

The Nasal Complex of a Semiaquatic Artiodactyl, the Moose (*Alces alces*): Is it a Good Evolutionary Model for the Ancestors of Cetaceans?

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ABSTRACT

Among Cetartiodactyla, cetaceans are the only obligate aquatic dwellers. Given morphological similarities between cetacean relatives such as *Indohyus* (the best represented Eocene raoellid artiodactyl) with other, later artiodactyls, any crown artiodactyl that engages in aquatic behaviors is of interest as an evolutionary model for the adaptations that accompanied the origins of cetaceans. The American moose (*Alces alces*) is the only non-cetacean artiodactyl to engage in aquatic foraging and, other than *Hippopotamus*, is distinctive in its diving behaviors. This study surveyed the soft and hard tissue nasal morphology of *Alces alces* to assess phylogenetic polarity and the presence of adaptations for diving and feeding in fresh water habitats. A fresh dissection of the facial musculature and nasal cavity was performed on one subadult male individual and osteological analyses were also performed on dry crania. This species was analyzed alongside fossil crania of *Cervalces* (its presumed ancestor), other cervids (e.g., *Odocoileus virginianus*, the white tail deer; *Dama dama*, the fallow deer), a bovid (*Bos taurus*, domestic cattle), and a carnivoran (*Ursus americanus*, the American black bear). A fresh dissection of the facial musculature and nasal anatomy of one fallow deer specimen was also performed for comparison with the moose. Results indicate that *Alces alces* exhibited a primitive configuration of maxillolabial muscles and, like *Dama*, exhibited a series of subcutaneous fibrous tissues connecting these muscles to skin. *Alces* and *Dama*, however, both exhibited autapomorphies in the soft tissue anatomy of the external nares. The former possessed a series of muscles that act to constrict the anterior nares, likely during diving. Extremely large fibrofatty pads that were perforated by muscle tendon supported their alar fold. Internally, a double-scrolled maxilloturbinal occupied nearly the entire volume of the anterior nasal cavity and protruded beyond the rim of the piriform aperture in dry crania. *Dama* had long, thin muscles

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taking origin on their nasal conchae and inserting onto the alar fold. Yet, despite these anterior nasal autapomorphies, the ethmoturbinal patterns of all observed cervids and the one bovid all appeared primitive with a posteroinferiorly oriented array of ethmoturbinals in close contact with a relatively straight cribriform plate, a macrosmatic condition. These differed from the curved cribriform plate of *Ursus* whose posterior nasal anatomy appeared hyper-macrosmatic. *Indohyus* exhibits no skeletal sign of a fleshy proboscis such as an enlarged piriform aperture or shortened nasal bones. Thus, there is little evidence that the early ancestors of cetaceans engaged in prolonged bouts of diving for aquatic foods but more probably were surface swimmers traveling between terrestrial food sources or fleeing predators. Anat Rec, 302:667–692, 2019. © 2018 Wiley Periodicals, Inc.

Key words: whale; comparative anatomy; cetacea; nasal complex; moose

INTRODUCTION

Cetaceans are among the major groups of living marine mammals. Named by Aristotle in the first book of his “History of Animals” (Book 1; see translation by Peck, 1965) from the Greek *Cete* or *Cetacea* meaning whale, they include whales, dolphins and porpoises with 89 currently recognized species (Berta, 2017). Cetaceans were formerly placed within their own order but are now considered an infraorder and are divided into two subgroups: the Odontoceti (toothed whales including dolphins and porpoises) and the Mysticeti (the baleen whales)—formerly suborders but now considered parvorders (i.e., a taxonomic category of related organisms ranking below an infraorder and above a superfamily). Recent genetic evidence suggests that the Cetacea are nested among the Artiodactyla, forming the new clade Cetartiodactyla and rendering Artiodactyla non-monophyletic without the inclusion of cetaceans (Berta, 2017). The new clade of Cetartiodactyla, however, is not without controversy (see Price *et al.*, 2005; Marcot, 2007; and Aagnarsson and May-Collado, 2008). When using the older terminology, Cetacea is considered the sister taxon to the even-toed ungulates such as hippopotamuses, giraffes, camels and deer (including moose; e.g., Shimamura *et al.*, 1997; Nikaido *et al.*, 1999, 2001, 2006, 2007; Meredith *et al.*, 2011; McGowen *et al.*, 2009), despite the long temporal gap in the fossil record between the origins of each clade. Cetacea are of great interest as one of only two mammalian groups to be obligate aquatic dwellers (other than Sirenia). Thus, aquatic adaptations found among other artiodactyls become important as they may serve as evolutionary models for the subtle beginnings of large-scale morphological adaptations. The artiodactyl *Alces alces* (including both the American “moose” and the Eurasian “Elk”) is one such species (Hundertmark *et al.*, 2002; Udina *et al.*, 2002; see below for discussion of taxonomic status), which may exhibit adaptations to aquatic foraging. Here, we discuss their bony and soft tissue nasal morphology within a comparative analysis. Consideration of such morphological features may inform analyses of the extinct raccoon-sized Eocene raoellid artiodactyls (that are closely related to the early ancestors of the Cetacea), considered the closest whale relatives (Thewissen *et al.*, 2007; Cooper *et al.*, 2012). They represent a close sister taxon to early cetaceans that likely

balanced the demands of both terrestrial and aquatic life-ways (Thewissen, 2014, see Fig. 1).

The nasal region is of importance as an area of extreme autapomorphy among Cetacea relative to other artiodactyls (or, indeed, all other mammalian groups) and among moose relative to other cervids. It has been argued that the notable proboscis of moose functions to close off the nasal cavity from incoming water, a vital function when diving for aquatic vegetation as part of its normal subsistence strategy (see below). Thus, study of its nasal morphology within the context of foraging behavior may be instructive when comparing them to early cetaceans, who may have also possessed aquatic adaptations in soft tissue nasal morphology that have not been preserved in the fossil record.

This study is largely an expansion of the detailed analysis of the American moose and its nasal anatomy by Clifford and Witmer (2004) who, based on dissecting four fresh heads (one adult male, one adult female, and two juvenile

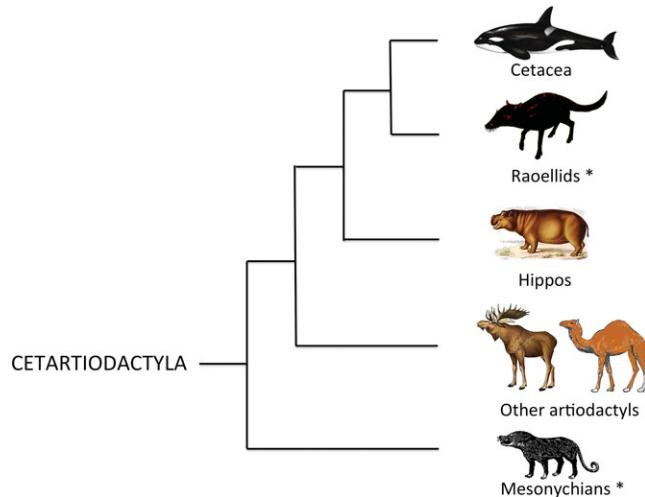


Fig. 1. Cladogram demonstrating the relationship between cetaceans and their terrestrial relatives. Note mesonychians are extinct four-footed taxon of small to large size carnivorous ungulates related to cetartiodactyla. Modified from Berta (2017).

specimens), described various highly specialized nasal morphologies. In particular, the series of muscles and cartilages of the external proboscis was documented in great detail. The present study builds on the analysis of Clifford and Witmer (2004), by focusing on a more limited number of structures and analyzing their potential usefulness in reconstructing the lifeways and selective forces that may have acted upon the ancestors of basal cetaceans.

BACKGROUND

Evolutionary History and Nasal Morphology of *Alces*

A constrictor function has been described for the external nasal musculature of *Alces* and it has been proposed that their anterior nares exhibit adaptations for enclosing the nasal antrum, preventing the flow of water into the upper airway (Clifford and Witmer, 2004). Supporting this function is an extensive network of cartilages and muscles that is accompanied skeletally by extreme reduction of the nasal bones and extreme elongation of the premaxilla, that are in the autapomorphic condition of lacking contact with the nasal bones. This skeletal morphology occurs alongside a highly reduced rhinarium (Clifford and Witmer, 2004) and has been hypothesized to allow greater labial mobility for grasping aquatic vegetation (Scott, 1885; Azzaroli, 1979), as evidenced by the lack of a well expressed labial frenulum of living *Alces alces*. Most other mammals that have lost the primitive rhinarium and labial frenulum do exhibit greater prehensility of the upper lip (Azzaroli, 1979). However, the ancestral Cervid morphology of relatively elongated nasal bones and foreshortened premaxillae (both being in contact with each other) is present among *Cervalces*, the presumptive fossil ancestor (Sher, 1987) of *Alces* (Azzaroli, 1952; Breda and Marchetti, 2005; Breda, 2008). This led Azzaroli (1979) to suggest that members of this genus lacked the prehensile upper labium of *Alces alces*, instead likely expressing a moderate labial frenulum and rhinarium as in most other cervids. Yet, some evidence of enlargement and “inflation” of the nasal bones has been found in *Cervalces*, leading Breda (2008) to suggest that there still may have been some enlargement of the external nasal apparatus and increased labial mobility. Given that both genera exhibit similarities in dental morphology, including premolar/molar length ratios and molarization of the premolars, *Cervalces* probably utilized many of the same food sources as *Alces*, despite the latter being a more obligate browser as can be deduced from a longer, more slender mandibular coronoid process and greater relative mandibular corpus length, suggesting that *Alces* engages in relatively less intensive masticatory grinding, as would be expected for a browser (Scott, 1885; Breda, 2008).

The first true *Alces* appears in the paleontological record during the late Pleistocene (Tazovian glaciation event, which occurred between 190 and 127 ka.; Gavshin *et al.* 1998) in Southern Siberia (Breda and Marchetti, 2005; Foronova, 2001). It appears in association with more forested environments, whereas species within *Cervalces* tended to inhabit more open environments as evidenced from antler size relative to body size (Flerov, 1952; Sher, 1987; Lister, 1993) and pollen analysis (Breda and Marchetti, 2005). Sher (1974) also used associated flora and fauna to determine that *Cervalces latifrons* (the

presumed ancestor of Eurasian *Alces*, but see Breda and Marchetti, 2005) lived in open steppe habitat. However, an extensive analysis of the postcranial morphology of *Cervalces* by Breda (2008) revealed few differences with living *Alces* in femoral morphology, tarsal fusion, and phalangeal elongation (which have all been identified as adaptations for locomoting in marshes), suggesting that *Cervalces* may have begun to utilize marshy, forested habitats as part of its foraging strategy. The subsequent diversification of Alceini in Asia and Pleistocene dispersal of *Alces* to North America are well represented in the fossil record (Breda and Marchetti, 2005; Heintz and Poplin, 1981; Kahlke, 1990).

The diversification of their fossil record has carried over to present day populations of *Alces alces* where six separate subspecies have been identified (i.e., *Alces alces alces*, *Alces alces pfitzenmeyeri*, *Alces alces cameloides*, *Alces alces buturlini*, *Alces alces gigas*, and *Alces alces andersoni*). These may be divided roughly into eastern and western populations, which have been separated geographically by a north–south boundary comprised of the Altai mountain range of Central Mongolia and the Yenesei river in Siberia. Differences in karyotype, pelage, and antler, craniofacial and, in particular, nasal morphologies separate the eastern and western populations. The western population exhibits premaxillae that extend further posteriorly toward the nasal bones than in Eastern *Alces* and ends in a spatulate process. Those of the eastern *Alces* end further rostrally and taper without a rounding of their posterior-most processes (Flerov, 1952; Lister, 2004). Such patterns of subspecific diversity indicate a degree of plasticity in nasal morphology and must be considered when describing the standard morphology of the bony nasal cavity in *Alces alces* as a species. Indeed, natural selection operates on morphological variability within a population to promote differing morphologies and selection exerts constant pressure on the population as a whole to become better adapted (Tattersall, 2010). Within this context the proboscis of *Alces* has evolved to fulfill differing biological roles (distinct from its functional role; Bock and Von Wahlert, 1965) in different regions and habitats, ranging from northern European Boreal forests, Siberian tundra, and fluvial/lacustrine marshlands across Alaska, Canada, and the northern United States.

