adult male African Black rhinoceros, killed 2 November 1778, at the Gamka River, Cape Province, South Africa. This unpublished and partial account of *Diceros* morphology is of historical interest as representing the earliest so far known attempt at the serious investigation of rhinoceros anatomy. The account itself was utilized by the early 19th century French naturalists and is the basis of their *Rhinoceros gordonii*. The illustrations of the viscera (tongue, liver, intestine, eye) which accompany the manuscript text are executed with fidelity to nature and were obviously prepared soon after the animal's death: those of the tongue and liver agree with drawings of these organs made by the present writer from other *Diceros* specimens.

This Gordon Atlas account contains two figures of the *Diceros* tongue showing the ventral and dorsal aspects of the same organ. The ventral view shows parallel, paramedian mucosal ridges indicating clearly the submucosal presence of a well-developed *lytta*. The dorsal view is more informative and depicts clearly the triangular outline and acuminate tip of the pars apicalis linguae, the relative size, shape and proportions of the corpus linguae, the presence of a large, prominent, marginated pars elliptica (some 70% the tongue length and 80% the tongue width) and, less distinctly, a sagittally furrowed intermolar eminence (Fig. 1). Thus in lingual configuration and morphology there is remarkable agreement between the 18th century adult male animal of the Gordon Atlas and the present young *Diceros* specimen (R 19).

#### *The circumvallate papillae*

In all rhinoceros specimens presently examined the circumvallate papillae are topographically confined to two clusters, a dextral and a sinistral, upon the corresponding moieties of the intermolar eminence: the eminence itself is prominent and invariably divided sagittally by a shallow furrow. This particular papillary-eminence arrangement is peculiar to the rhinoceros tongue among its perissodactyl congeners. The pale flesh-tinted papillae of the clusters contrast with their darker background of filiform papillae and are disposed in discontinuous longitudinal or oblique rows, convergent posteriorly.

In the *Rhinoceros unicornis* specimens the unilateral papilla count is remarkably constant at 10-12, in agreement with Owen's (1852) original findings: in the *Ceratotherium* specimens the count is similar save for an exceptional sinistral increase to 17 in one young individual. In the sole *Diceros* tongue available, the circumvallate papillae are more numerous, the dextral count being 22, the sinistral count 21. This single finding does not, however, suffice for assessment of the canonical generic complement of such papillae, for which further specimens require examination.

In all three rhinoceros forms studied (*Rhinoceros*, *Ceratotherium*, *Diceros*) the circumvallate papillae are broadly similar in shape and features. The individual papilla is of

flat-topped mushroom configuration, with stem encircled by the customary sulcus (fossula circularis) and rampart (vallum). The flattish expanded head is usually round or oval but occasionally polygonal in outline and projects but minimally above the general mucosa surface; in the smallest papillae its diameter is some  $3 \times 4$  mm, in the largest papillae  $9 \times 5.5$  mm. The virtually flat capitular free surface presents a central fovea, whence a series of sulci radiate to its periphery, which they severally indent, thus crenating the capitular margin (Fig. 3). The papilla head is thus sculpted into a series of radial segments, each sufficiently convex as to appear tuberculate under the microscope, and its subdivision may ensue from the precocious development of one such segment or more. Details of the capitular surface configuration differ somewhat in the three genera. Thus in *Rhinoceros* the central fovea is a simple shallow depression circumscribed by the contiguous apices of the more or less triangular peripheral segments of the papilla head, an arrangement encountered also in *Ceratotherium* and, more infrequently, in *Diceros*. In *Ceratotherium* the foveal area is relatively small and bears a single papilliform elevation surrounded by the larger capitular peripheral segments. In *Diceros* the foveal area is relatively large and is occupied by a series of small but variously sized papilliform elevations, which, with the larger peripheral segments of the papilla head, confer thereon a cobblestone appearance which tends to obscure its underlying radial subdivision (Fig. 3).

