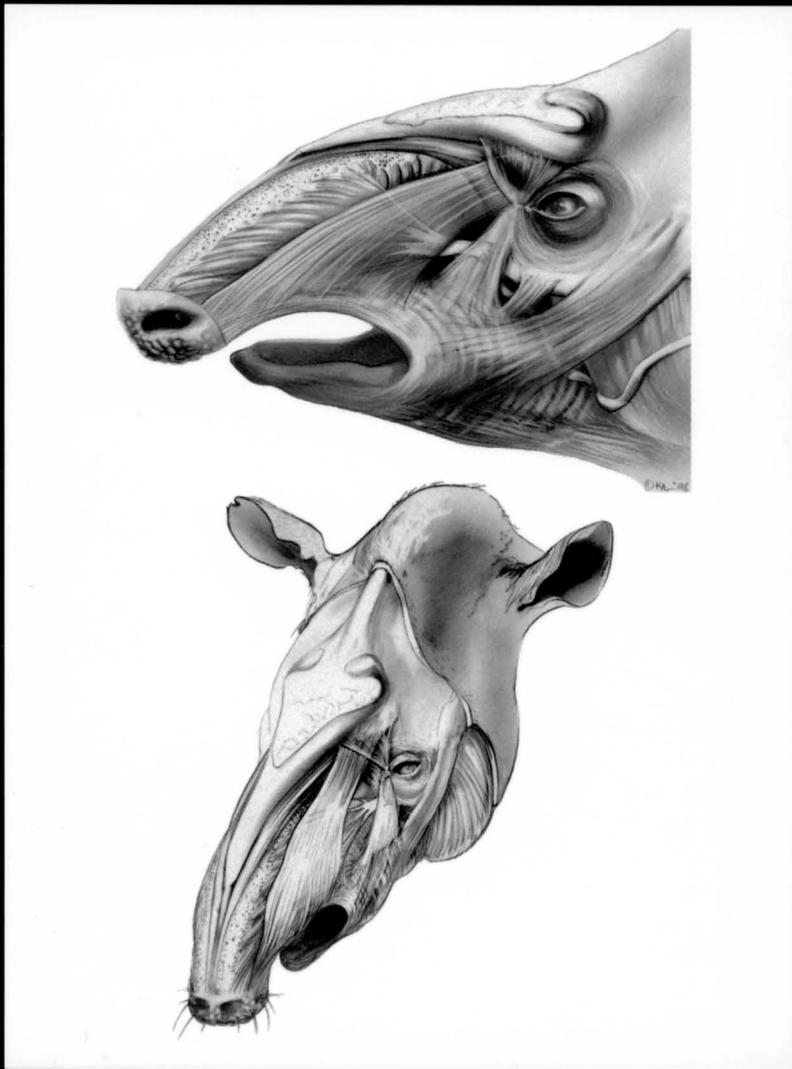


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The proboscis of tapirs (Mammalia: Perissodactyla): a case study in novel narial anatomy

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Abstract

The trunk-like proboscis of tapirs provides a prime case study in the evolution of anatomical novelty. Morphological study of this unique structure was undertaken employing several specimens and a combination of analytical techniques: gross anatomical dissection, radiographic imaging and histological sectioning. Evolution of the proboscis of tapirs entailed wholesale transformation of the narial apparatus and facial architecture relative to perissodactyl outgroups. This transformation involved retraction and reduction of the bony and cartilaginous facial skeleton, such that several structures present in outgroups are completely absent in tapirs, including cartilages surrounding the nasal vestibule (e.g. alar and medial accessory cartilages, rostral portion of the nasal septum) and associated musculature (dilator naris apicalis, lateralis nasi pars ventralis). At the same time, soft tissues surrounding the upper lip and nose became elaborated to form a mobile, fleshy proboscis. Several key facial muscles (e.g. levator labii superioris, levator nasolabialis, caninus, lateralis nasi) have been co-opted to function in movement of the proboscis. The nasal vestibule is expanded and occupies approximately 75% of the nasal cavity. Vestibular expansion has compressed and simplified caudal components of the nasal cavity (e.g. reduction of dorsal and middle nasal conchae, loss of plica recta and plica basalis). The airway has become dorsally arched causing the ventral conchal complex to become inclined relative to the long axis of the skull. A few anatomical enigmas remain, such as the complicated maxilloturbinate that rostrally contacts the nasal septum and vomeronasal organ. Similarly, the meatal diverticulum, despite being both ancient and anatomically complex, has no obvious functional significance; it is clear that it is not homologous to the nasal diverticulum of horses and other equids. The reduction of the osseocartilaginous portion of the proboscis, coupled with expansion of the muscular and connective tissue components, has resulted in an organ that is best interpreted as a muscular hydrostat.

Key words: Perissodactyla, *Tapirus*, nasal anatomy, proboscis, muscular hydrostat

INTRODUCTION

Among extant vertebrates, tapirs provide a dramatic example of transformation of the narial apparatus in that they have evolved an enlarged, mobile proboscis akin to that of elephants (Fig. 1). Tapirs, like equids (horses, asses, zebras) and rhinoceroses, are odd-toed ungulates and thereby members of Perissodactyla (Mesaxonia of Fischer & Tassy, 1993). Tapirs are an ancient group, represented from the Eocene to the present, with a broad geographic range that includes North America, South America, Europe and Asia (Radinsky, 1965; Prothero & Schoch, 1989; Nowak,

1991). Four extant species are recognized, all within a single genus, *Tapirus*, and all restricted either to Asia or to South America (Nowak, 1991). For the most part, they are crepuscular, solitary browsers preferring woody or grassy habitats close to permanent water supplies. They subsist predominantly on green shoots, though their diet also includes aquatic plants, twigs, leaves and fruits (Eisenberg, 1981; Nowak, 1991). The proboscis itself is used during feeding to manipulate shoots and branches; it is also held close to the ground during locomotion, presumably for olfactory detection of food items, predators, and other tapirs (Macdonald, 1985).

In comparison to other extant perissodactyls, tapirs are specialized in several aspects of their head morphology (Owen, 1831; Turner, 1850; Murie, 1872;

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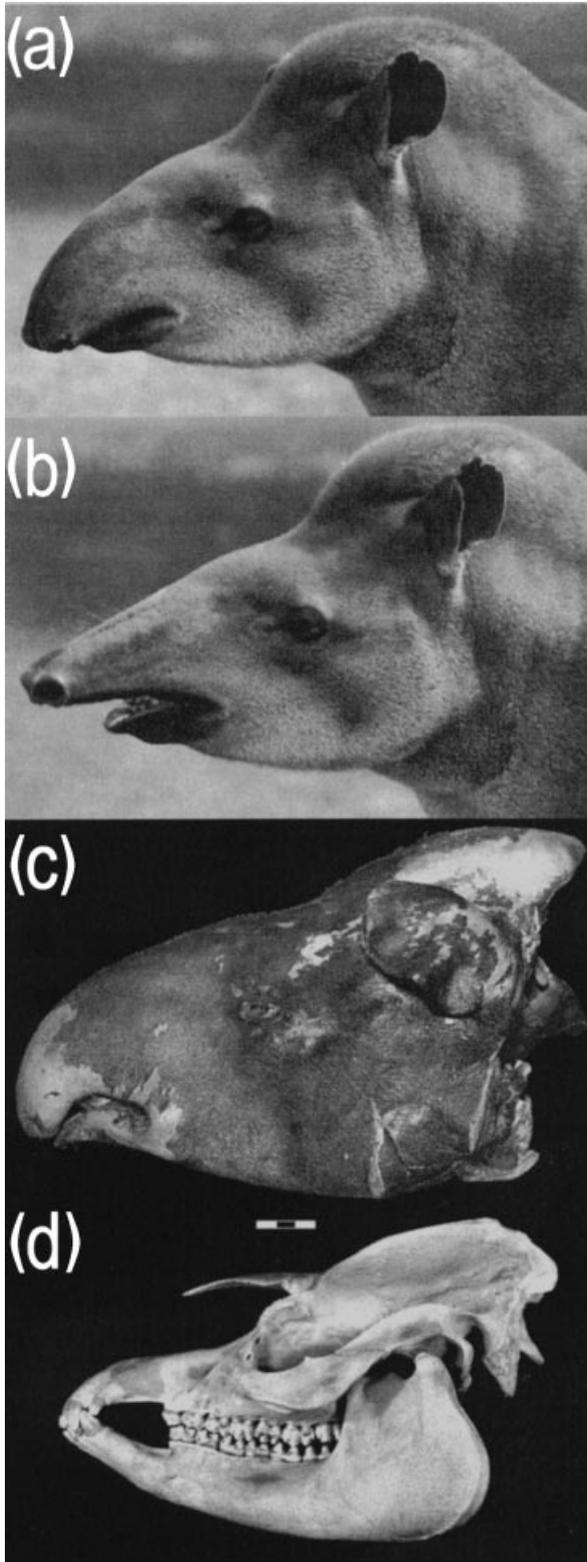


Fig. 1. Photographs of the head and skull of *Tapirus terrestris* in left lateral view. (a) Head of live tapir with proboscis at rest; (b) same animal with proboscis extended and nostrils dilated; (c) FMNH 155691, head before dissection of the facial region; (d) skull of FMNH 155691 prepared after dissection. Scale bar in (c) and (d) = 3 cm.

Bressou, 1961). In addition to the proboscis, their skulls have more rostrally positioned orbits, better developed sagittal crests, and more elongate and retracted nares (Fig. 1d). Skull anatomy was reviewed by Radinsky (1965) and Wall (1980). Of particular note is the work of Boas & Paulli (1908, 1925) who provided detailed descriptions and exquisite illustrations, comparing facial musculature of tapirs with that of elephants and other mammals. However, Boas & Paulli concentrated primarily on facial muscles, with only minor consideration of other aspects of morphology, such as neurovasculature and the cartilaginous nasal capsule. The present study addresses all major tissue types within the snout, including bone, muscle, cartilage, nerves, blood vessels and skin. Each tissue type is briefly described, with an emphasis on relationships between types. In particular, we focus on the interface between the soft and bony tissues of the narial region. This is followed by a brief anatomical review of the nasal cavity. The intent is not to provide an exhaustive treatment of all aspects of facial anatomy but rather to highlight those portions that are likely to impact significantly on interpretation of the narial apparatus.

This study is part of a larger project investigating novel narial anatomy in extant and extinct vertebrates. A major goal of the project is to provide primary descriptions of novel narial morphologies (e.g. inflatable integumentary bladders, fleshy probosces) among living taxa, with an eye toward establishing osteological correlates of soft-tissue structures. Ultimately, we hope to be able to associate particular soft tissues (e.g. muscles, cartilages, nerves, blood vessels) with specific bony morphologies (e.g. fossae, foramina, tuberosities, elemental configurations) in order to infer narial function in extinct taxa, for which only fossilized remains are available. A further goal is to go beyond current form and utility to investigate the evolution of apomorphic narial apparatuses generally. In other words, how does natural selection, together with other evolutionary forces, operate on available 'raw materials' to bring about often radical transitions in narial structure and function?