The Semi-Aquatic Moose

Native Americans and early explorers of the North American continent were well aware of moose and its affinity for aquatic environments but newly arriving settlers unfamiliar with the landscape associated this ungulate exclusively with terrestrial browsing activities as characterizes the Eurasian “Elk” (i.e., Reeves and McCabe, 2007). One of the earliest accounts of the American moose engaging in aquatic foraging behaviors dates back nearly 300 years ago when Paul Chamberlayne in 1720 communicated to the Royal Society the following observation:

“In the Summer they feed upon Plants, Herbs and young Shrubs, that grow upon the Land, but mostly, and with greatest delight on Water-Plants, especially a sort of wild Colts-foot and Lilly, that abound in our Ponds, and by the fides of the Rivers, and for which the Moose will wade far and deep, and by the noise they make in the Water, our

Hunters often discover them.” (Dudley and Chamberlayne, 1720–1721, p. 168).

The feeding behaviors of moose involving aquatic plants have been similarly documented ranging from newspaper accounts describing the common names of water plants consumed “....feeding on the pads and large roots of yellow water lilies” (Rice, 1896, p. 76) to scientific journals where a more detailed description of the kinds of aquatic plants preferred by moose have been reported from distinctly diverse geographic localities (e.g., McCabe and McCabe 1928; Murie, 1934; Peterson, 1955; DeVos, 1956; Ritcey and Verbeek, 1969; Fraser and Hristienko, 1983). The following studies identify the specific aquatic food item and their location, illustrating the large range of aquatic plants in the moose diet: swamp horsetail (i.e., *Equisetum fluviatile*; Ritcey and Verbeek, 1969; DeVos, 1958), large-leaved pondweed (*Potamogeton amplifolius*; Ritcey and Verbeek, 1969), the common floating pondweed (*P. natans*; Ritcey and Verbeek, 1969), bur-reed (*Sparganium* spp.; Ritcey and Verbeek, 1969; Peterson, 1955).

It is undeniable that the moose appears comfortable in water given the proportion of time it spends foraging for aquatic vegetation during the summer months and parts of fall (e.g., Joyal and Scherrer, 1978; Belovsky and Jordan, 1981), with some reports claiming that the time spent in water goes beyond the midsummer months (MacCracken et al., 1993). Adult moose have been observed diving underwater, completely submerging their bodies while grazing for aquatic plants with some sources witnessing moose swimming distances of 12–20 km, or 8–12 miles (Gest, 1999; Bubenik, 2007). Initially, there was speculation that moose sought out lakes, or ponds, in order to avoid the harmful insects that caused devastating tissue damage effects upon their bodies often leaving them bloodied (Caton, 1877; Kelsall and Telfer, 1974; Gest, 1999). It was presumed that when moose engaged in avoidance behavior by seeking refuge in aquatic environments from the various damaging inflicting insects (i.e., horse flies, biting midges, nose bot warbles, deer flies, stable flies, mosquitoes, black flies—see Lankester and Samuel (2007) for a list of the harmful flies from the order Diptera that target moose for their blood), the result was the incidental and unexpected discovery of an untapped food resource (Gest, 1999). On the other hand, the observed exploitation of water plants by American moose, which takes place across the northern continent, suggests that seeking an aquatic habitat also provided a new successful foraging strategy (Fraser et al., 1984).

Aquatic Plants Rich in Sodium

The “hunt” for aquatic plants by moose may also have been driven by a need to fulfill a dietary gap of certain trace elements important to their growth and development (Aho and Jordan, 1979; Jordan, 1987). Sodium, specifically, was the key trace element identified by Botkin et al. (1973) and Jordan et al. (1973) when they showed that the biochemical composition analyses of aquatic plants targeted by moose are rich in this highly reactive soft metal chemical element. Sodium has been shown to be a necessary mineral for animal nutrition (Dethier, 1977), playing a vital role in metabolism (see National Research Council of the National Academies, 1985), and being

essential for antler growth (e.g., Gest, 1999) with estimates of sodium being a major constituent comprising about 0.1% of the total chemical makeup of live mammals (Botkin et al., 1973). Denton (1982) has shown that prolonged sodium deprivation will lead to death demonstrating its importance in nutrition. Aquatic plants, however, are not the sole sodium resource exploited by moose. Many workers have documented moose making use of “Licks,” or “Natural Salt Licks,” which are natural geologic deposits containing a variety of mineral concentrations that include manganese and sodium (e.g., Chamberlin et al., 1977; Risenhoover and Peterson, 1986; Ayotte et al., 2008; Lavelle et al., 2014; also see Ayotte et al., 2006 for review on classification of licks). Sodium and chlorine, the composition of table salt, are required elements for the normal growth and development of bones, muscles, and maintaining homeostasis of the nervous system, while also assisting in the regulation of hematologic pH levels (e.g., Denton, 1982). Moose are not the only consumer of sodium as other mammals are always supplementing their diet with a variety of minerals (Mahaney et al., 1990; Cancelliere et al., 2014). Boreal ecosystems have been reported as non-suitable habitats for mammalian herbivores because plants and soils typically lack some essential minerals including sodium (Jacubas et al., 1995). Ultimately, it is in the foraging behaviors for underwater vegetation that we are able to observe the full repertoire of morphophysiological traits that facilitate moose delving into aquatic environments to explore, identify, and procure sodium-rich water plants.

Nasal Complex Structures: Morphological Indicators for Aquatic Adaptations?

Given the utilization of aquatic environments by moose, adaptations may be expected in their internal nasal morphology. The complex arrangement of the mammalian turbinal system has been a rich area of information, such as the inquiry into the origins of endothermy (Hillenius, 1992, 1994; Hillenius and Ruben, 2004), aquatic adaptations (Van Valkenburgh et al., 2011), climatic adaptation and/or diet (Green et al., 2012), and unique nasal airflow patterns for olfactory acuity and mapping (Craven et al., 2010, Pang et al., 2016). An examination of the moose maxilloturbinals, ethmoturbinals, and nasoturbinals may speak to its impressive olfactory acuity among the Artiodactyla from which surface water plants may be detected from far distances before engaging in deep diving behaviors to acquire submerged vegetation.

Some have described the prominent proboscis of the moose functioning as a valve to keep water from entering the nasal cavity and upper respiratory tract (e.g., Clifford and Witmer, 2004). This complex series of cartilaginous and muscular nasal structures of the moose may have predisposed them to develop a repertoire of functional behavioral adaptations for finding patches of aquatic vegetation. For example, one of the authors (KHA) observed a moose in a shallow pool employing short, powerful gusts of expired air (directed by their intricate series of internal nasal cartilaginous folds) toward submerged plant matter, thereby displacing the water surrounding the sodium-rich vegetation for easier access before mastinating it above water (see Fig. 2).

It, thus, appears that the nasal morphology of the moose is one of several ways in which it has adapted to

swamplands and marsh habitats. Here, we discuss the soft and hard tissue morphology of the moose nasal cavity and survey other artiodactyls in providing evolutionary context for their highly specialized noses, including a carnivore, to serve as an outgroup comparison. Being one of few terrestrial artiodactyls to have recently (during the Pleistocene) begun to utilize aquatic environments, they may serve as useful evolutionary models for the early ancestors of cetaceans.

MATERIALS

This study was the result of a MiniSymposium on Mysticete Anatomy and Evolution organized by Dr. Joy S. Reidenberg. It was sponsored by the Anatomical Record and held at the Icahn School of Medicine at Mount Sinai in New York (Oct 17–18, 2016). Invited participants included marine biologists, neurobiologists, pathologists, functional morphologists, and comparative anatomists. A range of wet specimens afforded the opportunity to explore various aspects of whale anatomy and evolution. Among the materials available for dissection was the head and neck of a subadult American moose, which was of comparative value as a related semi-aquatic artiodactyl.

Three representative artiodactyl species were chosen for soft tissue analysis, from which five specimens were dissected: the American moose, $n = 1$ (*Alces alces* [Linnaeus, 1758]), fallow deer, $n = 1$ (*Dama dama* [Linnaeus, 1758]) and domestic cattle, $n = 3$ (*Bos taurus* [Linnaeus, 1758]). CT scanning of dry crania included the Eurasian elk (*Alces alces*), white-tailed deer (*Odocoileus virginianus* [Zimmermann, 1780]), and the North American black bear (*Ursus americanus* [Pallas, 1780]), a member of the Order Carnivora used as an outgroup comparator. Age assessments for specimens were determined by molar dental eruption pattern based on published data (age assessment tables for bear see Marks and Erickson, 1966; all others see Márquez *et al.*, 2017). Dry cranial specimens were selected from the osteology collections of the Department of Anthropology, Lehman College, City University of New York (bear, $n = 1$), Center for Anatomy and Functional Morphology, Icahn School of Medicine at Mount Sinai (white-tailed deer, $n = 1$), and from the Department of Mammalogy, American Museum of Natural History (moose, $n = 3$; elk, $n = 1$). In addition, a cranium of *Cervalces*, (an extinct genus of deer that lived during the Pliocene and Pleistocene epochs and is thought to be ancestral to moose), from the Vertebrate Paleontology collection at the American Museum of Natural History, was studied. Dry specimens were chosen based upon the intact nature of the facial skeleton and complete and identifiable borders of foramina and fissures. In addition, transillumination of internal nasal morphology and examination of external appearance of the specimens were undertaken.

The moose (*Alces alces*) was a young, subadult male from the collection of the Center for Anatomy and Functional Morphology at the Icahn School of Medicine and generously made available for this dissection session by Dr. Joy Reidenberg. The animal was severely injured from a vehicular accident in Connecticut, was subsequently shot by state police providing a humane death, and was procured by Dr. Reidenberg. Other animals dissected were from the collections of Dr. Márquez at the Department of Cell Biology at SUNY Downstate Medical

Center and had been procured previously with permission from abattoir farms in the northeastern United States. The fallow deer was a subadult male based on dental tooth eruption. The cattle sample was comprised of one adult male and two subadult male specimens based on dental eruption patterns. All specimens had been frozen and then thawed for the dissections.

METHODS

The examination of the Moose nasal complex (external nose, nasal cavity proper, and its appendages—the paranasal sinuses, see Márquez and Laitman, 2008; Márquez *et al.*, 2014a,b, 2015 for a fuller treatment of their detailed definition) centered on the qualitative and quantitative assessments of two approaches: (1) anatomical serial dissection, and (2) CT imaging of dry crania.

Anatomical serial dissections of the moose were conducted in the anatomy laboratories of the Icahn School of Medicine at Mount Sinai in the Center of Anatomy and Functional Morphology. Dissections of the fallow deer and cattle heads were done in the embalming laboratory at SUNY Downstate Medical Center, department of Cell Biology. Photo documentation for each layer of dissection was undertaken using a Nikon D100 LRS digital camera. Specimens were measured for cranial lengths prior to dissection along with select nasal structures. Measures were taken during each phase of dissection. *Bos* specimens were frozen in a chest freezer and then were sagittally sectioned with a Butcher Boy SA20 Industrialized Bandsaw. Specimens were rinsed with tap water immediately following the bisection in order to clean the area of soft tissue debris. Description of the muscles found in these dissections follow the terminology of Clifford and Witmer (2004), who gave a detailed historical overview of their nomenclature and provide the most recent analysis of their origins, insertions, and functions in *Alces*.