(Microscopical search was not made for the taste buds invariably associated with the circumvallate papillae, these gustatory end organs being presumed to be present in their customary situations upon the walls of the fossulae circulares).

The other varieties of lingual papillae encountered during the present study are irrelevant to considerations of perissodactyl taxonomy and merit no more than passing mention. In all the rhinoceros forms examined filiform papillae invest most of the tongue dorsum with a dense "pile"; fungiform papillae are randomly scattered thereon (including the dorsum of the pars elliptica) but are more numerous implanted upon the margins and apex of the tongue: lenticular or simple papillae are irregularly distributed; conical papillae are confined to the radix linguae, appearing first in low parallel rows but rapidly succeeded by rows of taller, recurved papillae on the walls and floor of the epiglottic vallecula.

#### *The intermolar eminence*

The topographical distinction already indicated between the intermolar eminence and the pars elliptica linguae is plainly apparent in the undissected tongue and is expressed by the size and mutual association of the two anatomical entities. Thus whilst the eminence averages in length and width some  $100 \times 75$  mm, the pars elliptica averages half or more of the total length and width of the tongue: whereas the eminence is positioned opposite the posterior molar teeth, the pars elliptica lies opposite all the molar and the posterior premolar teeth: the smaller eminence is a nodular formation on the dorsum of the larger pars elliptica. This anatomical distinction merits formal descriptive recognition. Such recognition in no way however contradicts the findings of dissection, which demonstrate the two entities to share a common constitutional basis, namely, the collagenous specialization of the corium of the pars elliptica mucosa, a structural modification essential to the effective operation of the lingual musculature.

Owen (1852) seemingly dismissed the intermolar eminence as a mere incidental, presumably epithelial, feature of the tongue exterior, and considered neither its intrinsic