MATERIALS AND METHODS

The primary data for this study were derived from the heads of 3 tapirs, all zoo animals, representing 2 species and 3 age groups: a neonate *Tapirus terrestris* (South American, lowland, or Brazilian tapir), a 7-month-old female *T. indicus* (Asian or Malayan tapir), and an adult *T. terrestris* (FMNH 155691). In addition, several adult skulls (e.g. *T. terrestris*, AMNH 14103, AMNH 2592, FMNH 155691, NMNH 374864; *T. indicus*, AMNH 180030, NMNH 14648; *T. bairdii*, AMNH 208259, NMNH 11280; *T. pinchaque*, NMNH 11883) were used to facilitate description and elucidate osteological correlates. The bulk of the present description, however, is based on the adult specimen of *T. terrestris* (FMNH 155691; Fig. 1c, d). Institutional abbreviations

are: AMNH, American Museum of Natural History, New York City; FMNH, Field Museum of Natural History, Chicago; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, DC; NYCOM, New York College of Osteopathic Medicine; OU, Ohio University.

The descriptions and illustrations below were derived from a combination of radiographic imaging, gross anatomical dissection, and histological sectioning. Both the juvenile (*T. indicus*) and adult (*T. terrestris*) specimens were subjected to computerized tomographic (CT) imaging, and the latter was also analysed using magnetic-resonance imaging (MRI). Gross anatomical dissection of all three heads was carried out sequentially from superficial to deep. The heads were fresh-frozen and thawed before dissection. In addition, 2 transverse sections were made of the proboscis of the juvenile specimen, and the adult head was refrozen and sagittally sectioned using a band-saw in order to expose internal nasal structures. Histological sectioning was conducted on the 7-month-old *T. indicus* using standard techniques; 3 transverse sections through the fleshy proboscis at the level of the rostral limit of the skull were prepared. Additionally, heads and skulls of domestic horses (*Equus caballus*) were dissected and studied; 1 head was CT scanned, sagittally sectioned, dissected, and ultimately skeletonized. As far as possible, terminology follows Nomina Anatomica Veterinaria (1994; see also Schaller, 1992).

RESULTS

General description of the proboscis

The proboscis of tapirs is a mobile, fleshy organ derived from the tissues of the upper lip and nose (Fig. 1). It is a more-or-less tubular structure extending from a position caudodorsal to the orbit rostrally beyond the premaxillary rostrum to drape ventrally past the lower lip. The paired nasal airways pass through the proboscis, beginning rostrally at the terminally-positioned nostrils and entering the nasal cavity proper at approximately the level of the rostral tip of the nasal bones; left and right sides remain separate throughout their lengths. The length of the proboscis varies somewhat among the four extant species of *Tapirus*, being the longest in *T. indicus* and shortest in *T. terrestris*. These variations may well be reflected in craniofacial osteology; for example, the nasal cavity of *T. indicus* is considerably more vaulted than in *T. terrestris*, and the premaxilla (= Os incisivum (NAV, 1994)) is more rounded rostrally in the former taxon. Unless otherwise noted, the following description pertains to *T. terrestris*.

Integument

Tapirs are 'pachyderms' in the sense that their skin is relatively very thick (Figs 2 & 3; *i*; see Table 1 for an

explanation of abbreviations). On the head, the skin is thickest supracranially and thins considerably toward more distal portions of the proboscis. In the two species studied here (*Tapirus terrestris* and *T. indicus*), the fur of the head is short and bristly. The tip of the proboscis has numerous long, coarse hairs (i.e. vibrissae) that presumably have a mechanosensory function. The epidermis is thicker and more highly keratinized on the ventral side than the lateral side. The nostrils are transversely oriented. The skin immediately surrounding the nostrils is more heavily pigmented and keratinized, with a distinct pattern of roughened tubercles (Fig. 2).

Connective tissue pad

A pad of irregular dense connective tissue forms much of the dorsolateral wall throughout virtually the entire length of the proboscis (Fig. 2, *ctp*). For much of its length, the pad is interposed between levator labii superioris and the muscle complex formed by levator nasolabialis and caninus. The pad is oval in cross section, and histological analysis shows that it is an almost even mixture of fatty and fibrous connective tissue. It is traversed by radially arranged muscle bundles (rectus nasi, see below).

Musculature

The preorbital facial muscles are briefly reviewed below, including attachments, fibre orientation and relationships to adjacent structures. Muscular function and the mechanics of proboscis movement are addressed in the Discussion.

Muscles of the proboscis

Several facial muscles pass from the bony skull to the proboscis and may be regarded for purposes of discussion as extrinsic muscles of the proboscis. A single muscle, *M. rectus nasi*, occurs only within the proboscis and hence may be considered an intrinsic muscle.

M. levator labii superioris (= levatores [Owen, 1831], maxillolabialis superior [Boas & Paulli, 1908], pyramidalis nasi [Murie, 1872], caput infraorbitale quadrati labii superior [Bressou, 1961], levator labii maxillaris [Nickel *et al.*, 1986; Schaller, 1992]) is a longitudinal muscle of the proboscis (Figs 2–4; *mlls*). It originates as an extensive fan from a robust, roughened lacrimo-frontal ridge just rostradorsal to the orbit. Further rostrally, the levator labii superioris narrows to a cord, passing medially and dorsally (Fig. 2b). It follows the dorsal contour of the snout, tracking along the lateral edge of the dorsal lateral nasal cartilage (cartilago nasi lateralis dorsalis). The contralateral muscles converge at the rostral limit of the dorsal prong of the septal cartilage, eventually forming a conjoined median

Table 1. List of abbreviations used in the figures

ai	A. infraorbitalis	mm	M. malaris
avf	A. et V. facialis	mms	M. masseter
avls	A. et V. labialis superior	mn	nasal meatus formed by confluence of true dorsal and middle nasal meati
bo	bulbus oculi	mnc	meatus nasi communis
cac	cartilago alaris, cornu	mnd	meatus nasi dorsalis
cac'	lateral ala of nostril overlying the cornu of cartilago alaris	mnm	meatus nasi medius
cal	cartilago alaris, lamina	mnv	meatus nasi ventralis
cb	cavitas buccalis	mnv'	rostral extension of meatus nasi ventralis
ce	conchae ethmoidales	mooc	M. orbicularis oculi
ch	choana	moor	M. orbicularis oris
ci	canalis infraorbitalis	mrn	M. rectus nasi
cnam	cartilago nasalis accessoria medialis	mt	maxilloturbinate (os conchae nasalis ventralis)
cnd	concha nasalis dorsalis	mt ^d	dorsalmost turbinate structure of maxilloturbinate
cnld	cartilago nasi lateralis dorsalis	mt ^s	maxilloturbinate, septal portion
cnm	concha nasalis media	mt ^v	ventral turbinate structures of maxilloturbinate
cnv	concha nasalis ventralis	mx	os maxillare
cnve	concha nasalis vestibularis	mz	M. zygomaticus
ctp	connective tissue pad	mz'	M. zygomaticus, cut edge
d	dentes premolares	n	os nasale
dm	diverticulum meati	nf	N. facialis (CN VII)
dn	diverticulum nasi	nt	nasal tube (i.e. airway)
e	os ethmoidale, lamina perpendicularis	pa	plica alaris of ventral nasal concha
et1	endoturbinata I (os conchae nasalis dorsalis)	pa'	plica alaris, with lamina of alar cartilage dorsal to it
et2	endoturbinata II (os conchae nasalis media)	pb	plica basalis of ventral nasal concha
et3	endoturbinata III (ossa conchae ethmoidales)	pm	os premaxillare (incisivum)
f	os frontale	pr	plica recta of dorsal nasal concha
f'	median process of frontal bone	pv	plica vestibularis
fdm	fossa for meatal diverticulum	rc	communicating ramus between facial and infraorbital nerves
fi	foramen infraorbitalis	rne	N. infraorbitalis, ramus nasalis externus
fp	fissura palatina	rls	N. infraorbitalis, rami labiales superiores
fs	foramen sphenopalatinum	rni	N. infraorbitalis, ramus nasalis internus
i	integumentum	s	suture between maxilla and maxilloturbinate
in	incisura nasoincisiva	scv	sinus conchae ventralis
in'	position of incisura nasoincisiva	scv'	air sinus within septal portion of maxilloturbinate
l	lingua (tongue)	sf	sinus frontalis
li	labium inferius (lower lip)	sm	sinus maxillaris
m ¹	M. caninus + M. levator nasolabialis	sn	cartilago septi nasi (cartilaginous nasal septum)
m ²	M. caninus and overlying muscles	sn ¹	fibrous cord deriving from dorsal prong of cartilago septi nasi
m ³	M. levator nasolabialis + M. levator labii superioris	sn ²	hiatus between dorsal and ventral prongs of cartilago septi nasi
mb	M. buccinator	sn ³	cartilago septi nasi, cut edge
mc	M. caninus	vi	V. infraorbitalis
mc'	M. caninus, cut edge	vno	organum vomeronasale (vomeronasal or Jacobson's organ)
md	mandibula	vno'	bony fossa for organum vomeronasale within maxilloturbinate
mld	M. levator anguli oris		
mldom	M. levator anguli oculi medialis		
mlls	M. levator labii superioris		
mln	M. lateralis nasi		
mlnl	M. levator nasolabialis		
mlnl'	M. levator nasolabialis, cut edge		

tendon over the distalmost portion of the proboscis. This median tendon then courses distally along the dorsum of the proboscis to insert into the integument between the nostrils. Throughout most of its course, levator labii superioris is supported ventrally by the dense connective tissue pad.

M. levator nasolabialis (=levator labii superioris alaeque nasi [Murie, 1872], nasolabialis [Boas & Paulli, 1908], ventral part of caput angulare quadrati labii superior [Bressou, 1961]) is a broad, sheet-like muscle that passes obliquely down the long axis of the proboscis. It arises from the lateral margin of the nasal bone, the dorsal lateral nasal cartilage, and the medial

palpebral ligament (Figs 2–4; *mlnl*). Its caudal and ventral fibres descend rostrally toward the angle of the mouth whereas more dorsal fibres extend as a superficial longitudinal layer to the ventrolateral limit of the proboscis. All of these fibres ultimately merge with those of orbicularis oris. Levator nasolabialis is overlain proximally by levator anguli oculi medialis, whereas it partially overlies levator labii superioris, caninus, and lateralis nasi. In contrast to the condition in horses and at least some bovids, the levator nasolabialis of *T. terrestris* does not split into superficial and deep limbs that flank the caninus. It should be noted that Bressou (1961) reported such a split in *T. indicus*, though with

