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The rhinoceros faucial and laryngopharyngeal tonsils

A. J. E. CAVE
Zoological Society of London

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(With 1 plate and 16 figures in the text)

The literature of mammalian splanchnology contains but a single reference to the tonsillar morphology of the Rhinocerotidae, viz. Owen's (1852) cursory description of the faucial (palatine) tonsil in an Indian rhinoceros (*Rhinoceros unicornis*). Herein a fuller account is given of the tonsillar formations present in the lateral food channel of another Indian rhinoceros specimen and of specimens of the Sumatran rhinoceros (*Didermocerus sumatrensis*), the African White rhinoceros (*Ceratotherium simum*) and the African Black rhinoceros (*Diceros bicornis*). Attention is drawn to the invariable presence of tonsillar tissue in the rhinoceros pyriform fossa and to its frequent manifestation therein as an anatomically discrete and hitherto unrecognized organ, the laryngopharyngeal tonsil. This structure, functionally supplementary to the faucial tonsil, would appear to develop independently from the lympho-thymic primordium of the embryonal third pharyngeal pouch. Its anatomy is described and its morphological significance is discussed.

Contents

Introduction

Since mammalian body defence against antigen invasion depends largely upon lymphocyte activity, body regions specially vulnerable to such invasion are liberally equipped with defensive lymphoid tissue. Hence every segment of the alimentary canal is provided with its micro- or macroscopic complement of such tissue, which is morphologically separable into heterogeneous and homogeneous formations.

The heterogeneous lymphoid formations subserve local functional requirements: they are consequently multiple, histologically simple structures (essentially mechanical aggregations of unit lymphoid follicles) which vary widely in configuration and topography and which range in magnitude from the microscopic subepithelial patch to the obtrusively

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macroscopic agminated follicle. The homogeneous lymphoid formations subserve the general body requirements and are constant in number and situation: histologically more complex structures, they develop from specific and similar anlagen in the embryonal pharynx: they are represented by the faucial tonsil from the second pharyngeal pouch and the thymus gland from the third.

The embryological development of the faucial tonsil involves two distinct and dissimilar components—a primary diverticulum from the dorsal angle of the second pharyngeal pouch and a secondary lymphoid element, of disputed provenance, which becomes intimately associated therewith (Grosser, 1912; Frazer, 1931). The gross appearance of the mature tonsil is largely determined by the quantity of lymphoid tissue developed and the precise relationship of this tissue to the primordial diverticulum—hence a considerable diversity of tonsil configuration among mammals (Hett & Butterfield, 1909). A minimal lymphoid development may leave the primitive diverticulum virtually unaltered and readily recognizable by its patent ostium within the recesses tonsillaris: a maximal lymphoid development may reduce the diverticulum to a mere intratonsillar fossa or may obliterate certain evidence of its presence. Because the maximally lymphoid variety of faucial tonsil is associated with the human subject and is thus the most familiar variety of tonsil, it is commonly but erroneously considered to be "well developed" and is not infrequently assumed to represent the mammalian norm.

Whatever its precise macroscopic appearance, however, the mammalian faucial tonsil, like the closely allied thymus gland, is a canonical component of the body machinery. It occupies an invariable and specific site (the recessus tonsillaris) between the palatoglossal and palatopharyngeal arches of the isthmus faucium.

The rhinoceros faucial tonsil proves to be a relatively large, notably compact and conventionally "well developed" organ (markedly dissimilar from its equid counterpart) which protrudes medially from the tonsillar recess into the whole, or the most part, of the vallecula. Its embryology remains uninvestigated directly, but its total anatomy affords convincing if indirect evidence of its development in orthodox mammalian fashion from the second pouch of the embryonal pharynx.

The pioneer investigations of Indian rhinoceros anatomy comprise the published accounts of Parsons (1743) and Leigh Thomas (1801) and the unpublished memoir of Vicq D'Azyr (1793), duly summarized by Gervais & Gervais (1875). None of these early accounts made mention of the faucial tonsil and though Leigh Thomas (1801) commented particularly upon the oral mucosa and upon the capacity of the pharynx he curiously ignored the obtrusive lymphoid tissue of the oro-pharyngeal isthmus.

It thus fell to Owen (1852) to provide the earliest published account of Indian rhinoceros anatomy, which included a brief reference to the faucial tonsil, the sole literature reference to this organ for any rhinoceros species. Owen's subject was the first Indian rhinoceros specimen to be acquired (1834) by the Zoological Society of London and its anatomization (1849–50) established Owen's priority in the discovery of the parathyroid glands (Cave, 1953). Owen's tonsil account, however, is disappointingly brief and uninformative, possibly because of a poor state of preservation of the parts concerned. Inadequate distinction is made between the palatoglossal and palatopharyngeal arches, the nature of the latter is left obscure (particularly regarding its relationship to the pyriform fossa) and its termination is misleadingly described as being "near the sides of the glottis". A figure of the tonsil (Owen, Pl. 10, Fig. 1) shows the organ's mucosal surface but is

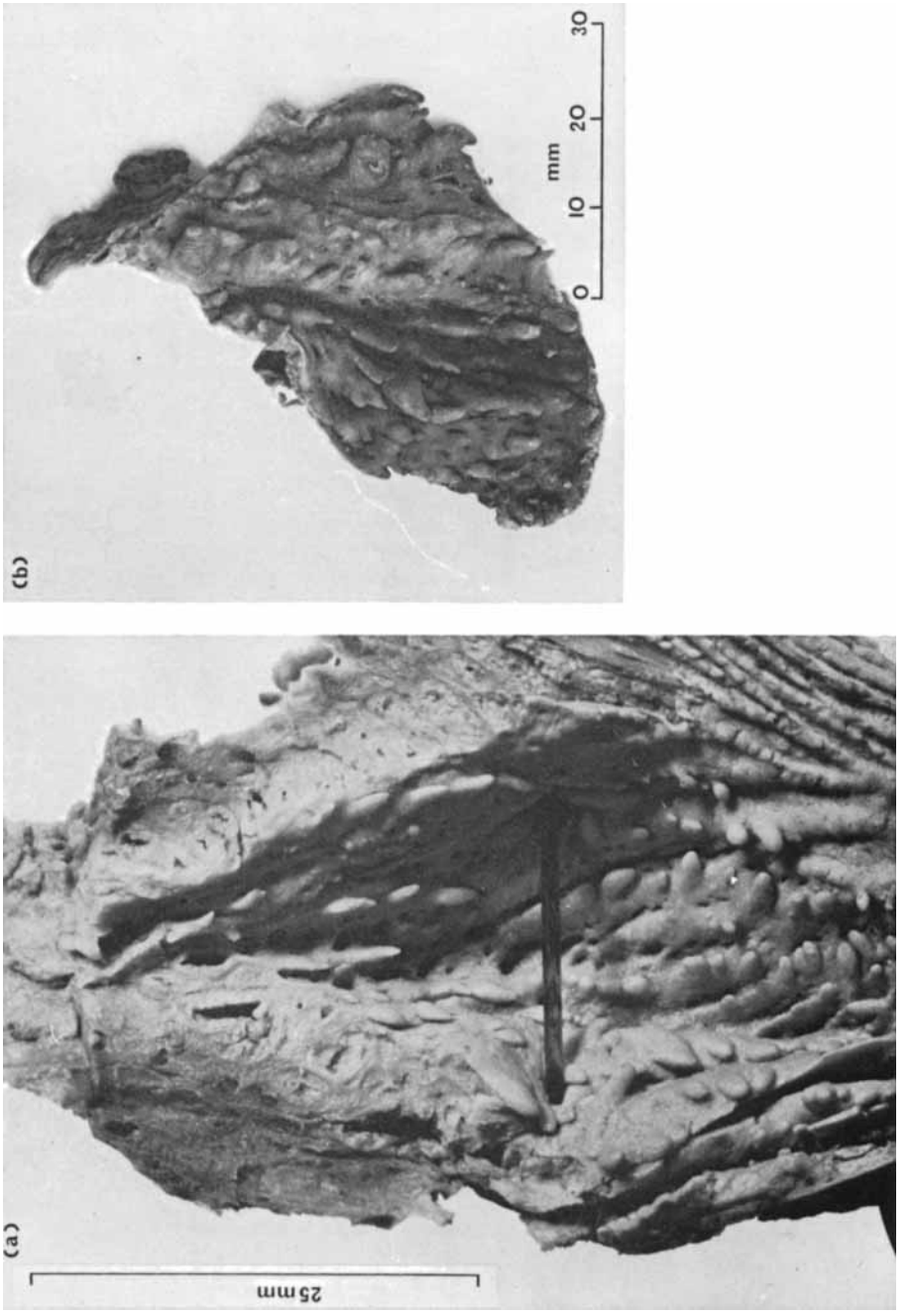

PLATE I. (a) *Ceratotherium simum*, juv. (specimen R20). Mucosal aspect of sinistral laryngopharyngeal tonsil. (b) *Ceratotherium simum*, ad. (specimen R76). Mucosal aspect of portion of laryngopharyngeal tonsil.

imprecise regarding its full extent: no reference is made to the presence of any processus retrolingualis or to any tonsillar invasion of the pyriform fossa, depicted (Owen, Pl. 15, Figs 12, 14, 17) as empty. Nevertheless the details of this tonsil figure are fully consistent with a caudal prolongation of the tonsil into the pyriform fossa. Owen's text—a mere verbalization of his tonsil figure—dismisses the organ summarily as "a reticulate structure at the sides of the soft palate having muciparous follicles in the interstices of its meshes, and many subcompressed conical processes of various lengths".

The faucial tonsil was not included in Burne's (1905) histological study of Indian rhinoceros organs and rhinoceros material was not available to Hett & Butterfield (1909) during their comparative review of the mammalian tonsil. A Burne dissection formerly in the Royal College of Surgeons Museum (Physiological Series, L.9.1) preserved the tonsils of either an Indian or an African Black rhinoceros, which were described in the catalogue as consisting of "a series of crypts covered externally by masses of glandular and adenoid tissue".

The faucial tonsil of the Javan rhinoceros (*Rhinoceros sondaicus*) was omitted from consideration in the classic memoirs of Garrod (1877) and Beddard & Treves (1887) as was also that of the Sumatran rhinoceros (*Didermocerus sumatrensis*) in those of Bell (1793), Garrod (1873) and Beddard & Treves (1889). Nothing has been recorded to date concerning the tonsil morphology of either the African White rhinoceros (*Ceratotherium simum*) or the African Black rhinoceros (*Diceros bicornis*).

Herein, therefore, observations are presented upon the tonsillar anatomy of particular specimens of the Indian, Sumatran and African rhinoceroses, which, though limited in scope, may afford a basis for more extensive investigation. These observations concern not only the faucial (palatine) tonsil of these forms but also the unsuspected presence of tonsillar tissue within the rhinoceros pyriform fossa, sometimes in the shape of an hitherto unrecognized lymphoid organ, herein described and designated the laryngopharyngeal tonsil (Plate I).

Material and methods

Examination was made of the gross and microscopic anatomy of the salivary, oral and palatine glands in the following rhinoceros specimens:

Rhinoceros unicornis	18 years.	R21	Zool. Soc. Lond. 1964
Diceros bicornis	11 years.	R162	Zool. Soc. Lond. 1964

From the following rhinoceros specimens the laryngo-pharyngeal viscera were excised in continuity during routine necropsy, were formalin-fixed and were later dissected with special reference to the structure and topography of tonsillar formations within the lateral food channel:

Rhinoceros unicornis	15 years.	R75	Zool. Soc. Lond. 1975
Didermocerus sumatrensis	14 years.	R72	Copenhagen Zoo 1972
Ceratotherium simum	3 years.	R20	Zool. Soc. Lond. 1964
Ceratotherium simum	10 years.	R76	Zool. Soc. Lond. 1976
Diceros bicornis	2–3 years.	R19	Zool. Soc. Lond. 1960

The organs of specimen R72 were additionally deep-frozen. Apart from some possible tonsillar senile atrophy in this specimen, the organs examined showed no evidence of pathological change. All the study material was uninjected and some of it was unavoidably mutilated during procurement, thus precluding determination of certain anatomical points. Mensural data were recorded where practicable.

The rhinoceros lateral food channel

The rhinoceros larynx is permanently elevated in the sense that the epiglottis tip is intra-narial in position and the laryngeal aditus is maintained in direct apposition to the air-containing epipharynx. During deglutition, therefore, food material traverses the pharynx along dextral and sinistral food channels which flank the raised larynx. Each such lateral food channel is an irregular gutter in the pharynx floor established by continuity of the vallecula anteriorly with the pyriform fossa posteriorly and is roofed by the arcus palatopharyngeus. The two channels unite dorsad of the cricoid cartilage, their common conduit opening immediately into the oesophagus. Each channel is liberally provided with lymphoid tissue in the minor form of scattered lymphoid follicles and in the major form of one or more ventral armillae of tonsillar tissue (Fig. 16(a)). A constant anterior armilla is formed by the faucial tonsil and its retrolingual process, an inconstant posterior armilla by the laryngopharyngeal tonsil.

The vallecula, a depression in the floor of the oro-pharyngeal junction, is bounded anteriorly by the tongue, posteriorly by the epiglottis, laterally by the recessus tonsillaris and medially by the glosso-epiglottic fold. (Despite its canonical designation this plica glosso-epiglottica mediana is no mere reflection of mucous membrane, but, contrariwise, a substantial intervallecular partition of notable length, height and thickness. It consists essentially of a sheet of dense connective tissue (lig. glosso-epiglotticum) almost as wide (thick) as tall, which encloses a small median muscle (m. glosso-epiglotticus) and is covered externally by a strongly papilliferous mucosa. This firm tripartite structure were more aptly named, as here, the vinculum glosso-epiglotticum). The vallecula is occupied, wholly or in great part, by the medially protruding mass of the faucial tonsil and is underlain by the organ's processus retrolingnalis. Its parietes thus present a reticulate appearance and are characterized by a multitude of gland ostia and well-developed conical papillae.