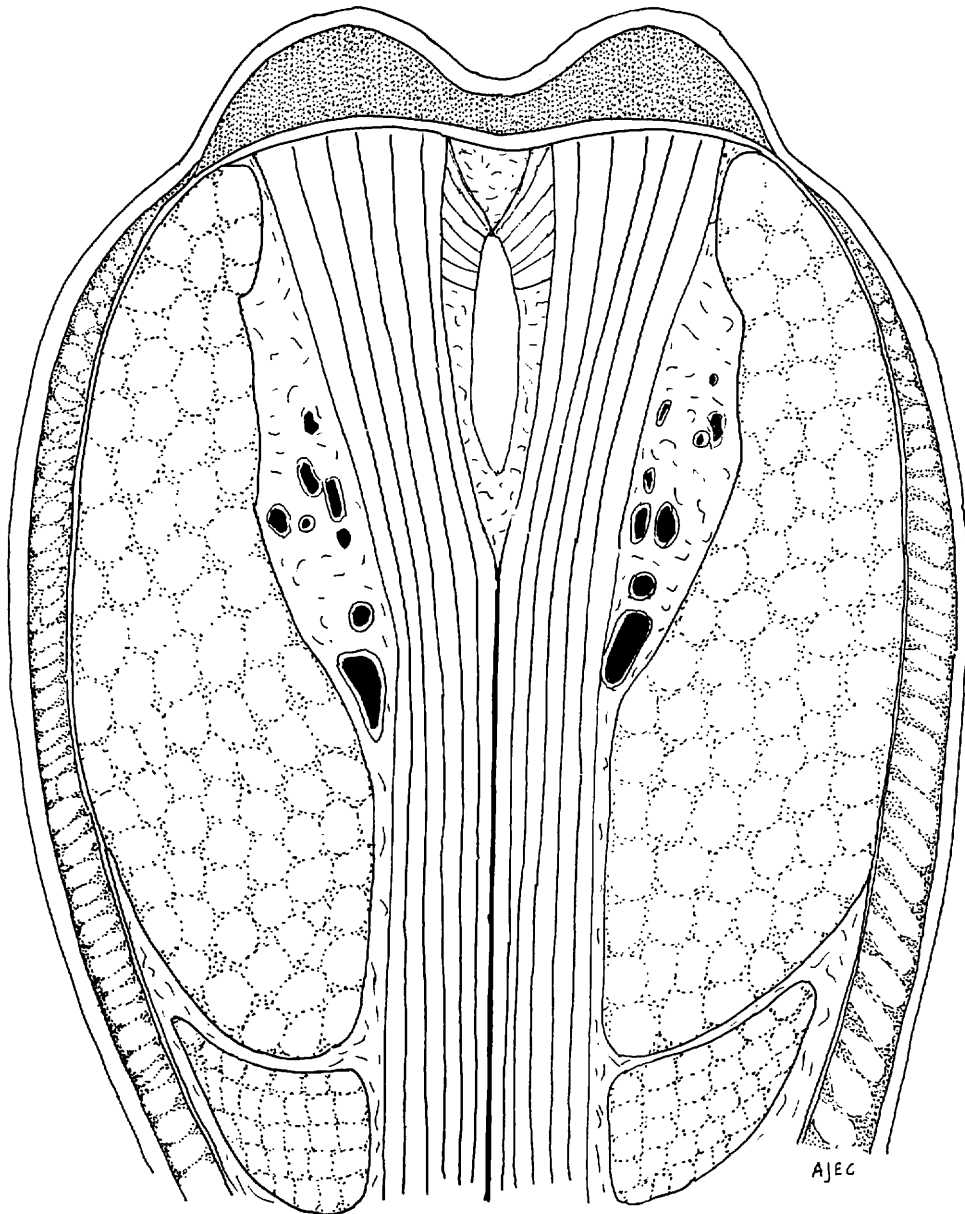


FIG. 5. Rhinoceros (*Ceratotherium*) tongue in coronal section. To show muscles (genioglossus paramedianly, hyoglossus laterally, styloglossus infero-laterally, U-shaped transversus-fasciculus from lingual septum), intermolar eminence, (stippled), subjacent galea tendinea continuous with hyoglossus fascia and mucous gland layer between hyoglossus fascia and mucosa. Details in text.

nature nor its differentiation from any pars elliptica: nothing therefore has been recorded to date concerning either intermolar eminence structure or the factors responsible for the development of a topographical pars elliptica linguae. These matters are therefore considered below.

Palpation alone suffices to establish the non-epithelial nature of the intermolar eminence, which thereby proves to be an intensely hard, unyielding, immobile lump, inseparable from the underlying tissues. Subsequent dissection confirms these findings and shows them to result from a basic connexion between the eminence and the lingual fibromuscular apparatus, indeed demonstrates the eminence to be simply a localized nodular enlargement of the specialized corium of the pars elliptica mucosa. Coronal sections of the tongue (Fig. 5) illustrate unequivocally the essentially collagenous nature of the eminence and its relationship to the subjacent musculature and to the superjacent epithelium. Such sections show clearly the mutual disposition of the several tongue components—the uniformly thick epithelial layer of the mucosa, the lateral submucosal layer of mucous glands, the posterior partial septum linguae, the sulcus limitans, the muscle fasciculi, their aponeurotic helmet of deep fascia and the collagenous core of the intermolar eminence.

The rhinoceros lingual mucosa comprises the customary two strata, *viz.*, a superficial epithelial stratum and a deep, supportive, connective tissue stratum or corium. Generally, the mucosa thickness averages some 3.5 mm, the epithelial layer accounting for 2.5 mm, the corium for about 1 mm. Upon the sides, root and under-surface of the tongue the mucosa maintains its average thickness and presents as a thin, wrinkled, semi-transparent, loosely attached membrane: upon the pars apicalis dorsum it is thicker, opaque and firmly attached to the musculature: over the pars elliptica it is stiff, thick and indurated, leather-like in consistency and inseparable from the underlying musculature.

Such local variation in mucosa thickness and consistency reflects a corresponding variation in mucosa structure, which since epithelial thickness remains everywhere constant, involves alteration in thickness of the corium.