Internal nasal morphology, particularly the maxilloturbinals and ethmoturbinals, were qualitatively assessed from wet specimens while dry crania were analyzed using two-dimensional and three-dimensional reconstructions derived from computer tomography scans. Patterns of paranasal sinus pneumatization were included in our analyses of bony nasal cavity morphology. Paranasal sinus reduction and loss has been described as an adaptation for diving behaviors among cetaceans as their bony boundaries may fracture under increasing pressure (see Reidenberg and Laitman, 2008). If moose were to also exhibit a reduction in sinus size relative to other non-cetacean artiodactyls despite the large, heavy antlers of males (necessitating lighter crania with larger sinuses), a diving adaptation may be indicated.

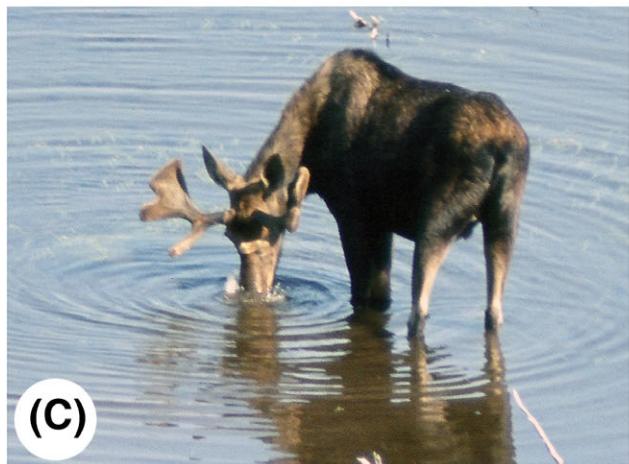
Two-dimensional reconstructions were used in supplying linear dimensions of such measures as anteroposterior length, maximum width, and height of the maxillary sinus. While a quantitative assessment of sinus morphology may lack the scientific rigor due to low sample numbers, it does offer a qualitative appreciation of which dimension varies as a function of craniofacial configuration. Three-dimensional reconstructions permitted contiguous structures (such as ethmoturbinals and dental arcade) to be graphically represented in conjunction with the sinuses, allowing for an appreciation of their size and shape dimension in a non-destructive way.



(A)



(B)



(C)



(D)



(E)



(F)

Fig. 2. A–F. Composite images of the American moose in its natural habitat showing its propensity and comfort in water. Note moose in (C) engaged in water-plant hunting in which the water ripple effect is caused by the gust of air expelled through its anterior naris. Adult moose in (D) may be seen demonstrating narial closure with rostrum partially submerged in water. (All photographs of moose from different National Parks taken by one of the authors - KHA).



Fig. 3. The fossil of *Cervales cervales* (AMNH 5899), the presumed ancestor of moose, shown in lateral views. **A.** Right lateral view showing bones comprising circumorbital and piriform aperture region. (F, frontal; La, lacrimal; Zy, zygoma; Mx, maxilla; Na, nasal; Pmx, premaxilla). White arrows showing sutural articulation of post orbital bar (POB) morphology with yellow arrows identifying the zygomaticotemporal (ZT) articulation. The composition of bones comprising the orbit, POB and ZT sutural pattern would classify *Cervales* as a Type 2, Category 3, and Configuration 1 patterns of cranial morphology (see Márquez et al., 2017 for definitions of classification terms). **B.** Left lateral view, demonstrating unlabeled elements of the facial skeleton. **C.** Dorsal view showing the midline articulation between the nasal bones and frontal bone.

Dry crania were scanned (GE HiSpeed Advantage CT scanner) at the Department of Radiology, Icahn School of Medicine at Mount Sinai. Coronal scans of variable slice thickness for all specimens were taken. Use of the smallest thickness minimizes partial volume averaging, which affords the best possible spatial resolution perpendicular to the scan plane (Spoor et al., 2000). All specimens were positioned in the supine position. Prior to scanning, scout beams insured the position of the specimen to be aligned centered within the CT opening, with the long axis perpendicular to the plane of opening (i.e., orientation of the X-ray beam). The CT digital capture intensity specifications of the scanning machine are reported for each specimen in the following section.

Four different software packages were employed for visualization and analysis of the CT digital dataset: (1) GE scanner console utilizing the NT Windows Scanning CT digital 3.11 software; (2) Avizo 9.2 to produce 3D volumetric renderings; (3) Osirix—to produce 2D and 3D reconstructions; and (4) a Silicon Graphics Indigo (SGI) 2-XZ Workstation using VoxelView 2.5 High-Performance 3D Imaging for Biomedicine software. The UNIX-based computer environment that the SGI 2-XZ Workstation provides is housed in the Center for Anatomy and Functional Morphology at Mount Sinai. In order to use VoxelView, a number of intermediate steps were performed. First, the digital data of the CT scans were transferred to a Digitized Audio Tape (DAT). The

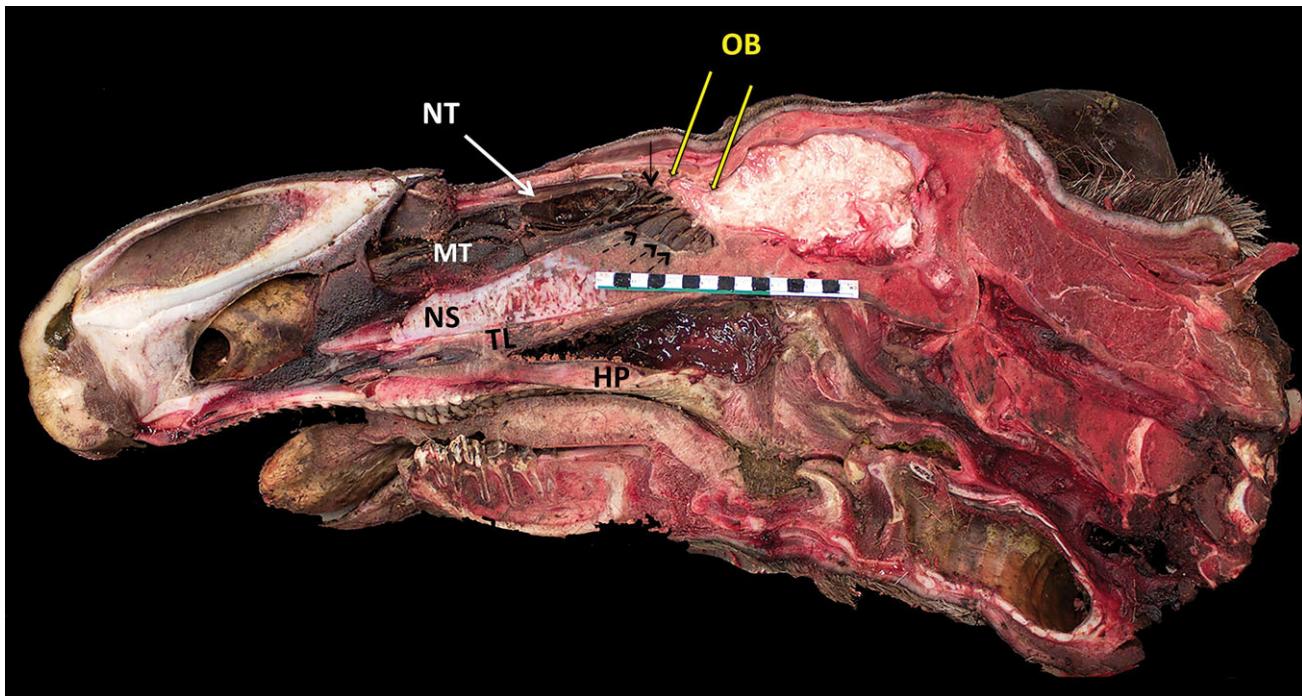


Fig. 4. Bi-section of a fresh subadult *Alces alces* male in the midsagittal plane. The overall size and complexity of the nasal proboscis is demonstrated in this view. The olfactory recess is well developed and contains a full complement of endo- (dashed arrows) and ectoturbinals (solid black arrow); NT, nasoturbinal; MT, maxilloturbinal; NS, cartilaginous nasal septum; TL, transverse lamina; HP, hard palate; yellow block arrows delimits the olfactory bulb (OB) of moose. (Scale = 1 cm bars).

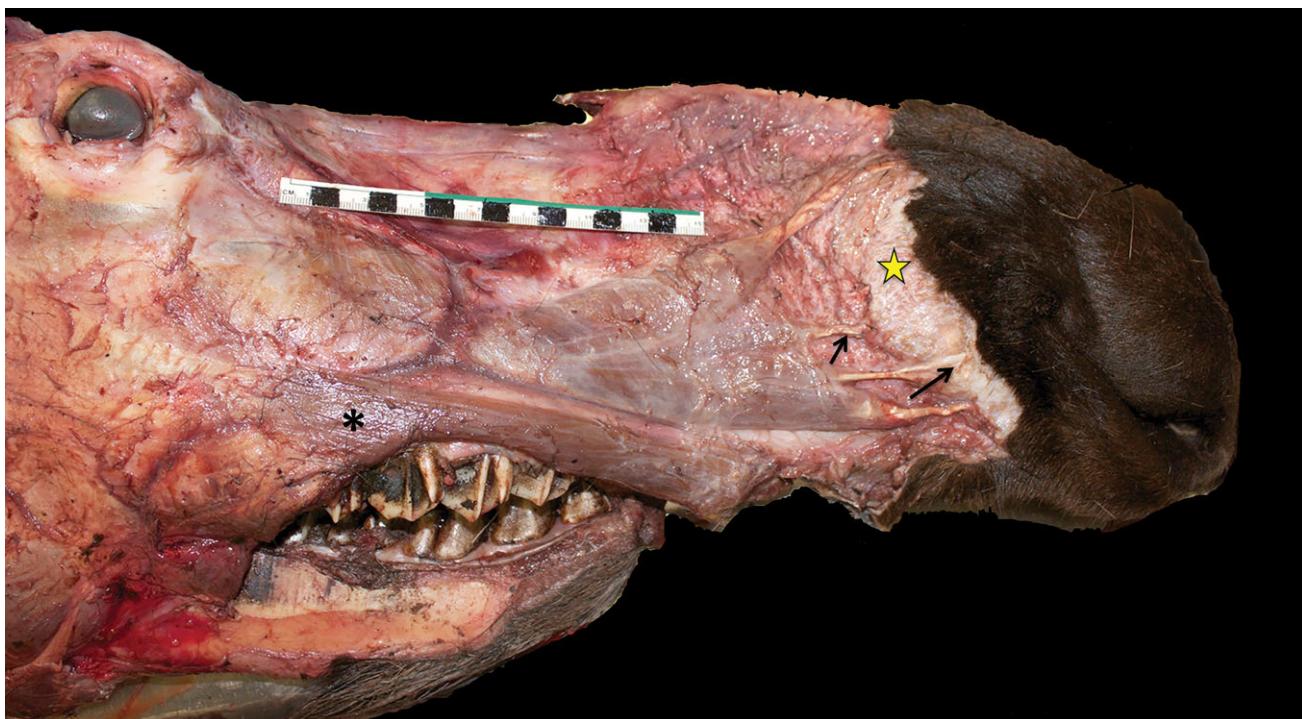


Fig. 5. External nasal anatomy of subadult male *Alces* is shown in dissection. Note the four separate tendons emerging from the maxillolabial muscle group (ML in text), two tendons associated with the caninus muscle (marked with black arrows) are inserting into a semi-fibrous fat pad (marked with a yellow star) that appears to comprise a large volume of the fleshy external proboscis. The orbicularis oris muscle is also expressed prominently (marked by black asterisk). (Scale = 1 cm bars).



Fig. 6. All four arms of the maxillolabial muscle group are demonstrated in this dissection of a subadult *Alces alces* male (muscle bellies are numbered). Note that the tendons extend to the limit of the alar fold, in which they are embedded in a dense network of fibrous and fatty tissue. Arrows track the tendinous path (black arrows) of the first muscle belly, that of the levator labii superioris muscle (dashed arrow) from its proximal origin to distal target (white arrows). The two muscle bellies of the caninus muscle (2 and 3) and the single muscle belly of depressor labii superioris (4) are visible in this dissection (Scale = 1 cm bars).

translation of the tape into a universal format Digital Imaging and Communications in Medicine (DICOM) took place at the American Museum of Natural History. The perimeter outline of the maxillary sinus was traced with the cursor on each CT scan image in the coronal plane by using the program “contour trace” in VoxelView. The surface contours of the maxillary sinus cavities were generated from the summed perimeters and graphically displayed both *in situ* and isolated.