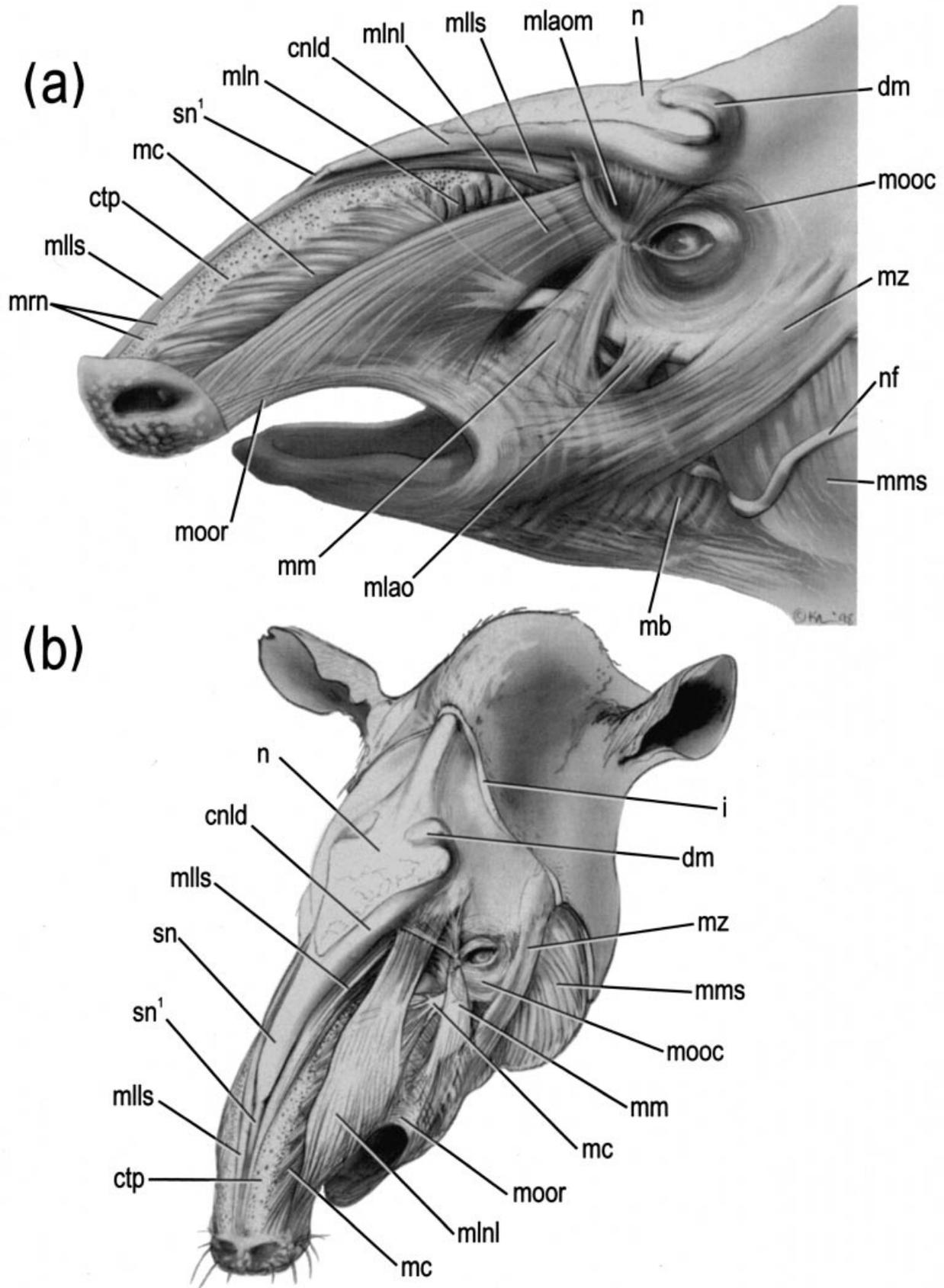


Fig. 2. Superficial dissection of the face of *Tapirus terrestris* in: (a) left lateral view; (b) oblique left rostradorsolateral view. See Table 1 for abbreviations.

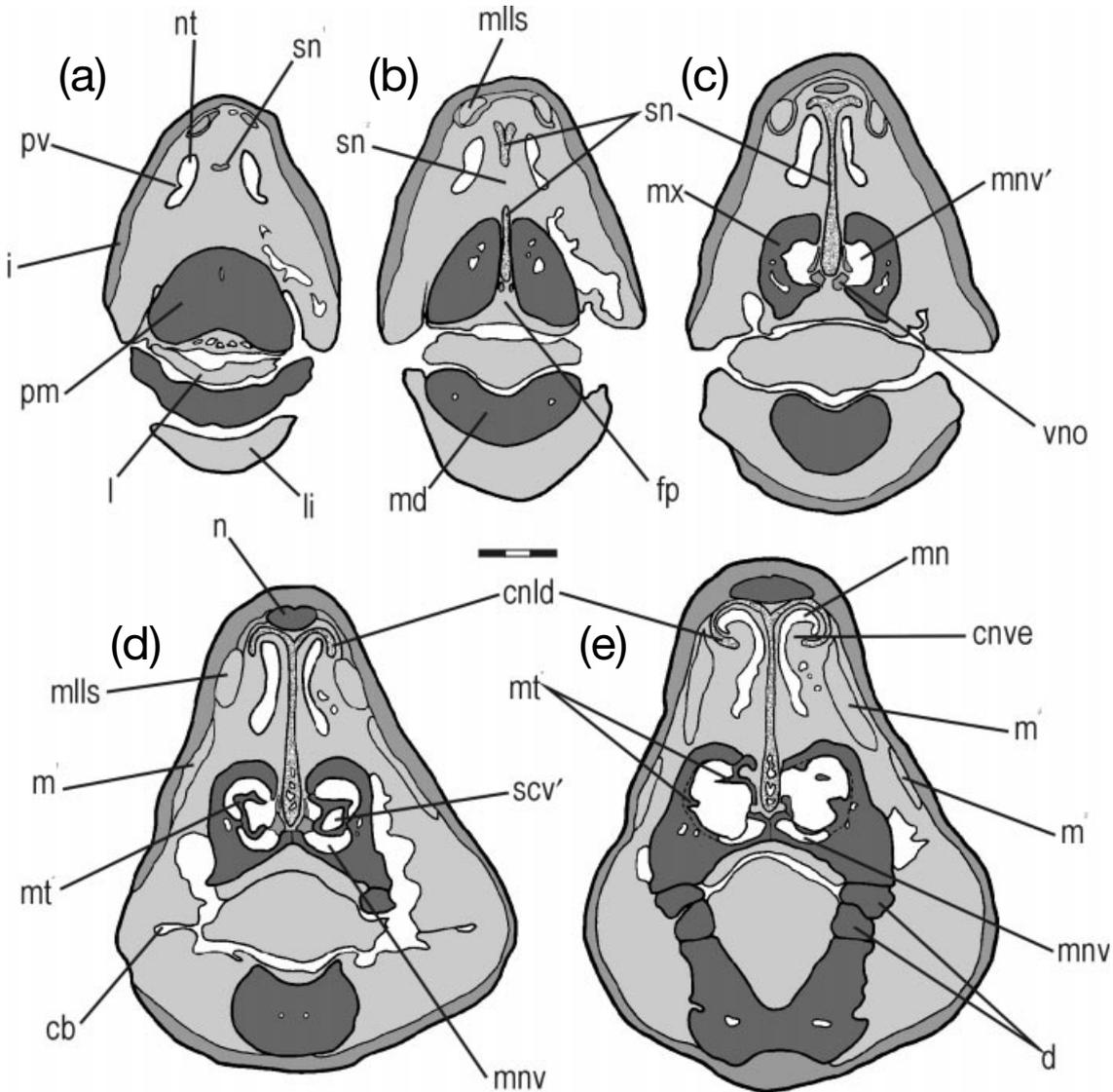


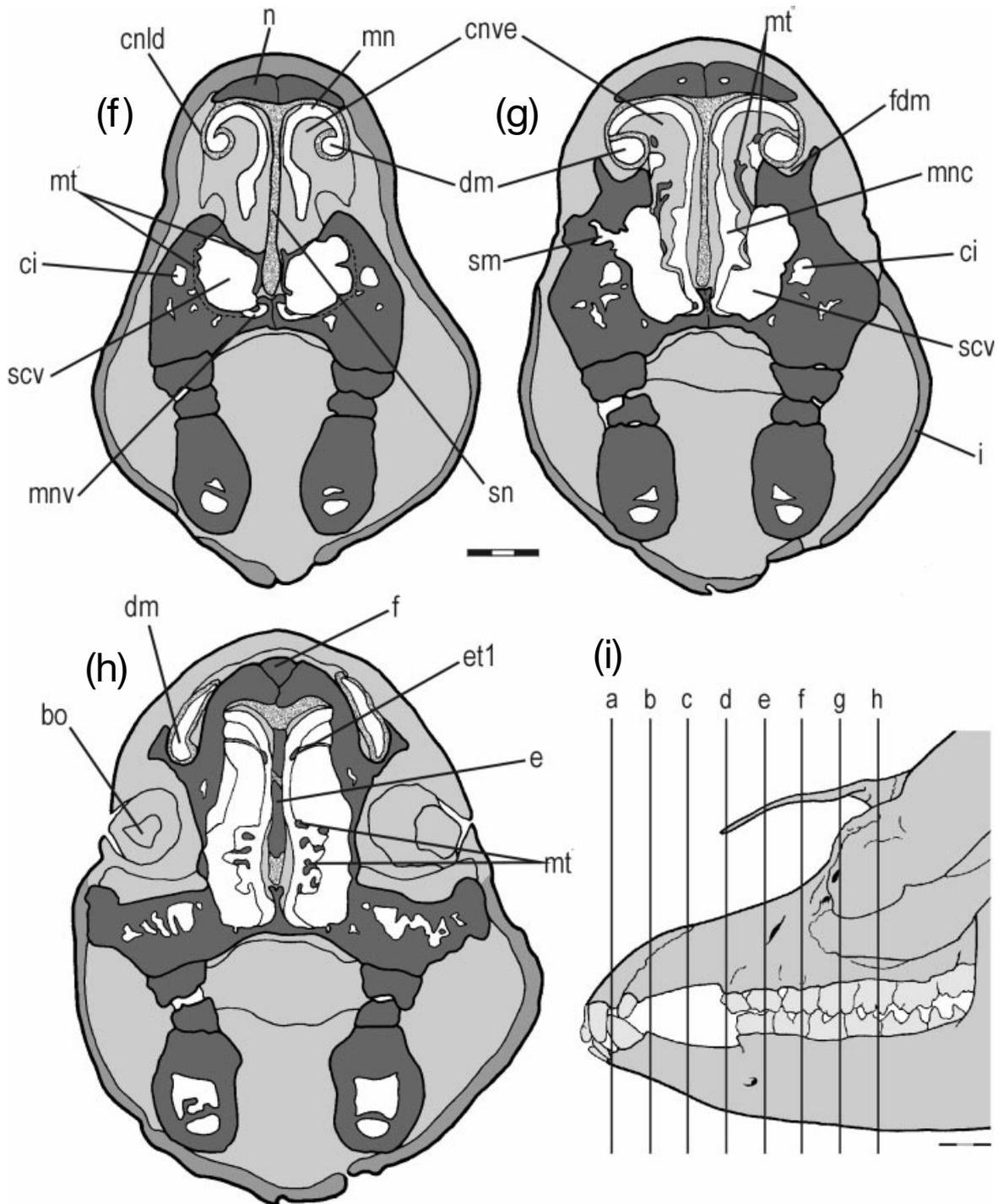
Fig. 3. Drawings of selected computerized tomographic (CT) images of the facial region of *Tapirus terrestris* (FMNH 155691), showing the nasal apparatus in successive transverse sections (a–h). The dashed lines in (e) and (f) show the approximate extent of the maxilloturbinate, which was not always clearly visible in the CTs because the scans were optimized to resolve soft tissue and not bone; the extent was determined after scanning by reference to the dried skull. (i) Skull in left lateral view to show the levels of the sections depicted in (a–h). Scale bar = 3 cm. See Table 1 for abbreviations.

both limbs remaining superficial. Close examination of Bressou's text and figures, however, shows that only the ventral limb is levator nasolabialis and the dorsal limb is actually part of caninus; viewed in this light, Bressou's findings are in accord with our dissections of both *T. indicus* and *T. terrestris* and the observations of Boas & Paulli (1908), a paper not cited by Bressou.

