

Case studies in novel narial anatomy: 2. The enigmatic nose of moose (*Artiodactyla*: Cervidae: *Alces alces*)

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Abstract

The facial region of moose *Alces alces* is highly divergent relative to other cervids and other ruminants. In particular, the narial region forms an expanded muzzle or proboscis that overhangs the mouth. The nose of moose provides a case study in the evolution of narial novelty within a phylogenetically well-resolved group (Cervidae). The function of the nasal apparatus of moose remains enigmatic, and new hypotheses are proposed based on our anatomical findings. Head specimens of moose and outgroup taxa were subjected to medical imaging (CT scanning), vascular injection, gross anatomical dissection, gross sectioning, and skeletonization. Moose noses are characterized by highly enlarged nostrils accompanied by specialized musculature, expanded nasal cartilages, and an increase in the connective-tissue pad serving as the termination of the alar fold. The nostrils are widely separated, and the rhinarium that encircles both nostrils in outgroups is reduced to a tiny central patch in moose. The dorsal lateral nasal cartilage is modified to form a pulley mechanism associated with the levator muscle of the upper lip. The lateral accessory nasal cartilage is enlarged and serves as an attachment site for musculature controlling the aperture of the nostril, particularly the lateralis nasi, the apical dilators, and the rectus nasi. Bony support for narial structures is reduced. Moose show greatly enlarged nasal cartilages, and the entire osseocartilaginous apparatus is relatively much larger than in outgroups. The nasal vestibule of moose is very large and houses a system of three recesses: one rostral and one caudal to the nostrils, and one associated with the enlarged fibrofatty alar fold. As a result of the expanded nasal vestibule, osseous support for the nasal conchae (i.e. turbinates) has retracted caudally along with the bony nasal aperture. The nasoturbinates and its mucosal counterparts (dorsal nasal concha and rectal fold) are reduced. The upturned maxilloturbinate, however, is associated with an enlarged ventral nasal concha and alar fold. Moose are the only species of cervid with these particular characteristics, indicating that this anatomical configuration is indeed novel. Although functional hypotheses await testing, our anatomical findings and published behavioural observations suggest that the novel narial apparatus of moose probably has less to do with respiratory physiology than with functions pertaining specifically to the nostrils. The widely separated and laterally facing nostrils may enhance stereolfaction (i.e. extracting directional cues from gradients of odorant molecules in the environment), but other attributes of narial architecture (enlarged cartilages, specialized musculature, recesses, fibrofatty pads) suggest that this function may not have been the evolutionary driving force. Rather, these attributes suggest a mechanical function, namely, an elaborated nostril-closing system.

Key words: Artiodactyla, Cervidae, *Alces*, nasal anatomy, proboscis, stereolfaction, nostril

INTRODUCTION

Modern moose *Alces alces*, the largest living member of Cervidae, are characterized by uniquely palmated antlers and a distinctively enlarged muzzle (Nowak, 1999; Fig. 1). As many as six subspecies of moose have been recognized,

reflecting the broad range of habitats this species occupies (Franzmann, 1981). Moose (also known as elk in Europe) are now recognized as a single species, and subspecies ranks have been abandoned in favour of recognition of somewhat distinct ecotypes, differing in features such as body size, antler size and shape, and coloration (Geist, 1999).

Alces is a member of the clade Odocoileinae, and as such, possesses a telemetacarpal structure in the feet

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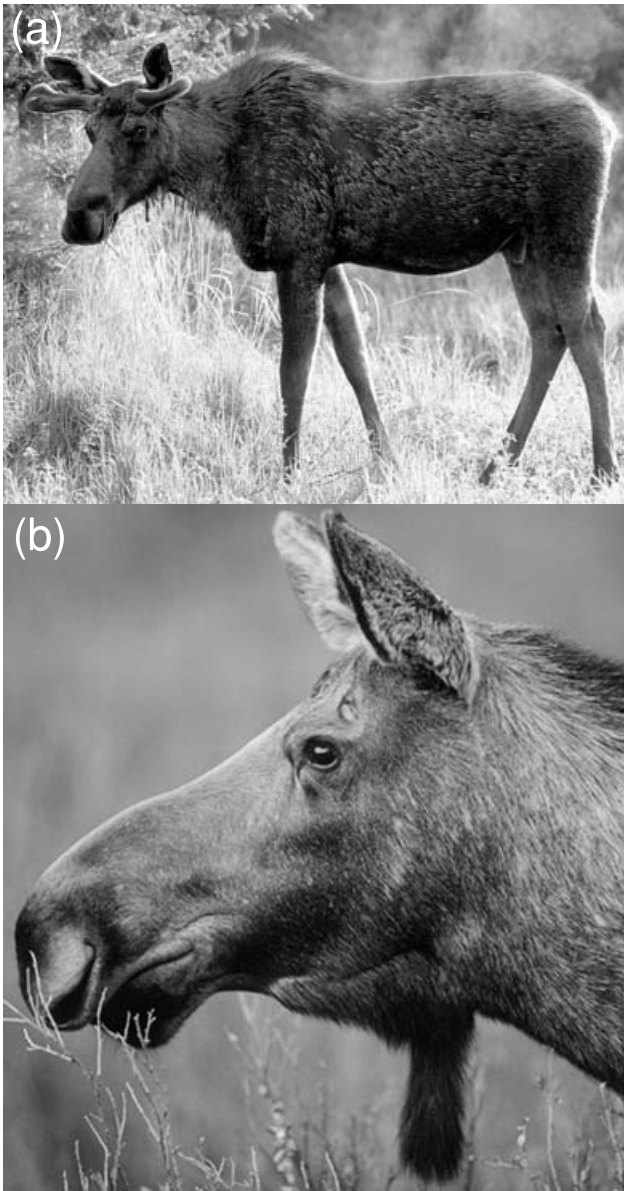


Fig. 1. Lateral view of male moose *Alces alces*: (a) in velvet; (b) lateral view of head showing unique muzzle. (a) Courtesy of M. Reichmann; used with permission. (b) Courtesy of G. and B. Corsi and the California Academy of Sciences; used with permission.

(Webb, 2000; Fig. 2). However, they are believed to have originated from a group separate from other New World cervids given their shortened neck (Scott, 1885), hair structure (Peterson, 1978), horizontally extending palmate antlers (Churcher & Pinsof, 1988), and vomerine septum (Groves & Grubb, 1987). *Alces* is a relatively young taxon, first appearing in the fossil record in middle-to-late Villafranchian deposits (*c.* 1.5 million years ago) in Europe (Franzmann, 1981). There clearly was interchange among members of Alcini between Eurasia and North America before the appearance of *Alces* (e.g. *Cervalces*, occurring as far back as Kansan deposits; Churcher & Pinsof, 1988). *Alces alces* does not appear in the North American fossil record until the late Wisconsinian (Franzmann, 1981). Some authors believe that there may

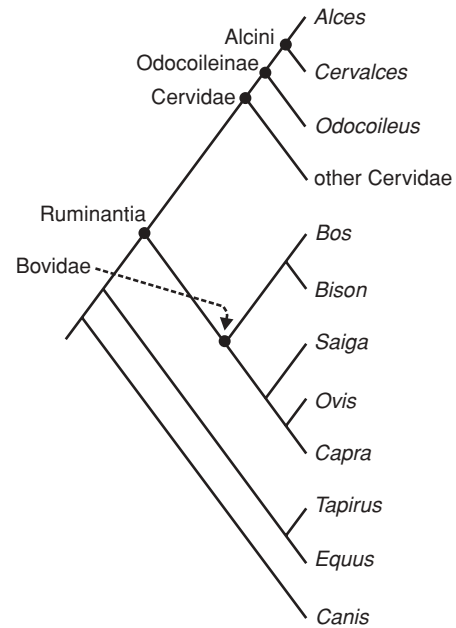


Fig. 2. Phylogenetic relationships of taxa and clades referred to in this study. Topology based on Novacek, Wyss & McKenna (1988) and Groves & Grubb (1987).

have been two separate crossings of modern moose into North America (Peterson, 1978).

Although their range has been much reduced in the face of human incursion into their native habitats (Heptner, Nasimovich & Bannikow, 1988), moose live throughout northern Eurasia and northern North America, occupying taiga and boreal forests. Some previously unoccupied North American areas, such as Rocky Mountain Wyoming and Idaho and Newfoundland have seen thriving human-augmented moose populations in the past 150 years (Karns, 1997). Moose are naturally limited in the south by habitats that exceed 27°C for long periods and do not provide adequate access to water and shade (Franzmann, 1981) and in the north by snow depths exceeding about 1m (Geist, 1999). They do not form herds or permanent groups, preferring habitats with access to abundant water and medium to dense cover (Peterson, 1978). Moose are selective browsers, or concentrate selectors (Hofmann, 1989), although their diet changes considerably during the year. In winter, moose subsist on tree bark, young branches, and lichens while they minimize the energy spent on foraging to conserve energy stores (Geist, 1999). During the northern growing season, moose forage for young branches of early successional deciduous trees, herbs, forbs, and aquatic plants, feeding often during daytime before the mating season (Peterson, 1978). At this time, moose never venture far from a source of aquatic vegetation, spending much of their feeding time partially or even completely submerged. Moose attain their largest size in forests where recent fires have given way to early-successional boreal vegetation (Geist, 1999). They are excellent exploiters of new environments, and although they do not thrive in mature habitats, they are often among the first species to establish in a new taiga or boreal habitat after a disturbance (Peterson, 1978; Geist, 1999).

The distinctive skulls and antlers of moose have been examined in numerous accounts (e.g. Scott, 1885; Flerow, 1952; Peterson, 1978; Geist, 1999). Beyond their antlers, the elongate fleshy muzzle of moose is probably their most remarkable attribute (Fig. 1). Very few studies, however, have been carried out on the soft-tissue cephalic anatomy in moose. Boas & Paulli (1908) included moose in their seminal work comparing the facial musculature of several different mammals to that of elephants. Meinertz (1955) carried out a detailed study of cranial muscles and their innervations in moose. Both of these studies, however, focused on musculature and lacked reference to osteological, vascular, and other soft-tissue features of the narial regions in moose. This study attempts to analyse the functional anatomy of the narial region in moose in reference to key differences from outgroups and with a mind on the enigmatic function of the nose of moose.

This research is part of a larger study attempting to describe the functional anatomy of unusual narial structures in modern amniotes (Witmer, Sampson & Solounias, 1999; Clifford & Witmer, 2001, 2002*a,b*, 2003; Witmer, 2001*a,b*). Peculiar narial structures are the product of natural selection acting upon a set of anatomical substrates, and this project attempts to determine how these differences result in causally-associated bony features in taxa with these apomorphies. A goal is to assess the presence or absence of novel soft-tissue structures in extinct taxa by appeal to the osteological correlates of these soft tissues as determined by their anatomy in extant taxa. Soft-tissue structures can be inferred in fossil taxa based upon common osteological correlates for certain structures shared between extant and extinct taxa (Witmer, 1995*a*), and ultimately this study seeks to determine how the functional anatomy of modern moose may bear on the reconstruction of soft-tissue narial structures in related fossil taxa.

MATERIALS AND METHODS

Four head specimens of *Alces alces* supplied by the Department of Natural Resources (DNR) in Newfoundland, Canada, were the primary source of data in this study. All 4 were wild animals that had been in accidental collisions with vehicles: 2 moose were killed outright, and 2 were finally shot by DNR officials. These specimens include a bull, a cow, a male calf, and a female calf (OUVC 9559, 9560, 9561, 9742, respectively). Two additional skulls (AMNH 207705, OUVC 9587) were examined before work on the study specimens to reveal modified bony narial structures. To determine anatomical structures in an outgroup, specimens of white-tailed deer *Odocoileus virginianus* of various ages and sexes (OUVC 9471, 9540, 9542, 9543, 9544, 9551, 9552, 9554, 9555, 9577, 9589, 9691, 9702, 9705, and 9742) were examined either as intact heads or as skulls.

Three moose (OUVC 9742, 9559, 9560) and 1 *Odocoileus* doe (OUVC 9741) were subjected to X-ray computed tomography (CT) at O'Bleness Memorial Hospital in Athens, Ohio, before dissection. Additionally, the

arterial system of 1 moose cow (OUVC 9741) was injected with a radio-opaque barium/latex solution (Sedlmayr & Witmer, 2002) and CT scanned again to visualize arterial branches occurring within and outside the nasal vestibule. Please see the online supplemental information (http://digimorph.org/specimens/Alces_alces/) for details on scanning protocols, as well as movies and animations of the CT data. The carotid arteries were injected while the occipital arteries were occluded to reduce extravasation of injection medium from bullet wounds in the cranial cavity. Both sectional anatomy and skeletal/arterial reconstructions were analysed in this specimen. All moose study specimens were dissected, sagittally sectioned, and skeletonized using Terg-A-Zyme (Alconox, Inc.) in lightly boiling water. Dissections were recorded with digital photography and videotaping. The nasal cartilages of the cow and bull were removed, fixed in 10% neutral buffered formalin, and preserved in 70% ethanol. Outgroup specimens were obtained either as skulls or as heads and then dissected, subjected to various kinds of sectioning (coronal or sagittal), and ultimately skeletonized. Veterinary anatomy texts (Getty, 1975; Nickel *et al.*, 1986; Schaller, 1992) and *Nomina Anatomica Veterinaria* (NAV, 1994) were used to standardize nomenclature of anatomical structures.