Structural Organization of the Turbinate System

To describe the turbinate system of the moose and other species for this study we follow the organization of Paulli (1900a, b, c) and Dieulafé (1906). This system was not created using developmental data, which was later used to show the non-homology of some of these structures (see review by Van Valkenburgh *et al.*, 2014). However, for the purpose of consistency and ease of comparison with older sources, we adopt the naming system in Paulli (1900a, b, c) as we are describing only adult morphology. Ethmoturbinals are defined as bony plates of bone that originate from the ethmoid and protrude into the nasal cavity in a scroll-like fashion. The characteristic curling (or revolutions) of these structures can range from

simple to elaborate, which is how they were named from the Latin *turban* for “spinning.” Ethmoturbinals are further subdivided based on the structural origin: those that protrude medially into the nasal cavity are termed endoturbinals (including the lamina semicircularis of Maier, 2000; see also Smith and Rossie, 2008); those that cluster laterally are termed ectoturbinals (including fronto- and interturbinals of Maier and Ruf, 2014) irrespective of whether they originate superiorly or laterally; and those that possess a turbinal that runs superiorly coursing the undersurface of the nasal bones are termed nasoturbinal (Moore, 1981). Note that our discussion of endoturbinals and ectoturbinals are relegated to structures residing within the olfactory recess.

RESULTS

Moose (Alces alces)

Soft tissues of the external rostrum. The most striking morphological trait of the moose remains its impressive proboscis. The muzzle is bulbous with long but wide-set anterior nares that are laterally displaced from the midline. The bulbous muzzle that overhangs the nasal region contributes overwhelmingly to the length of the snout and is supported inferiorly by the lengthened

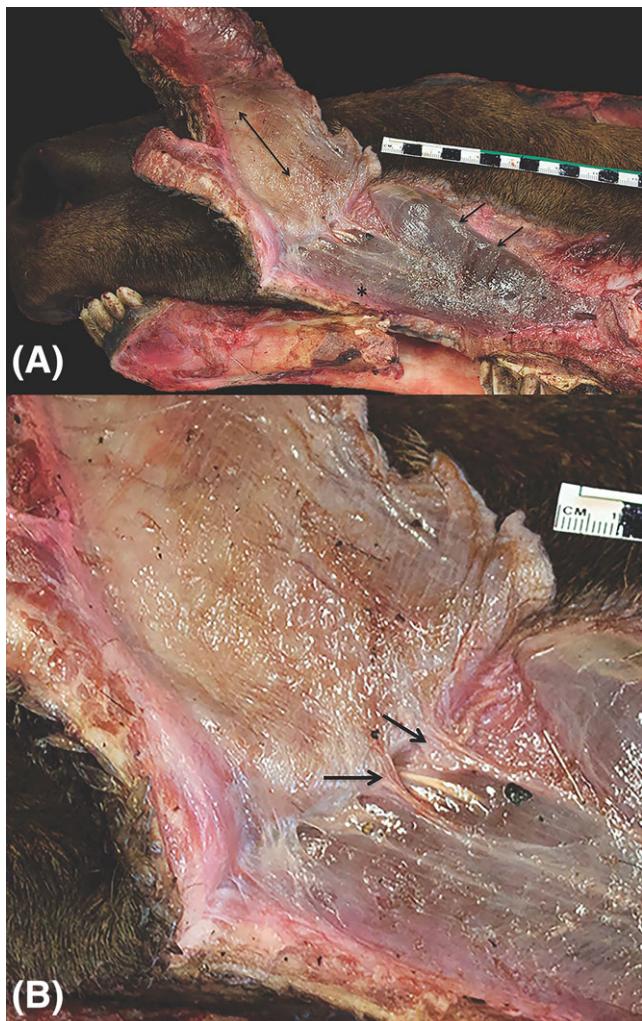


Fig. 7. Superficial dissection of a subadult *Alces alces* male. **A.** Skin reflected superiorly (double arrowheads) revealing the underlying muscle groups (including the *musculus levator labii superioris* [black arrows] and *musculus depressor labii superioris* [asterisk]). **B.** A close-up view of region shown in **(A)** showing skin appearing to be tethered to the underlying fibromuscular structures of the face via a dense network of fibrous tissues resembling the superficial musculaponeurotic system (or SMAS) of humans, which was first described in 1976 (Mitz and Peyronie, 1976).

premaxillary region. The considerably foreshortened nasal bones lose their contact with the premaxillae as they have migrated rostrally along with the anterior-most portion of the maxilla. Thus, the maxilla displaces the premaxilla from its ancestral position when compared with *Cervalces* (Fig. 3). The bony disengagement of the premaxilla from the shortened nasal bone creates a sizable piriform aperture whose space provides the room for the development of a prehensile nasal apparatus, which is offered still further mobility by the lack of a superior labial frenulum. This area is occupied by a cartilaginous partition of the distal nose that is continuous inferiorly with the cartilaginous nasal septum. This cartilage measured 19 cm in anteroposterior length compared with the 73.2 cm length of the whole head from snout to occiput (Fig. 4). The cartilaginous framework of the external nose appears reinforced by larger nasal fat pads that together create the majority of the volume within



Fig. 8. Close-up view of the internal nasal septum of *Alces alces*. There is a complex network of cartilages and muscles moving the fleshy proboscis. The superior incisive muscle can be seen from this section. (Scale = 1 cm bars).

the mobile proboscis (Figs. 4 and 5). The fat pad, in particular, gives both body and flexibility to the alar fold, providing the ability to be constricted inward, or pulled posteriorly and inferiorly during contraction of facial muscles (as confirmed from manual movement of the major muscle tendons therein). They pull caudally and, in that orientation, can narrow the nostril to a slit by aligning the two edges of the alar fold into straight or flat parallel edges. This is the opposite of relaxing the two ends of the alar fold into arc shapes that curve away from each other (forming the shape of two parentheses around an open nostril).

Superficial dissection reveals the maxillolabial (ML) muscles (Fig. 6), which comprise the dominant muscle group on the maxilla. Included in this group are the *levator labii superioris* muscle, the *caninus* muscle with its two



Fig. 9. Lateral view of an adult *Alces alces* cranium. The maxillae and nasal bones (dashed arrows) are reduced to such an extent that the maxilloturbinals (solid white arrows) protrude through the piriform aperture plane from the nasal cavity. The premaxilla (marked by an asterisk) is only present posteriorly as an extremely narrow projection of bone that does not contact the nasal bone in modern *Alces*. Black solid arrow is identifying the infraorbital foramen.

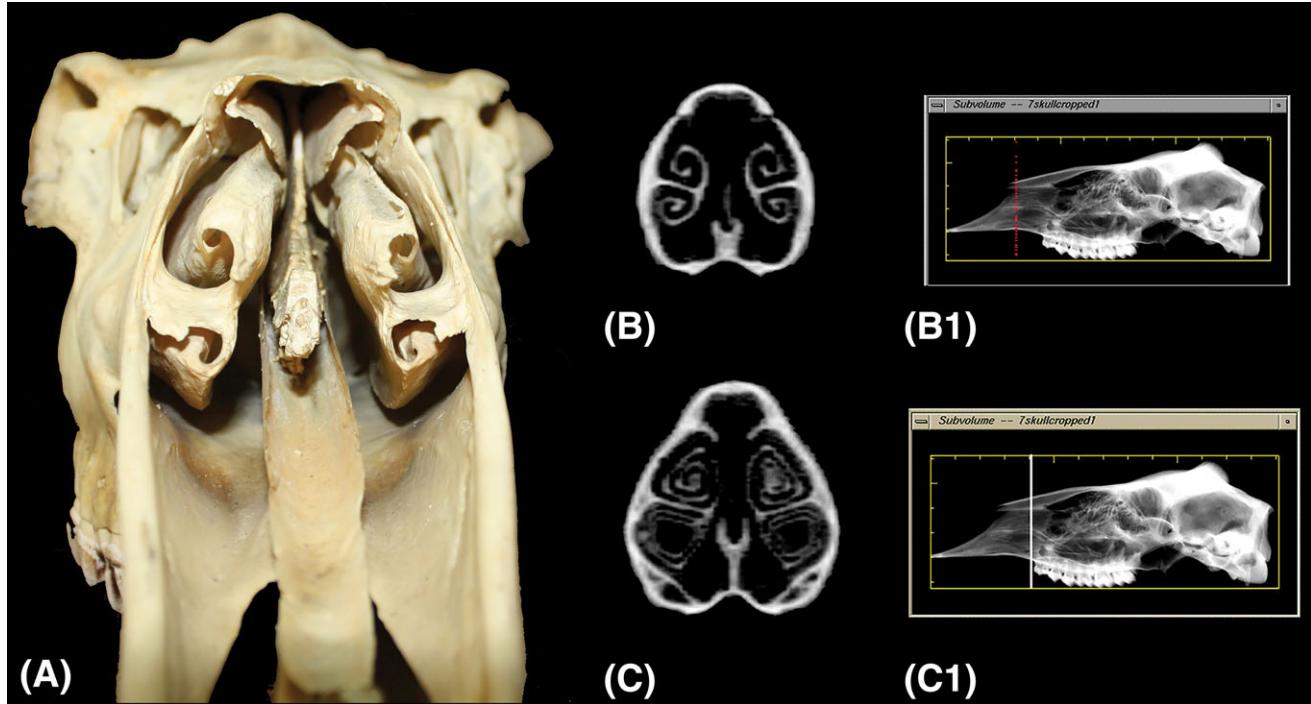


Fig. 10. Frontal view of an adult *Alces alces* cranium [AMNH 122674] (A) and a CT coronal plane slice through the piriform aperture of an adult white-tailed deer (B) with (B1) showing the reference CT slice. The maxilloturbinals of both species are visible through the piriform aperture and present in a double scrolled configuration. These bony coiled structures may redirect separately some respiratory airflow into the nasopharyngeal duct inferiorly while a large proportion of respiratory air is diverted superiorly to the olfactory recess, above the lamina transversalis. Tracking the extent and morphology of the deer's maxilloturbinal via CT imaging (B and C with C1 = reference window) revealed an increase of inrolling of their bony plates caudally.

muscle bellies, and the depressor labii superioris muscle. Tracking their four tendinous slips, they first run through the lateral nasal fat pad before continuing on to more distal zones of insertion (Figs. 5 and 6). The caninus muscle was confirmed as a caudal retractor of the alar fold and assisting in closure of the anterior nares upon manual pulling of the tendon toward the muscle belly (simulating normal

muscle contraction). The levator labii superioris and depressor labii superioris tendons also attach to the alar fold, suggesting a potential function in assisting with contraction of the anterior nares. Specifically, the tendon of the levator labii superioris runs superiorly and anteriorly over the enlarged alar fat pad, being redirected inferiorly toward the anteroinferior edge of the alar cartilage. When this tendon is manually retracted, the alar cartilage is lifted posteriorly and pressed into closer contact with its inferior end.

Tendinous slips of the maxillolabial muscles appear to attach and blend into a subcutaneous layer of fibrous tissue just deep to the skin of the nasal region where they may permit movement of both skin and cartilage surrounding the proboscis (Fig. 7). This fibrous layer extends further proximally on the face where the orbicularis oris muscle also exhibits attachment. The posterior continuation of the subcutaneous fibrous tissue layer has the appearance of a superficial musculopaponeurotic system (SMAS) as found in humans, which may assist in the integration of the proboscis with other facial regions while simultaneously allowing fine motor control of its dilatory function.