The fossa (*sinus, recessus*) *pyriformis* is the ventral pharyngeal compartment enclosed between the walls of larynx and pharynx and limited by their junction ventrally, anteriorly and posteriorly. It is a navicular, ventro-dorsally disposed recess with a deep and narrow fundus and a complete muscular roof separating it from the superjacent epipharynx. Its lateral wall comprises the short thyro-hyoid membrane and the lamina of the thyroid cartilage. Its medial wall is the structurally tripartite wall of the larynx. A ventral area of this wall is fibro-cartilaginous (epiglottis stem and thyro-epiglottic ligament), a larger dorsal area is muscular (muscles attached to arytenoid cartilage) and a narrow, trigonal intermediate area is fibro-elastic (conus elasticus). This intermediate area lodges the Wrisberg cartilage and provides a stout ligamentous band of attachment to such tonsillar mass as may occupy the fossa fundus, which is chink-like and convex both antero-posteriorly and ventro-dorsally, and may contain a laryngopharyngeal tonsil. The fossa roof (arcus palatopharyngeus) is entire but extremely tenuous and represents the conjoined pterygo-pharyngeal and palato-pharyngeal muscles. The fossa contains tonsillar tissue in a variety of formations, viz. as a caudal extension (cauda tonsillae) of the faucial tonsil along its lateral wall, as a caudal extension of the processus retrolingualis along its medial wall, as a discrete laryngopharyngeal tonsil within its fundus or as some combination of these formations. The quantity of such tonsillar tissue is determined by physiological requirement, its disposition by the lymphopoietic activity of the second and third pharyngel pouches without regard to considerations of taxonomy.

The pharynx roof (*arcus palatopharyngeus*), tenuous and complete, is pierced centrally

by a large, oval aperture through which the larynx projects in permanent communication with the epipharynx. The roof slopes caudo-ventrally from its palatal origin to its supra-oesophageal termination, each of its dextral and sinistral halves presenting an attached and a free border. The attached borders run caudo-medially along the pharynx wall to meet dorsad of the oesophageal ostium: the thin, sharp free borders sweep postero-medially from the palate to become continuous behind the rim of the laryngeal aditus, embracing tightly en route the raised larynx and by such sphincteric action assisting in its permanent elevation.

The arcus palatopharyngeus prevents the entrance into the larynx of material from the lateral food channels: its removal demonstrates their continuity and the facility with which the faucial tonsil may extend caudally into the pyriform fossa.

The rhinoceros soft palate (*velum palatinum*) resembles that of the horse in general constitution. It consists essentially of a thin, composite, strong aponeurosis sandwiched between a dorsal (epipharyngeal) and a ventral (oral) stratum of submucosal glands, which together account for some three quarters of the total palate thickness. No uvula is developed and the free concave margin of the velum is permanently overlain by the acuminate tip of the intranarial epiglottis. The aponeurosis is compounded of the virtually inseparable tendons of the mm. tensor palati, levator palati et palatopharyngeus. The m. azygos uvulae is represented by some small intrapalatal fasciculi and no m. palato-glossus is developed.

The tensor palati muscle is narrow, fusiform and largely tendinous. It arises, lateral to the m. levator palati, from the undersurface of the petrous temporal bone and from the lower edge of the lateral lamina of the cartilaginous portion of the Eustachian tube and descends obliquely to the level of the pterygoid hamulus where it is wholly tendinous: its flat, narrow tendon turns sharply around the hamulus and expands widely within the velum ventral to the tendon of m. levator palati. This latter muscle arises in medial contiguity to the tensor but is fleshy throughout its extra-palatal extent: its expanded intrapalatal tendon lies ventral to the azygos fasciculi and is apparently continuous with its contralateral fellow.

The extremely dense fascia (fascia of Weber-Liel) clothing the lateral aspect of m. tensor palati condenses into an obtrusive temporopterygoid ligamentous band (lig. temporo-pterygoideum), attached superiorly to the undersurface of the petrous temporal bone, inferiorly to the pterygoid hamulus, whereby it is separated from the pterygo-mandibular raphé. (This temporo-pterygoid ligament is not peculiar to the Rhinocerotidae and is observable in a wide variety of other mammals (prosimians, primates, cetaceans, carnivora) and is probably an unrecognized but canonical feature of mammalian anatomy. It is usually attached above to a special spine or process (spina Eustachiana) on the under-surface of the petrous temporal bone and below embraces a spiculate pterygoid hamulus.)

The rhinoceros palatine glands are principally mucous in function although the majority (the inferior palatine glands in particular) are essentially small salivary glands of mixed histological type. The palatal dorsal mucosa is relatively thick and lax, tending to be transversely wrinkled by an underlying layer of well-developed, yellowish-brown glands (glandulae palatinae superiores) disposed in roughly parallel linear series (Figs 4, 5(d)). Though predominantly mucous in type these glands reveal a mixed composition, odd serous cells being discernible within the parenchyma of each. The palatal ventral mucosa is uniformly thin, smooth and everywhere tightly adherent, with its epithelium produced

into a continuous brushwork of extremely fine filiform papillae: it conceals a subjacent and substantial stratum of close-packed, flask-shaped glands (glandulae palatinae inferiores) whose short ducts open by fine but macroscopially recognizable ostia over the entire undersurface of the velum. These inferior palatal glands—whose abundance in *Didermocerus* was noted by Garrod (1873)—are small salivary glands of mixed (mucoserous) type whose discharge of secretion is aided by palatal muscle activity. In adult Indian rhinoceros specimens they range in depth from 8–13 mm and in maximal breadth from 6–8 mm, each gland nestling within an investing plexus of extremely fine veins The superior and inferior palatine gland layers together comprise 70–75% of the soft palate total thickness.

The cartilaginous Eustachian tube is relatively long with an extremely narrow, almost slit-like lumen. It is formed by a typically mammalian plate of elastic cartilage folded upon itself superiorly into dorso-ventrally divaricating laminae—a larger, broader lateral and a shorter, narrower medial—ununited inferiorly. Its lining mucosa, unlike that of equids and tapirids, does not herniate to form a diverticulum (guttural pouch). The cartilaginous portion of the tube is attached superiorly to supporting projections from the undersurface of the petrous temporal bone whence it descends ventro-medially to the basisphenoid undersurface whereon it terminates immediately behind the uppermost part of the pterygoid lamina. Its epipharyngeal ostium is small, slit-like and remarkably inconspicuous since it lies flush with the epipharyngeal parietes and is undistinguished by any tubal "cushion" or any retro-tubal recess. (In an adult Indian rhinoceros (R21) the cartilaginous tube measures 11 cm in length, in an adult Black rhinoceros (R162) some 12 cm in length: in a young Black rhinoceros (R19) it is 7 cm long with an epipharyngeal ostium of 5·0 by 3·5 mm diameter.)

From the lateral surface and inferior border of the tube's lateral lamina arise the mm. tensor et levator palati: on the lateral surface lies the nerve to the tensor muscle.

Microscopically the tubal mucosa exhibits a pseudo-stratified columnar epithelium: it reveals a minor content of diffuse lymphoid tissue and a complement of small mucous glands. These last are numerous and have delicate ducts which traverse the thickness of the tubal medial lamina. The ducts are also remarkable for an individual accompaniment of many very fine arteries which are devoid of companion veins and surrounded instead by clusters of lymphocytes.

Observations on rhinoceros tonsil morphology

The tonsillar morphology of Indian rhinoceros R75

The faucial tonsil (Figs 1–5) is obtrusively "well developed" and bulges medially from the recessus tonsillaris so as completely to occupy the vallecula. It is the sole tonsillar mass present and comprises a principal portion (caput tonsillae) and two extensions therefrom, viz. a posterior (cauda tonsillae) and a medial (processus retrolingualis). It does not invade the tongue or the soft palate. Two notably large, elongated sacs (45 mm long and 5·0 × 3·0 mm in cross section) pass from the uppermost portion of the caput tonsillae in the direction of the soft palate, either or both of which may represent the primordial tonsillar diverticulum.

The caput tonsillae is a compact ovoid mass occupying the recessus tonsillaris and measuring some 90 mm antero-posteriorly, 45 mm ventro-dorsally and 30–35 mm in

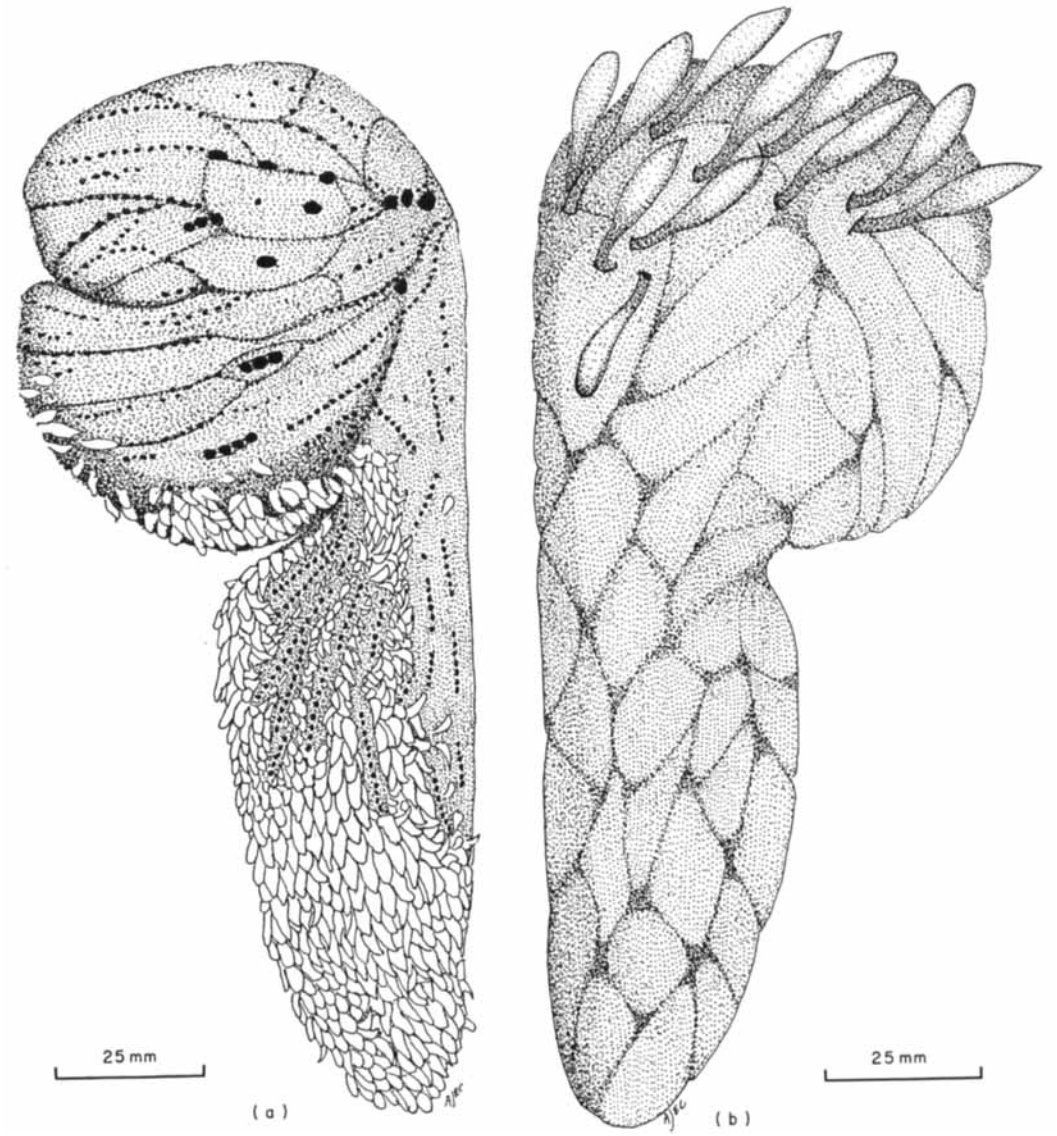

FIG. 1. *Rhinoceros unicornis* (specimen R75). Dextral faucial tonsil in (a) norma medialis, (b) norma lateralis.

transverse diameter (thickness) save where grooved medially by a vertical furrow: this furrow subdivides the lymphoid mass into an anterior portion (40 mm long) and a posterior portion (50 mm long) and reduces its thickness locally to some 15 mm. The organ is markedly convex medially, less so superiorly and laterally.