RESULTS

External anatomy

The enlarged nose of moose is characterized by a fleshy muzzle and mobile upper lip that, when relaxed, sags over the mouth. Rostrally, the muzzle takes on a flat shape, contoured only by the rostralmost portion of the nasal septum and the bulging lateral cartilages. In other cervids, the rhinarium covers much of the front of the nose, usually encircling both nostrils, but moose are highly divergent in this regard. The rhinarium of moose is a small triangular hairless patch of skin on the external surface of the nasal septum occupying *c.* 5 cm² in adults. The ventral apex of the rhinarium is continuous with the median upper lip cleft. The nostrils in moose are displaced such that they face almost entirely laterally (Fig. 1). Rostrally, the nostrils have a circular orifice bounded by skin with short dark hairs. As the nostril extends caudally, it takes on a slit-like shape for two-thirds of its length. The dorsal portion of the fleshy nostril is supported internally by the rostralmost extent of the alar fold (plica alaris), and a large fatty connective tissue pad here contributes to the slit-like shape of the caudal portion of the nostril. Within this terminal pad in the alar fold, the lateral accessory cartilages can be palpated, sending a thin process rostrally. When at rest, only the circular orifice of the nostril seems to be open, and this orifice is at a level below the plane of dental occlusion and is displaced laterally.

The nasal cavity of moose is an extremely long structure. Bubenik (1997) reported the length of the face in moose to be 70% of total head length, largest among any

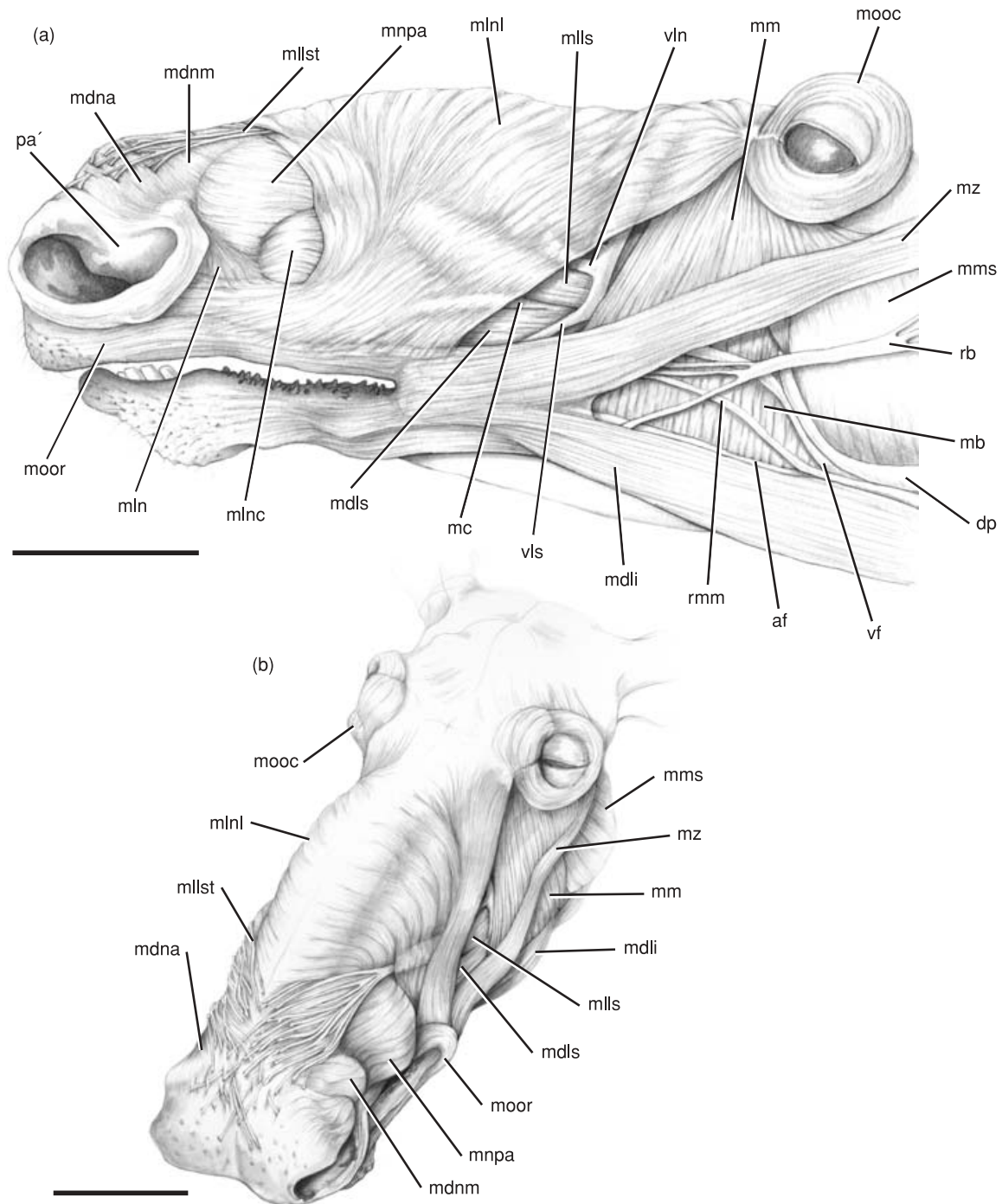


Fig. 3. Superficial dissection of the face of *Alces alces* based on OUV 9559: (a) left lateral view; (b) oblique left rostradorsolateral view. Scale bars = 10 cm. For abbreviations, see Appendix.

cervid. This number agrees well with our measurements of the nasal cavity, which, as measured from cribriform plate to the tip of snout (see Witmer *et al.*, 1999), accounts for 65% of total head length. This elongate nose is well-supported by extensive nasal cartilages. The upper lip and nostrils are very mobile, indicative of a herbivore specialized for browsing (Hofmann, 1989). Aside from the enlarged and modified nostrils, the upper and lower lips in moose also contribute to the increased length rostral to the orbit.

Integument

Moose are generally characterized as being covered in thick, dense fur. On the underside of the head, the fur is indeed thick, and the underlying skin approaches 3–4 mm in thickness. The skin overlying the nose and muzzle is much thinner, and the fur is much shorter. Although the skin remains fur covered on the entire exterior of the head, the fur on the nose is < 5 mm thick. In comparison, the fur of the bell on males may approach 10–12 cm. The skin

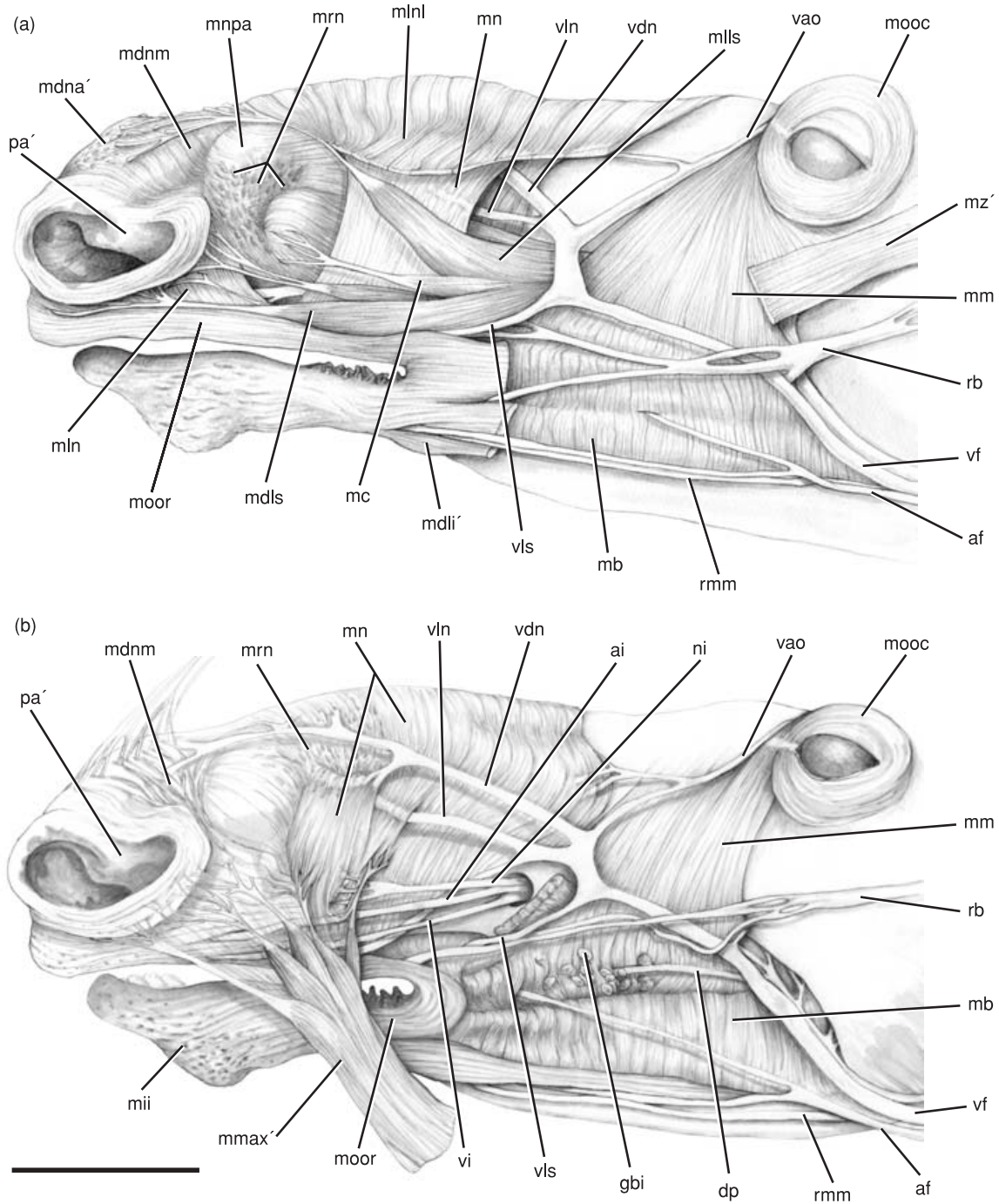


Fig. 4. Deep dissections of the face of *Alces alces* based on OUV 9559: (a) maxillolabial muscles are intact; (b) maxillolabial muscles reflected to reveal underlying structures. Scale bar = 10 cm. For abbreviations, see Appendix.

surrounding the nostril remains completely fur covered. In fact, the first few centimetres within the nasal vestibule are invested with hair-lined skin. One conspicuous feature missing from moose is a discrete mystacial pad. In many mammals, including the *Odocoileus* examined here, there is a dense subcutaneous connective tissue pad caudal to the nostrils containing follicles of thick bristles (vibrissae). A tightly packed mystacial pad is apparently replaced in moose by a series of longer hairs that grow directly away from the skin at regular intervals along the dorsal and lateral aspects of the nose.

Connective tissue pad

At the termination of the alar fold of the nasal vestibule and forming the caudodorsal aspect of the fleshy nostril there is a fatty connective tissue pad (Figs 3–5 & 7; pa'). At the nostril, the pad is directed mediolaterally, but, travelling caudally within the vestibule, the pad is directed dorsoventrally. Also travelling caudally, the mucosa of the pad changes (i.e. at the limen nasi) from a pigmented skin covered thinly in fur to the skinless moist mucosa characteristic of the rest of the nasal cavity and vestibule.

The pad is supported ventrally by cartilage, and dorsally and medially the pad moves freely within the enlarged nasal vestibule.

Musculature

Boas & Paulli (1908) grouped mammalian facial muscles on anatomical grounds whereas Huber (1930) used innervation (i.e. branches of the facial nerve, CN VII). These two groupings coincide almost entirely, and they have been kept for organizational purposes. Nomenclature of the muscle groups follows Boas & Paulli (1908) whereas nomenclature of individual muscles largely follows the NAV (1994).

Orbicularis oculi group

M. orbicularis oculi (Figs 3 & 4; mooc). The fibres encircling the orbit superficial to the protruding orbital margin belong to the orbicularis oculi. This muscle attaches on a tubercle on the lacrimal bone at the margin of the rostromedial angle of the orbit. The fibres of the orbicularis oculi then fan out to completely surround the orbit and the bones comprising the orbital margin. The orbital portion (*M. orbicularis oculi* pars orbitalis) forms a nearly complete circle around the orbit, except for its brief tendinous origin and insertion on the lacrimal bone. The palpebral portion (*M. orbicularis oculi* pars palpebralis) runs parallel to the margin of the eyelids, attaching to the palpebral ligaments medially and laterally. The action of this muscle is to approximate the eyelids and hence narrow the palpebral fissure (i.e. close the eye).

M. levator nasolabialis (Figs 3 & 4; mlnl). Originating from a connective tissue raphe along the midline of the head rostral to the orbit, the levator nasolabialis sends fibres laterally and ventrally. This muscle is very thin and lies just deep to the skin for about two-thirds the length of the nose, and no subcutaneous structures pass superficial to this muscle. As the muscle courses along the nose laterally, its rostrocaudal dimension decreases such that its widest point occurs at its origin and its narrowest point occurs at its insertion. Rostrally, the fibres form an arc roughly parallel to the extent of the lateral accessory cartilages and maintain an even distance from the nostril. Caudally, the muscle follows a path parallel to a line from the rostral margin of the orbit to the corner of the mouth. The levator nasolabialis inserts along the upper lip, attaching to the skin and interdigitating with fibres of other muscles around the mouth. Thus, the muscle sends fibres from a large attachment along the dorsal midline of the nose to converge on a much smaller area just dorsal to the margin of the upper lip. The levator nasolabialis, as its name suggests, elevates the upper lip, especially its caudal portions.