A parasagittal section through the proboscis reveals the superior incisive muscle (Fig. 8). This muscle appears broad and thin, running through a layer of fat, which underlies the supporting cartilages of the proboscis. It assists the levator labii superioris in elevating the upper lip, which is prehensile in *Alces*. Interestingly, this was one of two cases among cervids of muscle originating from an intranarial location. See the description of the fallow deer (*Dama dama*) below.



Fig. 11. An oblique frontal view of the *Alces alces* nasal cavity [AMNH 122674]. Of note is the well-developed nasoturbinal (asterisk) and extensive maxilloturbinal system whose upper scroll is larger than its lower scroll companion. The black arrow denotes the anterior limit of the basal lamella of the left maxilloturbinal.

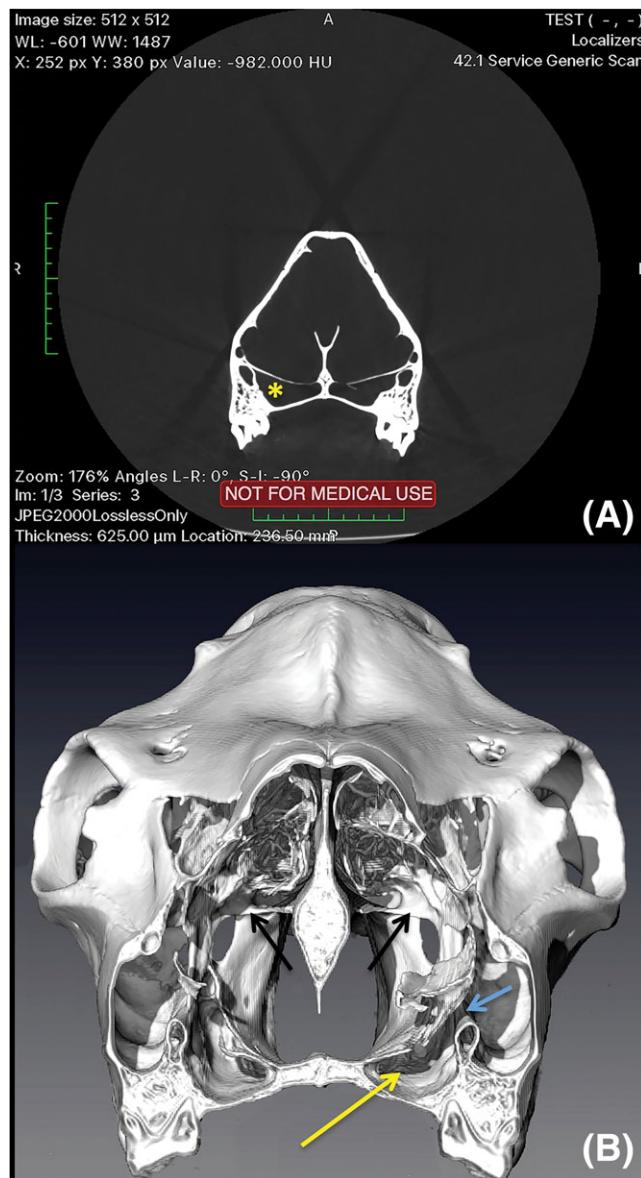


Fig. 12. CT imaging reveals *Alces alces* [AMNH 87098] exhibiting palatal pneumatization as do other cervids, which is likely a shared derived trait. **A.** The internal space of the pneumatized hard palate (yellow arrow) may be seen communicating with the maxillary sinus (yellow and blue arrows shown in **B**). **B.** A 3D CT reconstruction of same specimen showing a distinct transverse lamina (black arrows).

Endonasal morphology. The moose exhibits an extremely large, obliquely oriented piriform aperture, likely as a result of its extremely elongated premaxillae. The maxilloturbinal (MT) protrudes beyond the piriform aperture, unlike in other cervids (Negus, 1958; see Fig. 9). This appears to be a derived trait and may be related to the oblique re-orientation of the piriform aperture from the ancestral cervid condition. Indeed, this trend may begin in *Cervalces*, which exhibits obliquity in its piriform aperture but does not approach the extreme morphology of *Alces* as its nasal bones are relatively longer. Thus, the maxilloturbinals of *Cervalces* are nearly covered by the

coronal plane of the premaxillae, which were still in contact with the nasals.

When following the maxilloturbinals caudally, they exhibit a double-scrolled morphology. The medial bony plate of the MT is angled in which the upper scroll nearly contacts the bony septum while the lower scroll descends in an anterolateral manner nearly abutting the maxilla, which forms the lateral nasal cavity wall (Fig. 10). The convexity of the outer medial wall of the MT parallels the convexity of the outer wall of the maxilla creating a tubular pathway through which inspiratory and expiratory airflow must travel within each nasal compartment and in between the bony plate surfaces of the MT and septum (Fig. 11). In addition, the number of turns for each inroll increases from its anterior limit (i.e., one revolution) to nearly two and one half turns seen more caudally. However, unlike other cervids, the maxilloturbinal is extremely large, appearing highly pneumatized and swollen, and occupies nearly all of the space between the lateral nasal wall and the nasal septum. Whereas other cervids exhibit a divided anterior nasal cavity with an unobstructed inferior half dedicated to respiratory airflow and a superior half replete with maxilloturbinals and ethmoturbinals, *Alces* instead has the inferior half of the maxilloturbinal occupying the inferior space of its respiratory pathway. Thus, during quiet respiration, inspiratory airflow must first contact the inferior convolution of the maxilloturbinal and its mucosa before entering the nasopharyngeal duct. Of note, one adult female (AMNH 13795) exhibited extreme concha bullosa of the maxilloturbinal that resulted in septal deviation and may have predisposed this individual to unilateral nasal obstruction. Overall, *Alces* appears highly subject to extreme pneumatization, including invasion of the hard palate confirmed via CT imaging (see Fig. 12) that has been observed among other artiodactyls (see *Odocoileus* below).

Ethmoturbinal and transverse lamina morphology. Moose possess a full complement of endo- and ecto-turbinals that remain in close contact with the cribriform plate and are bounded dorsally by a nasoturbinal (Figs. 4 and 13). An extremely large nasoturbinal was found in the moose dissection while the remnant of its attachment to the ventral surface of the nasal bone was found in dry crania (Fig. 11). This confirms the observation of a large nasoturbinal continuous with the rectal fold (an extension of the lateral nasal wall).

The entire ethmoturbinal series appears irregular in size and spatial orientation among different individual specimens. However, its shape can be grossly described as having a larger bulbous anterior end before tapering posteriorly in a tubular-like fashion to its narrow caudal end which in parasagittal view, shows the moose turbinate resembling the cross-sectional outline of an airplane wing (Fig. 13). The sweptback nature of its morphology aids in the transportation of odorant molecules through the sieve-like structure of the cribriform plate before communicating with the rhinencephalon for olfactory discrimination during respiration. A greater appreciation of their elaborate branching as they approach the cribriform plate can be observed in CT imaging (Fig. 14). Most of the posterior ends of the distinct and individual ethmoturbinals abut against the cribriform plate, the latter appearing as a flattened but vertically angled plate of bone from the ethmoid providing a considerable surface area for the chemosensory function



Fig. 13. Mid-sagittal section through the head of a subadult male *Alces alces*. Note the junction between the braincase and olfactory portion of nasal cavity. Dashed black arrows indicate areas bounding the frontal cortex while the blue arrows are pointing around the large protruding olfactory bulb, which appears to occupy its own tubular-shaped recess. The ethmoturbinals appear arrayed perpendicular to the cribriform plate so that their posterior ends abut the cribriform boundaries (white arrows = endoturbinals; black arrows = ectoturbinals).

of olfaction (Fig. 15). The rhinencephalon appears to have a dedicated intracranial region for its olfactory bulb (Fig. 16) potentially heightening their keen sense of smell (Pihlström et al., 2005). Moving posteriorly to the olfactory recess, the transverse lamina appears well developed when viewed from coronal 3D CT reconstruction as observed in most other cervids (Fig. 12).

White-Tailed Deer (*Odocoileus virginianus*)

Maxillary sinus—general observations. The most anterior projection of the maxillary sinuses occurred in the coronal plane at the juncture of the distal-most maxillary premolars, with the most posterior excavation observed in the coronal plane of the maxillary tuberosity. The floor of the maxillary sinus extended over the premolar and molar dentition and slightly posteriorly beyond M^3 (the third maxillary molar). The lateral walls of the sinuses at the point of their maximum width were vertically disposed making these cavities appear narrow. Partitions, or septa, were not observed within the sinuses.

Right maxillary sinus. The following observations were made from coronal views with a reference window indicating the corresponding sagittal slice view. The greatest width occurred in the coronal plane intersecting the distal surface of the M^2 . In this plane, the lateral boundary of the maxillary sinus corresponded with the

approximate position of the zygomaticomaxillary suture whereas the medial boundary was the lateral nasal cavity wall. A mediolateral distance of 23.6 mm was recorded (Fig. 17). The greatest height was in the coronal plane at the juncture between M^2 and M^3 of the second and third maxillary molars, measuring 37.1 mm (Fig. 17). Antero-posteriorly, the greatest depth was 83.5 mm. The floor of the sinus dipped inferiorly at the level of the premolars to allow communication with a palatal pneumatization. This extension made near contact but did not communicate with the contralateral sinus in the midline of the hard palate (Fig. 18). Posteriorly, it terminates at the midportion of the M^2 but is observed anteriorly at the coronal plane of PM^2 . When visualizing the 3D reconstruction of the maxillary sinus (Fig. 19) the floor covers over the dental roots of the mesial-most maxillary premolar, extending well into the maxillary tuberosity.

Left maxillary sinus. The lateral and medial bony walls were similar to the right side. The greatest width (25.1 mm) occurred in the coronal plane at the distal border of M^2 . The greatest height (36.3 mm) in the coronal plane was measured at the juncture between M^2 and M^3 . From an axial view, the greatest anteroposterior length was 79.2 mm.

A medial extension into the hard palate was similarly observed. A thin bony partition at the midline of the hard palate prevented communication between the two

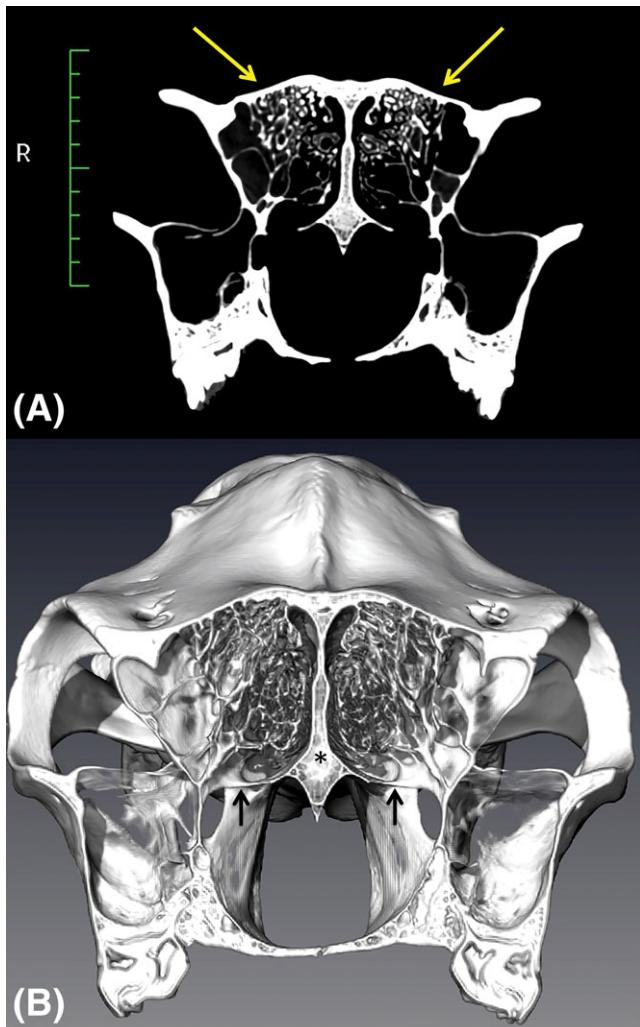


Fig. 14. **A.** A coronal CT slice of *Alces alces* cranium showing elaborate branching of ethmoturbinals in its olfactory recess (yellow arrows). **B.** The intricate branching of the ethmoturbinals within the olfactory recess above a well expressed lamina transversalis (black arrows) can be greatly appreciated via 3D CT reconstruction. Asterisk denotes nasal septum. The maxillary sinus shows a variety of incomplete bony septa.

sinuses. Palatal pneumatization in the coronal plane began anteriorly at the juncture of PM² and terminated at the midportion of M².