The medial (free, mucosal) surface of the tonsil (Fig. 1(a)) is beset by tall, recurved, conical papillae, which occur also, sparingly, upon the faucial pillars and, more abundantly, upon the vallecula parietes: this surface is reticulated, displaying a characteristic configuration of low, interlacing elevations and shallow intervening sulci, perforated by multiple

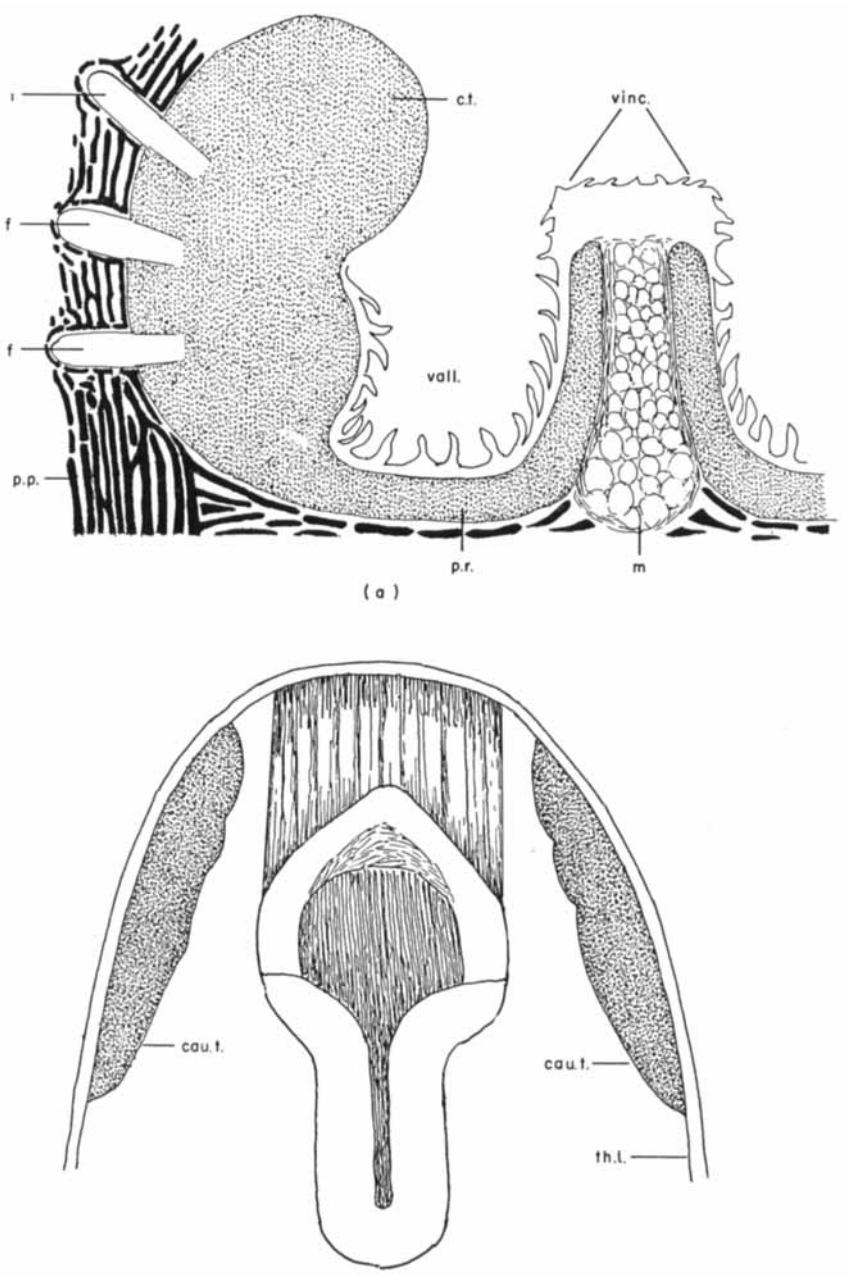

FIG. 2. *Rhinoceros unicornis* (specimen R75). Showing (a) caput tonsillae, processus retrolingualis and fossulae in vertical section, (b) bilateral extension of faucial tonsil into fossa pyriformis. cau.t. = cauda tonsillae: c.t. = caput tonsillae: f = fossula: m = glosso-epiglottic muscle: p.p. = paratonsillar venous plexus: p.r. = processus retrolingualis: th.l. = thyroid cartilage lamina: val. = vallecula: vinc. = vinculum epiglotticum.

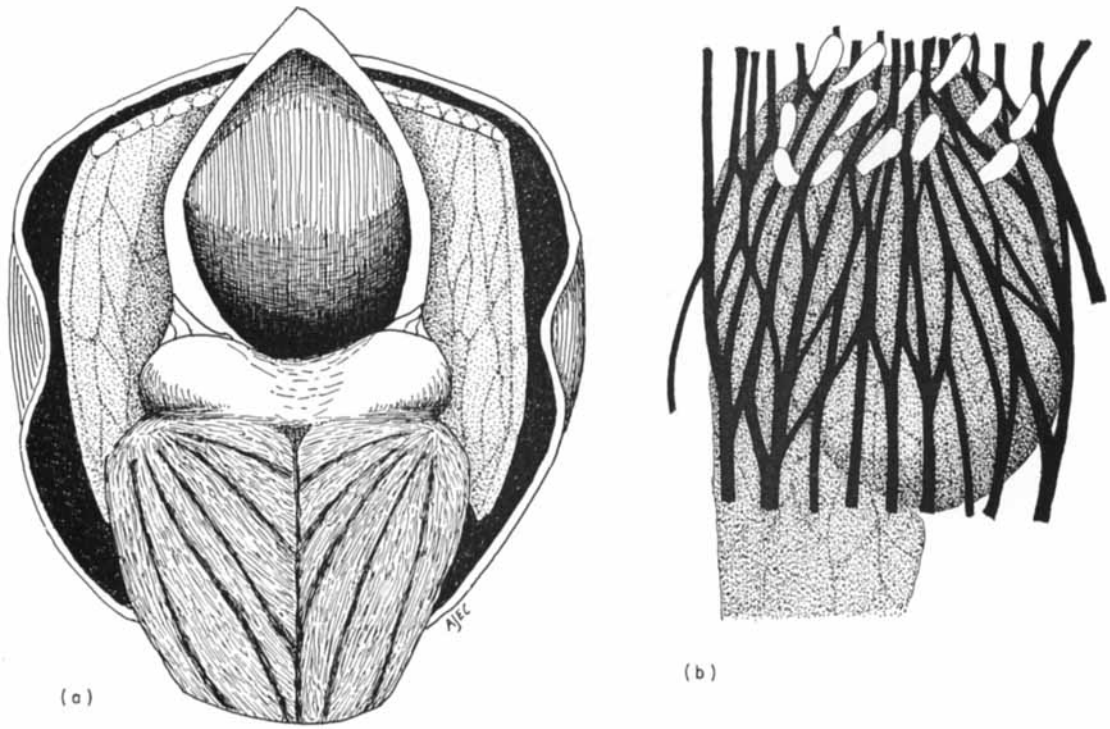

FIG. 3. *Rhinoceros unicornis* (specimen R75). Showing (a) presence of faucial tonsillar tissue within fossa pyriformis, (b) lateral aspect of caput tonsillae with projecting fossulae and paratonsillar venous plexus (black).

gland ostia. Most of these ostia are small, are arranged in intra-sulcal linear series and lead into flask-shaped mucous glands some few mm deep: a minority of ostia are relatively large (2–3 mm diameter), more irregularly disposed, and lead into fossulae. These last are Indian-club-shaped, epithelium-lined, fibrous sacs, averaging 35 mm in length, which tunnel the tonsil thickness to protrude in large part from the organ's lateral surface: their extra-tonsillar portions are individually invested with a network of extremely fine veins and collectively are enmeshed within a dense paratonsillar venous plexus (Figs 3(b), 5(a, b, c)).

The lateral surface of the caput tonsillae (Fig. 1(b)) is gently convex and is clothed by a dense connective tissue capsule, which is pierced by the tonsillar veins and supports the paratonsillar plexus. This plexus is a pallisade arrangement of large, vertically disposed and annectant veins which enmeshes the protruding fossulae, receives tonsillar and palatal veins as tributaries and drains indirectly into the internal jugular vein.

Infero-medially the caput tonsillae gives rise to a processus retrolingualis (Fig. 2(a)) which extends carpet-wise beneath the vallecula floor and ascends some distance upon the vinculum epiglotticum (a structure 65 mm long by 40 mm wide). This process does not involve the tongue proper or encroach posteriorly upon the epiglottis: its submucosal extent is indicated macroscopically by the surface appearance of elevations, sulci, gland ostia and conical papillae associated with its reticular configuration.

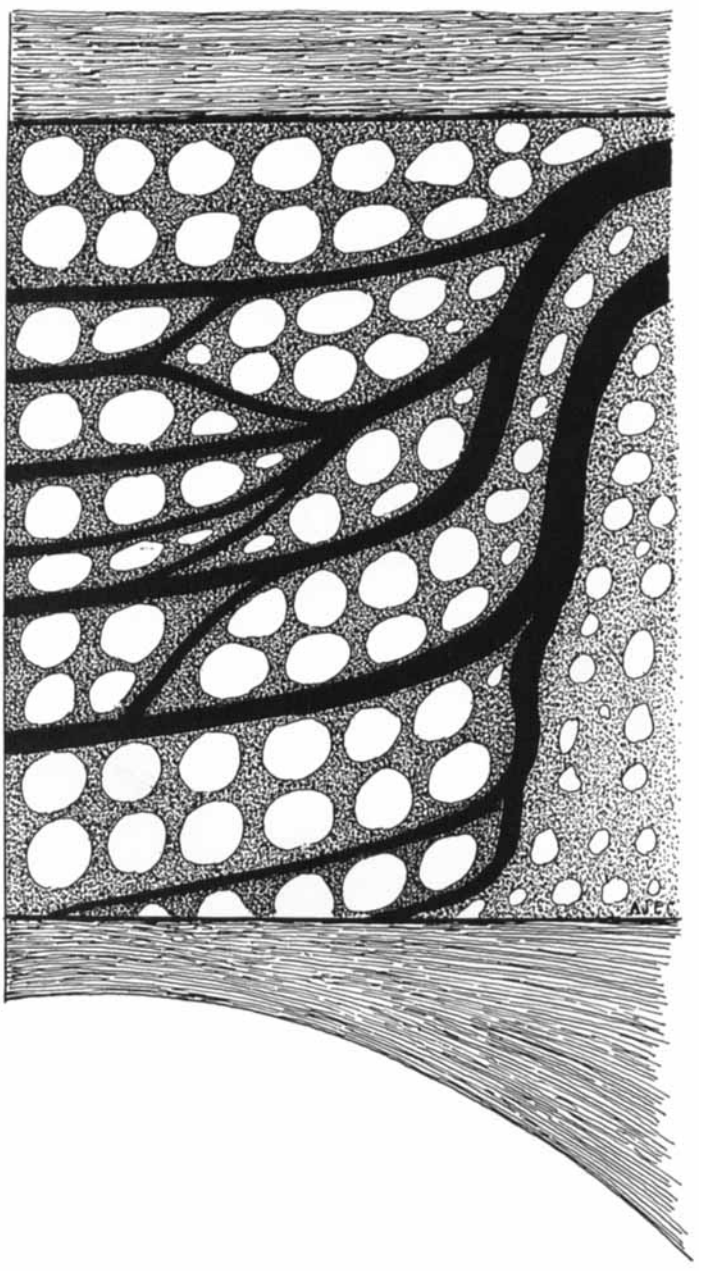

FIG. 4. *Rhinoceros unicornis* (specimen R75). Dorsal aspect of dextral moiety of soft palate dissected to show superior palatine glands and veins (black).

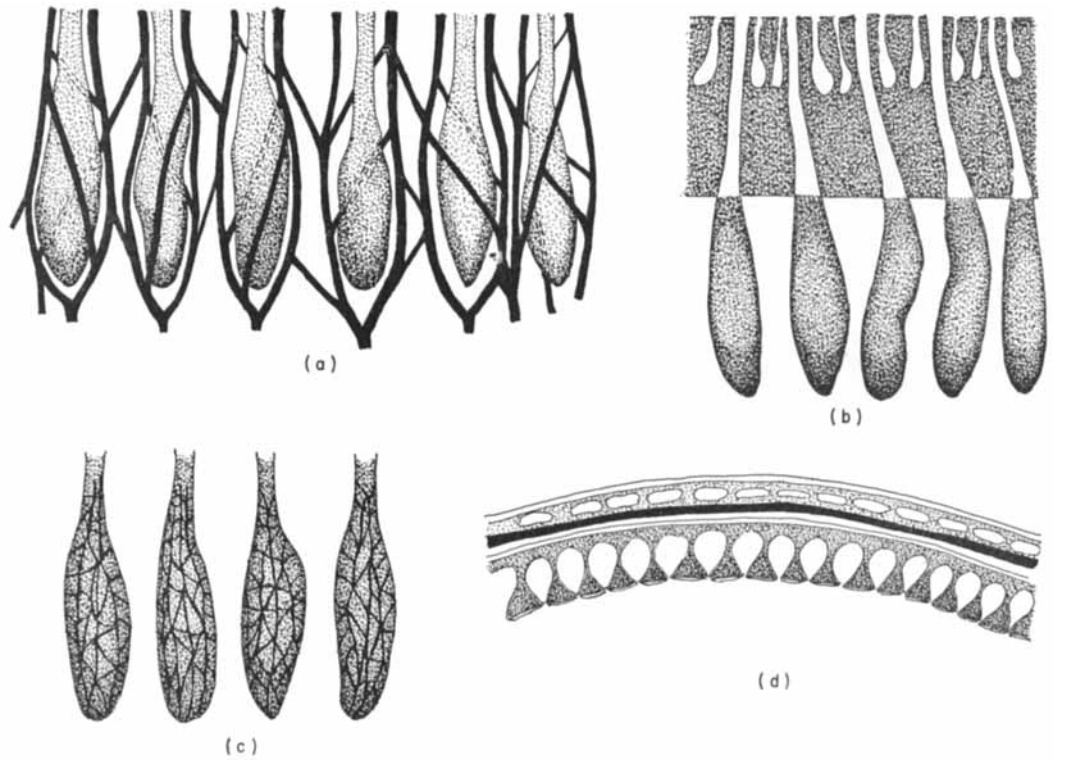

FIG. 5. *Rhinoceros unicornis* (specimen R75). Dissections of (a) fossulae and paratonsillar plexus (black), (b) fossulae and small glands in relation to (sectioned) caput tonsillae, (c) intrinsic veins (black) of individual fossulae, (d) soft palate showing dorsal and ventral gland layers.

Posteriorly the caput tonsillae is prolonged into a long, somewhat tapering process (cauda tonsillae) which invades the pyriform fossa along its lateral wall (Figs 2(b), 3(c)). This process is some 100 mm long and diminishes in dorso-ventral width from an initial 35 mm to a terminal 20 mm. Its flat lateral surface is applied to the thyroid cartilage lamina: its convex medial (mucosal) surface is reticulated (perhaps more finely so than that of the caput tonsillae), is densely clothed with conical papillae and presents the ostia of very numerous, uniformly small, mucous glands: its ventral edge occupies the fossa fundus. Fossulae are not developed in the cauda mass.

The tonsillar arrangements described for specimen R75 may well duplicate those which obtained, unnoticed, in Owen's Indian rhinoceros specimen: for though a cauda tonsillae was not mentioned by Owen, his tonsil illustration is fully compatible with the presence of such a formation and his figures of the fossa pyriform show an absence of any tonsillar tissue intrinsic to the fossa fundus.