M. malaris (= *M. præorbicularis* (Boas & Paulli, 1908), *M. retractor anguli oculi medialis profundus* (Meinertz, 1955)) (Figs 3 & 4; mm). The malaris is a thin muscle sharing an origin with orbicularis oculi on a tubercle of the lacrimal bone at the rostromedial margin of the orbit. The

muscle then fans out ventrally, widening as it courses to its insertion as a series of interdigitations with buccinator caudal to the corner of the mouth. It lies deep to the levator nasolabialis near the lacrimal tubercle and deep to the zygomaticus (*M. zygomaticus*), the facial vein, and the facial nerve ventrally. The fibres forming the caudal portion of the muscle are parallel to the ventralmost fibres of orbicularis oculi. The malaris is an elevator of the corner of the mouth and of the lateral walls of the oral vestibule (i.e. cheeks).

Maxillolabialis group (= *M. maxillolabialis* (Boas & Paulli, 1908; Meinertz, 1955))

M. levator labii superioris (Figs 3 & 4; mlls). The rostralmost member of the maxillolabialis group, this muscle originates from a common origin for the group at a point just caudodorsal to the infraorbital foramen on the lateral aspect of the maxilla. A tubercle here serves as the origin for the group, and the levator labii superioris occupies its dorsalmost portion. From this origin, the muscle courses, deep to the levator nasolabialis, rostrally and slightly dorsally, the fibres uniting into a single tendon about halfway between its origin and the caudalmost aspect of the nostril. Its tendon then passes rostradorsally over the hump formed by the lateral nasal cartilages (Figs 3, 4 & 6), using the hump as a pulley. Here, on the dorsal aspect of the nose deep to the levator nasolabialis, the tendon splits into several smaller tendons that ultimately insert on the dorsal aspect of the nostril and the flattened muzzle between the nostrils. Small muscle slips from the levator nasolabialis insert on the tendons of the levator labii superioris, and the tendons themselves sometimes possess small muscle bundles rostral to the main muscle bundle. Considerable overlap occurs between contralateral muscle tendons of the levator labii superioris between the nostrils at the continuation of the dorsomedian raphe from which the levator nasolabialis originates. Bilateral contraction of the levator labii superioris results in elevation and eversion of the upper lip and dorsal aspect of the nostril, rostral to the point of support by the lateral nasal cartilages. Unilateral contraction obliquely elevates the ipsilateral lip and elevates the dorsal portion of the nostril.

M. caninus (Figs 3 & 4; mc). This muscle originates from the common origin of the maxillolabial muscles, namely, a tubercle on the lateral aspect of the maxilla just caudodorsal to the infraorbital foramen. Sending out two or three muscle bundles, the caninus courses more or less directly rostrally from its origin. Each bundle of the muscle ends in a tendon at different rostrocaudal points. The differentiated tendons ultimately insert on the caudal aspect of the nostril and onto the lateral accessory cartilages caudal to the nostril. The action of the caninus is to retract the nostril and accessory cartilages caudally.

M. depressor labii superioris (Figs 3 & 4; mdl). The third member of the maxillolabialis group originates on the ventral portion of the common origin of the group. As with the levator labii superioris, the depressor labii

superioris sends a single large muscle belly rostrally. Taking a course more ventral than any other maxillolabial muscle, the depressor labii superioris unites into a single tendon more rostrally than any of the others, just caudal and ventral to the nostril. This single tendon courses rostrally ventral to the nostril and sends several small tendons dorsally to the ventralmost portion of the nostril. It ultimately ends in an area of the upper lip ventral to the rostralmost portion of the nostril. These small tendons serve as the point of attachment of some fibres from the lateralis nasi (*M. lateralis nasi*), in much the same way that the tendons of the levator labii superioris received inserted fibres from the levator nasolabialis. The action of this muscle is to depress and retract the ventral aspect of the nostril and parts of the upper lip. Taken together, the maxillolabial muscles overlie the contents of the infraorbital foramen and lie superficial to the deepest members of the buccinator group. They are all retractors of the nostril and upper lip and, depending on the angle of the muscle, have either a dorsal, ventral, or caudal action on the upper lip and nostril.

Buccinator group

M. buccinator (Figs 3 & 4; mb). The buccinator complex in moose consists of at least three, and possibly four, layers. Papp (2000) described the buccinator of moose and *Odocoileus* in detail, describing the layers of the buccinator and their attachments. Only those parts relevant to narial anatomy are discussed here. The superficial portion of buccinator (*M. buccinator pars buccalis* (NAV, 1994), *M. buccinator pars superficialis* (Boas & Paulli, 1908), *M. buccinatorius pars mandibulo-maxillaris superficialis* (Meinertz, 1955)) is a thin sheet of muscle passing dorsoventrally between its attachments to the maxillary and mandibular alveolar processes and the maxillary tubercle. This superficial sheet extends rostrally to the corner of the mouth, where it interdigitates with the orbicularis oris, and caudally to the ramus of the mandible. The buccal salivary glands are abundant deep to this sheet. The malaris interdigitates with the buccinator pars buccalis near its origin at the maxillary alveolar process, especially at the caudal end of the sheet. Rostrally, near the corner of the mouth, the insertions of the zygomaticus and the depressor labii inferioris converge upon the rostralmost fibres of the pars buccalis, making an area taken up by interdigitations of muscles coming from three different directions. This portion of the buccinator acts to compress the oral vestibule by apposing the cheek to the molar teeth.

The deep portion of the buccinator (*M. buccinator pars molaris* (NAV, 1994), *M. buccinator pars profundus* (Boas & Paulli, 1908), *M. buccinatorius pars mandibulo-maxillaris profundus* (Meinertz, 1955)) is thicker than the superficial portion, sending fibres in a rostrocaudal direction from the angle of the mouth to the ramus of the mandible between the alveolar processes of the maxilla and mandible. Caudally, the pars molaris interdigitates with intermediate layers of the buccinator. Rostrally,

the pars molaris interdigitates slightly with the common insertions of zygomaticus, depressor labii inferioris, and the caudalmost fibres of orbicularis oris. The action of the buccinator pars molaris is to retract the angle of the mouth and, along with the pars buccalis, compresses the oral vestibule.

M. orbicularis oris (= *M. buccinator pars rimana* Boas & Paulli, 1908), *M. buccinatorius pars oris* (Meinertz, 1955)) (Figs 3 & 4; moor). The orbicularis oris originates from the interdigitating intersection of the buccinator, the zygomaticus, and the depressor labii inferioris. From this point at the corner of the mouth, the muscle completely encircles the mouth within the upper and lower lips. Caudally, at the corner of the mouth, the orbicularis oris lies deep to other muscles, and the dorsal labial vessels lie on the dorsal aspect of the muscle along the lips. On the lateral face of the muscle is a series of interdigitations with the insertion of the levator nasolabialis and the lateralis nasi. The orbicularis oris acts as a sphincter of the mouth.

M. incisivus superior (= *M. buccinator pars supra-labialis* (Boas & Paulli, 1908)) (Fig. 7; mis). The incisivus superior is a thick, extensive, fan-like muscle arising from the rostralmost processes of the premaxillae (incisive bones). It radiates out from this point to insert on the upper lip, the connective tissue pad between the nostrils, the underside of the rhinarium, and the septal cartilage. The muscle is best seen in sagittal section, occupying almost entirely the underside of the muzzle between the dorsalmost rostral septum and the upper lip. The principal action of the muscle is to elevate and evert the upper lip and to retract the muzzle.

M. incisivus inferior (Fig. 4; mii). The incisivus inferior arises from the rostral portion of the mandibles and fans out to insert on the lower lip just ventral to the orbicularis oris muscle. It is less conspicuous than the incisivus superior, yet it performs a similar (albeit opposite) function by depressing and curling the lower lip.

M. depressor labii inferioris (Figs 3 & 4; mdli). The inferior labial depressor is a band of muscle originating from the fascia of the neck and partly from the *M. cutaneous faciei* (platysma) muscle. From this origin, it travels along the mandible, overlying the attachment of the buccinator below the tooth row. Its insertion interdigitates with the buccinator, the zygomaticus, and superficial portions of the orbicularis oris in addition to sending some fibres rostrally from this point to interdigitate with more rostral fibres of the orbicularis oris to insert on the skin of the lower lip. As its name suggests, it is a depressor of the corner of the mouth and the lower lip.

M. lateralis nasi (= *M. naso-labialis dorsalis profundus* (Meinertz, 1955)) (Figs 3 & 4; mln). This muscle arises from the lateral aspects of the premaxillae ventral and slightly caudal to the nostrils. It lies deep to the levator nasolabialis caudally and some portions of the orbicularis oris rostrally. Interdigitating with the orbicularis oris and the tendons of the depressor labii superioris, the muscle courses obliquely rostradorsally to insert on the underside of the nostril and the ventral aspects of the accessory cartilages. It is a thick, relatively well-developed muscle that acts to depress the caudal and ventral portions of

the nostril, thus dilating them. Caudally, a thin sheet of the lateralis nasi (*M. lateralis nasi pars caudalis*; Fig. 3; mlnc) courses obliquely caudodorsally to insert on the caudolateral surface of the lateral accessory nasal cartilages.

M. dilatator naris apicalis (= *M. lateralis nasi*, *m. transversus nasi* (Boas & Paulli, 1908), *M. nasolabialis dorsalis profundus pars nasalis* (Meinertz, 1955)) (Figs 3 & 4; mdna). The dilatator naris apicalis is a strong muscle lying superficially between the nostrils and running perpendicular to the superior incisive muscle at its dorsalmost extent. It originates in the connective-tissue septum dividing the halves of the narial vestibules at the rostralmost portion of the face. The muscle inserts onto the dorsal and slightly caudal portions of the nostril. As the muscle makes its way toward its insertion, it thickens, resulting from lateral fibres coalescing before attaching onto the skin of the nostril. The dilatator naris apicalis interdigitates caudodorsally with the elongate tendons of the levator labii superioris. The dilatator naris apicalis acts to pull the nostrils open, slightly rostrally, and dorsally.

M. nasalis (= *M. nasolabialis dorsalis profundus* (Meinertz, 1955)) (Figs 3 & 4; mn). The nasalis is a quadrangular, thick sheet of muscle lying deep to the maxillo-labial muscles ventrally and the levator nasolabialis dorsally. The muscle arises from the interalveolar margin along the maxilla (diastematic ridge; Fig. 6; ommi) and inserts on the underside of the levator nasolabialis and on the fascia near the midline of the dorsal surface of the head. The lateral and dorsal nasal veins irregularly pierce this muscle before travelling caudally superficial to it. The rostralmost fibres of the nasalis (*M. nasalis pars alaris*, Figs 3 & 4; mnpa) interdigitate with the caudal portion of the lateralis nasi, and both muscles run in the same direction at this point. The nasalis is the deepest muscle in the area of the nose between the malaris and the lateralis nasi, and vessels and nerves supplying the narial musculature and skin are all superficial to the nasalis at its caudal border.

M. dilatator naris medialis (= *M. nasolabialis* (Boas & Paulli, 1908), *M. nasolabialis dorsalis profundus* (Meinertz, 1955), *M. lateralis nasi* (Schaller, 1992)) (Figs 3 & 4; mdnm). The dilatator naris medialis (so named in accordance with terminology in Nickel *et al.*, 1986, rather than function) is a well-developed muscle originating from the ventral and caudal aspect of the lateral accessory nasal cartilages. From this origin, the dilatator naris medialis courses first caudally and ventrally to the caudal margin of the nostril, where it turns to travel in a rostradorsal direction. This muscle inserts on the dorsal portion of the nostril, between the dilatator naris apicalis and the fibrofatty termination of the alar fold. The fibre direction at its insertion is parallel to the fibre direction of the rostral fibres of the levator nasolabialis, but the fibres of the medial dilatator lie deep to the tendons of the levator labii superioris. Based on its attachments, the function of this muscle is ironically that of a constrictor of the nostril (not a dilatator, as its name suggests), as its fibre orientation indicates the ability to pull the lateral accessory cartilages and the caudal portion of the nostril up against

the fatty pad lying at the end of the alar fold of the nasal cavity.

Intrinsic musculature of the nose

M. rectus nasi (Boas & Paulli, 1908) (Fig. 4; mrn). Along the nasal vestibule, there are transverse muscle fibres. Generally, the rectus nasi is a diffuse muscle concentrated on the caudal and ventral portions of the nostril, extending from near the mucosa of the nasal vestibule to the underside of the skin. The action of the rectus nasi is presumably that of a dilatator of the nasal passages.

Major nerves and vessels

The vasculature and innervation of major structures involved with the musculature of the nose of moose are summarized below. This list is not intended to be comprehensive, but major anatomical structures contributing to the function of the nose are included here.

Arterial supply of the nose and face

A. facialis (Figs 3 & 4; af). The lingual and facial arteries arise from a common trunk from the internal carotid artery. The facial artery branches caudally from the linguofacial trunk to pass rostrally and ventrally around the edge of the mandible just rostral to the attachments of the masseter, where the artery turns dorsally to follow the rostral margin of the masseter. The two major branches of the facial artery occurring caudal to the corner of the mouth are the superior and inferior labial arteries. The inferior labial artery supplies the lower lip as far rostrally as the midline of the lower lip. The superior labial artery courses parallel to its counterpart in the lower lip, supplying structures along the upper lip from the corner of the mouth to the midline. Several unnamed branches of the facial artery branch off at various points to supply structures ventral to the inferior labial artery and dorsal and caudal to the point where the superior labial artery courses into the upper lip. The facial artery is the major blood supply to muscles of the buccinator group of muscles, especially the caudal and ventral members.

A. infraorbitalis (Fig. 4; ai). The infraorbital artery is a terminal branch of the sphenopalatine artery, itself a branch of the maxillary artery. The sphenopalatine artery branches into ophthalmic, septal, superior alveolar and infraorbital branches just caudal to the point where the infraorbital artery passes into the infraorbital canal. The infraorbital artery gives off no branches within the canal itself, remaining enclosed in the bony cavity coursing through the maxillary sinus. Rostral to exiting the infraorbital canal, the artery gives off numerous branches such as the dorsal nasal artery and lateral nasal artery that travel rostrally and dorsally along the exterior of the nasal vestibule, supplying muscles of the maxillo-labialis group, ventral and rostral members of the orbicularis oculi group, and dorsal members of the buccinator group. Branches of

the infraorbital artery follow the curvature of the nasal cartilages, and some rostral branches of the lateral nasal artery curve around the margin of the nostril to supply structures within the alar fold near the nostril.