Turbinate morphology. The maxilloturbinal begins anteriorly to the premolar dentition exhibiting a simple double scrolled arrangement (Figs. 10B, C and 18). The upper scroll had inrolled more than two full revolutions and the lower scroll made two revolutions (Fig. 18). From the coronal perspective and proceeding posteriorly, the upper scrolls continued to inroll and enlarge while the lower scroll became diminutive. At the level of the mesial border of M¹ the lower scroll was rudimentary but the upper scroll had only one full revolution present (Fig. 20). The basal lamella and the upper and lower scroll remnant of the maxilloturbinal are observed in the coronal plane at the mesial border of M².

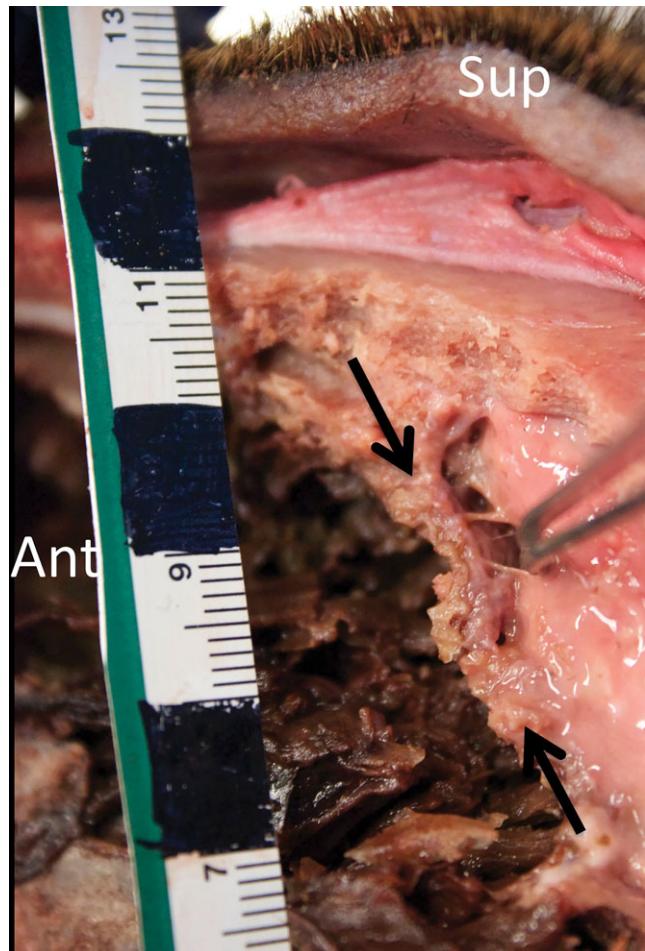


Fig. 15. Large olfactory filaments emerging from the hypertrophied cibiform plate (black arrows) and communicating with the olfactory bulb (forceps reflecting OB) may be seen in this subadult male *Alces alces*. (Sup, superior; Ant, anterior).

Coincident with the posterior ending of the maxilloturbinal, an elaborate branching of the ethmoturbinals appeared. The next sequential coronal cut posteriorly showed condensation of these plates to form thick spicules of bone that converged medially (see Fig. 17). These bony masses were housed in the olfactory region, separated from the respiratory air-currents by the transverse lamina. A coronal cut through the maxillary tuberosity still showed evidence of ethmoturbinals well into but below the anterior cranial fossa.

Fallow Deer (*Dama dama*)

The wet specimen measured approximately 28.6 cm in anteroposterior length from distal rostrum to occiput (Fig. 21A). Upon removal of the skin (with fur still attached), a membrane that appeared translucent over the rostrum and more opaque white caudally covered the muscles of the face (Fig. 21B). Dissection through this tissue layer revealed robust maxillolabial muscles, whose tendinous slips inserted onto large sections of the alar fold in a pattern similar to that of *Alces* (Fig. 21C). Upon

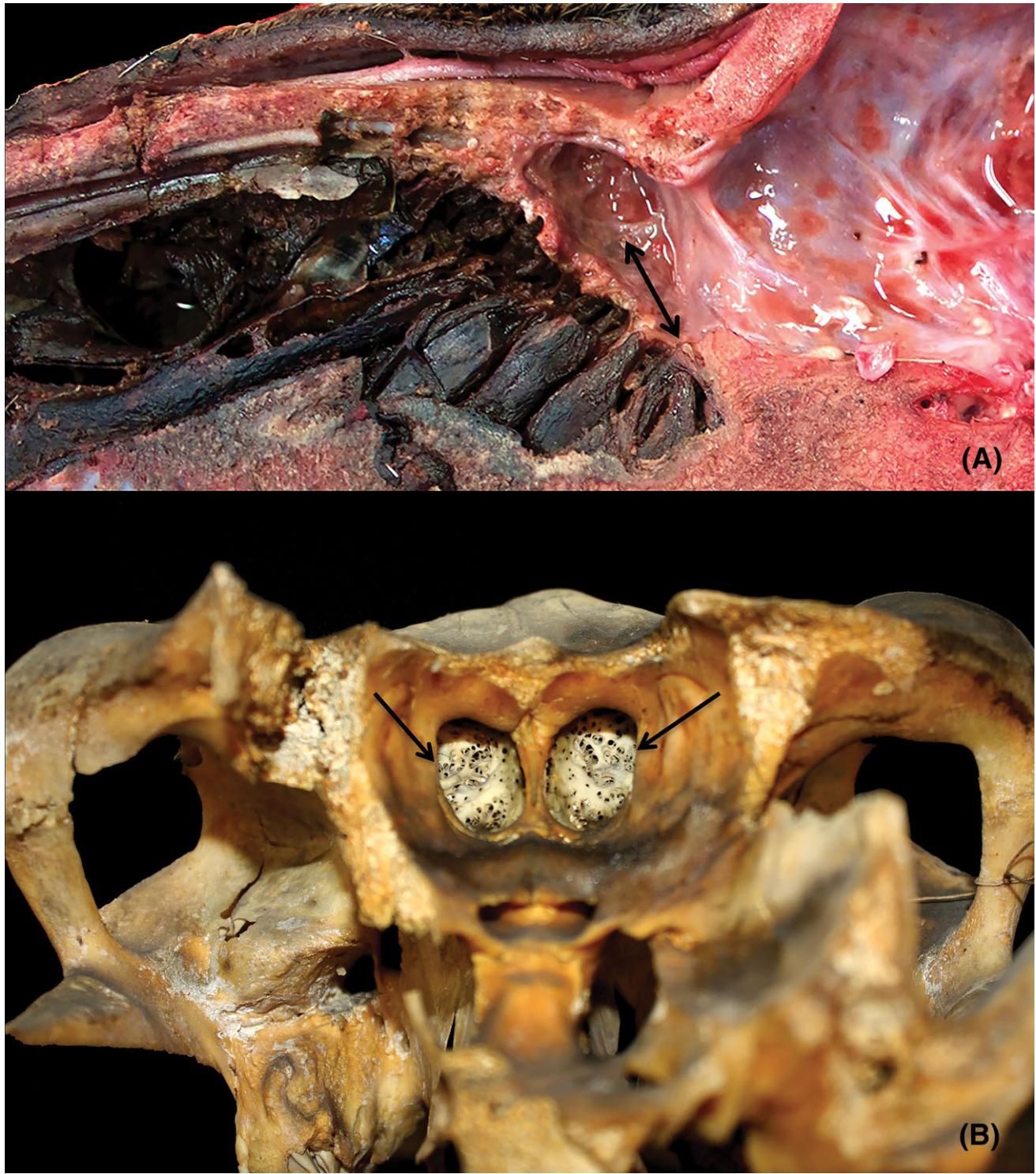


Fig. 16. A. Parasagittal view of dissected moose showing mediolateral depth of the cribriform plate area (see double arrow); B. Dry skull specimen of *Alces alces gigas* (AMNH 13795) with broken cranial vault allowing visualization of the posterior face of the cribriform plate (see black arrows). B. Note the numerous perforations of the cribriform plate through which the primary olfactory axons will course through communicating with the olfactory bulb.

manual pulling of the muscle tendons, it was found that some tendinous fibers of the levator labii superioris (the superior-most of the maxillolabial muscles) even extend

to the anterior surface of the alar fold and appear capable of inducing powerful posterior excursions of the fold. The maxillolabial muscles all have large bellies with a

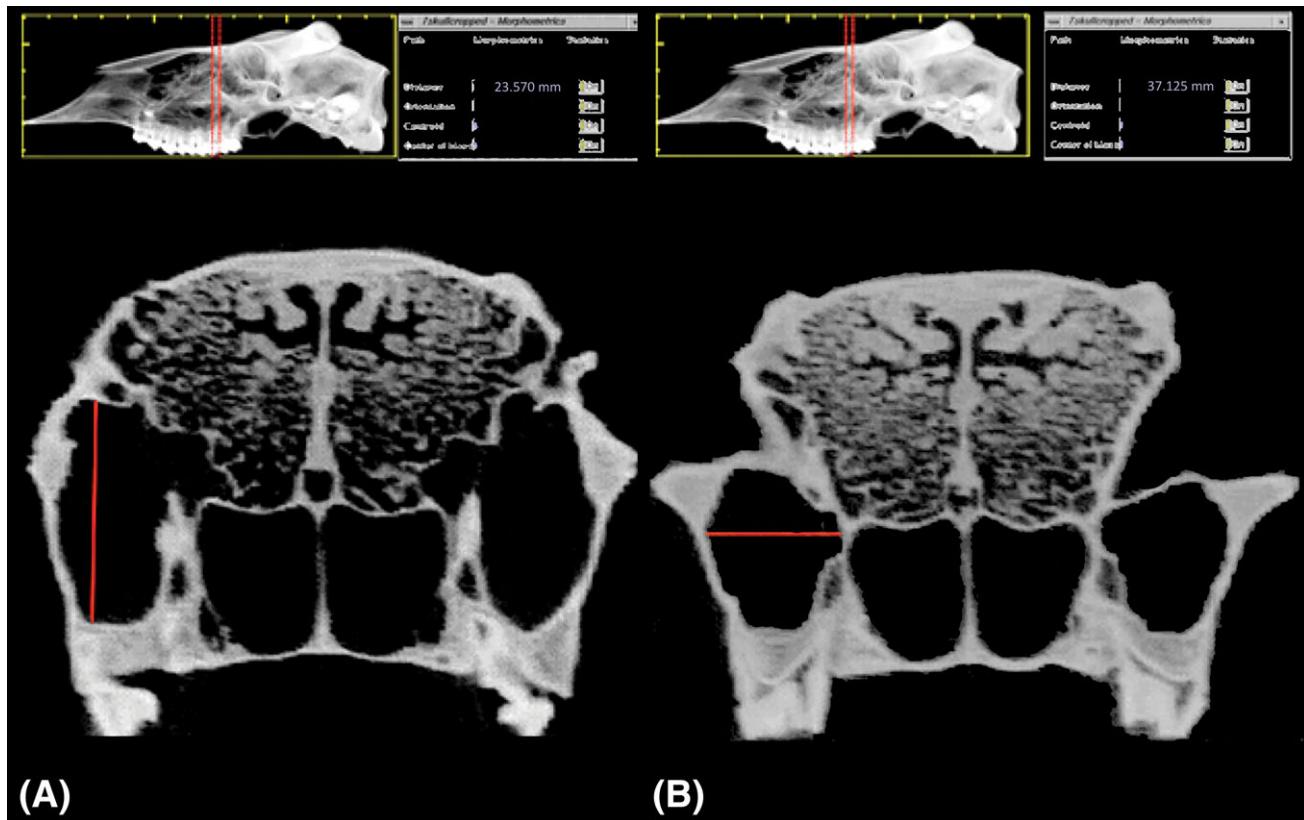


Fig. 17. **A.** Coronal view of *Odocoileus virginianus* cranium illustrating maximum height within the right maxillary sinus as indicated by the red line. **B.** Coronal view showing the largest width shown in red within the right maxillary sinus. Above are the reference windows showing the corresponding coronal cut slices. Note that the ethmoturbinals proliferated in their elaborate branching where they are dorsally exposed. Shown in (B) are the ethmoturbinals, which coalesce into thick and bony spicules.

common origin. As in *Alces*, the inferior tendons of this muscle group (including the caninus and depressor labii superioris) pierce through a fat pad that appears to give body to the alar fold. However, this fat pad does not appear as hypertrophied as that of *Alces*.