The tonsillar morphology of Sumatran rhinoceros R72

The specimen manifests mutilation of the palatal region and the tissue fragility resulting from deep-freeze preservation: tonsil invasion of the soft palate (though unlikely) cannot

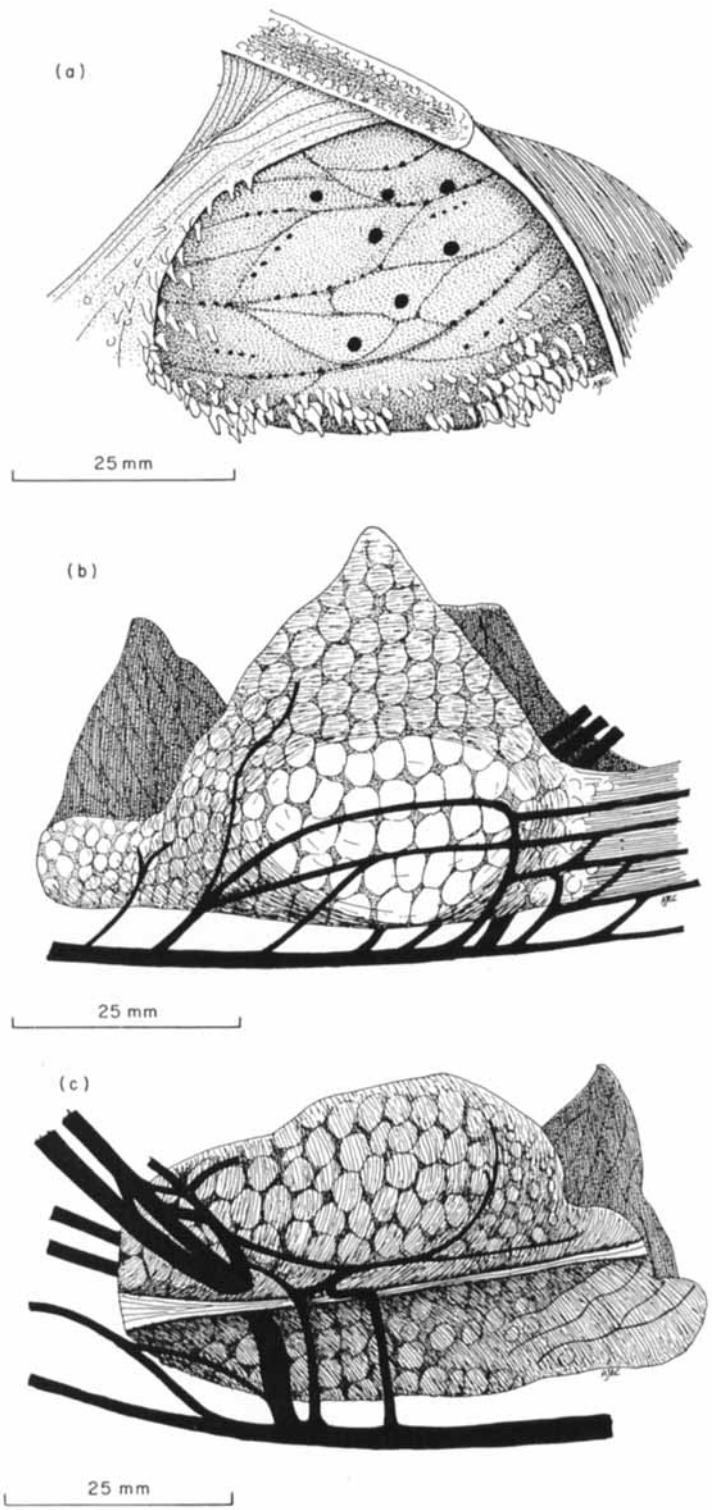

FIG. 6. *Didermocerus sumatrensis* (specimen R72). Showing (a) medial aspect of dextral faucial tonsil, (b) lateral aspect of dextral laryngopharyngeal tonsil and peritonsillar veins, (c) medial aspect of dextral laryngopharyngeal tonsil, associated veins and laryngotonsillar ligament. (Vessels black.)

therefore be excluded with certainty and the presence of a supratonsillar fossa is indeterminable. Tonsillar tissue present may reflect some degree of age-atrophy, since its surface reticulation is less emphatic than anticipated and the associated gland ostia and conical papillae are relatively few.

Notwithstanding such defects and possible age-change the disposition of the specimen's tonsillar tissue is strikingly apparent and differs radically from that obtaining in the previous (Indian rhinoceros) specimen. For this tissue is strictly localized into one or other of two and widely separate masses—one (faucial tonsil) occupying the canonical recessus tonsillaris, the other (laryngopharyngeal tonsil) occupying the fundus of the fossa pyriformis. This arrangement is not invalidated by a meagre scattering of atrophic lymphoid follicles over the fossa lateral wall which in no sense constitutes a cauda tonsillae.

The faucial tonsil, a laterally compressed ovoid mass of compact lymphoid tissue and mucous glands, is confined to the recessus tonsillaris and though least sharply defined posteriorly, is not prolonged into a cauda tonsillae. Convex generally, and markedly so medially, the organ projects from the recessus into the vallecula, occupying that space up to the vinculum epiglotticum. The dextral tonsil is 50 mm long, 35 mm high and 8 mm thick, the sinistral tonsil 40 mm long, 30 mm high and 10 mm thick.

The organ's medial (mucosal) surface (Fig. 6(a)) displays a characteristic, if not very emphatic, pattern of low elevations, intervening shallow sulci, gland ostia and conical papillae. The papillae are less numerous than expected as are also the uniformly small and mostly intra-sulcal ostia of the mucous glands. Some half dozen larger ostia which appear upon the elevations are those of fossulae, which range in depth from 10 to 20 mm and which tunnel the organ's substance so as to protrude from its lateral surface. This lateral (attached) surface lies in contact with a well-developed connective tissue capsule which supports a paratonsillar venous plexus containing in its meshes the protruding distal blind ends of the fossulae. The plexus comprises relatively large veins, vertically disposed in a pallisade arrangement, and receives tributaries from the tonsil and the soft palate. (The intrinsic vasculature of the tonsil itself escapes detailed determination.)

A processus retrolingualis arises from the infero-medial aspect of the tonsil mass. This extends beneath the vallecula floor and ascends a considerable distance upon the vinculum, without, however, encroaching upon the tongue anteriorly or upon the epiglottis posteriorly. Its area of distribution is indicated by a surface reticulation accompanied by multiple gland ostia and an abundance of conical papillae.

The laryngopharyngeal tonsil (Figs 6(a, b), 7(a)) is a discrete, sessile mass of typical tonsillar tissue ensconced immovably within the pyriform fossa fundus, and exceeding in bulk the faucial tonsil. Navicular in configuration it consists of two (medial and lateral) processes—conveniently termed moieties—which unite ventrally, dorsally and posteriorly to form, respectively, the prow, stern and prominently keeled hull of the lymphoid tissue "vessel". From the 12 mm wide body (or hull) of the structure the moieties ascend equidistally upon the medial and lateral walls of the pyriform fossa, gradually diminishing in thickness to a terminal 5 mm. Their anterior borders end freely, being neither continuous with, nor contiguous to, any other lymphoid formation within the fossa. Each moiety has a free, mucosal and an attached surface, the attached surfaces coinciding with those of the organ as a whole. The "hull" of the formation (Fig. 7(b)) has corresponding mucosal and attached surfaces.

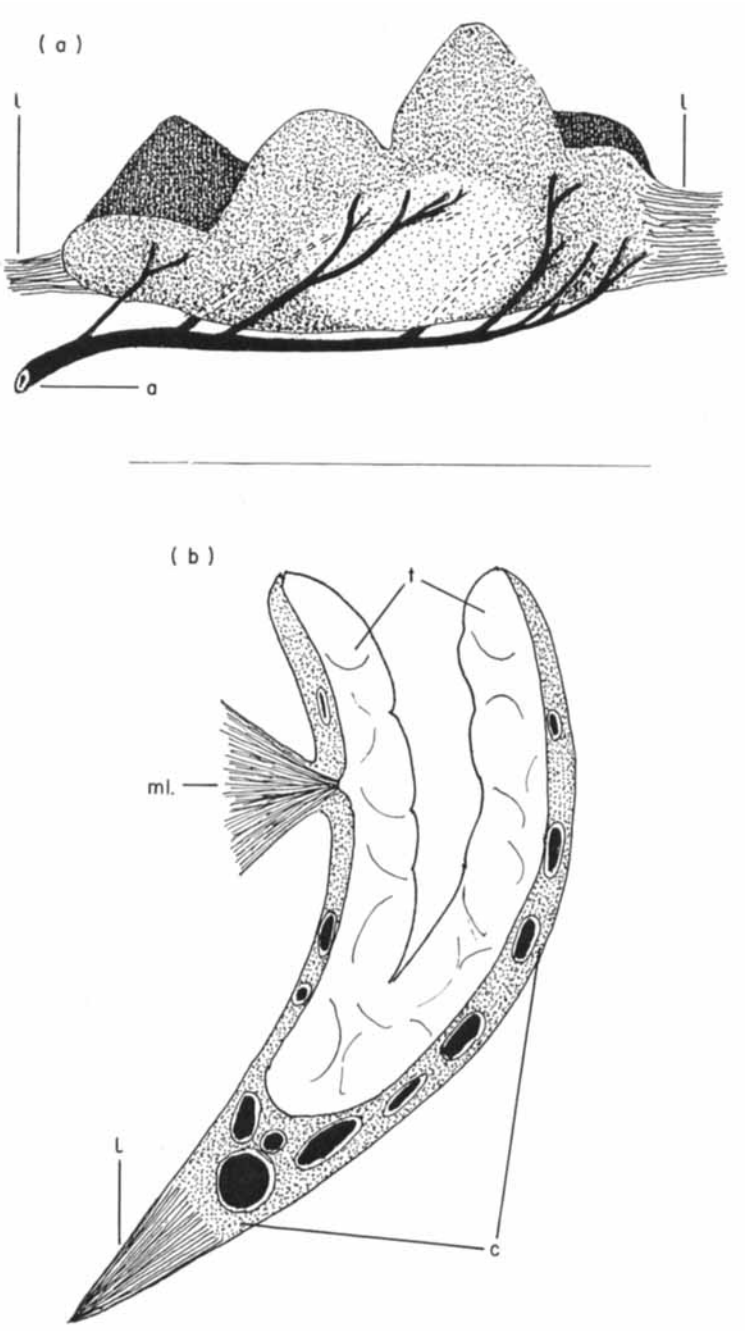

FIG. 7. *Didermocerus sumatrensis* (specimen R72). Dextral laryngopharyngeal tonsil (a) in norma lateralis, (b) in coronal section. a = arteria tonsillae laryngopharyngeae: c = capsule and embedded peritonsillar veins: l = ligamentous thickening of capsule: m.l. = medial (laryngo-tonsillar) ligament: t = tonsillar tissue.

The attached lateral surface of the laryngopharyngeal tonsil is everywhere convex and is sculpted into rounded or polygonal areas by the peripheral portions of constituent lymphoid follicles and mucous glands. The attached medial surface is concave and is ridged lengthways for the attachment of a ligamentous expansion (lig. laryngo-tonsillaris) from the larynx wall. This expansion (Fig. 7(b)) derives from the trigonum fibro-elasticum of that wall and ranges in ventro-dorsal thickness from 7–3 mm: it binds the laryngopharyngeal tonsil securely to the larynx, ensuring its excursion therewith during deglutitionary and respiratory movements. The mucosal surface of the tonsil body ("hull") and moieties is characteristically reticulated and is studded with multiple small gland ostia: from it, however, conical papillae are virtually absent (possibly from age-change) and are represented by a mere scatter of inconspicuous mucosal tags over its lateral area. Fossulae are wanting.

The laryngopharyngeal tonsil is invested with a thick connective tissue capsule, condensed locally into ventral, dorsal and posterior ("keel") ligaments which stabilize the organ: upon and around this capsule lies an obtrusive peritonsillar plexus of relatively large veins.

The dextral laryngopharyngeal tonsil, with its attached capsule and blood vessels is 75 mm in length, 45 mm in intermediate height and 15 mm in thickness: denuded of these adnexa it measures 70 mm in length, 40 mm in maximal height and 12 mm in maximal thickness. The organ is supplied by a special artery (a. tonsillae laryngopharyngeae) which enters the pyriform fossa through the large foramen thyroideum in the lamina of the thyroid cartilage: this vessal courses dorso-ventrally along the tonsil "keel", lying within the capsule deep to the peritonsillar veins. It gives one small and two larger branches to the organ's medial moiety and a series of unequal-sized branches to its lateral moiety. The peritonsillar plexus terminates in two or three large veins which leave the pyriform fossa (in company with conspicuously large lymphatic vessels) through the foramen thyroideum.

The laryngopharyngeal tonsil is manifestly intrinsic to the pyriform fossa and no mere invasion of that recess from elsewhere. Its structure, topography, and laryngeal connection are collectively suggestive (if not directly indicative) of its morphological independence and development *in situ*. Anatomical arrangements in this *Didermocerus* specimen would seem to indicate that the rhinoceros lateral food channel is dependent for its tonsillar tissue equipment upon the reciprocal activity of a cranial and a caudal source of such tissue, and that should the faucial tonsil fail adequately to "tonsilize" the pyriform fossa, such "tonsilization" may be completed by the development of a supplementary laryngopharyngeal tonsil.

The tonsillar morphology of White rhinoceros R20

The specimen is rendered less informative than anticipated by some mutilation of the palato-faucial region. This, however, nowise obscures the segregation of tonsillar tissue present into one or other of two anatomically discrete masses—a faucial mass within the recessus tonsillaris and a much larger laryngopharyngeal mass within the pyriform fossa.

The faucial tonsil manifests all the morphological and topographical features of such an organ and invades neither the soft palate nor the tongue. Surprisingly small for so young an animal its dimensions do not exceed 30 mm in antero-posterior length, 20 mm in ventro-dorsal height and 10 mm in transverse diameter (thickness). It does not protrude medially from the recessus into the vallecula. Its medial (mucosal) surface is gently convex, bears

numerous small, blunt-tipped conical papillae and displays a number of low elevations separated by shallow branching sulci, wherein appear the ostia of numerous, uniformly-small mucous glands. A few larger ostia appearing on the elevations represent fossulae. No supratonsillar fossa is identifiable. The tonsil lateral (attached) surface is flattish and much obscured by a pallisade arrangement of relatively large veins (paratonsillar plexus) among the interstices of which the protruding distal ends of three or four fossulae are distinguishable. The tonsil mass is not prolonged caudally into the pyriform fossa. Postero-inferiorly, however, it gives off a somewhat feebly-developed processus retro-lingualis which extends to the vinculum epiglotticum without ascending appreciably thereon and without encroaching posteriorly upon the anterior aspect of the epiglottis.