A. sphenopalatina. The sphenopalatine artery gives off branches that supply structures on the dorsal aspect of the oral cavity and the ventral and lateral aspects of the nasal cavity and vestibule. The palatine branches course rostrally through the soft palate and the palatal rugae of the hard palate. Branches supplying the nasal vestibule spread out to supply the mucosa lining the ventral nasal concha. These branches appear to make several anastomoses with each other while travelling in a mostly rostral direction.

Venous drainage of the nose and face

V. facialis (Figs 3 & 4; vf). The major vessel draining the facial musculature and exterior of the nasal cavity and vestibule is the facial vein. The vein is formed by a conspicuous confluence just rostral to the margin of the malaris of several branches draining the face. From this point, the vein travels caudally and ventrally along the rostral edge of the masseter. The facial artery and the facial vein travel parallel to each other at this point and wind together ventromedially underneath the mandible.

V. labialis superior (Figs 3 & 4; vls). The drainage of the upper lip is carried out by the superior labial vein, which travels parallel to the superior labial artery along the outer edge of the orbicularis oris muscle from about the midline of the nose to about halfway along the cheek to drain into the facial vein.

V. lateralis nasi and *V. dorsalis nasi* (Figs 3 & 4; vln and vdn, respectively). The dorsal and lateral nasal veins drain muscles and structures from the dorsal midline to the upper lip and from the nostril to the formation of the facial vein superficial to the masseter. Muscles of the orbicularis oculi group, maxillolabialis group, and buccinator group are drained by these veins. There are several anastomoses along the midline between the contralateral dorsal nasal veins. The lateral nasal vein also drains structures just inside the nostril, such as the alar fold rostral to the limen, and one of its small tributaries wraps around the nasal margin of the maxilla after anastomosing with vessels in the nasal vestibule.

V. angularis oculi (Fig. 4; vao). The drainage of most of the muscles of the orbicularis oculi group is carried out by the angularis oculi vein. This vein courses from the formation of the facial vein along the rostral margin of the malaris and enters the supraorbital foramen just medial to the margin of the orbit in the frontal bone. From this foramen, the angularis oculi vein communicates with ophthalmic vessels caudal to the orbit and ultimately with the internal jugular system at the cavernous sinus. This vein is an anastomosis between superficial drainage of the nose with blood draining deeper structures of the cranium.

V. infraorbitalis (Fig. 4; vi). The infraorbital vein drains structures deep to and including the maxillolabialis group. It lies ventral to the lateral nasal vein and dorsal to the superior labial vein, but it is deep to both of these veins.

The infraorbital vein makes a more or less straight line from the caudalmost margin of the fleshy nostril to the infraorbital foramen, where it enters the infraorbital canal to join veins draining the nasal cavity.

Sensory innervation of the nose and face

N. infraorbitalis (Figs 4 & 5; ni). The general somatic sensory innervation of the nose is carried by branches of the trigeminal nerve (CN V), principally by the infraorbital nerve (CN V₂). This nerve travels in the infraorbital canal with the artery and vein of the same name and exits the canal with the artery. From the opening of the infraorbital canal, the infraorbital nerve gives off several branches that travel rostrally, fanning dorsally and ventrally to supply the skin from the infraorbital foramen rostrally to the midline of the nose. The nerve, artery, and vein travelling through the infraorbital canal are bound together by fascia once they are in the canal itself, and this fascia disappears to allow the vessels and nerves to travel separately rostral to the foramen (Fig. 5).

Motor innervation of the nose and face

N. facialis (CN VII). The motor nerve supply for all of the muscles of the face and nose is carried by the facial nerve. The nerve branches into a buccolabial branch (ramus buccolabialis, Schaller, 1992; dorsal buccal branch, Getty, 1975, in ruminants) and a marginal mandibular branch (*R. marginalis mandibulae*, Meinertz, 1955, and Schaller, 1992; ventral buccal branch, Getty, 1975). These branches split from each other behind the caudal margin of the masseter and rejoin rostral to the rostral border of the masseter. Other branches, such as auricular, temporal, and zygomatic branches are not described here, as their contributions are minor in the facial region. Meinertz (1955) gave an extensive account of the course of the facial nerve and the muscles it innervates in the head. Many of our observations agree with those of Meinertz (1955), and the parts relevant to the current study are summarized here.

R. marginalis mandibulae (Figs 3 & 4; rmm). The marginal mandibular ramus of the facial nerve branches caudal to the masseter and courses ventrally along the caudal and ventral margin of the muscle. As it follows the outline of the muscle, it supplies the cutaneous faciei (platysma), the depressor labii inferioris, ventral parts of the orbicularis oris, and the incisivus inferior. At the rostral limit of the masseter, the marginal branch follows the facial artery and vein dorsally and slightly rostrally to join up with the buccolabial branch just rostral to the margin of the masseter.

R. buccolabialis (Figs 3 & 4; rb). The buccolabial branch of the facial nerve courses laterally along the masseter in a fascial sheath. A few smaller branches appear to break away from the buccolabial branch and join up with it a short time later, creating a small plexus of nerves along the masseter and just rostral to its margin. Some of these smaller nerves supply the zygomaticus

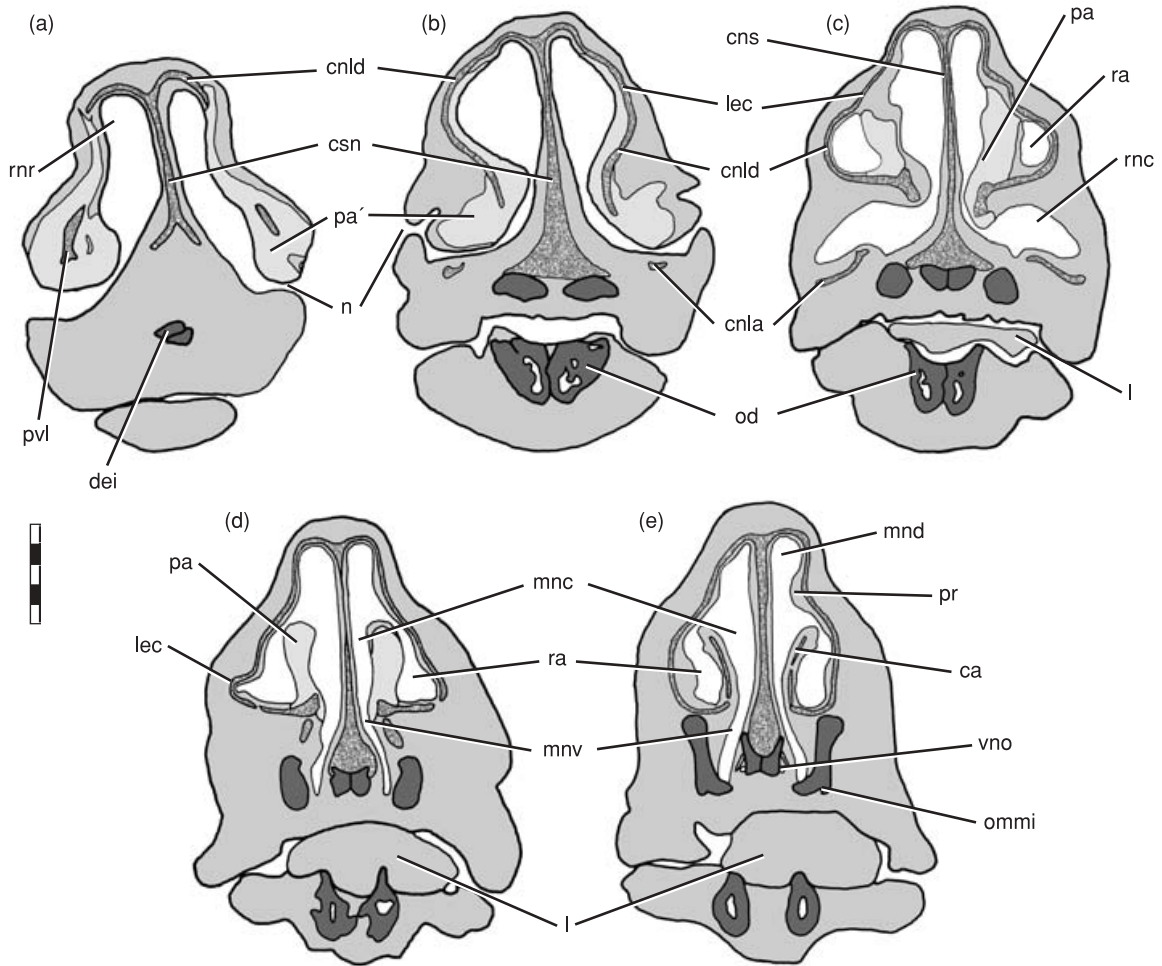


Fig. 5. For legend see facing page.

and the malaris. After rejoining the marginal branch, the buccolabial branch of the facial nerve then branches into dorsal and ventral buccolabial branches. The ventral buccolabial branch supplies superficial muscles along the upper lip, such as the orbicularis oris and the buccinator, and deeper muscles of the nose, such as the nasalis. The dorsal buccolabial branch sends various branches to supply the muscles of the maxillolabialis group and the orbicularis oculi group except the caudoventral portion of the orbicularis oculi and the dorsal portion of the malaris, which receive their innervation from the R. zygomatico-orbitalis of the facial nerve, as also noted by Meinertz (1955). Further rostrally, around the nostril, branches of the facial nerve are difficult to isolate and definitively differentiate from branches of the infraorbital nerve.

Nasal cartilages

Cartilago nasi lateralis dorsalis (Figs 5 & 6; cnld). The dorsal lateral nasal (parietotectal) cartilages of moose form an extensive framework for the support and attachment of muscles responsible for moving the nose. As a whole, the nasal cartilages of moose are elongated

both rostrally to accommodate the overhanging muzzle and caudally to assume much of the support of narial structures that would normally be taken up by the skull bones comprising the bony naris in many other mammals. Caudally, the dorsal lateral cartilage attaches to the nasal and maxillary bones, extending directly rostrally at their attachment. The cartilage expands laterally, creating a convex (with respect to the outside) hump supporting tendons of the levator labii superioris. At the rostral termination of the hump, the dorsal lateral cartilage ends laterally in a prong of cartilage that extends ventrally and rostrally to support the dorsal aspect of the caudalmost portion of the nostril. Ventral to the convexity, the dorsal lateral cartilage receives the attachment of the lateral accessory nasal cartilage, the two being connected by a mobile joint. Farthest rostrally, the dorsal lateral cartilage sends a median process ventrally. This terminal process does not attach to the premaxilla, cartilaginous nasal septum, or the ventral lateral nasal cartilage, as it does in other ruminants (Schaller, 1992). Rather, it ends just rostral to the termination of the premaxilla, supporting the rostralmost structures of the nose, including a rostromedial recess.

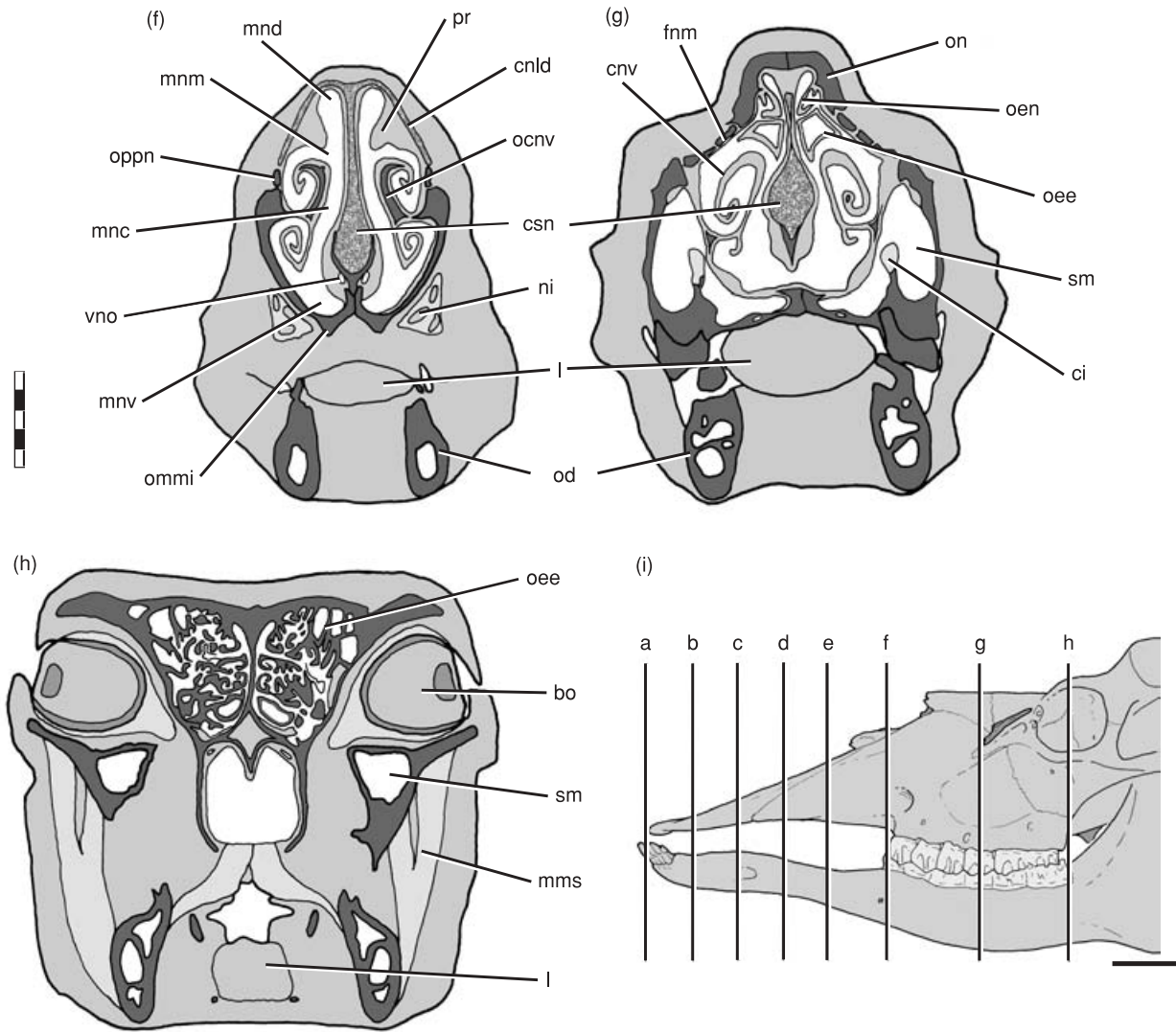


Fig. 5. Drawings of selected computerized tomographic (CT) images of the face of *Alces alces* (OUVC 9559) showing narial structures in successive transverse sections (a)–(h). Soft tissues that are more lightly shaded are less dense (e.g. fat). (i) Skull in left lateral view showing rostrocaudal levels of sections depicted in (a)–(h). Scale bars = 5 cm. For abbreviations, see Appendix.