Corium thickness and consistency are determined by the mechanics of muscle insertion. The inserting fasciculi of the strong and active tongue muscles require a sufficiently stable platform of attachment which the corium alone is capable of providing. Hence the greater the local incidence of inserting fasciculi the thicker, firmer, more rigid does the corium become. In the rhinoceros tongue this physiological reaction of the corium attains its apotheosis in that of the pars elliptica mucosa. For into the corium here insert the vast majority of the tongue muscle fasciculi, namely all the fasciculi of *m. hyoglossus* and the longest and largest fasciculi of *m. genioglossus*. The pars elliptica corium adapts to the requirements of such maximal fasciculus insertion by thickening into a substantial plate of collagen. Since the genioglossus and hyoglossus muscles are the most powerful and antagonistic of all the tongue muscles, and since their longest and strongest fasciculi insert into the hind end of this collagen plate, special provision is required for their attachment thereto, and this is made by the development upon, and from, that plate of a dorsal nodule—the intermolar eminence.

The insertion of the genioglossus and hyoglossus muscles into the specialized corium and eminence of the pars elliptica mucosa is effected by a multitude of minute, thread-like and immensely strong tendons from their component fasciculi. These filiform tendons traverse the deep fascia (epimysium) of the tongue dorsum to enter the undersurface of the corium, wherein they terminate. Prior, however, to such termination they interweave



in complicated fashion with and upon the dorsal deep fascia, transforming it into an exceptionally strong, dense, almost aponeurotic sheet which covers the muscle surface as a distinctive helmet (galea tendinea). The fascicular tendons and stroma, the galea tendinea, the specialized corium of the pars elliptica and the intermolar eminence are in direct structural continuity: collectively they constitute a collagenous framework essential to the mechanics of tongue activity and designed to ensure maximal muscle efficiency in effecting such activity.

Intrinsically therefore the intermolar eminence is a localized ovoid nodular enlargement of the plate-like collagenous corium of the pars elliptica mucosa. Inferiorly it is continuous with the galea tendinea and the entrant tendons of the muscle fasciculi: superiorly it is invested by the lingual epithelium and is sagittally divided by a shallow furrow. Each of its moieties averages some 100 mm in length, 25 mm in width and 11 mm in thickness, the corium of the intervening furrow being some 4 mm thick. The filiform tendons of the hyoglossus, genioglossus and transversus fasciculi are directly traceable into its substance.

#### *The pars elliptica linguae*

Sufficient indication has been given above of the external and internal features of this specialized (elevated, marginated, demarcated, indurated) dorsal region of the tongue as to obviate further justification of its claim to topographical and nomenclatorial independence. Its differentiation from the remainder of the tongue is due to its constituting the insertion area for the largest, strongest and most active of the tongue muscles, from which primary anatomical arrangement stem all its peculiarities of feature and physical property. The key thereto is the obligatory transformation of its mucosa corium into a collagenous plate designed to meet the mechanical demands of intensive muscle insertion. In this respect the pars elliptica linguae illustrates admirably the Hunterian doctrine of the subservience of anatomical form to the requirements of functional activity.

#### Commentary

The *Rhinoceros*, *Ceratotherium* and *Diceros* tongues examined manifest a commonalty of morphological characters. In all the tongue is topographically divisible into pars apicalis, corpus linguae, pars elliptica and radix linguae and displays a prominent, anatomically distinct, intermolar eminence. This last rises from the hind end of the pars elliptica, is divided sagittally by a shallow furrow, and each of its moieties is crowned by a collection of circumvallate papillae. In the nature of its intermolar eminence and the relation thereto of the circumvallate papillae the rhinoceros tongue is distinctive among perissodactyl organs.

The pars apicalis is dorso-ventrally compressed, contains a litta and its mucosa corium is moderately thick: the corpus linguae is laterally compressed with an unthickened mucosa corium through which submucosal glands are discernible: the obtrusively elevated and marginated pars elliptica is ventrally demarcated by a circumferential sulcus limitans, bears posteriorly the intermolar eminence and is characterized by an indurated mucosa resulting from a collagenous corium. A complete septum linguae is not developed and a distinct lingual "tonsil" is wanting.