From a lateral view (see Fig. 21D), when these external muscles are reflected, bony contact appears to be prevented between the premaxilla and nasal bone by the nasal process of the maxillary bone, a primitive morphology for cervids. This specimen may exhibit some obliteration externally of the superior-most portion of the suture separating the maxilla from the premaxilla where it meets the nasal bone. When viewed dorsally, a thin, membranous layer of translucent fibrous tissue overlies several unnamed muscles that originate from within the nasal cavity (Fig. 22). Reflection of the rostral skin reveals tendinous connections with this fibrous tissue layer that, as in *Alces*, appear similar in morphology to the human SMAS. An additional unnamed, fan-shaped muscle originates from the ventral and distal most surfaces of the nasal bones, protruding beyond the piriform aperture. These muscle fibers insert into the dorsum of the external nares and appear to function in retraction of the alar fold dorsally and posteriorly. These fibers are extremely thin and likely assist the more hypertrophied maxillolabial muscles.

Upon reflection of these dorsal muscles and fascia, a separate group of deeper muscles become visible. Their

respective origins are exclusively intranarial, lying on the anterior tips of the maxilloturbinal and the first and second ethmoturbinals (Fig. 22). However, each tendon inserts distally into the inner surface of the alar fold. The bellies of these muscles are similar to the nasal conchae in caliber but each tapers distally into thin tendons that in life are covered over by mucosa. It is worth noting that these muscles have been seldom described in either *Dama dama* or any other cervid species. Indeed, the origins of these muscles among the nasal conchae appear exceedingly rare among mammals overall and may be an autapomorphic feature. The first ethmoturbinal of *Dama* is broad mediolaterally but dorsoventrally compressed, potentially offering a mechanical advantage for anchoring the large muscle taking origin on its distal anterior margin. The remaining ethmoturbinals are far shorter anteroposteriorly, curving in a superomedial direction and lying in a tightly packed and curved array, following the shape of the cribriform plate.

The endoturbinals and ectoturbinals do not appear completely differentiated, a potential consequence of this individual's young age at death. However, their caudal tips do abut the cribriform plate as in *Alces* (Fig. 23). The cribriform plate of *Dama* is curvilinear in sagittal view with its inferior half oriented anteriorly and its superior half tilting posteriorly. The concavity created by this curve is occupied by a blunt projection of the rhinencephalon. The cribriform plate of *Alces*, in contrast, is less

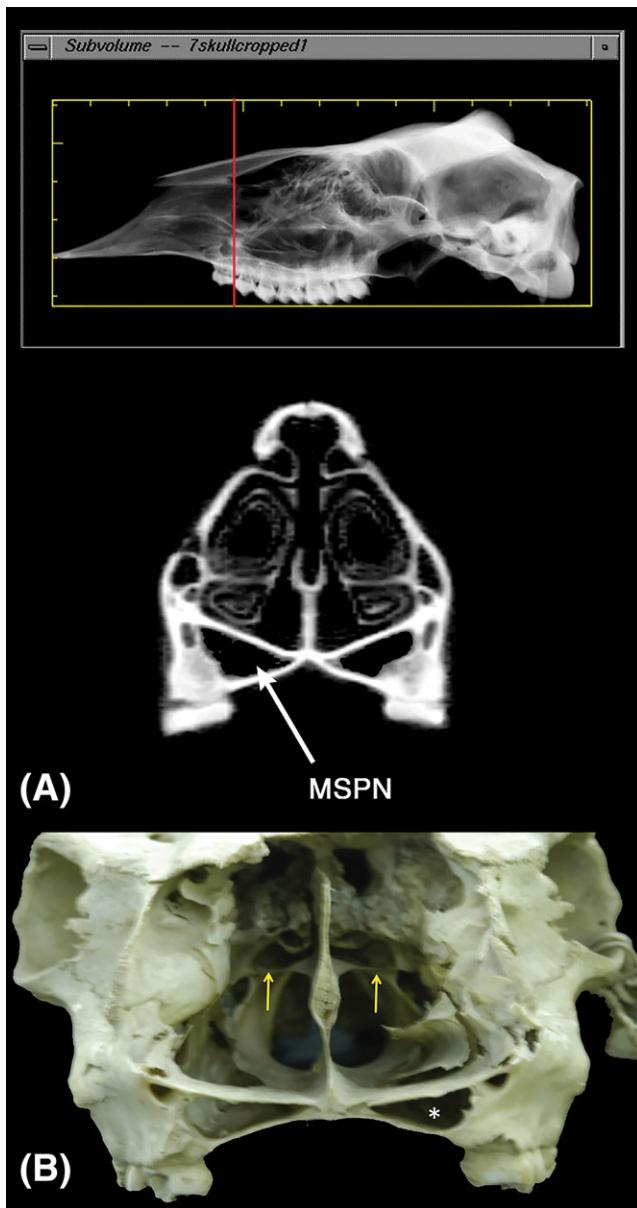


Fig. 18. **A.** A coronal CT of *Odocoileus virginianus* cranium sectioned through the distal border of PM² showing the medial invasion of the maxillary sinus into the hard palate extending to the midline (MSPN, maxillary sinus palatal pneumatization) with reference window shown above; **B.** Dry deer cranium with broken nasal region exposing the pneumatized hard palate (white asterisk) with clearly defined transverse lamina enclosing the olfactory recess (yellow arrows).

curved (i.e., straight) and tilted toward a vertical orientation.

Cattle (*Bos taurus*)

The external nasal anatomy of adult and subadult *Bos* included many of the muscles noted in cervids. Among these was the maxillolabial muscle group that had many thin tendinous attachments both at the alar fold and the inferior narial margin instead of a lesser number of

robust tendons as among cervids. *Bos* lacked the clear autapomorphies of *Alces* and *Dama* as its external narial anatomy appears less complex structurally.

The nasal cavity of *Bos* is divided by a well-developed transverse lamina in the subadult and adult but with a highly pneumatized hard palate observed only in the latter (Figs. 24 and 25). The palatal pneumatization represents an invasion by the epithelial diverticula of the maxillary sinus that results in the maxilla and hard palate remaining in communication in subadult and adult specimens (Fig. 25). *Bos* also exhibits partial and complete septated frontal sinus morphology (Fig. 25). The ethmoturbinal systems of both the adult and subadult specimens appear to have well differentiated endoturbinals and ectoturbinals. As in *Alces*, there is a long, pneumatized nasoturbinal that overhangs a large, club-like first ethmoturbinal (Fig. 25). The caudal half of the nasoturbinal also has its own site of lamellar attachment posteriorly while its anterior half projects rostrally. All other ethmoturbinals appear attached to each of their basal lamellae along their lateral margins although the first two ethmoturbinals appear to come together at their posterior ends when abutting with the cribriform plate (Fig. 25). In this morphological configuration, the ethmoturbinals are in close contact with a straight and vertically oriented cribriform plate (Fig. 25).

Black Bear (*Ursus americanus*)

The specimen exhibited three paranasal sinuses: (1) maxillary; (2) frontal; and (3) sphenoid. The maxilloturbinals are well developed and are anteroventrally positioned at the nasal cavity, with the maxillary sinus positioned topographically caudal to them. The ethmoturbinals were present and exhibited pronounced, elaborate branching. In parasagittal view, the specimen exhibited a distinct transverse lamina that enclosed the olfactory ethmoturbinals above (Fig. 26). The transverse lamina was confluent with the nasal septum superiorly.

Multiplanar CT imaging from anterior to posterior direction viewed in coronal, sagittal, and axial perspective showed the following characteristics of the skull of *Ursus americanus*. The maxilloturbinal and ethmoturbinal morphology appear compartmentalized being housed anteriorly and posteriorly within the nasal cavity, respectively, when viewed transversely (Fig. 27). CT visualization showed evidence of a maxillary sinus with pneumatization extending up to the frontal bone. A parasagittal slice through the midportion of the ethmoid bone showed the transverse lamina dividing the nasal cavity into olfactory and respiratory regions (see Fig. 26). The ethmoturbinals were assembled superior to this plate and were elaborately scrolled, with numerous branches projecting into the frontal sinus and sphenoid sinus regions (see Fig. 28). Posteriorly, in coronal perspective, the extensive branching of the ethmoturbinals coalesced into as a mass of bony spicules surrounding the cribriform plate.

Maxillary sinus. The floor of the maxillary sinus approached the nasal cavity floor but did not proceed below it. The lateral walls of the sinuses were vertically orientated. The sinus was confined to the maxillary bone with no evidence of palatal or zygoma pneumatization.