Cartilago nasi lateralis accessoria (Figs 5 & 6; cnla). The lateral accessory cartilage of moose forms a rough triangle. The caudoventral apex of the cartilage attaches to the underside of the dorsal lateral cartilage, forming a movable joint that is capable of a considerable amount of excursion. The caudodorsal apex curves upward to almost meet the convexity of the dorsal lateral cartilages. The rostral apex of the accessory cartilages extends directly rostrally roughly parallel to the terminal process of the dorsal lateral cartilages. These last two processes support the caudal end of the nostril, and rostradorsal and caudoventral movements of the lateral accessory cartilages facilitate the compression or dilatation of the nostril, respectively.

Cartilago nasi lateralis ventralis (Fig. 6; cnlv). The ventral lateral cartilage has an indefinite separation from the dorsal lateral cartilage. Both lateral cartilages attach to each other for a considerable distance along the nose, but

there is a clear distinction ventrally between structures belonging to the ventral lateral cartilage. The ventral lateral cartilage thinly lines the bones underlying them, namely the premaxilla and maxilla, on the surfaces of these bones within the nasal cavity. Extending dorsally from this position, the ventral lateral cartilage supports a cartilaginous process (Fig. 5; ca) that sweeps upward to support the plica alaris and the fatty pad that blocks the entrance to a lateral recess in the nose. The cartilage supports this fatty pad only on its most ventral portions, leaving the pad apparently free to move medio-laterally.

Cartilago septi nasi (Fig. 5; csn). The septal cartilage of moose separates the halves of the nasal cavity rostrally as far as the termination of the premaxilla and caudally as far as the perpendicular plate of the ethmoid bone. At the rostralmost extent, the separation of the halves of the nasal cavity is carried out by mucosa extending between the

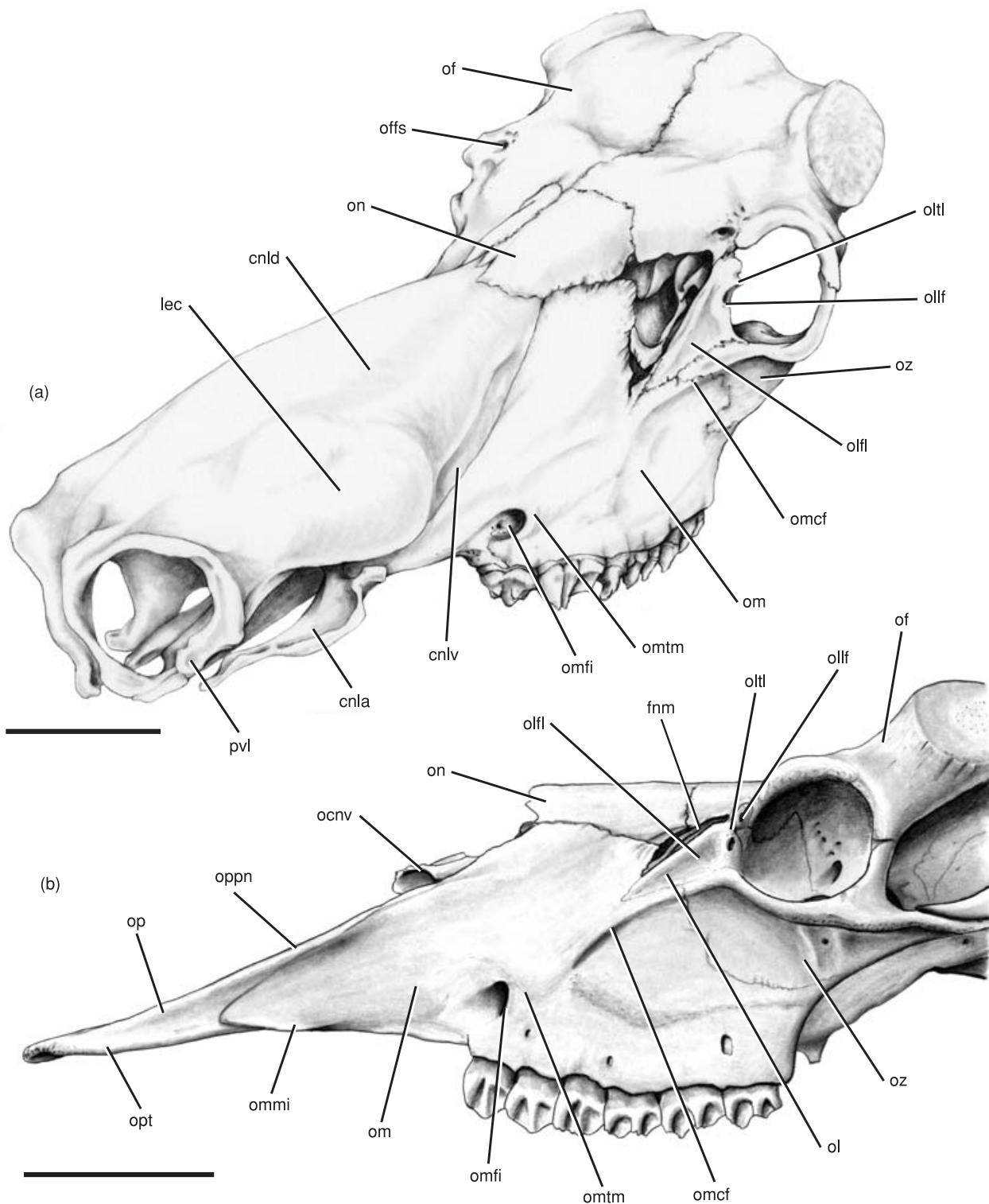


Fig. 6. Skull of *Alces alces* based on OUV 9559: (a) left rostradorsolateral view with cartilages in place to show cartilaginous framework of nose; (b) left lateral view. Scale bars = 10 cm. For abbreviations, see Appendix.

rostralmost septal cartilage and the rostromedian process of the dorsal lateral cartilages. Between its rostral and caudal limits, the septal cartilage extends from the vomer bone dorsally to the dorsal lateral cartilages, being thicker at its base than at its apex.

Overview of nasal cavity

The nasal cavity in moose is composed chiefly of three mucosal conchae and the surrounding air spaces. The largest of these spaces is the ventral nasal meatus

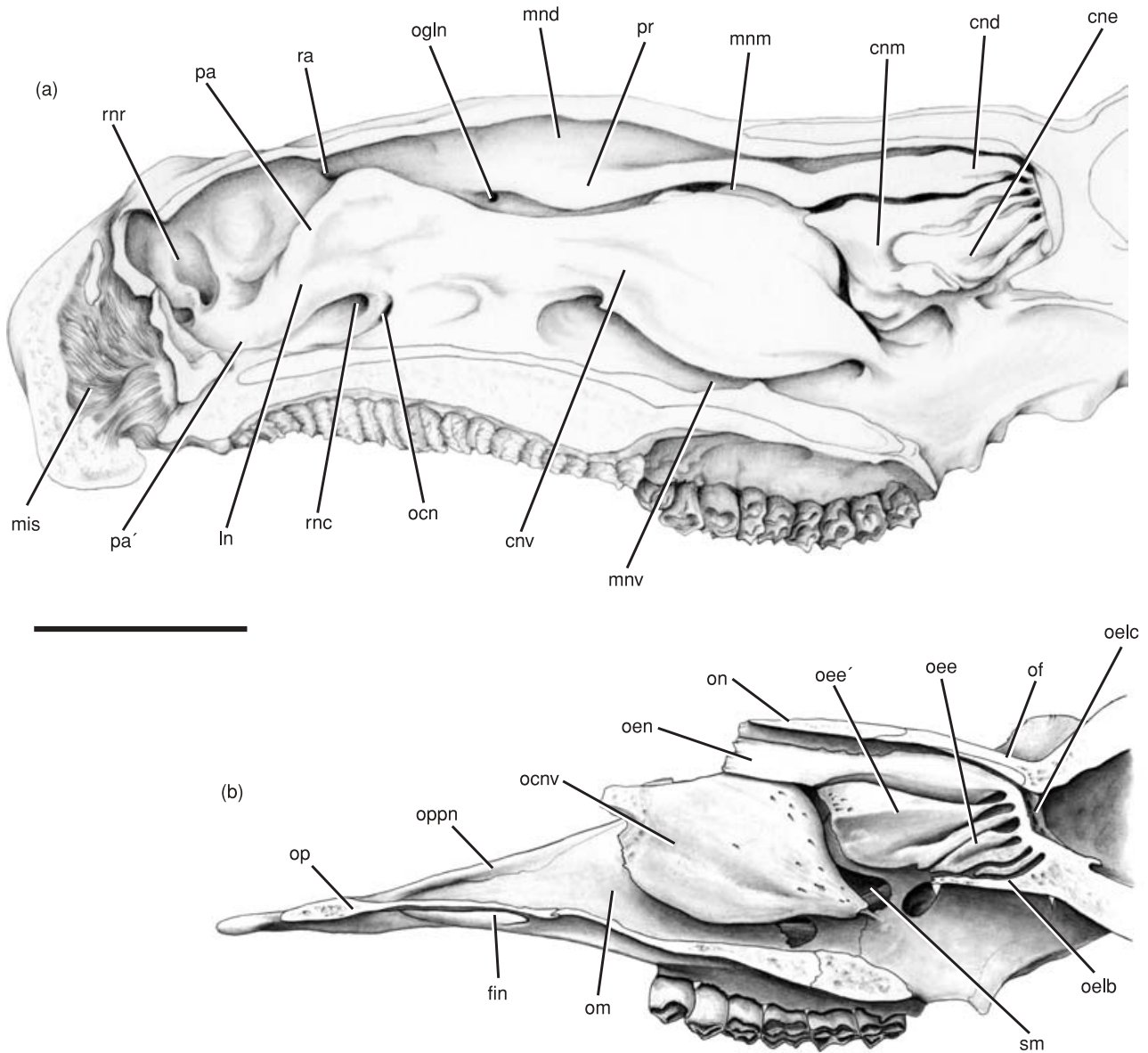


Fig. 7. Medial view of right side of sagittally sectioned head (a) and skull (b) of *Alces alces* (OUVC 9559) with nasal septum and vomer removed to show internal nasal structures. Scale bar = 10 cm. For abbreviations, see Appendix.

(Figs 5 & 7; mnv). This space communicates freely with the nostril rostrally and the choana ventrally. Dorsal to this space is a greatly enlarged concha nasalis ventralis (Figs 5 & 7; cnv). The ventral nasal concha is supported in its caudal half by the maxilloturbinate (Figs 5–7; ocnv) and farther rostrally by the lateral nasal cartilages. Rostral to the maxilloturbinate, the ventral nasal concha is composed of the plica alaris (Figs 3–5 & 7; pa). The alar fold attaches to the lateral wall of the nasal vestibule through a robust mucosal and fibrofatty connection. Caudal to the nostril, the alar fold changes its orientation from more or less directly medial to rostromedial. At this point, the fibrofatty dorsal expansion of the alar fold forms the boundary of a caudally-open, rostrally-blind sac, termed here the recessus naris alaris (Figs 5 & 7; ra). Rostral and ventral to the dorsal fibrofatty pad of the alar fold, a ventral pad

forms the rostralmost extension of the alar fold and the caudodorsalmost portion of the nostril.