M. caninus (= maxillolabialis inferior [Boas & Paulli, 1908], dorsal part of caput angulare quadrati labii superior [Bressou, 1961]) originates as a tendinous band from a ridge on the maxilla located just caudoventral to the infraorbital foramen near the maxillozygomatic suture (Figs 2–4; *mc*). The muscle fans rostrally into a

thin sheet, its fibres passing deep to levator nasolabialis. Its caudodorsal fibres tend toward a more vertical orientation, arching rostrally as they emerge from beneath levator nasolabialis. Its rostroventral fibres, however, form a more longitudinal layer within the substance of the proboscis, again deep to levator nasolabialis. The distal ends of all of the fibres attach along the length of the connective tissue pad and skin down to the area of the nostril.

M. lateralis nasi (= nasalis [Boas & Paulli, 1908], incisivus superior [Bressou, 1961]) is a deeply placed, elongate band of vertically-oriented fibres that extends from near the nasoincisive incisure (= nasal incision of



Radinsky, 1965; Wall, 1980) almost to the tip of the proboscis (Figs 2, 4; *mln*). Ventrally, it arises from the rounded dorsal portion of the maxilla and premaxilla, whereas dorsally it attaches to the dense connective tissue pad. Lateralis nasi is deep to the previous three muscles. Boas & Paulli (1908: pl. 14) described and illustrated a transverse band of muscle fibres ventral to the nasal tubes and dorsal to a large mass of muco-

serous glands; our material confirms this finding. Boas & Paulli regarded this band as a portion of *M. rectus nasi* (see below). Shoshani (1996) identified a similar transverse muscle in the elephant *Loxodonta africana* as *M. transversus nasi*. However, our observations indicate that this transverse band is derived from fibres of lateralis nasi. Following this interpretation, fibres of lateralis nasi rostral to the limits of the premaxilla

pass transversely across the midline to interdigitate with the contralateral side and form a median raphe.

M. orbicularis oris, as in other mammals, is a superficial muscle that encircles the mouth and merges with several other facial muscles, including levator nasolabialis, caninus, malaris, buccinator, levator anguli oris, and zygomaticus (Figs 2, 4; *moor*). In tapirs, orbicularis oris is also an important component of the proboscis, forming its ventrolateral portion.

M. rectus nasi is an intrinsic muscle of the proboscis that radiates transversely from the mucosa of the nasal tube (Fig. 2, 4; *mnn*). Dorsally and laterally, the fibres pass radially to the integument. Medially, the fibres pass across the midline to the contralateral nasal tube (Bressou [1961] called these fibres 'transversus nasi'), whereas ventrally, they blend with those of the transverse band of lateralis nasi. As Boas & Paulli (1908) described for their material, the rectus nasi fibres are more numerous medially and ventrally than laterally and dorsally. Many of the fascicles are spirally arranged and alternate with a compact matrix of connective tissue which is also oriented transversely. In the area of the proboscis where the dorsal prong of the septal cartilage occurs, the medial rectus bundles diverge around the prong, forming alternating concentric layers of muscle and connective tissue; in locations rostral to the termination of the prong (e.g. see Boas & Paulli, 1908: plate 14), the fibres are oriented more strictly transversely. Lateral to the nasal tube, the rectus nasi fascicles alternate with longitudinal bundles of caninus and levator nasolabialis.

Related facial musculature

M. levator anguli oculi medialis (= preorbicularis pars dorsalis [Boas & Paulli, 1908]) is a superficial, rhomboidal muscle located rostral and dorsal to the eye (Fig. 2, *mloam*). It is firmly attached to the medial canthus of the eye and overlies both levator nasolabialis and orbicularis oculi.

M. malaris (= preorbicularis pars ventralis [Boas & Paulli, 1908], lacrymalis [Bressou, 1961]) is a triangular sheet of muscle originating from the medial canthus of the eye (Fig. 2, *mm*). It descends rostrally, interdigitating with fibres of orbicularis oris. In doing so, its fibres pass superficially to those of caninus and buccinator.

M. levator anguli oris (= sphincteris profundus, pars palpebralis [Boas & Paulli, 1908]) is a small band of muscle arising from the fascia overlying the zygomatic arch and merging with fibres of orbicularis oris, buccinator, and zygomaticus (Fig. 2, *mloa*).

M. zygomaticus (= zygomaticus platysmatis [Boas & Paulli, 1908]) is a thin sheet of muscle attaching proximally to the fascia overlying the angle of the zygomatic arch (Fig. 2, 4; *mz*). Its fibres sweep rostroventrally where they overlie buccinator and merge with fibres of orbicularis oris at the corner of the mouth.

M. buccinator, as noted by Boas & Paulli (1908), consists of at least two sheets of muscle adhering to the

lateral surface of the buccal mucosa (Fig. 2, 4; *mb*). It attaches dorsally to the alveolar process of the maxilla and ventrally to the lateral aspect of the mandible. The superficial portion, buccinator pars buccalis, runs vertically and is composed of relatively coarse fibres caudally and finer fibres rostrally. The deeper portion, buccinator pars molaris, has more longitudinally oriented fibres (Boas & Paulli, 1908). Buccinator is overlain by zygomaticus, levator anguli oris, malaris, caninus, and levator nasolabialis. The rostral fibres of buccinator pars buccalis tend to occur in series with those of lateralis nasi.

Nerves and blood vessels

This section addresses selected elements of the neurovasculature in the facial region of *Tapirus terrestris*. The list of structures is by no means exhaustive, but rather represents major nerves and blood vessels that are likely to be of critical importance in proboscis function.

The *facial artery and vein* (accompanied by the parotid duct) emerge onto the face immediately rostral to the ventral portion of the masseter. They then assume a diagonal course, passing through a fascial tube along the rostral border of masseter. The superior labial and angularis oculi vessels branch within this fascial tube, the former curving rostradorsally to ramify over the caudal region of the face (Fig. 4, *avf*, *avls*). The angularis oculi vessels are very short in tapirs due to the apomorphic rostral orientation of the orbit. In their course across the face, the superior labial vessels pass deep to zygomaticus, levator anguli oris, malaris, and levator nasolabialis, and superficial to buccinator, to some extent coursing within the substance of caninus. These vessels anastomose with branches of the infraorbital vessels just rostral to the orbit. Due to these anastomoses, it could not be determined whether the lateralis nasi and dorsalis nasi vessels, though observable, branched from the superior labial, facial, or infraorbital vessels.

The *facial nerve* (CN VII) has a large ramus buccalis dorsalis that, after crossing the masseter, takes a course similar to the superior labial vessels, although it is rostral to and not within their fascial tube (Figs 2 & 4; *nf*). This nerve ramifies to supply motor innervation to all of the muscles noted above. Otherwise, the major trunk of the dorsal buccal ramus follows the course of the superior labial vessels within caninus. Just rostral to the infraorbital foramen the facial and infraorbital nerves communicate via the typical ramus communicans (Fig. 4, *rc*).

The *infraorbital artery and vein*, which are branches of the maxillary vessels, emerge from the infraorbital foramen with the vein dorsal to the artery (Fig. 4, *ai*, *vi*). They pass rostrally deep to levator nasolabialis and caninus, ramifying en route and ultimately reaching the tip of the proboscis. The infraorbital vessels, via their lateral and dorsal nasal branches, are the largest vessels in the facial region and appear to be the major blood supply of the proboscis.

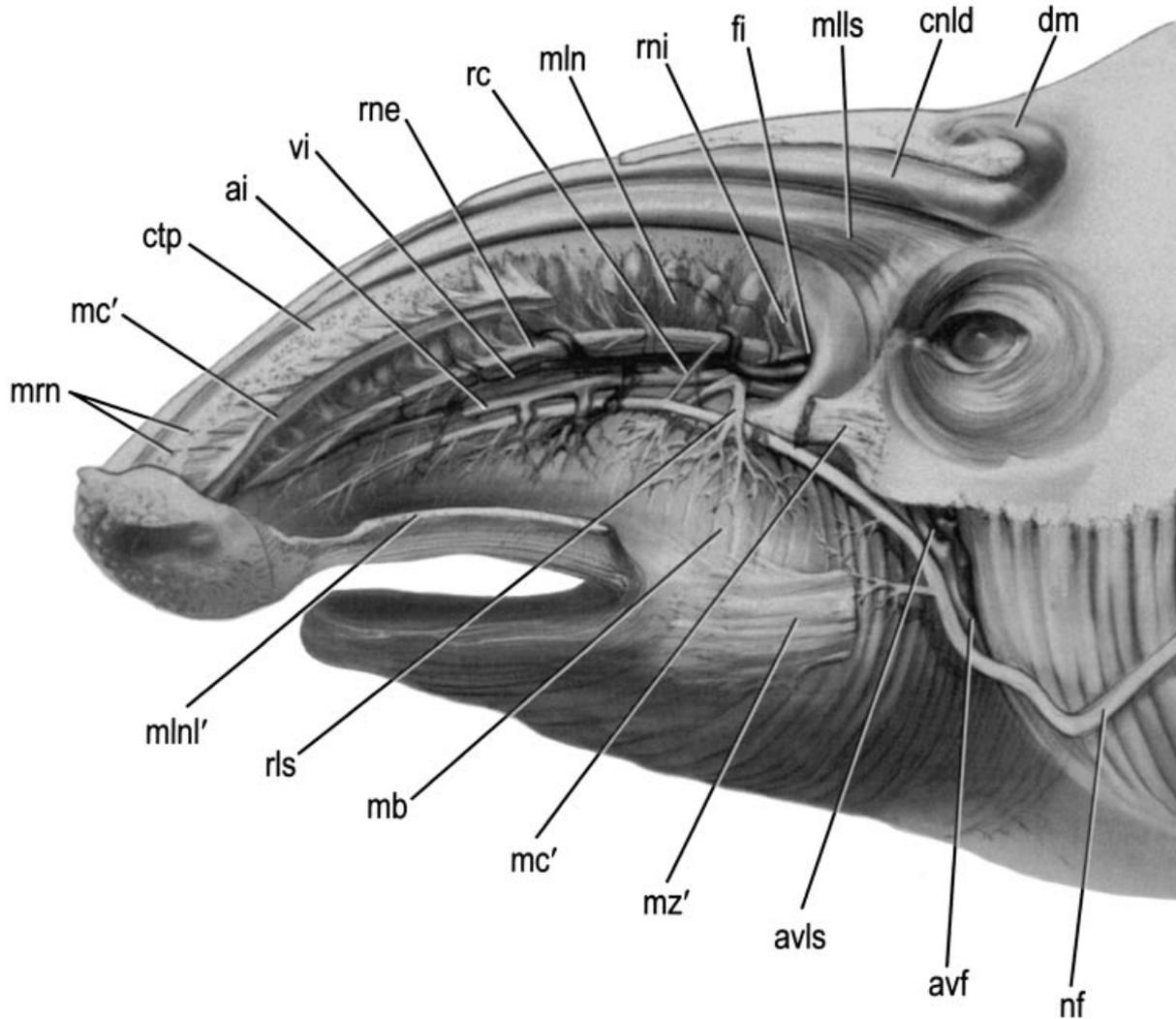


Fig. 4. Deep dissection of the face of *Tapirus terrestris* in left lateral view. Several muscles have been resected, and the cut ends of caninus, levator nasolabialis, and zygomaticus have been retained for reference. Likewise, much of the anastomotic network between the facial and infraorbital vessels has been removed to clarify underlying relationships. See Table 1 for abbreviations.