The laryngopharyngeal tonsil (Figs 8, 9), in contrast, is maximally developed. It takes the form of a sessile, navicular mass of reticulated compact lymphoid tissue, firmly embedded within, and wholly occupying, the fundus and ventral region of the pyriform fossa. Of canoe-like configuration the organ is a natural cast of this cavity, being convex laterally, concave medially and prominently keeled posteriorly. The "hull" of this navicular formation occupies the fossa fundus, whence its sides (moieties) ascend equidistantly upon the fossa walls, the medial almost to the ary-epiglottic fold, the lateral to a corresponding level upon the thyroid cartilage lamina.

The tonsil lateral surface (coincident with that of the lateral moiety) adheres to the thyroid lamina, the medial surface (coincident with that of the medial moiety) is firmly attached to the larynx wall, principally by a stout expansion from the fibro-elastic portion of that wall (ligamentum laryngo-tonsillaris). The tonsil lateral moiety, a flattish slab of tissue, has its medial (mucosal) surface subdivided by more or less parallel shallow sulci and displays multiple small gland ostia and numerous conical papillae: the thicker and laterally convex medial moiety is longitudinally divided into two elongate elevations and is similarly beset with gland ostia and conical papillae.

Isolated from its connective tissue matrix the dextral laryngopharyngeal tonsil is 100 mm long, 28–30 mm in maximal thickness and 28 mm high: the sinistral tonsil is 100 mm long, 28 mm thick and 30 mm high. The gland ostia on the mucosal surface of the tonsil are mostly of uniform small size, though a few larger ostia occur at the ventral fusion of the tonsil moieties. Fossulae, however, are not developed. The conical papillae which abound on the mucosal surface are small (2·5–5·0 mm tall) blunt-tipped structures, the smallest being mere tags of mucosa: the apices of all are caudally directed.

The laryngopharyngeal tonsil is invested with a dense connective tissue capsule, thickened locally into distinct ventral, dorsal and posterior ("keel") ligaments, which, together with the stout laryngo-tonsillar ligament from the larynx wall, secure the organ firmly within the pyriform fossa and render difficult its enucleation undamaged. These ligamentous connections compel the tonsil to accompany the larynx in all excursions made by that organ.

The capsule supports an elaborate peritonsillar venous plexus, the efferent vessels of which pass ventro-dorsally alongside the tonsil "keel" to leave the pyriform fossa, accompanied by large lymphatic vessels, through a capacious foramen thyroideum (15 by 10 mm in diameter) in the lamina of the thyroid cartilage. Through this foramen a special artery (a. tonsillae laryngopharyngeae) enters the fossa to course dorso-ventrally along the tonsil "keel" and to expand itself in a succession of fine branches to the tonsil substance.

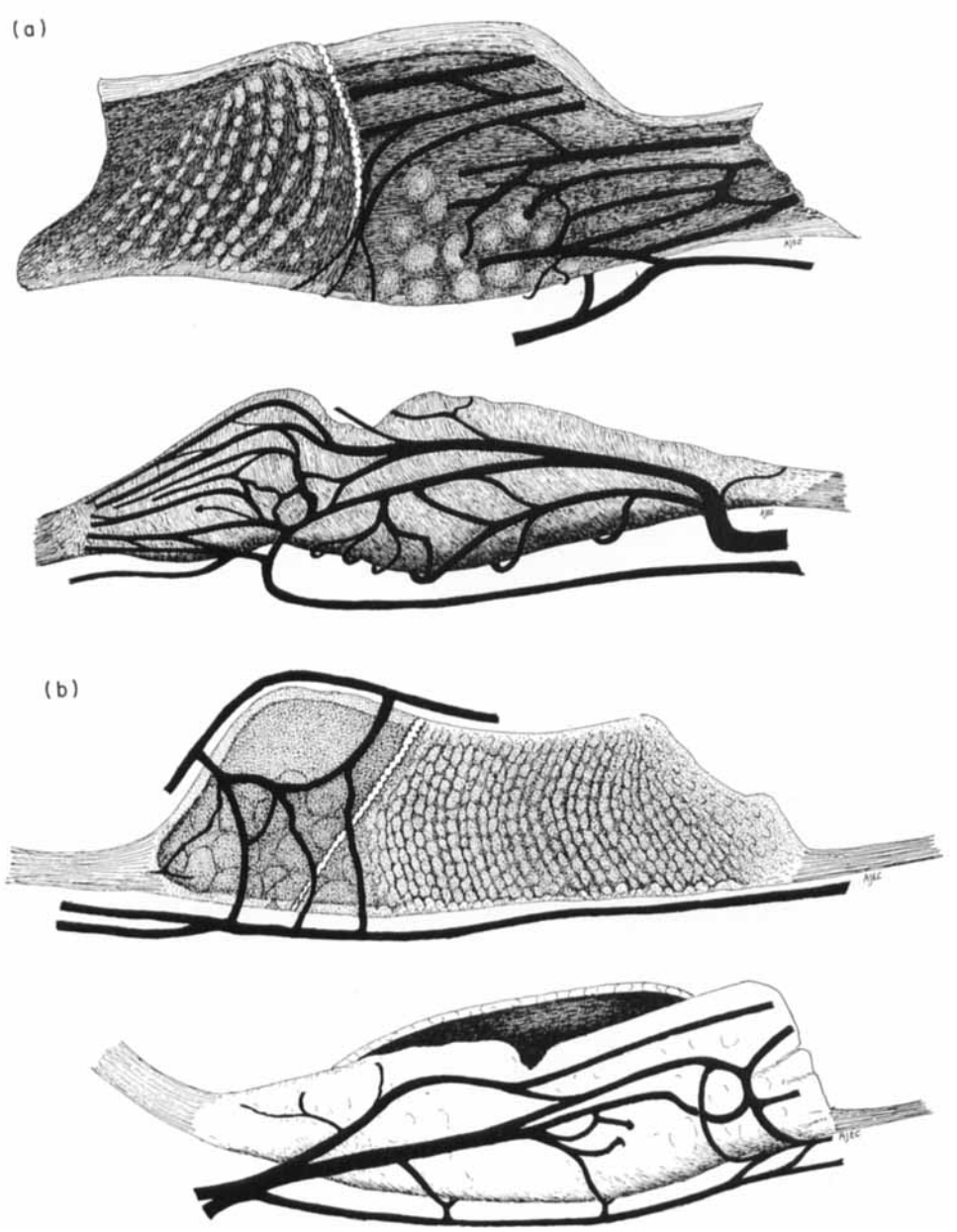

FIG. 8. *Ceratotherium simum* (specimen R20). Gross appearance of (a) sinistral, (b) dextral laryngopharyngeal tonsil and associated veins (black). The upper figures represent the medial, the lower figures the lateral, aspects of the two organs. The bulkier end of each is the anterior.

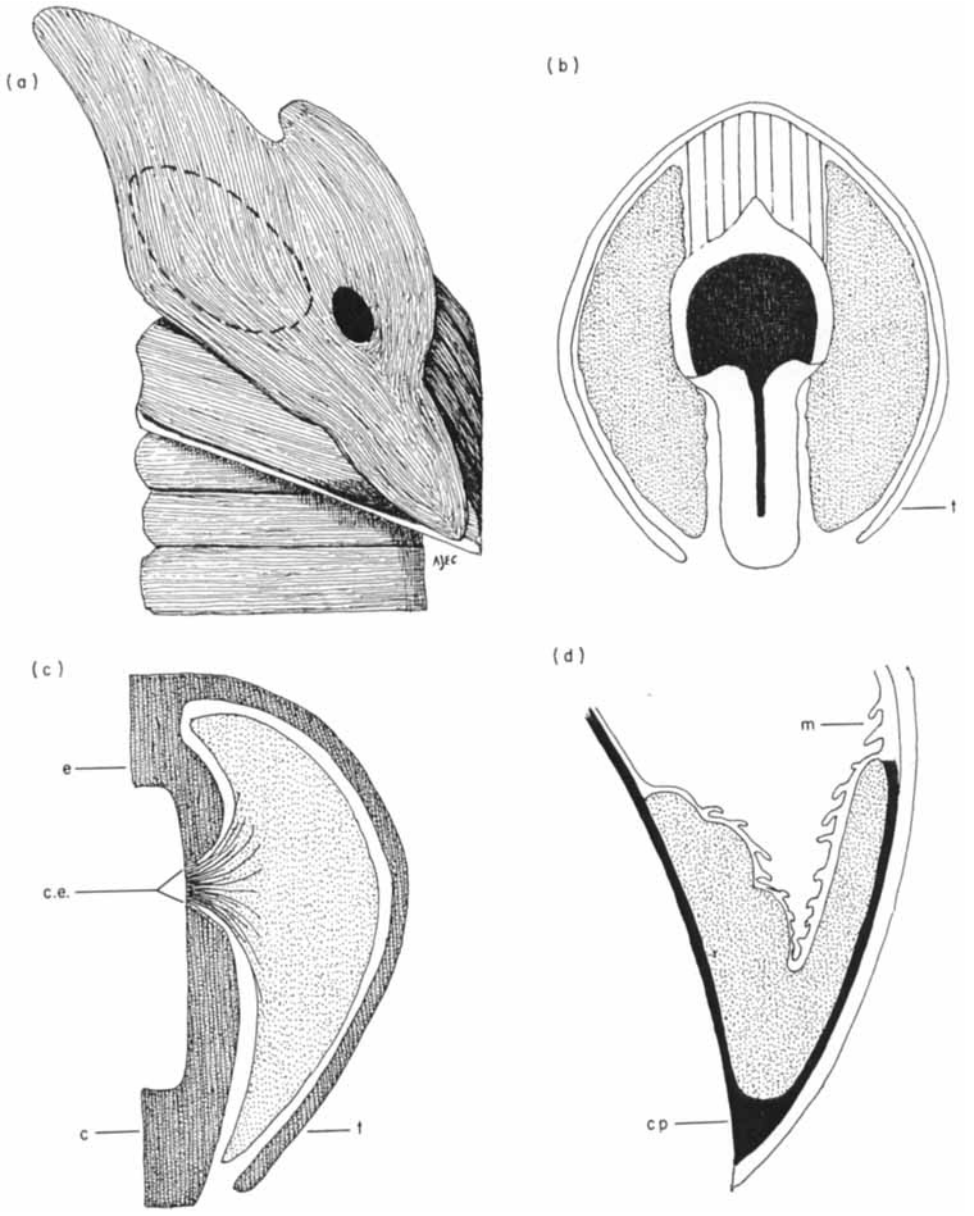

FIG. 9. *Ceratotherium simum* (specimen R20). Laryngopharyngeal tonsil. Showing (a) relationship of sinistral organ (broken outline) to thyroid cartilage and thyroid foramen (black), (b) dextral and sinistral organs occupying pyriform fossae, (c) dextral organ in horizontal section, (d) dextral organ in vertical section. c=cricoid cartilage lamina: c.e.=conus elasticus: cp=capsule: e=epiglottis stem: m=mucous membrane: t=thyroid cartilage lamina. Tonsillar tissue stippled.

The laryngopharyngeal tonsil, so obtrusively intrinsic to the pyriform fossa, is a larger anatomical structure than the faucial tonsil and presumably functioned as the physiologically dominant of the two organs.

The tonsillar morphology of White rhinoceros R76

In this adult animal both a faucial and a laryngopharyngeal tonsil are developed, the former predominantly so: the processus retrolingualis is exceptionally extensive: the pyriform fossa is invaded laterally by a small cauda tonsillae and medially by the processus retrolingualis.

The main mass of the faucial tonsil (caput tonsillae) is a prominent, compact, ovoid body occupying the sinus tonsillaris and projecting thence far into the vallecula (Fig. 10(a)). The dextral and sinistral organs are identical in configuration: each is some 70 mm in antero-posterior length, 40 mm in ventro-dorsal height and 35 mm in maximal transverse diameter (thickness) and is wider above than below. Neither invades either the tongue or

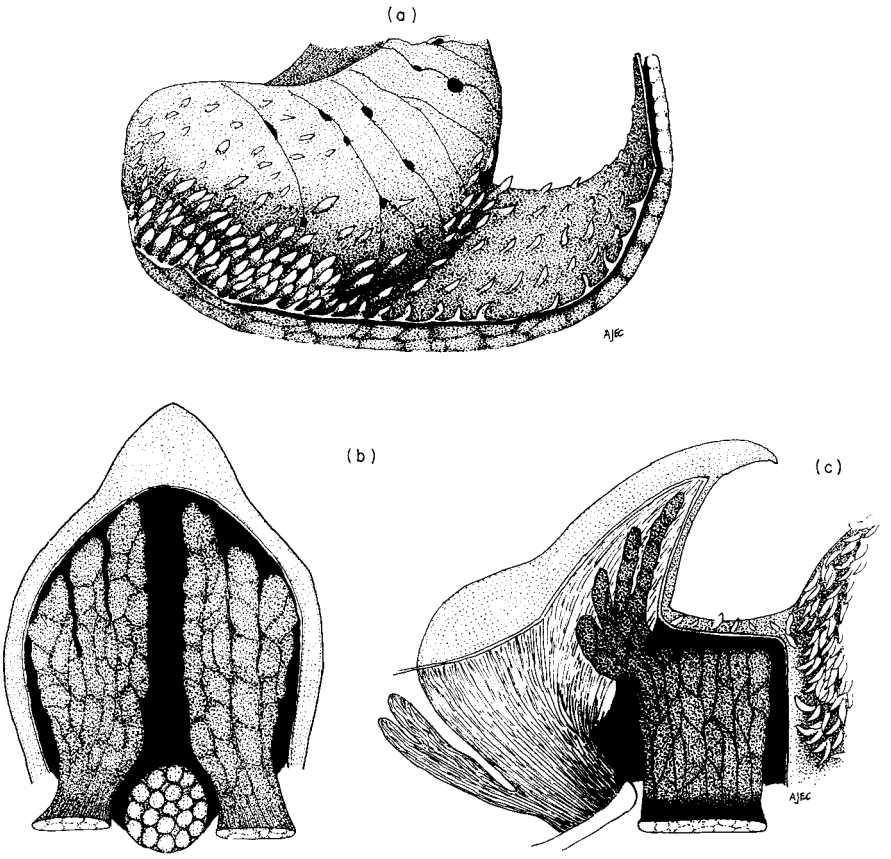

FIG. 10. *Ceratotherium simum* (specimen R76). Showing (a) anterior aspect of caput tonsillae and processus retrolingualis, (b) anterior and (c) lateral aspect of processus retrolingualis in relation to vinculum and epiglottis. Tonsillar tissue stippled.

the soft palate and neither displays any recognizable intratonsillar cleft or supra-tonsillar fossa. Each is entered below by a considerable artery of unascertained provenance and each is continuous infero-medially with a maximally developed retrolingual process (Fig. 10(b)), prolonged caudally upon the epiglottis within the pyriform fossa. Each caput tonsillae is prolonged caudally into the fossa in the shape of a small cauda tonsillae. Vertical sections show the caput tonsillae to be traversed by numerous relatively large veins pursuing an oblique medio-lateral course to the tonsil lateral surface.