Dorsal and caudal to the ventral nasal concha are the concha nasalis dorsalis (Fig. 7; cnd), concha nasalis media (Fig. 7; cnm), and conchae ethmoidales (Fig. 7; cne), which are situated in a more or less dorsoventral series at the caudal end of the nasal cavity. The space between the ventral and middle nasal conchae (meatus nasi medius, Figs 5 & 7; mnm) extends for the entire rostral extent of the middle concha and the caudal half of the maxilloturbinate-supported portion of the ventral concha. The ventral surface of the middle nasal concha is open to the choana, and the ethmoid conchae are partially enclosed by the lamina basalis of the ethmoid (Fig. 7; oelb) (transverse lamina of Moore, 1981). The dorsal nasal concha is much less complex than the other

conchae, as it is only gently curved ventrally and does not contain multiple scrolls. The dorsal nasal concha is supported caudally by the nasoturbinates (Figs 5 & 7; oen) (endoturbinates I of Paulli, 1900), and rostrally, it continues as the plica recta (Figs 5 & 7; pr). The rectal fold does not extend as far rostrally as the fibrofatty extensions of the alar fold, instead terminating just rostral to the mucosal ostium of the lateral nasal glands (Fig. 7; oln). The middle nasal meatus is between the dorsal and ventral nasal conchae rostral to the middle nasal concha. The middle nasal meatus is continuous with the alar recess bounded by the fibrofatty dorsal extension of the alar fold. The air passageway dorsal to the dorsal nasal concha (meatus nasi dorsalis, Figs 5 & 7; mnd) is widened rostrally between the cartilaginous roof of the nasal vestibule and the rectal fold and becomes dorsoventrally constricted caudally ventral to the nasal bones. The mucosa of the dorsal nasal meatus is pigmented caudally (olfactory mucosa) whereas more rostrally it is unpigmented like the rest of the respiratory mucosa.

The nasal vestibule, the area of the nose where air first enters from the nostril, is characterized by three distinct spaces. First, the largest space in the nasal vestibule – the recessus naris rostralis (Figs 5 & 7; nr) – is a rostral expansion of the space dorsal and rostral to the nostril opening. When the narial musculature is at rest, the rostral narial recess is minimized and results in the squared and broadened muzzle. Second, the sac dorsal to the alar fold – the recessus naris alaris – beginning at the caudodorsal margin of the nostril occupies the nasal vestibule dorsally and caudally. It occupies the space created by the lateral expansion of the dorsal lateral nasal cartilages (i.e. the ‘hump’ mentioned earlier that serves as a pulley for the levator labii superioris tendons). This space is bordered rostrally, medially, and ventrally by the attachment of the fatty pad on the alar fold and laterally by the dorsal lateral nasal cartilages. It opens caudally into the nasal cavity proper. Third, the recessus naris caudalis (Figs 5 & 7; rc) begins at the ventral portion of the nostril, ventral to the alar fold, and occupies the caudoventral portion of the nasal vestibule. This caudal narial recess is open to the circular portion of the nostril lined with hair and rostral to the fatty pad of the alar fold.

The nostril opens into the ventral nasal meatus. All nasal meatuses can communicate with each other through the common nasal meatus (meatus nasi communis, Fig. 5; mnc), which is the open space between the cartilaginous septum and the conchae. The dorsal and middle conchae do not lie in the most direct path of air, but rather occupy a more caudodorsal position.

Glands

Moose and other cervids are characterized by relatively large salivary glands to accommodate a browsing diet (Hofmann, 1989). As this study focused on the narial anatomy of moose, the salivary glands were not a major focus of attention (for a discussion of moose salivary glands see Papp, 2000). Caudal to the masseter, moose

possess an enlarged parotid gland that also has been described elsewhere (Hofmann, 1989). Although the gland does not approximate any of the other relevant tissues described here, the duct of the parotid gland (Fig. 3; dp) is associated with several facial structures. The duct first appears at the caudoventral portion of the gland and extends ventral to the angle of the mandible with the facial artery, facial vein, and ramus marginalis mandibulae. Rostral to the masseter and caudal to the angle of the mouth, the parotid duct then courses rostrally to pierce the superficial part of the buccinator and ultimately opens in the oral vestibule opposite the second upper molar. Among non-salivary glands, the lateral nasal glands are a diffuse series of glands that open via a common ostium within the middle nasal meatus near the rostral termination of the rectal fold. Although many ruminants possess a well-developed preorbital gland (Frey & Hofmann, 1996), no gland or glandular orifice of such a gland could be found in any of the moose specimens we dissected.

Osteology

The skulls of moose are easily distinguishable from those of even closely related cervids by virtue not only of their size, but also by the highly modified shape of the bony nasal aperture. The aperture in moose is highly angled back toward the orbits, shortening the nasal bones and excavating the premaxillae and maxillae. Overall, the skull is easily classified as a cervid by virtue of the toothless premaxillae and large nasomaxillary fissure (Fig. 6; fnm). As this study focuses on anatomical details of the nose in moose, only those facial skeletal features relevant to the nose are included here.

Os premaxillare (= os incisivum, NAV, 1994; intermaxillary, Boas & Paulli, 1908) (Figs 6 & 7; op). The premaxilla in moose is fairly typical for a ruminant, i.e., it is thin and edentulous. Remaining shallow for its entire length, it possesses two caudally directed processes. The medial process contacts both the medial process of the contralateral premaxilla and the rostralmost extent of the vomer. Laterally, the nasal process (Figs 5–7; oppn) of the premaxilla, which contacts the nasal bones in most other mammals, forms the margin of the bony naris up to about the rostral extent of the maxillary spine of the maxilla. The nasal process flares laterally as it extends caudally along the bony narial aperture. Between these two processes, an elongate incisive foramen (Fig. 7; fin) typical of many ruminants conducts the incisive duct and the vomeronasal organ. The body of each premaxilla contains two roughened tubercles (Fig. 6; opt) serving as the attachment of the superior incisive muscle (rostrally) and the lateralis nasi (laterally). The premaxillae are discontinuous from each other rostrally, each sending processes directly rostrally that have oval margins medially. Ventrally, the hard palate is continued rostrally by the premaxilla.

Os maxillare (Figs 6 & 7; om). The largest and most robust skeletal component of the narial anatomy of moose is the maxilla. Laterally, this bone is roughly triangular,

with a dorsal apex that contacts the nasal bone for its entire lateral suture, a caudal margin that borders the nasomaxillary fissure and contacts the lacrimal and zygomatic bones, a ventral margin containing six teeth (P2–P4, M1–3) in adults, and a rostral margin covered partially by the nasal process of the premaxilla and partially forming the bony nasal aperture. Ventrally, the interalveolar margin (Fig. 5; ommi) is the narrowest part of the bone. The palatal and buccal mucosae meet at the interalveolar margin before they part to accommodate the tooth row. Immediately dorsal to the root of the first molar, the infraorbital canal (Fig. 5; ci) exits the skull through a large, oval foramen (Fig. 6; omfi). Dorsal and slightly caudal to the infraorbital foramen, a roughened tubercle serves as the point of origin for the three maxillolabial muscles (Fig. 6; omtm). Caudal to this maxillolabial tubercle, the facial crest (Fig. 6; omcf) extends along the rest of the maxilla from the tuber faciale and onto the zygomatic bone. Dorsal to the facial crest and maxillolabial tubercle, the maxilla slopes medially to form the rostral margin of the nasomaxillary fissure and to meet the nasal bone. The maxilla forms the middle third of the hard palate and supports the vomer bone. On its medial surfaces, the maxilla possesses an upturned maxillary spine supporting a large, double-scrolled maxilloturbinate. The maxilloturbinate is roughly oval shaped, with the rostral end projecting beyond the margin of the bony narial aperture. About halfway along the ventral surface of the maxillary spine, the bony nasolacrimal duct opens into the nasal cavity. Caudodorsal to the maxillary spine is a large opening into the maxillary sinus (Fig. 7; sm). The turbinates of moose are specialized in that they extend rostrally past the margin of the bony nasal aperture and are visible in lateral view (Fig. 6).

Os lacrimale (Fig. 6; ol). The triangular lacrimal bone of moose contacts the maxillary and zygomatic bones ventrally, the nasomaxillary fissure rostrally, the ethmoid medially, and the orbit and frontal bone caudally. A ridge on its sloping rostral margin contacts the thin cartilaginous plate overlying the nasomaxillary fissure. Along the margin of the orbit, the lacrimal bone holds two lacrimal foramina (Fig. 6; ollf), serving as the caudodorsal opening of the nasolacrimal duct. Between these two foramina, a rough tubercle (Fig. 6; oltl) serves as the origin of members of the orbicularis oculi group. A concave fossa (Fig. 6; olfl) occupies the lateral face of the lacrimal bone. In many other ruminants, this fossa accommodates a preorbital gland, but, as noted above, moose lack the preorbital gland.

Os ethmoidale. The ethmoid bone in moose consists of a perpendicular plate forming the bony portion of the nasal septum and a labyrinth of ethmoturbinates and nasoturbinate. The nasoturbinate (endoturbinale I of Paulli, 1900; Fig. 7; oen) extends from the dorsalmost area of the cribriform plate (Fig. 7; oelc) along the dorsal margin of the ethmo- and maxilloturbinates and terminates at the rostral edge of the nasal bone. Ventral to these, the numerous, scrolled ethmoturbinates (Fig. 7; oee) occupy the rest of the nasal cavity dorsal and caudal to the maxilloturbinate and connect to the cribriform plate. The

dorsalmost of these (endoturbinale II of Paulli, 1900; Fig. 7; oee') is enlarged and supports the middle nasal concha.

Os nasale (Figs 5–7; on). The relatively simply shaped nasal bone of moose is unique among cervids in that its rostral extent is severely limited. As stated above, the nasal bone does not contact the premaxilla, but rather terminates a few centimetres caudal to the nasal process of the premaxilla. The nasal bone is roughly quadrangular in shape, taking on the appearance of a rectangle half as wide as long that is bent at 90° along its long axis so as to contact its fellow medially and the maxilla ventrolaterally. The lateral and dorsal faces of the nasal bone are smooth, having no obvious specialized features except for the jagged rostral margin that contacts the dorsal lateral cartilages. The nasofrontal suture is arched such that the frontal bones send processes rostrally on the lateral and medial sides of each nasal bone.

DISCUSSION

Novel aspects of narial anatomy in moose

The nose of moose is an obviously distinctive structure differing in many ways from the condition found in other cervids and in other ruminants. Aside from external differences, visible from quite a distance, there are many other differences apparent upon dissection. These anatomical specializations have long warranted special attention (see Boas & Paulli, 1908; Jacobi, 1921; Meinertz, 1955).

Inside the nasal vestibule and main nasal cavity, there are several differences between moose and closely related cervids and other ruminants. Overall, the nasal vestibule of moose is greatly enlarged in all dimensions, having the effect of caudally displacing and telescoping more caudally located structures such as the maxilloturbinate and nasoturbinate. Moreover, the ventral nasal concha (overlying the maxilloturbinate) is inclined somewhat dorsally going from caudal to rostral (Fig. 7), a situation unique among the cervids examined here. Other species possessing a proboscis, such as tapirs (Witmer *et al.*, 1999) and saiga antelope (Frey & Hofmann, 1996) share this inclination of the ventral concha, suggesting that enlargement of the nasal vestibule may impart some morphogenetic rotation of more caudally located structures (Witmer *et al.*, 1999). Another manifestation of this telescoping phenomenon is that the nasal ostium of the lateral nasal gland, which generally marks the caudal end of the nasal vestibule in amniotes and is located far forward (Witmer, 1995b), is displaced caudally in moose to a position almost midway along the nasal cavity (Fig. 7a; ogln).

The meatuses are greatly enlarged in moose such that the nasal cavity is a relatively wide-open chamber. In mammals in general, the ventral nasal meatus is the largest (Getty, 1975), and this condition is true in the cervids examined here (Fig. 8). Moose, however, have relatively enlarged the middle and dorsal nasal meatuses,

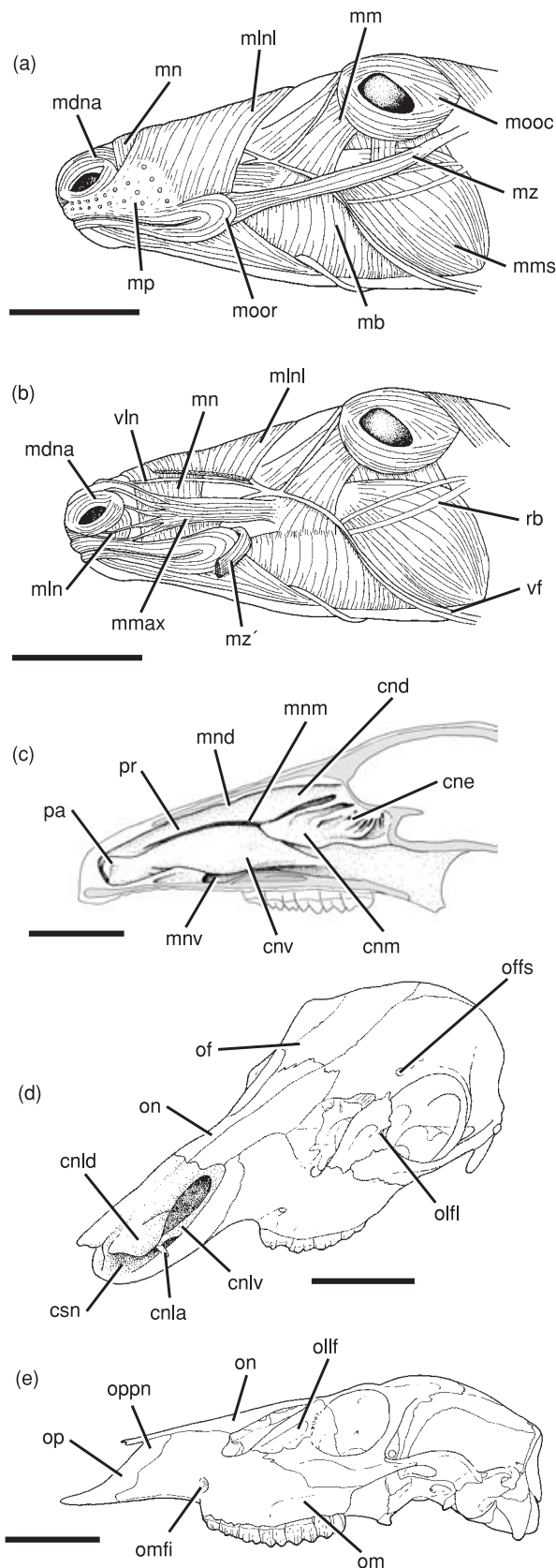


Fig. 8. White-tailed deer *Odocoileus virginianus*. Musculature of face and nostril: left lateral view of (a) superficial and (b) deep dissections. (c) Medial view of right side of sagittally sectioned head with nasal septum and vomer removed to show internal nasal

as well as the common nasal meatus between the conchae and the septum. Some of the mucosal components of the conchae (e.g. the alar fold; Fig. 7a; pa) are also somewhat enlarged but occupy relatively less space in the nasal cavity, whereas other components (e.g. the rectal fold; Fig. 7a; pr) are reduced, perhaps again reflective of the telescoping imparted by the enlarged vestibule. The nasal conchae are tightly packed in *Odocoileus*, filling up almost the entire available space (Fig. 8c). Indeed, other ruminants, such as oxen, sheep, and goats (Getty, 1975), as well as many mammals outside ruminants, such as dogs (Dawes, 1952) and horses (Schaller, 1992), also have tightly packed conchae. Moose, however, have relatively much larger spaces between the conchae. The conchae remain tightly packed only at the caudodorsal portion of the cavity, at the intersection of the dorsal, middle, and ventral conchae. As they extend rostrally, the meatuses enlarge between the conchae. Thus, the inner structures of the nose are characterized by open spaces rostrally with an altered but generally typical condition caudally.