The general dorsal mucosa is rendered pseudo-hairy in appearance and silky in texture from its development of innumerable filiform papillae: it shows scattered lenticular

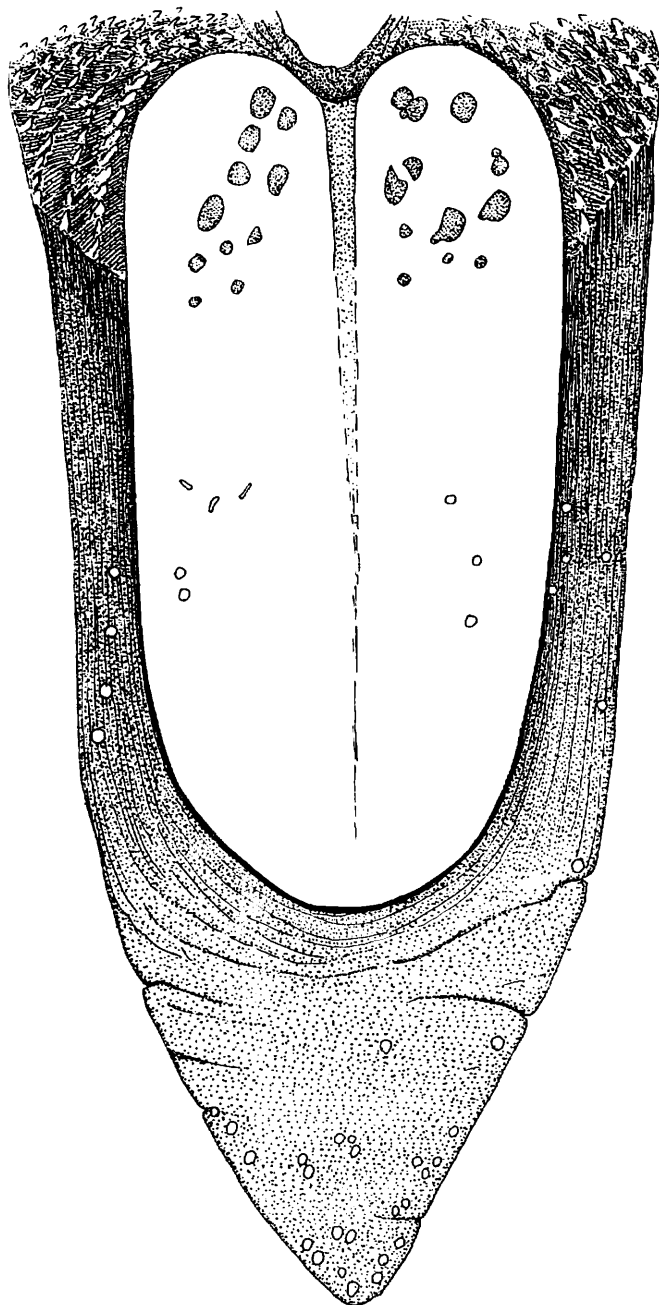


FIG. 6. White rhinoceros (*Ceratotherium simum*). juv. Undissected tongue in norma dorsalis, showing pars elliptica, intermolar eminence and papillae. Semi-diagrammatic.

papillae and an irregular distribution of fungiform papillae, mainly over the apical and marginal regions: it exhibits dextral and sinistral clusters of circumvallate papillae upon the intermolar eminence and parallel rows of low conical papillae immediately behind that eminence.

Intergeneric differences lie in the configuration of the apex linguae and in the relative proportions of pars elliptica and total tongue mass. Thus in *Rhinoceros* the tongue apex is expanded and spatulate, in *Ceratotherium* and *Diceros* of triangular outline narrowing to an acuminate tip. In *Rhinoceros* the pars elliptica is some 50% the tongue length and width, in *Ceratotherium* (Fig. 6) some 70% and in (a single specimen of) *Diceros* 50% that length and 70% that width.