The caput tonsillae medial surface is convex (especially superiorly), irregularly sulcated and invested with conical papillae: it presents the ostia of numerous small glands and those of a few fossulae. Its sulci are faint, rendering the surface fairly uniform in appearance: the gland ostia are generally distributed over this surface and are somewhat fewer than anticipated: they pertain to small, flask-shaped structures averaging 4·0 mm in depth by 2·5 mm in width. Fossulae are remarkably few and relatively small: they average but 12–15 mm in depth and hence remain totally intratonsillar and undetectable from the tonsil lateral surface. (The impression is gained that, for whatever reason, the proportion of glandular to lymphoid tissue is less in this specimen than in others of the present series.) The conical papillae vary in size and distribution: the smallest (some 2 mm tall) are confined to the dorsal area of the surface, the largest (6·0–6·5 mm tall) are crowded upon its ventral area where they adjoin the equally tall papillae of the vallecula.

The caput tonsillae lateral surface lies in direct contact with the branching glossopharyngeal nerve, is flattish and adherent to a thick connective tissue capsule. This last supports a paratonsillar plexus composed of large veins in pallisade formation, which receive as transcapsular tributaries the intrinsic veins of the caput tonsillae.

The tonsil superior surface is unremarkable. The inferior surface is continuous medially with the processus retrolingualis, laterally with the tonsil bed.

The cauda tonsillae is relatively short (50 mm) and lies within the pyriform fossa. Its flat lateral surface is adherent to the thyro-hyoid membrane and cranial portion of the thyroid cartilage laminia: its medial surface is mucosal and convex. The cauda is remote from, and manifestly unconnected with, the more caudally situate laryngopharyngeal tonsil occupying the pyriform fossa fundus.

The processus retrolingualis (Figs 10(a, b); 11(a, b, c)) is exceptionally developed and exceeds in mass its counterpart in any previous specimen of the present series. It is a notably thick (15 mm) and distally digitiform carpet of compact lymphoid tissue, more reticulated in configuration than the caput tonsillae, from whose infero-medial aspect it arises. It underlies the vallecula floor and ascends over the entire lateral aspect of the vinculum, whence it extends posteriorly to clothe the antero-lateral aspect of the epiglottic cartilage. It is everywhere firmly adherent to subjacent structures and is immediately underlain by a well-developed venous plexus. Its distribution, where superficial, is surface-marked by the presence of a characteristic tonsillar association of interlacing elevations, intervening sulci, gland ostia and conical papillae. Its relatively enormous epiglottic prolongation extends over the stem of that cartilage and thus comes to lie upon the ventral area of the pyriform fossa medial wall.

The laryngopharyngeal tonsil is a very much smaller structure than the faucial tonsil. It is an anatomically independent sessile mass of reticulated compact lymphoid tissue confined to the pyriform fossa fundus. Of navicular configuration it measures 60 mm in length, 28 mm in height and 15 mm in maximal thickness. The "hull" of this boat-like

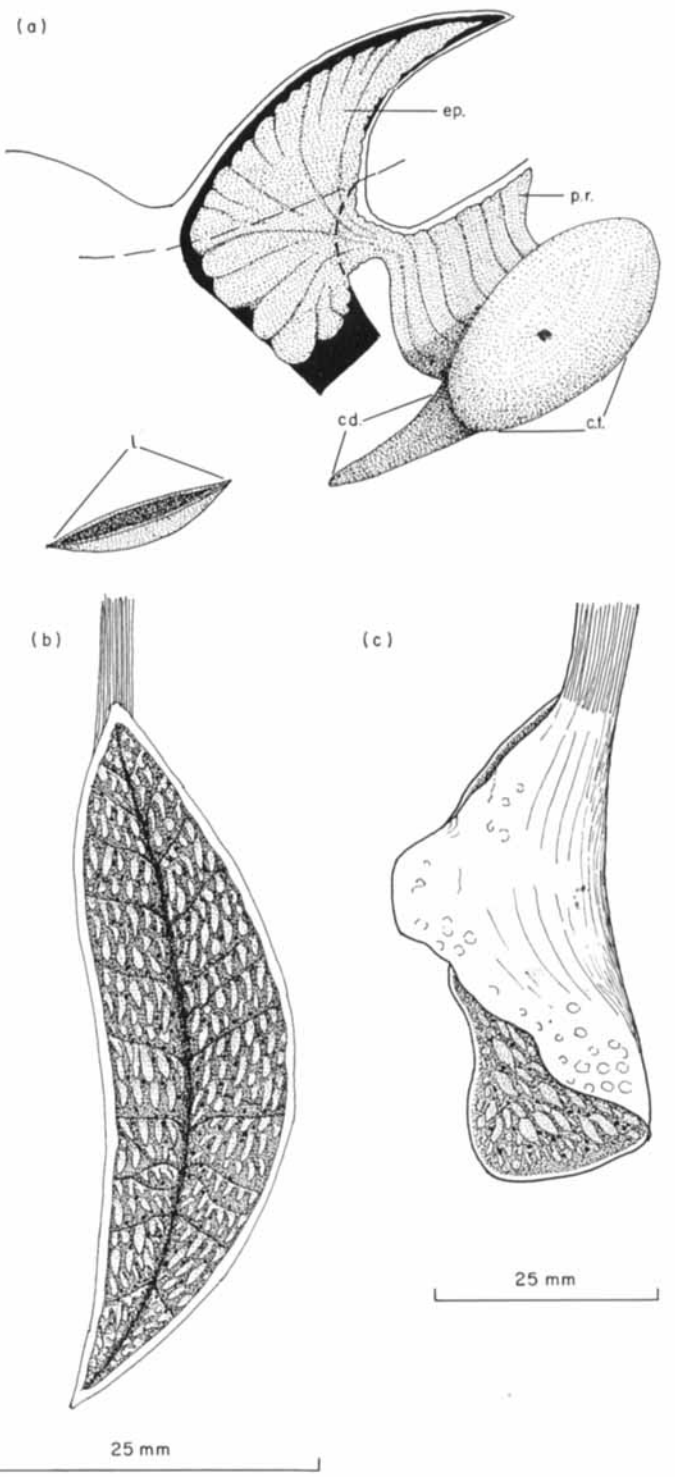

FIG. 11. *Ceratotherium simum* (specimen R76). Showing (a) associated major faucial and minor laryngopharyngeal tonsillar formations, (b) mucosal aspect of laryngopharyngeal tonsil, (c) lateral aspect of dextral laryngopharyngeal tonsil. Tonsillar tissue stippled; epiglottis black; pyriform fossa inlet indicated by broken line. c.t. = caput tonsillae: c.d. = cauda tonsillae: ep. = epiglottic extension: l = laryngopharyngeal tonsil: p.r. = processus retrolingualis.

formation is composed of medial and lateral moieties separated by the fossa cavity: the prow, stern and keeled bottom of the "boat" are formed by their fusion ventrally, dorsally and posteriorly. The tonsil mucosal surface ("hull" interior) is reticulated and exhibits the multiple, uniformly small ostia of mucous glands (some 3–4 mm deep by 2·0–2·5 mm wide) and great numbers of stout conical papillae (ranging in length from 3·5–8·5 mm). Fossulae are not developed (Fig. 11(b, c)).

The organ's external surfaces are encapsulated with strong connective tissue which is condensed ventrally, dorsally and posteriorly to form local ligaments of tonsil attachment. A stout band of tissue (lig. laryngo-tonsillaris) passes from the trigonum fibroelasticum of the larynx wall to the medial aspect of the tonsil, still further ensuring its stability. The connective tissue capsule supports a peritonsillar plexus of relatively large veins, the terminal vessels of which, accompanied by prominent lymphatics, leave the pyriform fossa through the foramen thyroideum.

In *Ceratotherium* R76 the faucial tonsillar formation with its extensions greatly exceeds in bulk the laryngopharyngeal tonsil and presumably functioned as the effective tonsil of the lateral food channel. Its massive retrolingual process is remarkable for its invasion of the pyriform fossa in series parallel with the cauda tonsillae. This fossa invasion, though considerable, is nevertheless subtotal and a laryngopharyngeal tonsil is accordingly developed to supplement the fossa "tonsilization". The anatomical disposition of the fossa tonsillar tissue indicates forcefully that such tissue derives from the mutual and reciprocal activity of the second and third pharyngeal pouches, in which the second pouch exerts a preponderant role.

The tonsillar morphology of Black rhinoceros R19

This young *Diceros* specimen is unique in the present series in respect of its mode of pyriform fossa "tonsilization", which takes the form of a complete submucosal carpeting of the fossa by the faucial tonsil alone, but by means of conjoint caudal prolongations of both caput tonsillae and processus retrolingualis (Fig. 13(c)). These prolongations cover the fossa walls, are continuous through the fossa fundus and thus render unnecessary the development of any supplementary laryngopharyngeal tonsil. The tonsillar tissue of the specimen is also notable for an intrinsic preponderance of glands to lymphoid tissue and for the presence on its mucosal surface of papillae of quadrate outline, not observable in the remaining specimens of the series.

The sole tonsillar formation developed in the lateral food channel is the tadpole-shaped faucial tonsil, 100 mm long dextrally, 115 mm long sinistrally. The organ comprises a large ovoid caput tonsillae (Fig. 12(a)), which gives off an exceptionally well-developed retrolingual process and a tapering cauda tonsillae. Both the process and the cauda extend posteriorly into the pyriform fossa (Fig. 13(c)). The tonsil mass does not invade either the tongue or the soft palate: a dorsally situate slit on its medial surface is the ostium of an angulated saccule representing the original tonsillar diverticulum from the second pharyngeal pouch. The caput tonsillae occupies the anterior vallecular region and impinges permanently upon the vinculum so as to reduce its local thickness by one third. (The vinculum itself is a robust partition 50 mm long, 30 mm high, 20 mm thick anteriorly, 30 mm thick posteriorly).

Dextrally the caput tonsillae is 58 mm long, 27 mm high and 27 to 18 mm in diminishing antero-posterior width, sinistrally 53 mm long, 27 mm high and 21 to 15 mm in

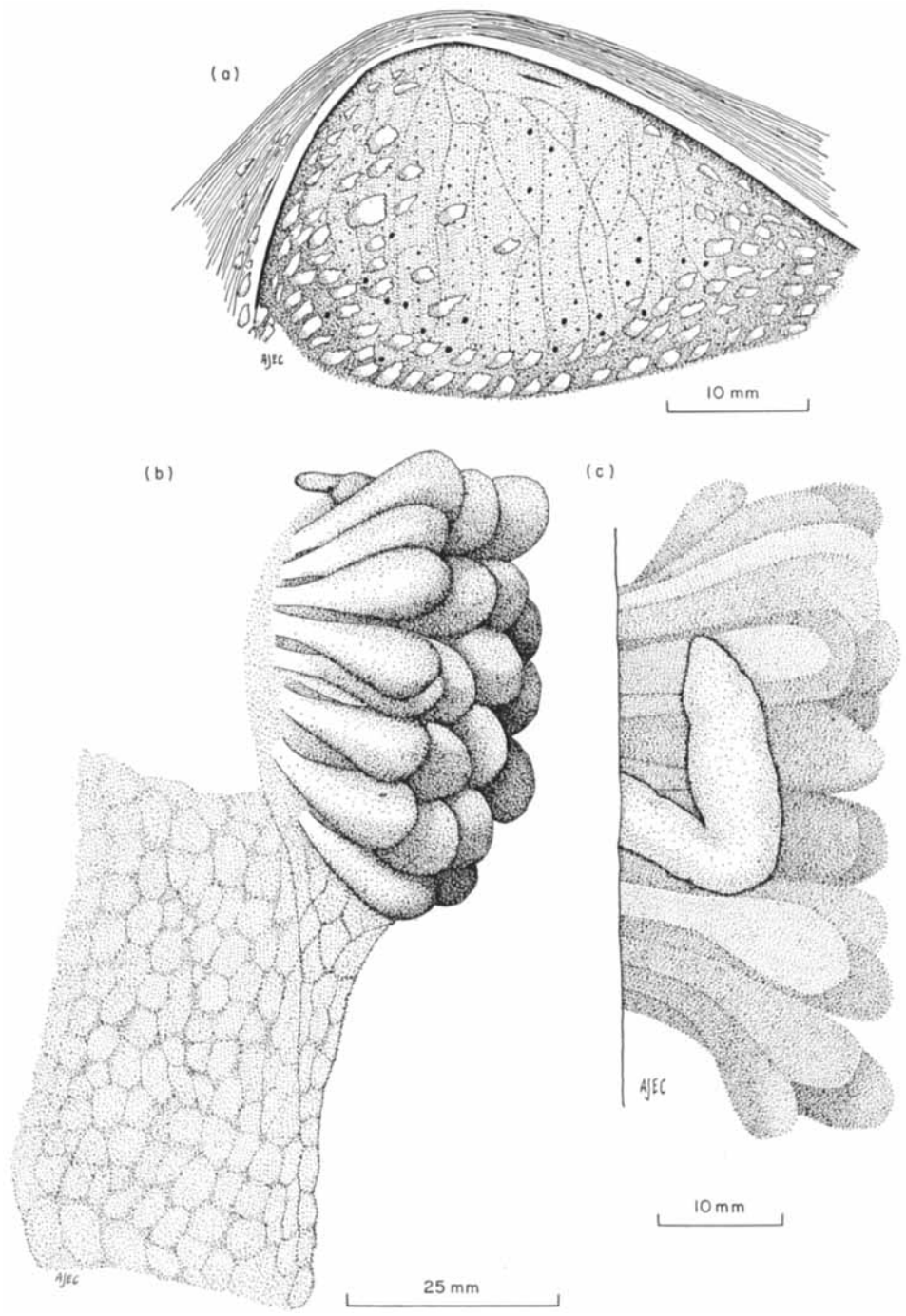

FIG. 12. *Diceros bicornis* (specimen R19). Showing (a) dextral aspect of caput tonsillae in norma medialis, (b) sinistral faucial tonsil and fossulae in norma lateralis, (c) dextral tonsillar fossulae and superjacent tonsillar diverticulum in norma cranialis.