The alar fold of the ventral concha in both moose and *Odocoileus* extends as far rostrally as the middle of the nostril and sends a fatty process dorsally. In moose, however, this fatty process is greatly enlarged, extending farther rostrally and farther medially than in *Odocoileus*. The alar fold is supported laterally in this area by the lateral cartilages. The presence of the fatty pad, coupled to better-developed musculature, may aid in nostril closure (see below). In both moose and *Odocoileus*, the attachment of the ventral concha undergoes a rotation, changing from lateral to ventral as the concha extends rostrally (Getty, 1975; Schaller, 1992). In moose, the result of this rotation and the enlargement of the fatty pad is an enlarged sac, the alar recess, caudodorsal to the nostril. *Odocoileus* has a homologous recess but it is much smaller.

The general narial musculature of moose is characteristic of other ruminants, namely, a well-developed malaris, three maxillolabial muscles, and marked specialization of the orbicularis oris muscles (Boas & Paulli, 1908; Getty, 1975; Schaller, 1992). However, as a result of enlargement of the nasal vestibule and nostrils, many of these muscles are modified in the condition in closely related groups. In general, the attachments (origins and insertions) of the facial muscles remain similar, but, because of the dramatic conformational changes in the nasal capsule, it is the relative sizes and/or courses of the muscles that have changed. For example, whereas in other ruminants the maxillolabial muscles (the caninus, in particular) have bellies that separate distally along the snout, in moose the tendons that extend rostrally from each separate muscle belly are very long, reflective of rostral elongation of the nasal capsule. Moreover, interaction of

structures. Skull: (d) left rostradorsolateral view with nasal cartilages intact; (e) left lateral view. Scale bars = 5 cm. For abbreviations, see Appendix.

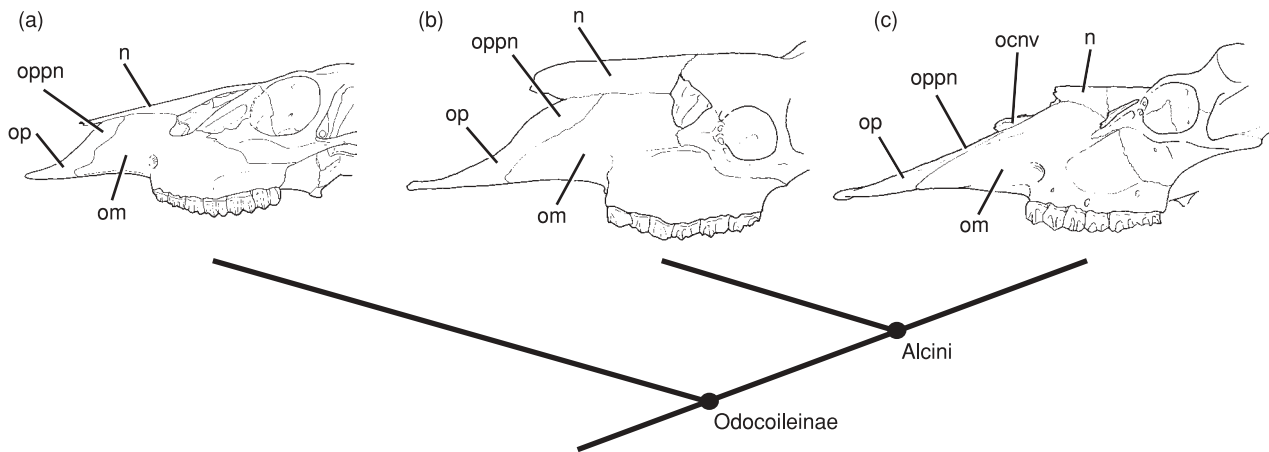


Fig. 9. Cladogram of skulls in left lateral view to illustrate transformation of the bony naris: (a) *Odocoileus virginianus*; (b) *Cervalces scotti*; (c) *Alces alces*. (b) Redrafted from Scott (1885). For abbreviations, see Appendix.

the tendons with the specialized lateral nasal cartilages has produced another functional differentiation in the nose of moose. The angle taken by the levator labii superioris and its tendons in deer (Fig. 8b) and bovids is such that contraction of the muscle would depress and caudally displace the nostrils and the snout (Boas & Paulli, 1908; Getty, 1975; Schaller, 1992). In moose, however, the levator labii superioris has become more of a true levator by wrapping around the lateral enlargement of the dorsal lateral nasal cartilages (Fig. 6a; lec) which act as a pulley redirecting the muscle's line of action (Fig. 4a; mlls). In this way, the tendon of the levator labii superioris angles ventrally at its rostralmost extent, enabling contraction of the muscle to produce elevation of the upper lip more easily in moose (Fig. 3b; mllst) than in other ruminants.

Muscles of the buccinator group are also specialized in moose. The nasalis, which in moose is broad and very well-developed, is not even described in the veterinary literature for ruminants (Getty, 1975; Schaller, 1992) and only briefly described in Boas & Paulli (1908). This muscle was found in *Odocoileus* (Fig. 8), maintaining similar attachments but being considerably less developed than in moose. Given in moose the maintenance of primitive attachments but an apomorphic narial conformation, the nasalis now has both a novel size and potentially a novel action, i.e. as a depressor and compressor of the nasal cavity, decreasing the distance between the dorsal lateral and ventral lateral nasal cartilages and potentially affecting intranasal pressures. It is not clear whether the expansion of this muscle in moose reflects simply enlargement of the cartilages themselves, enhancement of the particular actions of the muscle, or some combination of these two.

The nostrils of moose are greatly enlarged relative to those in other cervids and other ruminants. Thus, it is not surprising that the muscles associated with the nostrils are enlarged as well. Moreover, the enormous nostrils of moose are directed laterally and have virtually

lost the rhinarium that in other ruminants binds the nostrils together. The nostrils of moose are not only larger than in other ruminants but also are more mobile. Dorsal and ventral to the caudal, slit-like portion of the nostril, a suite of muscles such as the narial dilators and the lateralis nasi are much more conspicuous in moose. These muscles have been variably named by different workers or completely ignored by others (Boas & Paulli, 1908; Meinertz, 1955; Getty, 1975; Schaller, 1992), reflecting both their small size in outgroups and the difficulty in isolating particular muscles. These muscles in moose interact closely with the hinged lateral accessory nasal cartilage forming the caudal aspect of the nostril and with the tissue surrounding the fleshy nostril. We regard the enlargement of the nostril, the elaboration of the nostril musculature, and the mobile joint of the lateral accessory cartilage to be indicative of increased control over the external aperture to the nasal vestibule.

Moose narial anatomy with respect to fossil alcines

Present-day *Alces alces* is a fairly young species, first appearing < 100 000 years ago and migrating to North America only 10 500 years ago (Geist, 1999). The closest fossil relatives of *Alces* are species of *Cervalces* (synonymous with *Libralces*; Breda, 2001). Several specimens of *Cervalces* have been found throughout Eurasia and North America, but specimens possessing well-preserved facial structures are rare. For this reason, alcines are distinguished from other cervids mainly by features of antlers and limb bones (Churcher & Pinsof, 1988). *Cervalces* show characters of the foot and of antlers that unite them with *Alces* as members of Alcini, but the facial skeletons in fossil alcines do not approach the level of specialization seen in present-day moose (Fig. 9) (Scott, 1885). The nasal bones in *Cervalces* are much longer than in moose, and these nasals contact the ascending process

of the premaxillae for at least 3 cm (Scott, 1885; Breda, 2001). In addition, the articulations between the nasals and frontals and between the nasals and the nasal cartilages differ between fossil alcines and moose, particularly in that moose have a process of the articulation of the frontals that divides the caudal end of the nasals (Scott, 1885). Even specimens of *Alces latifrons* do not show any separation of the nasals and premaxillae or the modifications of the articulations of the nasal bones with surrounding osseocartilaginous structures (Churcher & Pinsof, 1988). Nasal-premaxilla contact is a feature frequently used to infer the presence (but not the structure) of probosces in mammals (Scott, 1885; Jacobi, 1921), and so no fossil alpine has been reconstructed with the conspicuous narial specializations seen in moose.

We consider additional osteological features in addition to the separation of the nasal and premaxillary bones to be indicative of highly modified narial anatomy in moose. The specimens of *Odocoileus* that were examined in this study showed variable contact between these bones, although the two bones were much closer to each other than in moose. The nasals in moose are wider and have lateral and dorsal faces that meet at roughly 90°. The nasal bones in other cervids and other ruminants examined in this study are not evenly widened, nor do they form an angle between dorsal and lateral parts. The dorsal face of the nasal bones is almost perfectly flat in moose, whereas these bones in *Odocoileus*, *Bos*, *Bison*, *Ovis*, and other ruminants have a slight ventral curvature to them at their rostral ends. No ruminant examined here has the modified articulations of nasal bones that are described in fossil alcines. *Cervalces* and *Alces latifrons* both possess nasal bones that have dorsal and lateral faces that meet at right angles, even though the nasal and premaxillary bones contact each other. Present-day moose are the only cervids with the particular narial specializations described here, although the evolution of this peculiar set of anatomical structures may be traced through the fossil record of alcines by virtue of the subtle differences in facial anatomy beyond simply a lack of articulation between the nasal and premaxillary bones.

The cartilaginous capsule and the modified nostril musculature found in moose leave causally associated osteological correlates that separate moose from any other known cervid. The squared-off rostral edges and quadrangular shapes of the nasal bones serve as evidence of the more extensive attachment of the dorsal lateral nasal cartilages, signalling modification of the caudal portion of the cartilaginous nasal capsule. Of course, the most dramatic cartilaginous modifications are seen in the expanded rostral portions of the capsule (Fig. 6a), and bony evidence for these modifications can be identified. For example, the lateral hump of the dorsal lateral nasal cartilages modifies the nasal process of the premaxillae, causing it to flare outward near its caudalmost extent along the bony nasal aperture. The enlarged and highly developed lateralis nasi, which acts as a ventral dilatator of the nostrils, leaves a tubercle on the lateral face of the body of the premaxillae. In addition, the superior incisive muscle leaves another, more medial, tubercle on the body

of the premaxilla. Both of these muscular attachment sites are undetectable in either closely related cervids or other large-bodied ruminants, indicating the reliance upon nostril musculature in moose rather than simply allometric effects of having a large face. Admittedly, the inference of missing soft-tissue anatomy in mammalian narial anatomy is difficult (Witmer, 1995a). However, the enlarged cartilaginous capsule and highly developed nostril musculature (unique in moose among cervids) do leave causally associated bony signatures.

Functions of moose noses based on anatomical specializations

Despite studies that deal with moose ecology (see Flerow, 1952; Geist, 1999) and narial anatomy (Boas & Paulli, 1908; Jacobi, 1921; Meinertz, 1955), no study has explained why moose have such apomorphic noses relative to very closely related outgroups or what novel functions may be carried out by these novel anatomical structures. Modified narial structures serve many adaptive functions for an animal (Witmer, 2001a), such as acting as a muscular hydrostatic organ of manipulation (Witmer *et al.*, 1999) or as an essential water-conservation device (Langman *et al.*, 1979). The nose of moose, however, remains enigmatic in terms of its function. We attempt here to address the adaptive significance of the modified narial anatomy in moose by appeal to its anatomy. While we hypothesize that this highly derived structure performs adaptive functions, a single, driving *raison d'être* for these modified structures is not implied. Noses in general simultaneously serve diverse functions for animals (Witmer, 2001a), and presumably moose are no different.