The differentiation of the pars elliptica as a topographical component of the tongue results from the arrangement and insertion pattern of the fasciculi of the genioglossus and hyoglossus muscles. A minority of the m. genioglossus fasciculi insert with those of m. styloglossus into the pars apicalis mucosa but the remaining more powerful fasciculi, together with the equally powerful fasciculi of the m. hyoglossus, insert into the mucosa corium of this particular area of the dorsum linguae. The fasciculi insert by a multitude of individual filiform tendons for the reception of which the mucosa corium is compelled to thicken and strengthen, so that it becomes modified into a plate of collagen, inseparable from the underlying musculature and leather-like in consistency. Posteriorly this collagenous plate enlarges dorsally as a nodular elevation, the intermolar eminence. It is this region of the plate which affords insertion to the longest and strongest fasciculi of the mm. genioglossus and hyoglossus. The intermolar eminence is clearly the physiological response to the insertion of such fasciculi and constitutes a common insertion node and fixation point for these two mutually antagonistic muscles. It may itself receive further stabilization from certain U-shaped fasciculi of the m. transversus which apparently arise from the local partial septum linguae and insert into the eminence from below.

The relatively fixed position of the intermolar eminence no less than its prominence, ensure its almost continuous apposition with the undersurface of the palate, with which, during mastication, it must make repetitive contact, and between eminence and palate the triturated food material suffers momentary arrest prior to deglutition. Hence the epithelial stratum of the mucosa clothing the eminence provides the optimum anatomical arena for the distribution of the taste-buds and precisely here accordingly are disposed the taste-bud bearing circumvallate papillae. The eminence thus subserves a primary myo-mechanical function and a secondary gustatory function.

The circumvallate papillae are topographically restricted to the intermolar eminence: their number is remarkably similar and constant in *Rhinoceros unicornis* and *Ceratotherium simum*, but is doubled bilaterally in the single *Diceros bicornis* specimen examined. The canonical complement of such papillae in *Diceros* remains unknown, pending study of additional material. In all rhinoceros genera the circumvallate papillae are grouped in a dextral and a sinistral cluster upon the corresponding moieties of the intermolar eminence, whereon they lie in irregular longitudinal or oblique rows; in all forms they show a corresponding variation in size and a comparable sculpting of their capitular free surface.

### Summary

Certain particulars of tongue morphology are reported for specimens of *Rhinoceros unicornis*, *Ceratotherium simum* and *Diceros bicornis*. These three genera display a common

lingual topography which includes an hitherto unrecognized specialized component, here described and named *pars elliptica linguae*.

The rhinoceros tongue is characterized by a prominent, sagittally divided, intermolar eminence, with each eminence moiety surmounted by a cluster of circumvallate papillae. The intermolar eminence is shown to be a nodular enlargement of the collagenous corium of the *pars elliptica mucosa*: its function is indicated. The incidence, arrangement and features of the circumvallate papillae are described and the functional association of the papillae with the intermolar eminence is indicated.

In *Rhinoceros* the apex linguae is spatulate and the *pars elliptica linguae* relatively small: in *Ceratotherium* and *Diceros* the apex is acuminate and the *pars elliptica* relatively larger.

Present observations on *Rhinoceros unicornis* confirm and amplify Owen's (1852) original findings and vindicate Sonntag's (1925) taxonomic assessment of the rhinoceros tongue. Observations on *Ceratotherium simum* and *Diceros bicornis* are new to the published record.

Gratitude is hereby tendered to the Council of the Zoological Society of London for the gift of the material forming the basis of the present observations, to the Society's Senior Veterinary Officer (Mr D. M. Jones) and its Curator of Whipsnade Park (Mr V. J. A. Manton) for facilitating its procurement and preservation, to Mr L. C. Rookmaaker for photocopies of the Gordon figures of *Diceros* viscera, and to Mr Michael Lyster for the excellent photographs of the circumvallate papillae.

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