The *infraorbital nerve*, a branch of the maxillary nerve (CN V²), emerges from the infraorbital foramen ventral and deep to the infraorbital vessels and subsequently splits into two divisions, one dorsal and one ventral (Fig. 4). The ventral division of the infraorbital nerve ramifies immediately into a number of small branches (*rami labiales superiores*, *rls*) that supply sensory innervation in the lower facial region. The dorsal division splits immediately upon exiting the infraorbital foramen. One branch, *ramus nasalis externus* (*rne*), travels with the *dorsalis nasi* vessels to supply the caudodorsal portion of the proboscis and adjacent part of the nasal capsule. The second branch divides into superficial and deep branches which pass on either side of caninus, the former giving off small branches as it passes forward to the distal portion of the proboscis and the latter, *ramus nasalis internus* (*rni*), entering the nasal capsule.

Cartilages

In general, the nasal cartilages of *Tapirus* (Figs 3 & 5) are extremely simple and apomorphically reduced relative to those of other extant perissodactyls (Fig. 5). The cartilaginous side-wall of the nasal cavity is minimal, being composed solely of the dorsal lateral nasal cartilage (*cnld*, see below). The absence of a ventral lateral nasal cartilage is shared with horses (the condition is unknown in rhinoceroses). However, whereas horses retain the alar (*cah*, *cac*) and medial accessory (*cnam*) cartilages that support the nostril and provide attachment for dilator musculature (Fig. 5b), these cartilages are absent in tapirs (Fig. 5a). The nasal cartilages of tapirs are restricted to the septal cartilage and its outgrowths, the dorsal lateral nasal cartilages.

The *septal cartilage* (*sn*) is confluent caudally with the perpendicular plate of the ethmoid bone. As with

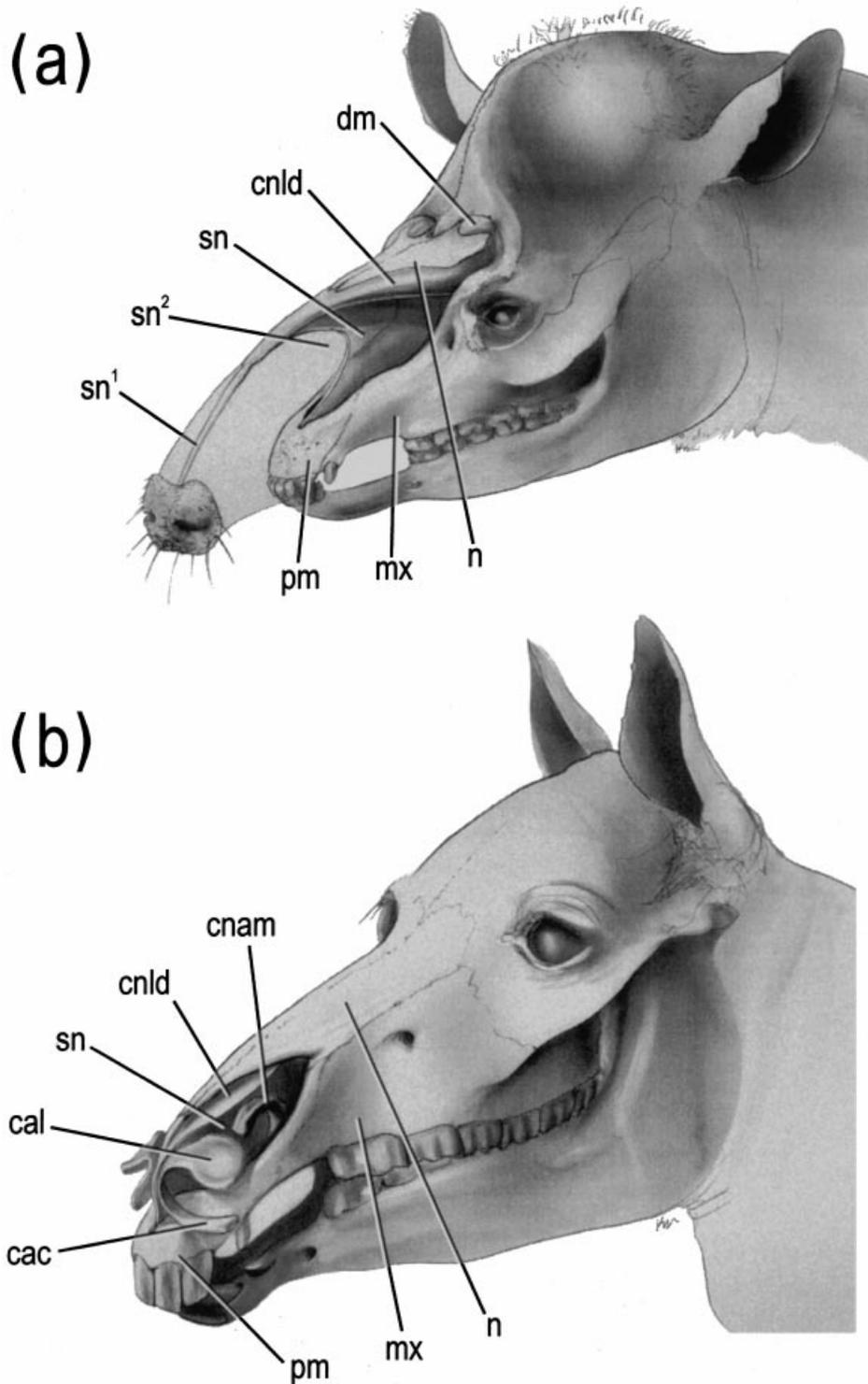


Fig. 5. Oblique view (a) of a tapir skull (*Tapirus terrestris*) with nasal cartilages in place, compared with the same view (b) of a horse skull (*Equus caballus*) to show the difference in extent of the narial region and nasal cartilages. Relative to horses, tapirs have a dramatically enlarged narial region, yet have highly reduced and simplified the osseocartilaginous components. The nasal cartilages in (b) were modified from Schummer *et al.* (1979). See Table 1 for abbreviations.

the perpendicular plate of the ethmoid, the septal cartilage is moderately thin throughout most of its height, but swollen ventrally where it is lodged within the sulcus septalis, a longitudinal channel within the maxilla and vomer (Fig. 3). More dorsally, the septal

cartilage is flanked by a dorsomedial rim formed by the maxillae and premaxillae. The rostral portion of the septal cartilage is deeply emarginate, separating into elongate dorsal and ventral prongs that form a C-shape in lateral view (Figs 3b & 5a; *sn*²). The ventral prong

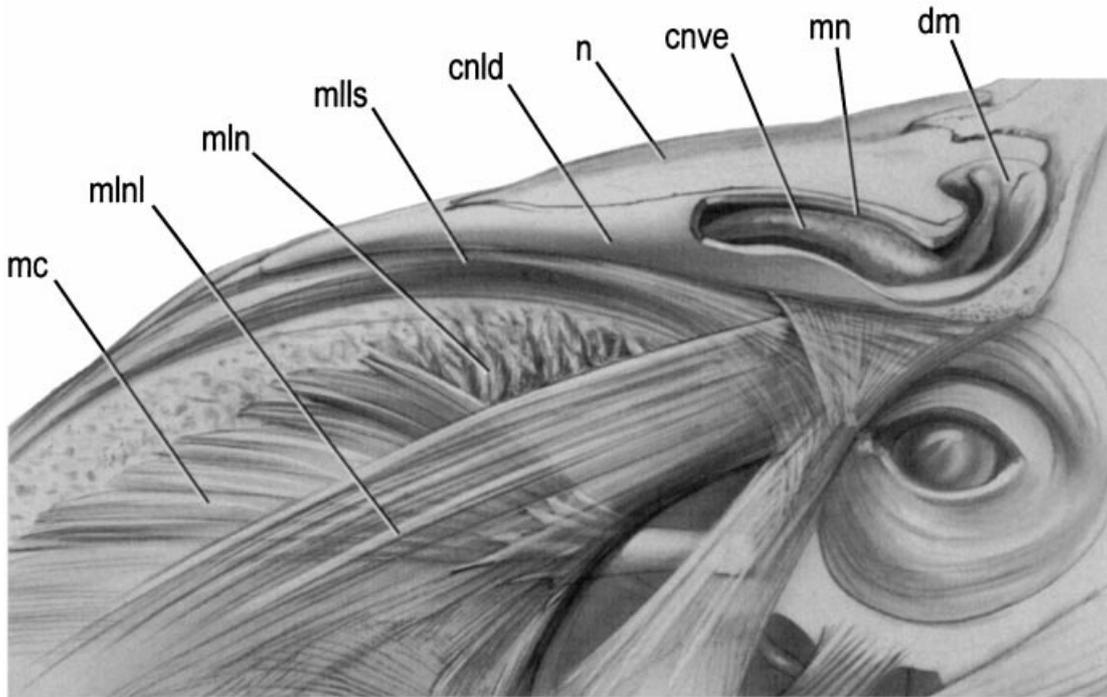


Fig. 6. Meatal diverticulum of *Tapirus terrestris* in left lateral view. Its external cartilaginous wall has been partially removed to reveal internal structure. See Table 1 for abbreviations.

passes through a deep premaxillary slot where it is lodged in the dorsal half of the palatine fissure, rostral to the termination of the sulcus septalis and just dorsomedial to the paired vomeronasal organs (Fig. 3b–d). The dorsal prong of the septum tapers to a fine tip, terminating at approximately the level of the rostral margin of the premaxilla. The dorsal portion of the septum, as well as this dorsal prong, is sheathed by dense connective tissue that seems to be continuous with the periosteum of the nasal bone. Beyond the termination of the dorsal prong, the connective tissue continues rostrally as a cord almost to the distal limit of the proboscis (Fig. 5a, *sn*¹). As the dorsal prong (and its sheath) passes rostrally, it becomes embedded within the substance of the proboscis and eventually comes to lie between the nasal tubes (Fig. 3a–c).

The *dorsal lateral nasal cartilages*, homologues of the parietotectal cartilages of other amniotes (Witmer, 1995), form as winglike, dorsal laminae that flare laterally from the septal cartilage (Fig. 3b–f, *cnld*). Throughout much of its length, the dorsal lateral nasal cartilage underlies and projects laterally beyond the nasal bone such that the two together form the osseocartilaginous roof of the nasal tube (Figs 2–6). Rostrally, each dorsal lateral nasal cartilage extends ventrolaterally first to roof and then to flank the dorsal portion of the airway. At progressively more caudal levels, it scrolls into a ‘vestibular nasal concha’ (Fig. 3e, *cnve*) of uncertain homology (see below). Dorsal to this concha is a nasal meatus, again of questionable homology, which is just internal to the cartilage (Fig. 3e, *mn*). Upon completion of a full turn, the scrolling

cartilage essentially ‘captures’ a portion of this meatus (Fig. 3e–g). This evagination is the meatal diverticulum (*dm*; = nasal diverticulum of Beddard and Treves, 1889; Gregory, 1920), which is located near the nasoincise incisure, at about the rostrocaudal level of the first molar.

The *meatal diverticulum* (*dm*) is a mucocartilaginous pouch of uncertain function generally homologized with the nasal diverticulum of equids (see below). Whereas the main airway heads caudoventrally into the nasopharynx, the meatal diverticulum turns laterally, housed within the tube-like dorsal lateral nasal cartilages (Figs 2–6). The diverticulum passes predominantly caudolaterally, travelling initially within the trough-like floor of a deep fossa on the surface of the skull formed in *T. terrestris* by the maxilla and frontal bones. Within this meatal diverticulum fossa, the diverticulum takes a full turn, first passing rostromedially and then looping caudolaterally around a cartilaginous pillar that is an extension of the vestibular nasal concha (Fig. 6). The meatal diverticulum is not a blind sac, as previously described (Turner, 1850, and others), but rather re-enters the nasal cavity proper between the dorsal nasal concha, ventral nasal concha, and vestibular nasal concha.