The physiological role of the nasal cavity in regulating heat and water balance has been well studied in ruminants (e.g. Langman *et al.*, 1979), and hence enhancement of this role is a potential explanation for narial novelty in moose. Indeed, Flerow (1952) hypothesized that the enlarged narial structures in moose contribute physiologically to predator escape behaviour, allowing moose to run rapidly and for prolonged periods in cold, dry habitats. This physiological mechanism has indeed been found in other cervids, by which cooled blood from the nasal mucosa ultimately cools arterial blood supplying the brain (Johnsen & Folkow, 1988). This mechanism permits selective brain cooling during periods of heat stress, a feature that seems to be ubiquitous within Mammalia, to varying degrees (Kuhnen, 1997). However, this mechanism does not seem to be enhanced in moose for at least three reasons. First, selective brain cooling in artiodactyls is dependant upon patterns of blood flow allowing heat exchange within the nasal cavity (Ghoshal, 1985). Our dissections and injections of moose, however, do not reveal an increased vascularity of the nasal cavity. In fact, the alar fold in moose, which is well placed to participate in heat exchange, seems to be less vascularized than expected, as it is filled with

loose connective tissue and fat. Secondly, from a design standpoint, enhancement of heat exchange mechanisms should involve not only increased vascularity (the means of heat transfer) but also increased surface area (over which heat transfer occurs), which is accomplished most efficiently by developing more elaborately scrolled conchae (Negus, 1958; Schmidt-Nielsen, Hainsworth & Murrish, 1970). However, the nasal cavities of moose do not show hypertrophied exchange surfaces. On the contrary, their nasal cavities are much less densely packed with conchae than outgroups, and the greatly enlarged nasal vestibule is basically devoid of surfaces optimized for heat exchange. Certainly, expansion of the nasal vestibule and transformation of the nostrils did not evolve to house expanded, physiologically relevant exchange structures. Thirdly, prolonged running escape is not a behaviour moose preferentially use in the wild (Geist, 1999). Although moose are capable of extended periods of 'trotting,' they prefer to escape through moderately dense cover strewn with obstacles that they can easily clear (by virtue of leg length) and that their pursuers (e.g. wolves and coyotes) cannot, thus minimizing their energy expenditure in fleeing (Geist, 1999). Thus, the derived noses of moose apparently did not evolve as an adaptation to enhance the physiological functions of the nasal cavity.

The behavioural ecology of moose can produce several other lines of evidence concerning the evolution of the moose nose. Scott (1885) and Jacobi (1921) attributed the modified narial anatomy of moose to the evolution of a mobile and sensitive upper lip to enhance browsing selectivity. Moose do indeed have a sensitive upper lip by virtue of rich innervation of the nose and upper lip (Meinertz, 1955; Geist, 1999), and thus it is reasonable to hypothesize that moose evolved their novel noses as a tactile adaptation. However, other cervids species likewise are browsers and have similarly sensitive and mobile upper lips for selecting food items (Hofmann, 1989); the branches of the trigeminal nerve that supply the nose and lips in moose are not particularly large or unusual. In fact, moose have lost the mystacial pad of vibrissae (present in other cervids) that serves a major tactile role in other mammals. Thus, the proboscis of moose did not evolve as an adaptation to enhance the sense of touch, and, if anything, this sense has been compromised (e.g. loss of the mystacial pad).

Moose do have certain anatomical specializations that suggest a lip more mobile than other ruminants. The pulley mechanism of the levator labii superioris creates an angle of movement for the upper lip that is considerably more dorsoventral than other ruminants. In *Odocoileus*, for example, the contraction of the incisivus superior is the only way to achieve dorsal elevation of the upper lip directly, based on its attachments and fibre direction. Moose, on the other hand, would be able to achieve this movement through a combination of contraction of the incisivus superior and the levator labii superioris. This levator in tapirs runs more dorsally than in ruminants, and this leads to more efficient elevation of the proboscis in tapirs (Witmer *et al.*, 1999). In this way,

the modified lateral nasal cartilages and the levator labii superioris tendons of moose may analogously contribute to proboscis-like movement of the upper lip. This enhanced mobility, however, fails to explain other aspects of narial anatomy, such as the enlarged nostrils and specialized internal structures.

Many observers of moose have noted their keen sense of smell (Flerow, 1952; Peterson, 1978; Geist, 1999). Indeed, moose do seem to have acquired unusual characteristics that may enhance the information content of olfactory cues. Their widely spaced nostrils permit odorant molecules to be collected from different locations in the environment. This physical separation of the two nostrils opens the possibility of stereolfaction. That is, moose may derive directional information from olfactory cues, a notion previously suggested by Geist (1999). Wide separation of the nostrils is certainly apomorphic for moose in that, in other cervids (indeed most other mammals), the two nostrils open almost on the midline, being separated only by the thickness of the septum. In general, internarial width seems to decrease in vertebrates, indicating a reliance on klinotaxis (orientation using one chemical sensor) rather than tropotaxis (orientation using two sensors) to derive directional information (Stoddart, 1979). Moose potentially represent a rare exception to this rule. It is currently unknown whether moose actually engage in stereolfaction, and, in fact, stereolfaction is a generally under-studied phenomenon (Kobal, Van Toller & Hummel, 1989). Nevertheless, it may be significant in this regard that humans can derive directional information from olfactory stimuli, albeit by a different mechanism (e.g. the nasal cycle; Sobel *et al.*, 1999). Moose likewise may benefit from these characteristics of odorant detection. Moose rely heavily on 'scent urination' to coordinate mating and oestrus, and this information needs to be communicated over long distances (Miquelle, 1991). This behaviour has not been found in other cervids (Miquelle, 1991), and the uniqueness of this activity in moose, coincident with anatomical diversification, is intriguing. Whether or not moose use stereolfaction awaits experimental confirmation. The point here is that moose have evolved an anatomical conformation that would enhance such a function.

One aspect of their behavioural ecology that separates moose from other large cervids is their reliance upon aquatic vegetation as a mineral-rich source of food (Geist, 1999). It has been suggested that the large antlers of male moose increase mineral demand, and foraging for aquatic vegetation is one means of increasing mineral uptake (Peterson, 1978). Coincident with the formation of unique narial structures is a unique foraging method, and this perhaps could be an important factor in the evolution of the moose nose (Witmer, 2001a). Moose are the only cervid that consistently feed on aquatic vegetation; moreover, they spend a great deal of time with the head submerged as they forage for vegetation underwater (Peterson, 1978; Geist, 1999). Moose also dive periodically to search for food, remaining submerged for a minute or more and reaching depths of at least 5 m (Peterson, 1978). These

behaviours would place increased demands on narial structures that are not faced by other non-diving cervids, such as nostril closure, the ability to detect food items underwater, etc. The nostrils of moose are specialized in several ways, including lateral displacement, increased mobility, and proximity to an enlarged and highly mobile alar fold. The lateral enlargement of the dorsal lateral nasal cartilages, together with the rostral portion of the alar fold, forms a sac (the alar recess). This mobile portion of the alar fold lies against the caudal two-thirds of the nostril. In addition, contraction of the levator labii superioris, resulting in dorsal displacement of the upper lip and nostril, would align the ventral face of the nostril against the alar fold. Therefore, we suggest a possible mechanism of nostril closure in moose consisting of evacuation of air from the rostral and caudal recesses in the nasal vestibule, compression of the alar fold against the nostril by air in the alar recess, and apposition of the dorsal and ventral faces of the nostril by contraction of maxillolabial and lateral nasal musculature. It might seem that nostril closure could be accomplished more efficiently by having small nostrils surrounded by a muscular sphincter; indeed, the system in moose may not be optimal, but rather may be simply adequate and represents the best solution given the anatomical substrates that moose inherited. Although validation of the mechanism proposed here has not been tested experimentally, narial anatomy clearly indicates that this hypothesis is both feasible and merits testing.

At present, the adaptive significance of the specialized nose of moose remains somewhat enigmatic. We have presented anatomical findings that suggest that the key to deciphering this enigma resides in the highly derived nostrils. It would seem that the evolutionary driving force is not enlargement and separation of the nostrils for stereolfaction, although moose may nevertheless benefit from this arrangement. Instead, a more compelling hypothesis is elaboration of the nostrils and related structures for nostril closure in association with underwater feeding, because it more fully explains narial complexity. Indeed, both explanations require substantiation, and this situation highlights the dearth of experimental work on non-physiological nasal functions. In fact, it is the extensive experimental data on the physiology of heat and water balance that provides enough understanding to allow exclusion of an enhanced physiological role as the principal explanation for moose narial apomorphies. In any case, anatomical investigation has clarified the functional components of moose noses and outlined predictions that can be tested by subsequent investigation.

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Appendix. List of abbreviations used in the figures

af	arteria facialis (Figs 3 & 4)	mp	mystacial pad (Fig. 8)
ai	arteria infraorbitalis (Fig. 4)	mrn	musculus rectus nasi (Fig. 4)
bo	bulbus oculi (Fig. 5)	mz	musculus zygomaticus (Figs 3 & 8)
ca	cartilage of the alar fold (Fig. 5)	mz'	musculus zygomaticus, cut edge (Figs 4 & 8)
ci	canalis infraorbitalis (Fig. 5)	n	naris (Fig. 5)
cnd	concha nasalis dorsalis (Figs 7 & 8)	ni	nervus infraorbitalis (Figs 4 & 5)
cne	conchae nasalis ethmoidales (Figs 7 & 8)	ocn	ostium canalis nasolacrimalis (Fig. 7)
cnla	cartilago nasi lateralis accessoria (Figs 5, 6 & 8)	oee	os ethmoidale, ethmoturbinate (Figs 5 & 7)
cnld	cartilago nasi lateralis dorsalis (Figs 5, 6 & 8)	oee'	os ethmoidale, ethmoturbinate underlying cnm (Fig. 7)
cnlv	cartilago nasi lateralis ventralis (Figs 6 & 8)	oelb	os ethmoidale, lamina basalis (Fig. 7)
cnm	concha nasalis media (Figs 7 & 8)	oelc	os ethmoidale, lamina cribrosa (Fig. 7)
cnv	concha nasalis ventralis (Figs 5, 6 & 8)	oen	os ethmoidale, nasoturbinate (Figs 5 & 7)
csn	cartilago septi nasi (Figs 5 & 8)	of	os frontale (Figs 6 & 8)
dei	dentes incisives (Fig. 5)	offs	foramen supraorbitale (Figs 6 & 8)
dp	ductus parotideus (Fig. 3)	ogln	ostium glandulae lateralis nasi (Fig. 7)
fin	foramen incisivum (Fig. 7)	ol	os lacrimale (Fig. 6)
fnm	fissura nasomaxillaris (Fig. 5)	olfl	os lacrimale, fossa lacrimalis externa (Figs 6 & 8)
gbi	glandulae buccalis intermediae (Fig. 4)	ollf	os lacrimale, foramen lacrimale (Figs 6 & 8)
l	lingual (Fig. 5)	otl	tuberculum lacrimale (Fig. 6)
lec	lateral expansion of cnld (Figs 5 & 6)	om	os maxillare (Figs 6–9)
ln	limen nasi (Fig. 7)	omcf	os maxillare, crista facialis (Fig. 6)
mb	musculus buccinator (Figs 3, 4 & 8)	omfi	os maxillare, foramen infraorbitalis (Figs 6 & 8)
mc	musculus caninus (Figs 3 & 4)	ommi	os maxillare, margo interalveolaris (Fig. 5)
mdli	musculus depressor labii inferioris (Fig. 3)	od	os dentale (mandibula) (Fig. 5)
mdli'	musculus depressor labii inferioris, cut edge (Fig. 4)	ocnv	os conchae nasalis ventralis (maxilloturbinate) (Figs 5–7 & 9)
mdls	musculus depressor labii superioris (Figs 3 & 4)	omtm	tuber maxillolabiale (Fig. 6)
mdna	musculus dilatator naris apicalis (Figs 3 & 8)	on	os nasale (Figs 5–9)
mdna'	musculus dilatator naris apicalis, cut edge (Fig. 4)	op	os premaxillare (Figs 6–9)
mdnm	musculus dilatator naris medialis (Figs 3 & 4)	oppn	os premaxillare, processus nasalis (Figs 5–9)
mii	musculus incisivus inferior (Fig. 4)	opt	os premaxillare, tubercule (Fig. 6)
mis	musculus incisivus superior (Fig. 7)	oz	os zygomaticum (Fig. 6)
mlls	musculus levator labii superioris (Figs 3 & 4)	pa	plica alaris (Figs 5, 7 & 8)
mllst	musculus levator labii superioris tendons (Fig. 3)	pa'	nostril connective tissue pad (Figs 3–5 & 7)
mln	musculus lateralis nasi (Figs 3, 4 & 8)	pr	plica recta (Figs 5, 7 & 8)
mlnc	musculus lateralis nasi, portio caudalis (Fig. 3)	pvl	processus ventrolateralis of cnld (Figs 5 & 6)
mlnl	musculus levator nasolabialis (Figs 3, 4 & 8)	ra	recessus naris alaris (Figs 5 & 7)
mm	musculus malaris (Figs 3, 4 & 8)	rb	nervus facialis, ramus buccolabialis (Figs 3, 4 & 8)
mmax	maxillolabial muscle group (Fig. 8)	rmm	nervus facialis, ramus marginalis mandibulae (Figs 3 & 4)
mmax'	maxillolabial muscle group, cut (Fig. 4)	rnc	recessus naris caudalis (Fig. 5)
mms	musculus masseter (Figs 3 & 5)	rnr	recessus naris rostralis (Figs 5 & 7)
mn	musculus nasalis (Figs 4 & 8)	sm	sinus maxillaris (Figs 5 & 7)
mnc	meatus nasi communis (Fig. 5)	vao	vena angularis oculi (Fig. 4)
mnd	meatus nasi dorsalis (Figs 5, 7 & 8)	vdn	vena dorsalis nasi (Fig. 4)
mm	meatus nasi medius (Figs 5, 7 & 8)	vf	vena facialis (Figs 3, 4 & 8)
mnpa	musculus nasalis pars alaris (Figs 3 & 4)	vi	vena infraorbitalis (Fig. 4)
mnv	meatus nasi ventralis (Figs 5, 7 & 8)	vln	vena lateralis nasi (Figs 3, 4 & 8)
mooc	musculus orbicularis oculi (Figs 3, 4 & 8)	vls	vena labialis superior (Figs 3 & 4)
moor	musculus orbicularis oris (Figs 3, 4 & 8)	vno	organum vomeronasale (Fig. 5)