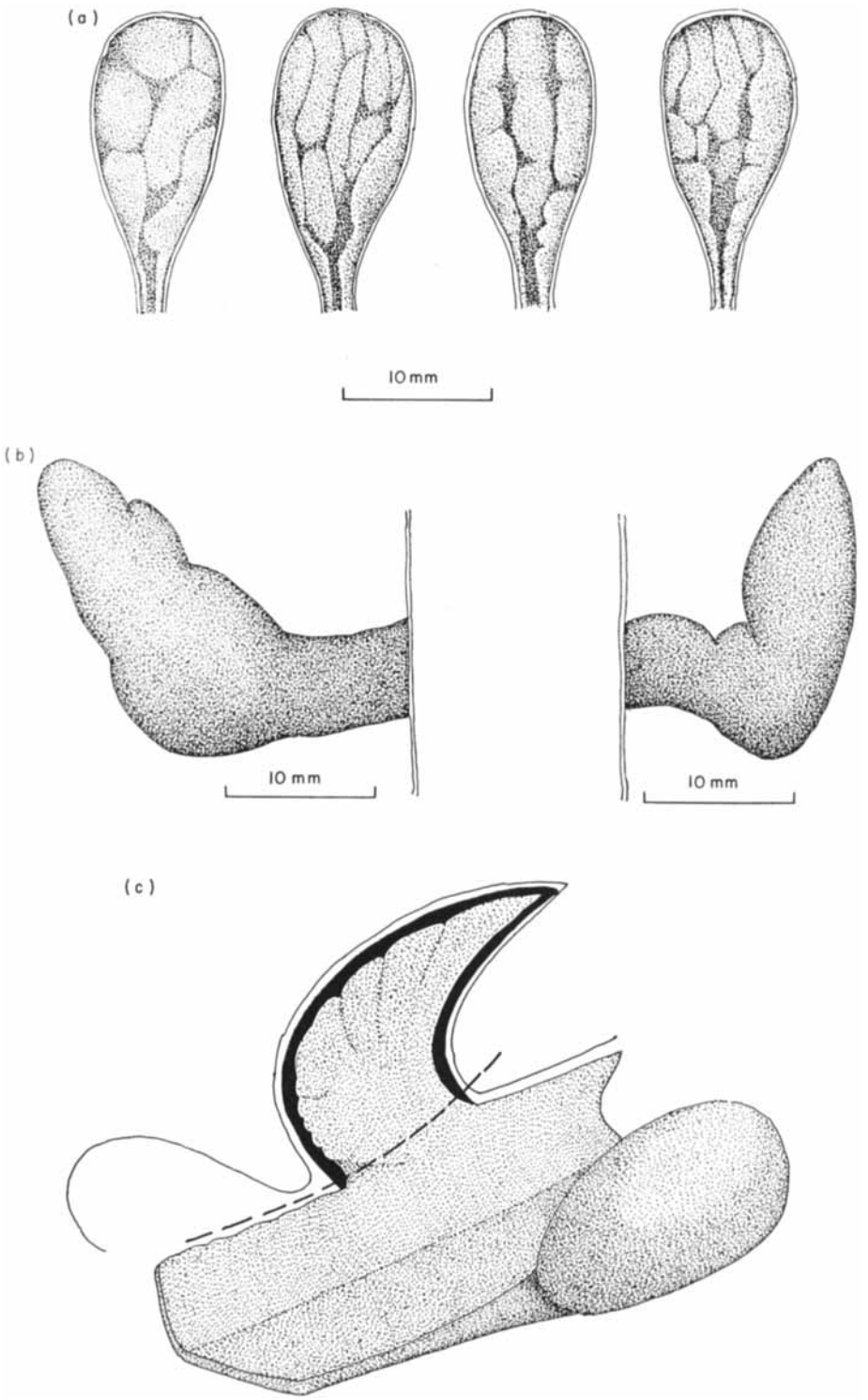

FIG. 13. *Diceros bicornis* (specimen R19). Showing (a) fossulae opened to display mucosal lymphoid content, (b) the sinistral and dextral tonsillar diverticula, (c) the maximally developed (dextral) faucial tonsil.

corresponding width: each mass is wider dorsally than ventrally and is largely composed of fossulae: each is essentially a multitude of small glands embedded in compact lymphoid tissue plus a smaller though considerable number of fossulae, similarly embedded proximally and mutually connective-tissue bound distally. The predominance of the glandular element in both caput and cauda tonsillae may reflect the specimen's immaturity. The caput medial (mucosal) surface, everywhere convex, is reticulated and beset by multiple gland ostia and papillae. Most of these ostia are small (under 1 mm diameter) and disposed in linear series: a smaller number, those of fossulae, are larger (1 mm or more in diameter) and more randomly distributed over this surface. The fossulae (Fig. 12(b, c)), some 25 in number, are capacious, club-shaped, sacs, some 18–21 mm long and 7–9 mm in maximal width, lined by a thick mucosa which is macroscopially laden with lymphoid tissue (Fig. 13(a)). The sacs are lymphoid tissue-free externally and are so bound together by dense connective tissue as to form a fairly solid mass constituting most of the caput tonsillae thickness.

Close to its dorsal border this medial surface of the caput tonsillae presents an inconspicuous slit-like mucosal orifice, some 5–7 mm long, which is the ostium of the primordial tonsillar diverticulum. The orifice leads into a blindly ending saccule (Fig. 12(c)) some 20 mm long and some 13–15 mm wide: from the orifice the saccule proceeds dorsolaterally for some 13 mm and then becomes angulated anteriorly for about 20 mm. The sinistral saccule is the larger of the two structures. Each is lined by a mucosa heavily impregnated with lymphoid tissue and lies alongside, but slightly above, the fossulae, from which it is readily distinguishable by its greater capacity and distinctive angulation. Neither saccule invades the soft palate.

The less convex lateral surface of the caput tonsillae is almost completely obscured by the emergent cluster of wide-bodied fossulae and lies in contact with a well-developed connective tissue capsule. This last provides a fascial support to the fossulae, both individually and collectively, and supports a paratonsillar plexus of relatively large veins.

The cauda tonsillae, an elongated tapering mass of lymphoid tissue developed around small mucous glands, is 42 mm long dextrally, 60 mm long sinistrally. It enters the pyriform fossa, covers the whole of the fossa lateral wall and in the fossa fundus becomes continuous with the caudal prolongation of the retrolingual process. It differs structurally from the caput tonsillae solely in its non-development of fossulae. Its attached lateral surface adheres to the thyroid cartilage lamina, its mucosal medial surface is reticulated, manifesting gland ostia and papillae. The ostia are uniformly small and lie mostly in continuous rows: the papillae are of the quadrate variety and crowd the surface in serried rows.

The processus retrolingualis is developed in thickness and extent to a degree unmatched in any previous specimen of the series. It not only ascends upon the whole lateral extent of the vinculum but also extends thence to cover both the lateral aspect of the epiglottic cartilage and the remaining (dorsal) area of the pyriform fossa medial wall. It clothes this wall completely and in the fossa fundus becomes continuous with the expanded cauda tonsillae. It is 7 mm thick upon the vinculum, 3 mm thick in the pyriform fossa: its overlying mucosa is heavily papillated by parallel linear series of quadrate papillae.

The pyriform fossa is carpeted submucosally by a continuous sheet of tonsillar tissue constituted by the continuity of the expanded cauda tonsillae with the caudal prolongation

of the processus retrolingualis. Its reticulated surface displays multiple small gland ostia and regular rows of quadrate papillae.

The papillae of this specimen's mucosal surfaces (Fig. 14(d)) are caudally recurved and tend to lie in parallel linear series: the smallest are 2·0–2·5 mm long, the largest 4·0–4·5 mm, their average length being 3·5 mm. Their variation in configuration resolves them into three distinct varieties, viz. (1) large or small papillae of typically conical shape with bodies narrowing more or less abruptly into short, acuminate apices, (2) papillae of conical shape, but with indented, notched or serrated margins, (3) non-conical structures of bilaterally compressed, quadrilateral shape, wherein an apex is replaced by a distal border, of serrated or pectinate outline. Such papillae quadratae are particularly abundant upon the vinculum and the pyriform fossa walls. Their counterpart is not observable in any other specimen in the present series. It is possible that a quadrate papilla is compounded of several conical papillae which for some reason have remained undifferentiated. In an earlier specimen of this series (*Ceratotherium* R76) the pyriform fossa is "tonsilized" from the second and third pharyngeal pouches in dual fashion, i.e. in part by antomically independent caudal prolongations of the caput and retrolingual process of the faucial tonsil and in part by a discrete laryngopharyngeal tonsil. In the present specimen (*Diceros* R19) the fossa is "tonsilized" solely and entirely by the second pouch faucial tonsil by means of similar, but larger and anatomically confluent, prolongations of caput and retrolingual process, thus obviating all necessity for the development of any laryngopharyngeal tonsil. The tonsillar tissue of the pyriform fossa derives clearly from a single embryonal source and yields no indication of developmental duality.

Commentary

Examination of the present limited series of specimens establishes, for all rhinoceros genera, not only the anticipated presence of tonsillar tissue within the recessus tonsillaris (canonical faucial tonsil) but also the hitherto unrecognized presence of such tissue within the pyriform fossa. This fossa tissue is constant in occurrence and considerable in quantity, yet variable in its topographical disposition (Fig. 15(a–e)). It may present as a caudal extension (cauda tonsillae) of the faucial tonsil along the fossa lateral wall, or as a caudal extension of the processus retrolingualis along the fossa medial wall, or as a discrete lymphoid mass (laryngopharyngeal tonsil) within the fossa fundus, or as some combination of such formations. The presence of tonsillar tissue within the rhinoceros pyriform fossa became initially suspect when an earlier investigation of local lymphatic arrangements (Cave, 1978) showed the outflow of lymph from the fossa to exceed that expectable from its lining mucosa alone.

Of the five rhinoceros specimens presently studied a faucial tonsil alone is present in two (*Rhinoceros* R75, *Diceros* R19) and is entirely responsible for the "tonsilization" of the pyriform fossa: in the remaining three specimens (*Didermocerus* R72, *Ceratotherium* R20, R76) faucial and laryngopharyngeal tonsils co-exist and share this "tonsilization" in varying measure—the faucial tonsil assuming a major share in one specimen (*Ceratotherium* R76), the laryngopharyngeal tonsil assuming this share in two specimens (*Didermocerus* R72, *Ceratotherium* R20). The indications are that the precise topographical disposition of pyriform fossa tonsillar tissue is subject to an intraspecific individual variation greater than present limited findings might suggest and that such variation is therefore wholly devoid of taxonomic significance.

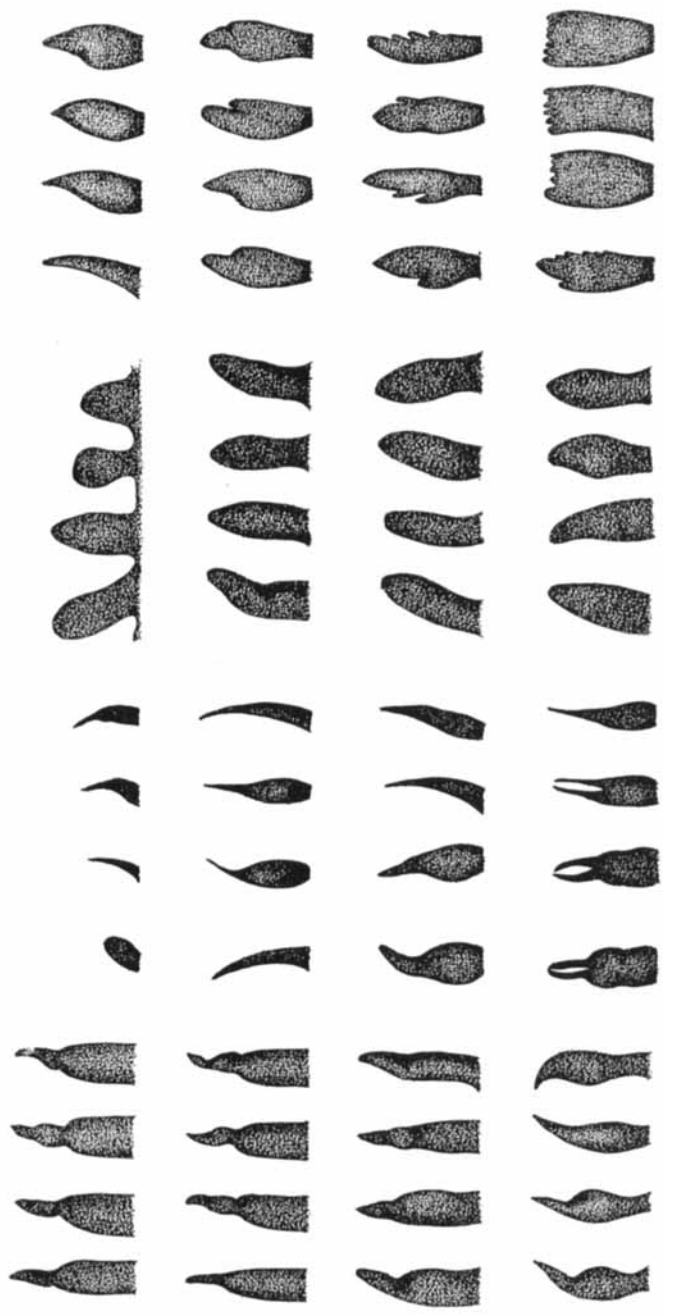

FIG. 14. Rhinoceros tonsillar papillae. Showing papilla configuration in specimens of (a) *Rhinoceros*, (b) *Didermocerus*, (c) *Ceratotherium*, (d) *Diceros*.