Osteology

In general, the osteology of the face in tapirs is highly modified to accommodate the fleshy proboscis (Figs 1, 3, 5 & 7). Below is a brief description of the bony

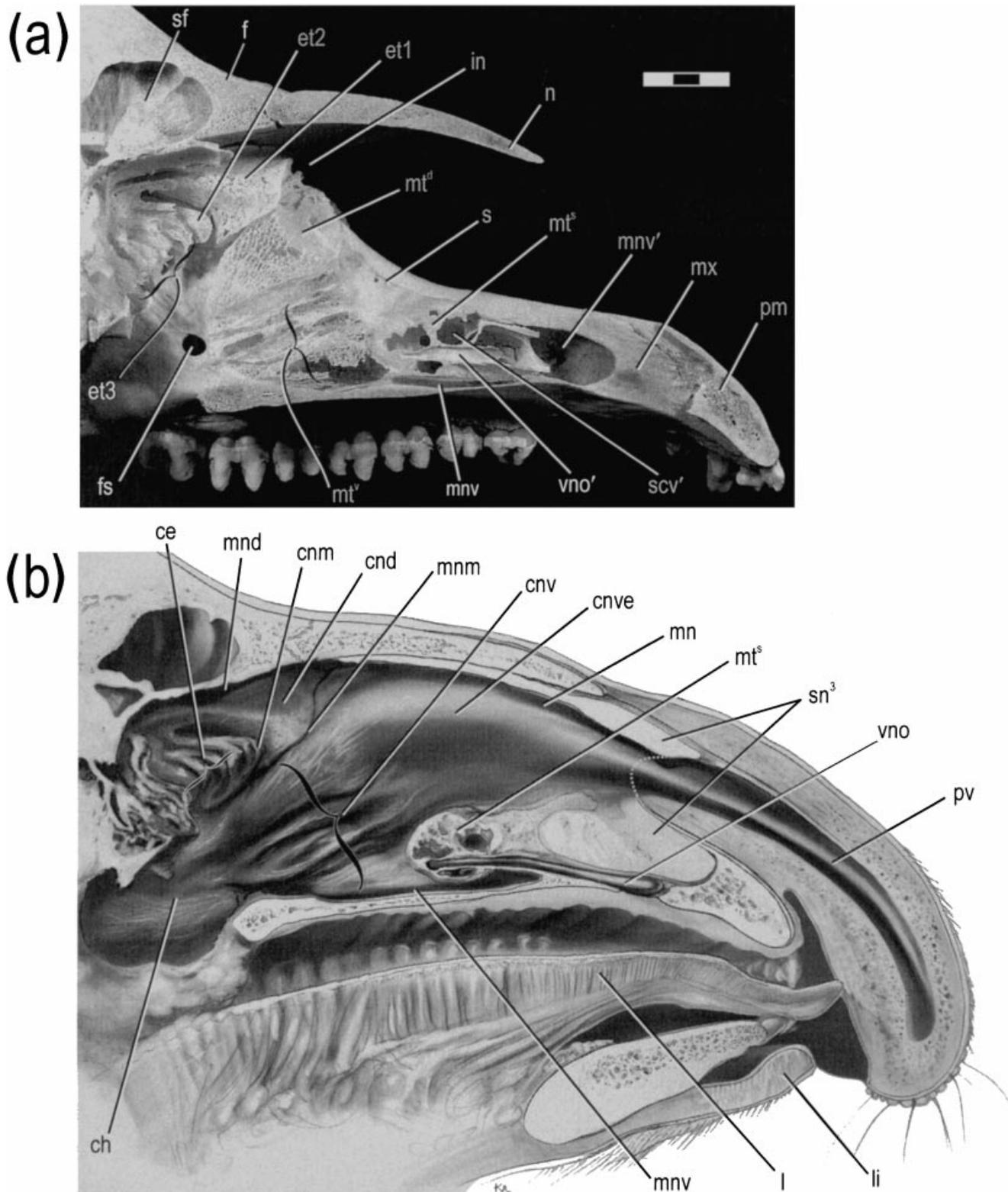


Fig. 7. Medial view of sagittally-sectioned skull (a) and head (b) of *Tapirus terrestris* (FMNH 155691) with nasal septum removed to show internal nasal structures. Scale bar in (a) = 3 cm. See Table 1 for abbreviations.

elements of the facial skeleton, particularly as they relate to the proboscis.

The *premaxilla* (*pm*; = intermaxillary [Boas & Paulli, 1908]; os incisivum [NAV, 1994]) is somewhat thickened

vertically, well-fused to its counterpart, and rounded both laterally and rostrally, with three large teeth per side. A relatively small canine is present at the premaxilla-maxilla junction. Unlike the general perissodactyl

condition, there is no ascending process of the premaxilla contacting the nasal. Dorsally, opposing premaxillae form a narrow, median slot for the cartilaginous nasal septum. Ventrally, the premaxillae form the rostral border of the unpaired palatine fissure.

The robust *maxilla* (*mx*) has a rounded and relatively featureless dorsolateral surface, bearing few obvious manifestations of the overlying proboscis (in comparison with, for example, the pronounced maxillary ridges of *Saiga tatarica*, AMNH 119649). Medially, the opposing maxillae clasp the intervening cartilaginous septum nasi (Fig. 3c); in *T. terrestris* and *T. indicus*, this dorsal medial edge is relatively low and rounded, whereas in *T. bairdii* this edge flares dorsally forming an extensive support for the more ossified septum. It should be noted that this dorsomedial edge is not part of the maxillary palatal process (which is present ventromedially), but rather represents an apomorphic in-rolling of the facial surface. The frontonasal process projects caudodorsally, forming a large portion of the narial border and part of the bony lateral wall of the nasal cavity. It terminates in a relatively gracile flange juxtaposed between the nasal and frontal. Together, the maxilla, frontal and nasal form a deep external fossa that houses the meatal diverticulum. The infraorbital foramen is large, with dorsal and ventral sulci for transmitting the infraorbital nerves and blood vessels to the face. The conformation of the infraorbital foramen varies within taxa and even within individuals; one specimen of *T. indicus* (AMNH 180030) has a single large foramen on the right and three smaller foramina on the left. The diastematic region has a well-defined depression ventrolaterally and a ventral ridge for attachment of the buccinator. The muscle scar for caninus varies from being a rugosity in the area of the maxillozygomatic suture in *T. terrestris* to being a discrete, vertical raised ridge in *T. bairdii*. In transverse section (Fig. 3c), the rostral portion of the maxilla is C-shaped (concave medially) and houses a rostral extension of the ventral nasal meatus in the diastematic region (Figs 3c & 7a; *mnv'*). In contrast to the condition in horses, the maxillary sinus is virtually absent, apparently as a result of both expansion of the maxilloturbinate (= os conchae nasalis ventralis [NAV, 1994]) and reorientation of the orbital contents to a more rostral position.

The *nasal* (*n*) is highly modified from the ancestral perissodactyl condition. It lacks any contact with the premaxillae, and is retracted to such a great extent that the nasoincise incisure (the caudal corner of the naris) overlies the caudal portion of the orbit (Figs 1d, 5a & 7a; *in*). The nasal also is relatively abbreviated and freely projecting rostrally. In dorsal view, it is triangular, broadest caudally and tapering to a point rostrally (Fig. 5a). The lateral edge of the bone is roughened for attachment of the dorsal lateral nasal cartilages. The caudal margin is complex, with a large median notch for contact with a rounded, peg-like extension of the frontals. Lateral to this notch is a shallow, parasagittal depression that, together with the

deep ventrolateral fossa in the frontal and maxilla, houses the meatal diverticulum. A ventral, hooklike process of the nasal forms the dorsomedial portion of the meatal diverticulum fossa. The morphology of the nasal bone is considerably more elaborate in *Tapirus indicus* and *T. bairdii* than in *T. terrestris* and *T. pinchaque*. For example, the dorsal depressions of the nasals in *T. indicus* form deep excavations that include the frontals, and the ventral hook is elaborated into a lateral projection that overlies a portion of the frontal.

The *frontals* (*f*) also are highly modified in several respects from other extant perissodactyls. A thick, median process of the frontal slots into a notch within the nasals (Figs 3h, 5a, 6 & 7a; *f*). Rostrolateral processes of the frontal slope downward at an angle of about 45° to meet the lacrimal and maxilla. These frontal processes form a large portion of the meatal diverticulum fossa (Fig. 6), including a robust lateral wall (absent in *T. indicus*). The dorsolateral margin of this wall is roughened in the area of attachment of levator anguli oculi medialis, orbicularis oculi, and fascia orbitalis (Fig. 6). This rugosity is continuous rostrally with a low ridge on the lacrimal for attachment of levator labii superioris.

The *lacrimal* is a roughened, wedge-shaped bone bounded dorsally by the frontal, ventrally by the zygomatic, and rostromedially by the ascending (nasal) process of the maxilla. Two large lacrimal foramina pierce this element along the rostral margin of the orbit. A pronounced tabular process projects laterally and provides area of attachment for malaris, levator anguli oculi medialis, and levator nasolabialis, as well as supporting orbital contents. As mentioned above, the lacrimal has a well-developed ridge rostrally for levator labii superioris. Ventromedial to the lacrimal is a large passage in the floor of the orbit for the infraorbital blood vessels and nerves.

The *vomer* resembles that of other perissodactyls. It is a narrow, elongate, median structure situated on the palatal processes of the palatines and maxillae. A well-developed V-shaped trough (sulcus septalis) forms the ventral support for both the ethmoidal and cartilaginous portions of the nasal septum. The walls of this trough are highest caudally and taper rostrally, becoming virtually non-existent at the caudal margin of the incisive foramen.

The *ethmoid* is a complex structure with a median, perpendicular plate (lamina perpendicularis) forming a portion of the nasal septum (Fig. 3h, *e*), a dorsal, horizontal lamina (lamina tectoria), and the convoluted ethmoidal labyrinth supporting the ethmoidal conchae (Fig. 7a). The perpendicular plate is relatively thin and of uniform thickness dorsally whereas the ventral portion is swollen and elliptical in cross section. It has an irregular, concave contact with the cartilaginous nasal septum. The tectorial lamina contacts the ventral surface of the nasals and forms a substantial portion of the roof of the nasal cavity. Ossification of the perpendicular plate is variable both within and among species of

tapirs. *Tapirus bairdii* is most divergent in that virtually the entire cartilaginous nasal septum ossifies as the perpendicular plate of the ethmoid, even preserving the C-shaped rostral emargination. The nomenclature used here for the ethmoidal labyrinth follows Nickel *et al.* (1986) in referring to bony structures as 'turbines' and reserving 'concha' for the mucosa-covered structures. The ethmoidal labyrinth (Fig. 7a) is composed of a discrete endoturbinete I (*et1*; = the bony portion of concha nasalis dorsalis [NAV, 1994]; nasoturbinete of other authors), a small endoturbinete II (*et2*; = the bony portion of concha nasalis media), and about five other turbines comprising the endoturbinete III complex (*et3*). Relative to the condition in horses and other ungulates, endoturbinete I is strikingly reduced. Endoturbinete II resembles that of horses in being small relative to other ungulates, but is even more so in tapirs such that it gives the appearance of being simply the dorsalmost of the endoturbinete III series. The middle nasal meatus (*mm*) is oblique, passing between endoturbinete I and the maxilloturbinate (Fig. 7).

The maxilloturbinate (*mt*; = os conchae nasalis ventralis [NAV, 1994]) of tapirs is drastically modified relative to other mammals. Rather than being a separate element having only a relatively short suture with the maxilla as in other mammals, the maxilloturbinate of tapirs is very extensive, occupying a large recess within the maxillary bone to which it is broadly sutured (Figs 3d–h & 7a; *s*). For purposes of discussion, the maxilloturbinate may be divided into a caudal turbinate portion and a rostral septal portion (Fig. 7a). The caudal portion runs from the middle meatus down almost to the bony palate such that the ventral meatus (*mv*) is restricted. The bones of the caudal portion are extremely delicate and lacy. Five turbinate structures are elaborated from the maxilloturbinate. The dorsalmost (*mt^d*) is largest and forms the ventral border of the middle meatus; its rostradorsal border is deeply concave where a broad mucosal fold attaches. The three more ventral turbines (*mt^v*) are relatively simple ridges, whereas the ventralmost is a larger, hollow shell. This caudal portion of the maxilloturbinate is pneumatized by a paranasal air sinus (*scv*; ? = sinus conchae ventralis of horses) (Fig. 3g–h). The rostral septal portion (*mt^s*) is a discrete chamber that is separated from the turbinate portion by a partial bony wall. The septal portion is itself divided into rostral and caudal pneumatic chambers by a transverse wall (Fig. 7a). The septal portion is so-called because it contacts the nasal septum (Figs 3d–f & 7), walling off this rostral part of the nasal cavity from the main flow of air. In fact, the major communication between this region and the main nasal cavity is via the ventral meatus, which is formed into a complete tube by the contact of the septal portion of the maxilloturbinate to the nasal septum (Fig. 3d–f, *mv*). The septal portion also bears an elongate fossa housing the cartilage of the vomeronasal organ (Fig 7a, *vno*). The nasolacrimal duct passes dorsally over the septal portion of the maxilloturbinate.

Overview of nasal cavity

The nasal cavity of amniotes may be divided into three major parts (Parsons, 1971; see also Witmer, 1995): vestibulum nasi, cavum nasi proprium, and ductus nasopharyngeus. The nasal cavity proper is often further divided into regio respiratoria and regio olfactoria (NAV, 1994). Evolution of a proboscis in tapirs has resulted in reorganization of these components. The nasal cavity of tapirs, measured from the tip of the proboscis to the cribriform plate, occupies some 70–75% of total head length. That tapirs have a large nose is hardly surprising, but what may be more unexpected is that most other ungulates have comparable values (e.g. 60–75% in horses, bison, oxen, deer, and pigs). The quantity that differs between tapirs and these other ungulates is the relative size of the rostralmost portion of the nasal cavity, the vestibulum nasi. The nasal vestibule of tapirs occupies some 75% of the total length of the nasal cavity, whereas in horses, only 42% is vestibule.

The nasal vestibule of tapirs extends from the nostril back to the region of the nasoincisive incisure (Fig. 7). The vestibular portion of the nasal tube traverses the length of the proboscis, such that the nasal cavity proper and its contents are telescoped and restricted to the region between the orbits. Arising from the lateral wall of the nasal tube is a longitudinal mucosal ridge, the plica vestibularis, projecting into the nasal tube (Figs 3 & 7; *pv*). It is present at the very tip of the proboscis, where it is cornified, and is continuous caudally with the concha nasalis vestibularis. As this vestibular fold passes caudally, the dorsal lateral nasal cartilage scrolls into it, transforming the fold into the vestibular nasal concha (Fig. 3a–e, *cnve*). This transformation is gradual but a vestibular concha can be regarded as present at the rostrocaudal level of the second upper premolar. The plica and concha vestibularis divide the nasal tube into dorsal and ventral spaces, which do not correspond exactly to the definitive dorsal and ventral nasal meati of other ungulates. The dorsal space passes caudally dorsal to the vestibular fold and concha and is continuous caudally with both the true dorsal and middle nasal meati. In fact, this dorsal space is perhaps best regarded as a confluence of the two meati (Figs 3 & 7b). Frey & Hofmann (1996a) described an analogous confluence in the dik-dik *Madoqua guentheri*, an artiodactyl with a short proboscis. The ventral space passes caudally into the respiratory region of the nasal cavity proper in the area of the middle series of ventral nasal conchae (Fig. 7b). The most significant aspect of this morphology is that the nasal vestibule does not communicate directly with the ventral nasal meatus, but is separated from it by the expanded maxilloturbinate structures and by the in-rolling of the maxillae and premaxillae noted above.

The nasal cavity proper, as mentioned, is compressed caudally due to expansion of the vestibule. The mucous membrane covering the bony turbines is not generally elaborated into complex conchal folds, but rather

faithfully reflects the underlying bony structure (compare Fig. 7a & b). For example, the dorsal and ventral nasal conchae clearly lack a plica recta and a plica basalis, respectively. The status of the plica alaris of the ventral nasal concha is equivocal. There is a mucosal fold arising from the dorsalmost component of the ventral nasal concha, which would seem, therefore, to correspond to the alar fold of, say, horses (e.g. Schummer, Nickel & Sack, 1979) (Fig. 8b, *pa*). However, in tapirs the dorsal lateral nasal cartilage scrolls into this fold (Fig. 3c–e), whereas in other ungulates the plica alaris is supported by the medial accessory nasal cartilage, with the dorsal lateral nasal cartilage supporting the plica recta (Fig. 8b). Thus, lacking decisive evidence of homology, we have chosen to refer to these structures simply as the vestibular concha and fold.

In general, the nasal conchae are highly modified relative to those of other ungulates (Fig. 7b). As noted above, the maxilloturbinate supporting the ventral nasal concha (*cnv*) is expanded and subdivided into five smaller conchae. In most other mammals, the ventral nasal concha is more or less horizontal. In tapirs, caudodorsal expansion of the nasal vestibule has caused the entire airway to become arched, resulting in rotation of the ventral conchal complex and middle meatus such that they are now steeply inclined. Inclination allows the conchal complex to remain in line with the direction of airflow. As just mentioned, the dorsalmost component of the ventral nasal concha supports and is continuous with the vestibular mucosal fold; in doing so, it presents a broad concave surface facing rostr dorsally (Fig. 7a), resembling the ‘umbrella-shaped cartilage’ described by Frey & Hofmann (1996a) for Guenther’s dik-dik *Madoqua guentheri*. Although highly modified, the surface area of the ventral conchal complex and the ethmoidal conchae are not substantially reduced relative to those of most other ungulates. In contrast, the dorsal nasal concha (*cnd*) is extremely reduced and out of the main flow of air. Similarly, elaboration and reorientation of the maxilloturbinate, coupled with the arching of the airway and infolding of the maxillae and premaxillae, has resulted in isolation of the ventral nasal meatus from the main flow of air; Frey & Hofmann (1996a) again reported similar findings in *M. guentheri*.

DISCUSSION

Meatal diverticulum homology and function

The meatal diverticulum of tapirs is an elaborate, highly derived, yet enigmatic structure. Until now, the meatal diverticulum of tapirs was thought to be homologous to the nasal diverticulum of equids. The first statement of this hypothesis of homology can be traced to Beddard & Treves (1889), who also referred to a similarly placed structure in the rhinoceros *Dicerorhinus sumatrensis* as a nasal diverticulum (Fig. 8c). This view became widely accepted after the authoritative treatment of Gregory (1920), such that in all later discussions (e.g. Radinsky,

1965; Wall, 1980) the homology of the nasal diverticulum in perissodactyls has been unquestioned. There never has been a critical appraisal of this hypothesis, and even Gregory (1920) appears to have taken it as an assumption.

The term ‘nasal diverticulum’ was first applied to extant horses, where it colloquially is known as the ‘false nostril.’ The nasal diverticulum in horses (Fig. 8a, b, *dn*), situated lateral and just caudal to the definitive nostril, is a blind, fur-lined, cutaneous pouch extending from the nostril to the nasoincisive incisure (see also Schummer *et al.*, 1979). It is wholly external to the cartilaginous nasal capsule and accessory cartilages (Fig. 8b). The meatal diverticulum of tapirs is superficially similar in that it also is a diverticulum that comes to lie in direct association with the nasoincisive incisure. In fact, this similarity seems to be the sole basis for homologizing these structures in horses and tapirs. Closer examination shows fundamental differences. As described above, the structure in tapirs (i.e. the meatal diverticulum) is not an external, cutaneous, blind pouch, but rather an intracapsular, mucocartilaginous tube that maintains communication with the nasal cavity at both ends (Fig. 6). Moreover, the meatal diverticulum of tapirs is derived from the scrolling of the dorsal lateral nasal cartilage (Fig. 3e–h; see above). The dorsal lateral nasal cartilage is also present in horses, but it scrolls into the plica recta (*pr*) and has nothing to do whatsoever with the nasal diverticulum (Fig. 8b). In fact, the nasal diverticulum is external even to the alar cartilage (Fig. 8a, *pa*). The situation in horses shows that the hypothesis of homology fails Patterson’s (1982) test of conjunction in that both putative homologs (i.e. nasal diverticulum and scrolling dorsal lateral nasal cartilage) co-occur in the same animal.

Beddard & Treves (1889: 11) figured a rhinoceros snout and briefly mentioned ‘cartilages of nasal diverticulum’ that appear to be scrolled (Fig. 8c). Unfortunately, this is to our knowledge the only report in the literature of the nasal anatomy of rhinoceroses, and it is difficult to relate the figured structures to those of other extant perissodactyls. If the structures are indeed cartilaginous, then perhaps they are related to the meatal diverticulum of tapirs, which would not be unreasonable given that tapirs and rhinoceroses are extant sister groups (Prothero, Manning & Fischer, 1988; Prothero & Schoch, 1989). In any case, it seems highly unlikely that the figured structures in rhinoceroses have any relationship to the nasal diverticulum of horses.

The function of the meatal diverticulum in tapirs remains unknown. Its relatively minuscule volume would argue against its having any significant role as a resonating device in phonation. The mucosa is unremarkable and shows no unusual glandular or cavernous tissue. It does not seem to be a correlated by-product of proboscis evolution in that other animals with probosces – such as dik-diks, saiga and elephants – lack meatal diverticula (Boas & Paulli, 1908, 1925; Frey &

Hofmann, 1995, 1996*a,b*). At the same time, the meatal diverticulum and its osteological correlates comprise an elaborate anatomical system that has a long fossil history, dating at least to the Oligocene (Radinsky, 1965). Thus, whereas it would seem that the system must function in some way (or did in the past), this function remains totally obscure.

Novel aspects of the proboscis of tapirs

Throughout this paper we have documented numerous anatomical attributes of the facial region of tapirs that are strongly divergent from those of most other ungulates. The intent of this section is to provide an overview of these novelties. In doing so, we will use horses rather than rhinoceroses as our outgroup because horses are the only perissodactyl for which adequate comparative data are known. This section is not intended to be a comprehensive analysis of the phylogenetic transformation leading to the proboscis of modern tapirs; such an analysis would require extensive information on not only extinct tapiroids and other extinct perissodactyl groups, but also robust data on extant rhinoceroses. Neither will this section be a comparative study of probosces across Mammalia; such a study is beyond the scope of the present work, and will be the subject of a future paper.