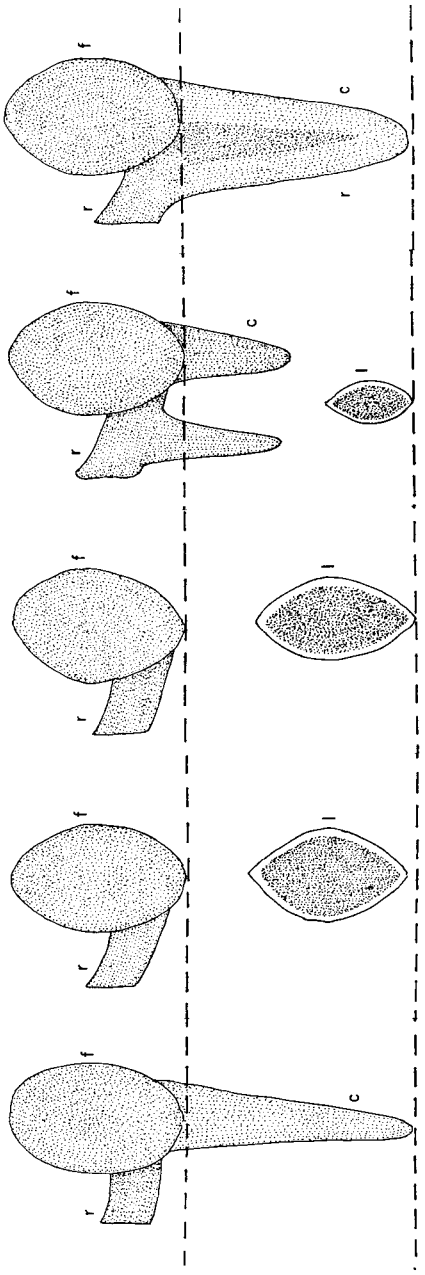

FIG. 15. Diagram of rhinoceros tonsillar formations and relationship to pyriform fossa. c=cauda tonsillae: f=caput tonsillae: l=laryngopharyngeal tonsil: r=processus retrolingualis: broken lines=pyriform fossa limits.

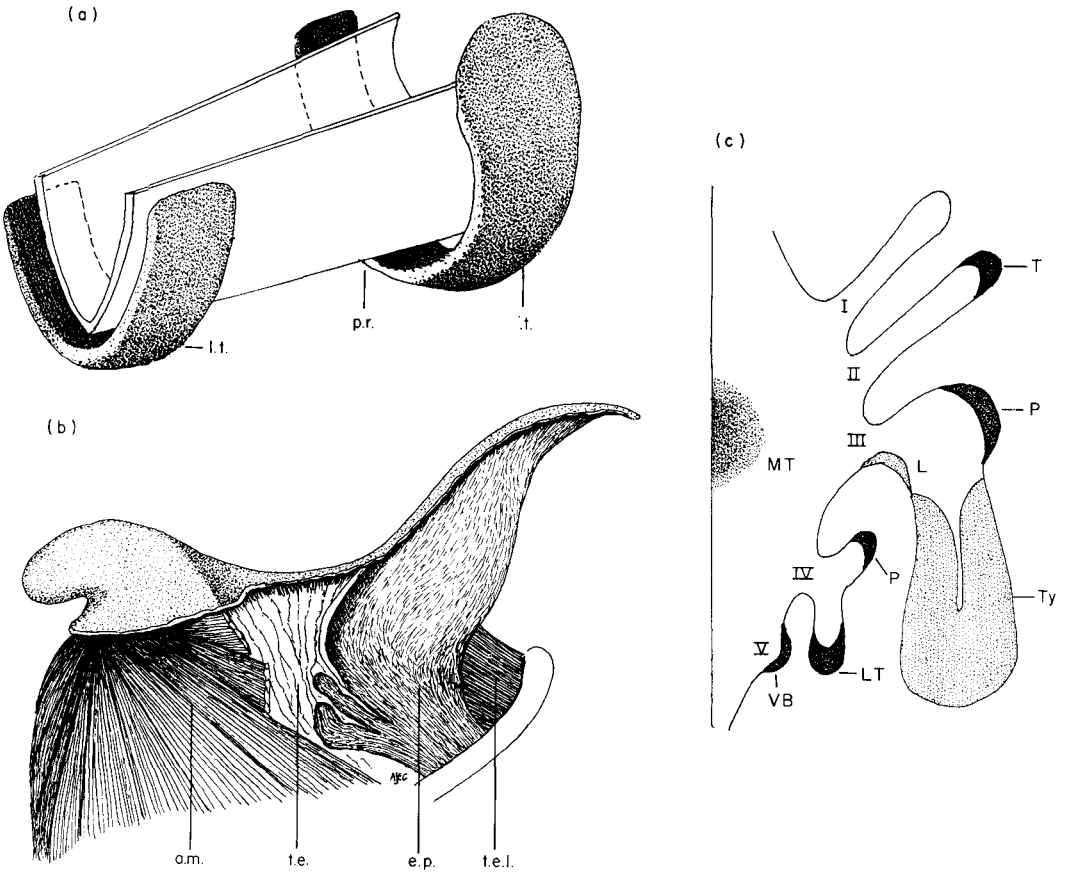

FIG. 16. Diagrammatic representation of (a) rhinoceros lateral food channel and tonsillar armillae, (b) tripartite medial wall of pyriform fossa, (c) embryonal relationship of laryngopharyngeal tonsil to thymus gland. am = arytenoid musculature: ep = epiglottis: f.t. = faucial tonsil: l.t. = laryngopharyngeal tonsil: p.r. = processus retrolingualis: t.e. = trigonum elasticum: t.e.l. = thyro-epiglottic ligament: L = laryngopharyngeal tonsil: LT = lateral thyroid: MT = medial thyroid: P = parathyroid: T = faucial tonsil: Ty = thymus: UB = ultimobranchial body: I to V = pharyngeal pouches.

Present anatomical evidence indicates that the quantum of tonsillar tissue essential to the functional activity of the rhinoceros pyriform fossa derives primarily from the faucial tonsil but may require supplementation by a specially developed laryngopharyngeal tonsil. It also indicates that co-existent intra-fossal faucial and laryngopharyngeal tonsillar formations, whilst physiologically complementary, are nevertheless distinct morphological entities. Since, as noted below, the rhinoceros faucial tonsil undoubtedly develops from the second pharyngeal pouch and the laryngopharyngeal tonsil from the third, these two pouches are jointly and exclusively responsible for the "tonsilization" of the rhinoceros lateral food channel. Their respective roles therein are mutually reciprocal and are subject to an inherent variation which accounts sufficiently for the observed differences of tonsillar tissue disposition within that channel.

A canonical faucial (palatine) tonsil is expectedly present in every rhinoceros specimen examined. The organ is relatively large, compact and sharply circumscribed and conventionally "well developed": it occupies the recessus tonsillaris whence it protrudes into the whole or greater part of the vallecula. In present material at least it does not invade either the tongue or the soft palate and in one specimen only does it manifest any recognizable remains of the primordial tonsillar diverticulum. The impression is gained however that the organ's abundant lymphoid tissue is concentrated within and around the ventral lip of this structure.

In every specimen examined the faucial tonsil gives off inferomedially a carpet-like process (processus retrolingualis) which underlies the vallecula floor and ascends a variable distance upon the vinculum glosso-epiglotticum, whence it may be prolonged caudally over the lateral aspect of the epiglottic cartilage or even over the entire medial wall of the pyriform fossa. The main tonsil mass (caput tonsillae) may be prolonged caudally into the fossa by a tail-like process (cauda tonsillae), sometimes of considerable size. Caput tonsillae, cauda tonsillae and processus retrolingualis share with the laryngopharyngeal tonsil an identical pattern of mucosal surface configuration and differ structurally in but a single particular, viz. the restriction of fossulae to the caput tonsillae.

The laryngopharyngeal tonsil (developed in the *Didermocerus* and *Ceratotherium* specimens) is an obtrusively independent lymphoid organ. A discrete, sessile, navicular mass of reticulated compact lymphoid tissue, it is confined to the pyriform fossa fundus and is patently distinct from any co-existent tonsillar formation within the fossa. Intrinsic to the fossa fundus its truly tonsillar nature is evidenced by its close resemblance to the faucial tonsil in histological structure, in its strong encapsulation, in its association with an extrinsic venous plexus and in its occupancy of an anatomical cul-de-sac of pharyngeal pouch origin. Its total morphology proclaims it an organ of independent genesis, developmentally in series with the faucial tonsil and physiologically supplementary thereto, but nevertheless a distinct morphological entity, whose mass may indeed exceed that of the faucial tonsil.

The ontogenesis of both the faucial and the laryngopharyngeal tonsils remains unascertained by any specific investigation of the embryonal rhinoceros pharynx, but indirect anatomical evidence renders morally certain the pharyngeal origin of both these lymphoid organs. Thus the rhinoceros faucial tonsil resembles so precisely in structure and topography the tonsils of known development in other mammals that its origin from the second pharyngeal pouch cannot be doubted, whilst the rhinoceros laryngopharyngeal tonsil is so intimately associated with the pyriform fossa fundus that its presence therein is explicable only on the assumption of its development *in situ*. Since the pyriform fossa develops largely from the third pharyngeal pouch such an assumption is not only justifiable but also virtually inescapable in view of the known pattern of mammalian pharyngeal pouch organopoiesis.

In higher vertebrates the second and third pharyngeal pouches manifest a predilection for lymphoid tissue production, as evidenced by the development of the faucial tonsil from the second pouch and of the thymus gland—Keith's (1948) "buried tonsil"—from the third. The intensely lymphopoietic third pouch contributes very largely to the formation of the definitive pyriform fossa and may therefore reasonably be presumed to carry into the developing fossa some rudiment of its primordial lymphoid endowment, capable of subsequent elaboration therein into a laryngopharyngeal tonsil (Fig. 1(b, c)). Indeed

such a presumption will alone account satisfactorily both for the laryngopharyngeal tonsil's total morphology and for its close histological similarity to thymic tissue.

On the indirect basis of anatomical evidence it is therefore inferred that in the rhinoceros embryonal pharynx the lymphoid primordium of the third pouch normally differentiates into two disproportionate masses, viz. a major, migratory mass which develops into the definitive thymus gland, and a minor, residual mass potentially capable of development into a laryngopharyngeal tonsil.

Present anatomical findings indicate that the considerable quantity of tonsillar tissue invariably present in the rhinoceros pyriform fossa is provided entirely by the second pouch faucial tonsil and the third pouch laryngopharyngeal tonsil, and that the faucial tonsil has priority in such provision. For clearly the faucial tonsil may "tonsilize" the fossa either unaided (as in specimens R75, R19) or with the assistance of a supplementary laryngopharyngeal tonsil (as in specimens R72, R20, R76).

The precise pattern of pyriform fossa "tonsilization" (i.e. the proportionate contribution thereto made by faucial tonsil, processus retrolingualis and laryngopharyngeal tonsil) is a matter of individual variation and has no taxonomic relevance.

The presence of tonsillar tissue in some quantity within the rhinoceros pyriform fossa is correlated with the development of a large vascular foramen (foramen thyroideum) in the lamina of the thyroid cartilage: this foramen transmits a considerable, and otherwise inexplicable, leash of blood vessels and lymphatics entering or leaving the fossa interior, and appears to be peculiar to the Rhinocerotidae among perissodactyls.

The rhinoceros lateral food channel tonsillar formations are characterized by great intrinsic vascularity and by close individual association with an extrinsic venous plexus—the faucial tonsil with a paratonsillar plexus, the laryngopharyngeal tonsil with a peritonsillar plexus, the processus retrolingualis with a vallecular plexus. Such morphological disposition testifies to a sustained lymphoid tissue metabolism and to the rapid passage into the bloodstream of the organic (cellular) and inorganic products of such metabolism.

The tonsillar morphology of the rhinoceros lateral food channel differs in certain particulars from that obtaining in the Tapiridae and Equidae: whether its pattern is peculiar to the Rhinocerotidae amongst mammalian families in general remains, however, open to enquiry.

Conclusions

A canonical faucial tonsil is prominently developed in all rhinoceros genera. The organ is prolonged into an infero-medial processus retrolingualis associated with the vallecula, and may be prolonged posteriorly as a cauda tonsillae into the pyriform fossa. Its retrolingual process may be similarly prolonged posteriorly either independently of, or in continuity with, a cauda tonsillae.

Tonsillar tissue is present submucosally in the rhinoceros pyriform fossa, its disposition taking the form of a caudal extension of the faucial tonsil along the fossa lateral wall, or of a caudal extension of the processus retrolingualis along the fossa medial wall or of a discrete laryngopharyngeal tonsil within the fossa fundus or of some combination of such formations. Such variation in disposition is of developmental, not taxonomic, significance.

The presence of tonsillar tissue in the rhinoceros pyriform fossa occasions the development of a vascular foramen (foramen thyroideum) in the lamina of the rhinoceros thyroid

cartilage. The tonsillar tissue of the rhinoceros lateral food channel derives exclusively from the reciprocal activity of the embryonal second and third pharyngeal pouches.

The laryngopharyngeal tonsil is an independent and hitherto unrecognized lymphoid organ, functionally supplementary to the faucial tonsil. Its morphology indicates its development in association with the thymus gland from the lymphoid primordium of the third pharyngeal pouch. A Eustachian tube diverticulum (guttural pouch) is not developed in the Rhinocerotidae.

Summary

A description is given of the structure and topography of the tonsillar formations obtaining in the lateral food channel of individual Indian, Sumatran, African White and African Black rhinoceroses. The rhinoceros pyriform fossa is shown to contain tonsillar tissue. Rhinoceros pyriform fossa tonsillar tissue may be represented, wholly or partially by a previously unrecognized lymphoid organ—the laryngopharyngeal tonsil—of which an account is given.

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