The conformation of the snout region of horses resembles that of most other large ungulates, but differs sharply from that of tapirs. In addition to lacking a flexible proboscis, horses lack the derived caudal extension of the nasoincise incisure present in tapirs, retaining instead relatively long snouts, rostrally extensive nasals, contact between nasal and premaxilla, and relatively small nares (Fig. 5). Hence, the bony side-wall of the nasal cavity extends far more rostrally in horses, and the nasal conchae extend correspondingly further forward. The main airway follows the long axis of the skull. The cartilages of the nasal cavity are elaborate, with a rostrally extensive septal cartilage, prominent dorsal lateral nasal cartilages, and two additional pairs of cartilages (i.e. alar cartilages and medial accessory cartilages); these cartilages function as support structures for vertically-oriented nostrils as well as attachment sites for dilator musculature (Figs 5 & 8). The nostril of horses is crescent-shaped when relaxed

and elliptical when dilated. The principal muscles responsible for this dilation are lateralis nasi and dilator naris apicalis (= dilator naris lateralis, transversus nasi), both of which anchor to the alar and/or medial accessory cartilages (see also Schummer *et al.*, 1979).

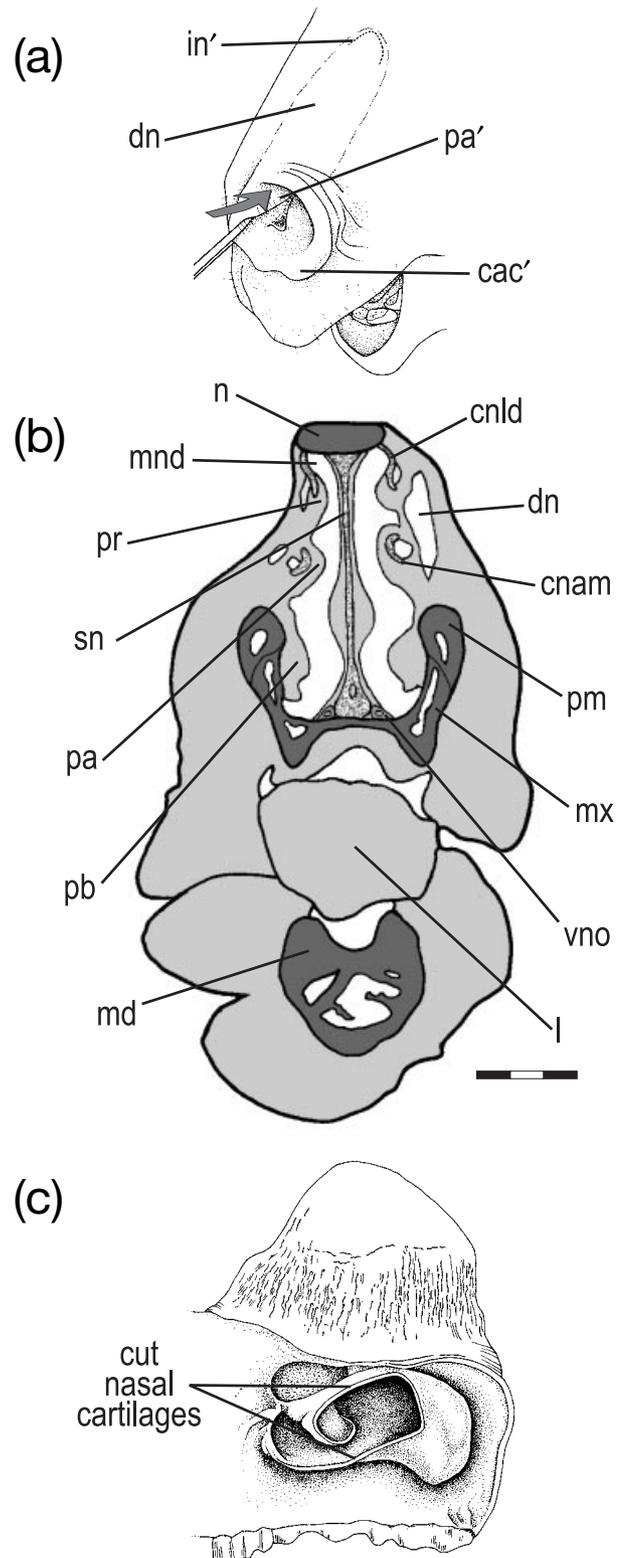


Fig. 8. (a) Snout of a domestic horse in oblique view, showing the position and extent of the nasal diverticulum. A rod has been inserted to displace the nostril medially. The arrow shows the entrance to the nasal diverticulum. (b) Drawing of a CT slice through the middle of the naris of a horse, showing the relationship of the nasal diverticulum to other narial structures. (c) Nose of the rhinoceros *Dicerorhinus sumatrensis* in right lateral view to show its enigmatic nasal cartilages. Scale bar in b = 3 cm. (a) Modified after Ashdown & Done (1987). (c) Redrawn from Beddard & Treves (1889). See Table 1 for abbreviations.

Obviously the major facial novelty of tapirs is the presence of a fleshy proboscis, a structure that has required dramatic re-organization of virtually the entire head. One might predict that a highly mobile proboscis would be coupled with reduction and retraction of the osseocartilaginous elements of the face to create space for movement. More importantly, such a re-organization would permit the co-opting of existing facial musculature for new functions and enhanced mechanical advantage. Tapirs fully meet these expectations. Radinsky (1965) and Wall (1980) reviewed the bony manifestations of this transformation. For example, the nasoincisive incisure has migrated caudally to a position behind the orbit. The premaxilla and nasal are no longer in contact, resulting in the maxilla forming a portion of the narial border. The nasals are reduced and retracted. The length of the skull rostral to the orbits is reduced, particularly the distance between the orbit and infraorbital foramen. Moreover, this study revealed no evidence in *Tapirus* of accessory nasal or alar cartilages (Figs 3 & 5); as a likely consequence, the dilatator naris apicalis and lateralis nasi pars ventralis are absent. Likewise, the nasal septum is highly emarginate rostrally in tapirs (Fig. 5a) rather than extending all the way up to between the nostrils as in horses (Fig. 5b). As a result, the rostral half of the proboscis of tapirs is virtually without any internal bony or cartilaginous support. Furthermore, the nostrils of tapirs are horizontally oriented, and it seems plausible that loss of the intrinsic dilator musculature required reorientation of the nostril to permit active dilation with existing longitudinal musculature (e.g. levator nasolabialis, caninus; see Fig. 1b). Otherwise, tapirs have simply co-opted facial muscles already present in other perissodactyls (and in mammals generally) for use in the proboscis – in particular, levator labii superioris, levator nasolabialis, caninus, and lateralis nasi (pars dorsalis).

The presence of a proboscis also has resulted in major transformation of the internal anatomy of the nasal cavity (Fig. 7). Most notably, the nasal vestibule is expanded to encompass approximately three-quarters of the nasal cavity. This vestibular expansion has had the effect of compressing and simplifying more caudal elements. For example, the bony endoturbinates I and its mucosal counterpart, the dorsal nasal concha, are markedly reduced, and a plica recta is absent. Similarly, the endurbinates II (and the middle nasal concha) is reduced to being just the dorsalmost of the ethmoturbinate series. Furthermore, the plica basalis is absent, as is the plica alaris, unless the single remaining mucosal fold, the plica vestibularis, bears some phylogenetic relationship to the latter. Expansion of the nasal vestibule also has altered the overall conformation of the nasal airway such that it is no longer straight and in line with the long axis of the skull, but rather is dorsally arched. In accordance with this arching, the components of the ventral nasal conchae are inclined such that they remain in line with the main flow of air. There are a few features within the nasal cavity that are clearly apomorphic, but whose functional relationship to the

proboscis is problematic. For example, the meatal diverticulum is diagnostic of modern tapirs, but has no obvious functional connection to the proboscis. The same can be said for the effective isolation of the ventral nasal meatus and for the rostral portion of the maxilloturbinate that contacts the nasal septum and vomeronasal organ.

The proboscis of tapirs as a muscular hydrostat

One of the most important findings of this study is that tapirs, in building their probosces, have radically transformed their snouts. Not only have they reduced and retracted the bony components, but they also have apomorphically lost several of the cartilaginous elements. Thus, the rostral half of the proboscis lacks any significant internal osseocartilaginous support. Rather, the proboscis is composed almost entirely of soft tissues. In short, tapirs have replaced a relatively rigid, osseocartilaginous narial support structure with a flexible, mobile apparatus constructed of connective tissue and muscle. The proboscis of tapirs has all the characteristics of a muscular hydrostatic organ.

Kier & Smith (1985; see also Smith & Kier, 1989) have described the unique biomechanical properties shared by such diverse organs as elephant trunks, lizard tongues, and squid tentacles. All such organs are composed primarily of muscle and lack typical internal skeletal support. Due to their muscular composition, these organs are generally flexible and capable of a variety of complex movements. Kier & Smith have dubbed such structures 'muscular hydrostats'. Although there is considerable variation in the morphology of muscular hydrostats, the constituent muscles typically fall into one of three groups (Kier & Smith, 1985; Smith & Kier, 1989): (1) longitudinal muscles, oriented parallel with the long axis; (2) transverse muscles, generally oriented perpendicular to the long axis of the organ; (3) helical muscles, obliquely arranged fibres along one or two sides forming a portion of a helix.

Because total volume of a muscular hydrostatic organ remains constant (being composed mostly of incompressible water), a decrease in any one dimension produces a compensatory increase in at least one other dimension. In general, contraction of longitudinal muscles results in shortening, while contraction of transverse (or radially oriented) muscles produces elongation. More complex actions such as bending and twisting require the simultaneous action of multiple muscle groups. Smith & Kier (1989) note that in muscular hydrostats capable of the most complex movements (e.g. elephant trunks), longitudinal musculature tends to be superficial to transverse musculature.

The tapir proboscis is an excellent example of a muscular hydrostat, and evolution of the narial apparatus is best viewed in this context. The proboscis muscles of tapirs can be allocated to the three categories noted by Kier & Smith (1985), although few of the muscles are purely longitudinal, transverse, or helical

along their entire lengths. The principle longitudinal muscles are levator labii superioris, levator nasolabialis, caninus, and orbicularis oris. Deep to this group are the transverse muscles, including rectus nasi, lateralis nasi, and the rostral fibres of buccinator. Some of the muscles just noted also can be regarded as helical muscles, such as levator labii superioris, levator nasolabialis, and caninus. Interestingly, these last three have both helical and longitudinal components, with the helical portion being more proximally located and the longitudinal portion more distal.

Based on attachments and fibre orientations, one can make predictions about actions of the proboscis muscles. Levator labii superioris is clearly the major elevator of the proboscis when acting bilaterally (Fig. 1b), and contributes to lateral flexion (side-bending) and twisting when acting unilaterally. Levator nasolabialis has complicated movements. When acting bilaterally it will retract the proboscis, dilate the nostrils, depress the elevated proboscis, and raise the depressed proboscis. When acting unilaterally, it is involved in lateral flexion and twisting of the proboscis and dilation of the nostril. Attachments of caninus suggest that it will depress the elevated proboscis when acting bilaterally, will contribute to lateral flexion and twisting of the proboscis during unilateral contraction, and will dilate the nostril in both cases. Orbicularis oris is probably involved in depressing the elevated proboscis and retraction when acting bilaterally as well as some lateral flexion unilaterally. The transverse muscles – rectus nasi, lateralis nasi, and buccinator – will act primarily to dilate the entire vestibular portion of the nasal tube; in addition, they may play a role in protrusion, although the proboscis is probably capable of only minimal elongation.

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