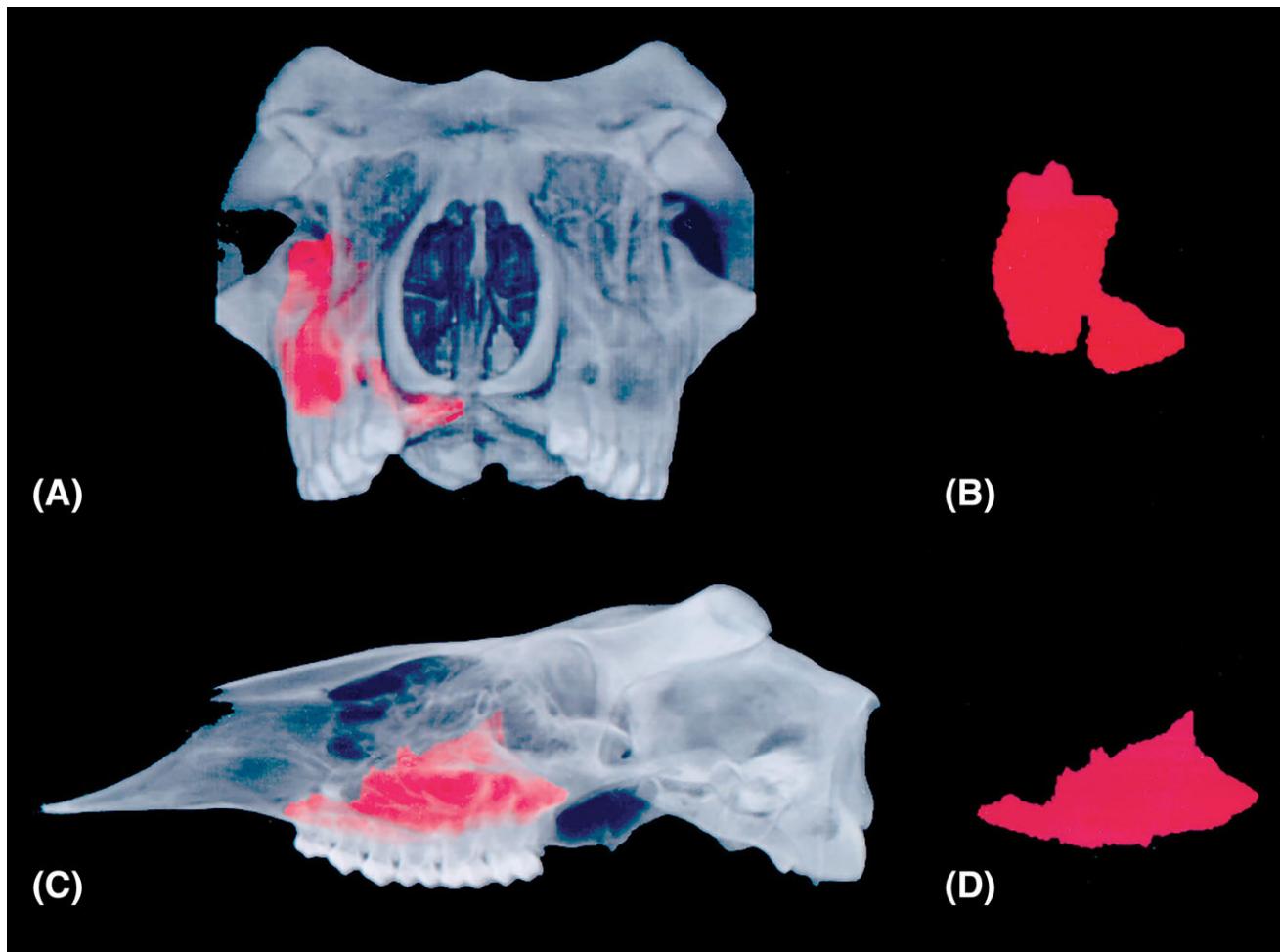


Fig. 19. A–D. A frontal and lateral view composite of the white-tailed deer showing the maxillary sinus both *in situ* and extracted. Note the floor of the sinus spans immediately superior to the roots of the maxillary tooth row and extends into the maxillary tuberosity region in lateral view.

Frontal sinus. Frontal sinus pneumatization was quite extensive with the pockets of air extending into several bones, including temporal, parietal and occipital bones. A series of complete and incomplete bony septal divisions were seen sagittally, with ethmoturbinals encroaching into the sinus in coronal view (see Fig. 28).

Sphenoid sinus. A large sphenoid sinus was present in the black bear. In a midsagittal view, the sinus was expansive and appeared to be compartmentalized by coronal septal barriers. However, in a parasagittal perspective the septal divisions appeared to be incomplete falsely giving the impression of multiple sphenoid sinuses. The intrusive nature of the ethmoturbinals was observed at the anterior aspect of the sphenoid sinus inferiorly and frontal sinus territory superiorly.

DISCUSSION

The nasal morphology of moose may be best described as a combination of derived and ancestral traits relative to other cervids. Their large proboscides are a derived trait, related to extreme nasal bone reduction and posteriorly receding piriform aperture boundaries. These are

expressed alongside relatively elongated premaxillae (a derived trait), related to a lack of a labial phrenulum to provide greater mobility of the upper lip during browsing (see Fig. 29). Despite possession of the ancestral complex of facial muscles with homologous points of insertion, the extremely large dimensions of the cartilaginous proboscis has re-oriented some of these tendons into a novel orientation. As discussed by Clifford and Witmer (2004), the tendon of the levator labii superioris muscle (the dorsal-most of the maxillolabial muscle group) has been re-oriented vertically. Our dissection (Fig. 7) revealed that the pulley-like morphology of this muscle was mostly the result of extreme enlargement (relative to other cervids and bovids) of the fibro-fatty pad that reinforced the alar fold of the external nose. Thus, when manually pulling the tendon toward its muscle belly to mimic a normal contraction, a partial closure of the anterior nares is observable. This same motion produced a narial dilation when performed on the fallow deer. When contraction of the levator labii superioris in moose is combined with actions of other muscles of the maxillolabial group such as the caninus (that functions to partially retract the alar fold), and superior incisorus (moving the upper lip), a mechanism for narial closure is exhibited.

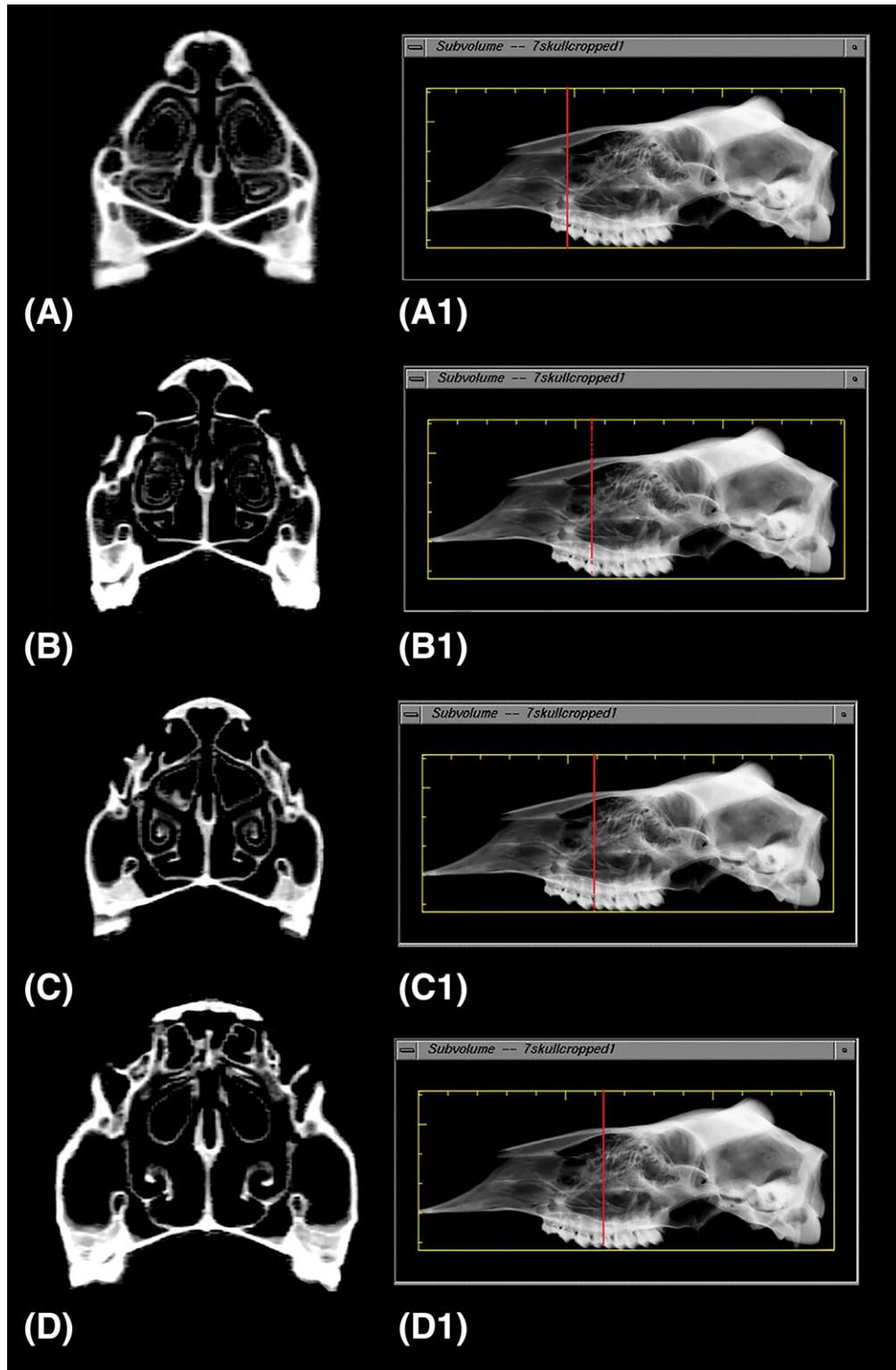


Fig. 20. The upper scroll portion of the maxilloturbinal in an *Odocoileus virginianus* cranium begins elaborate inrolling and is larger than its lower scroll partner (A); the reference coronal slice is shown in (A1). Note the palatal pneumatization in (A) and the patent communication with the maxillary sinus in (B) (see reference plane in B1). A coronal cut at the mesial border of the first molar dentition shows the lower scroll with a slight inroll of its extremity while the upper scroll inroll shows a full turn revolution (C, C1). A coronal cut at the midportion of the first molar shows the lower scroll almost absent while the upper scroll exhibits a half turn revolution. This continues posteriorly (D) to the coronal plane of the first maxillary molar (D1).

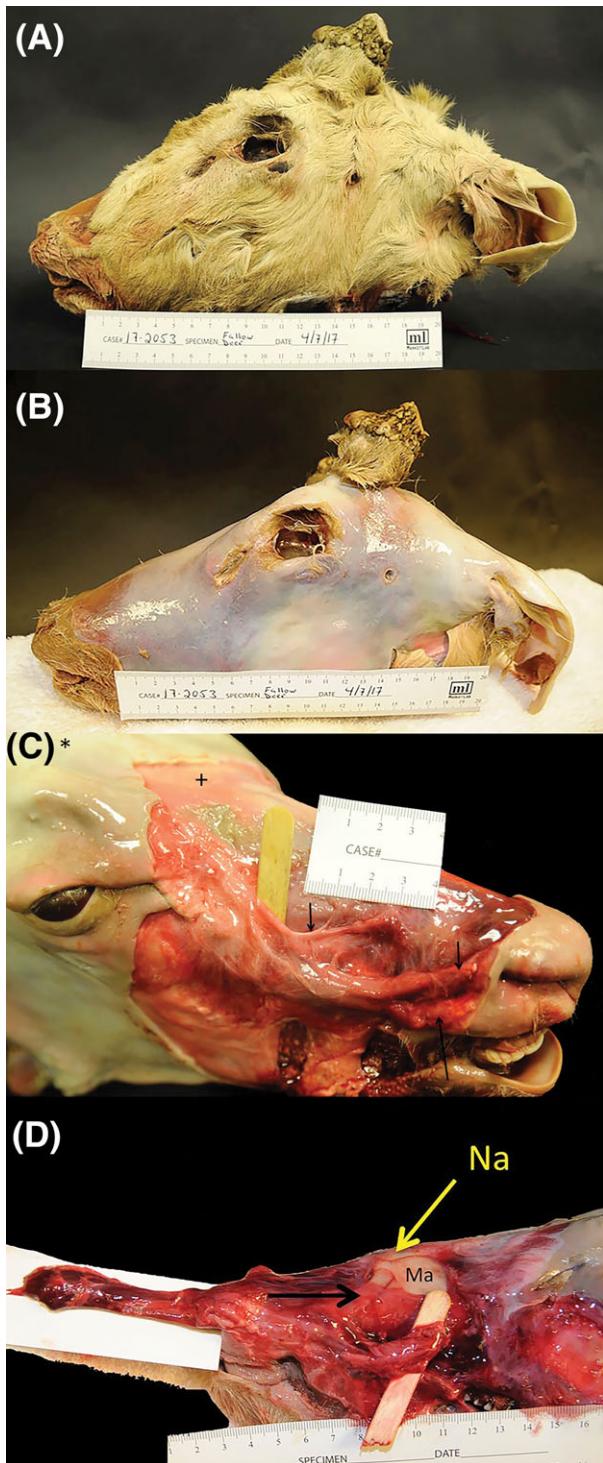


Fig. 21. Left lateral views of superficial dissections of *Dama dama* (**A** and **B**). A large maxillolabial muscle group (highlighted by tongue depressor) was visible with tendons (black arrows) extending to the alar fold (**C**, right side shown). (asterisk = dermis seen in **C**; "+" = tissue similar to the SMAS of humans). **D** (Left side shown) Note that the premaxilla (black arrow) and nasal bone (Na) are prevented from contacting each other by a slip of the maxillary bone (Ma), a departure from the typical cervid condition (see Results). This is made visible by anterior reflection of the levator labii superioris (onto a white sheet of paper).

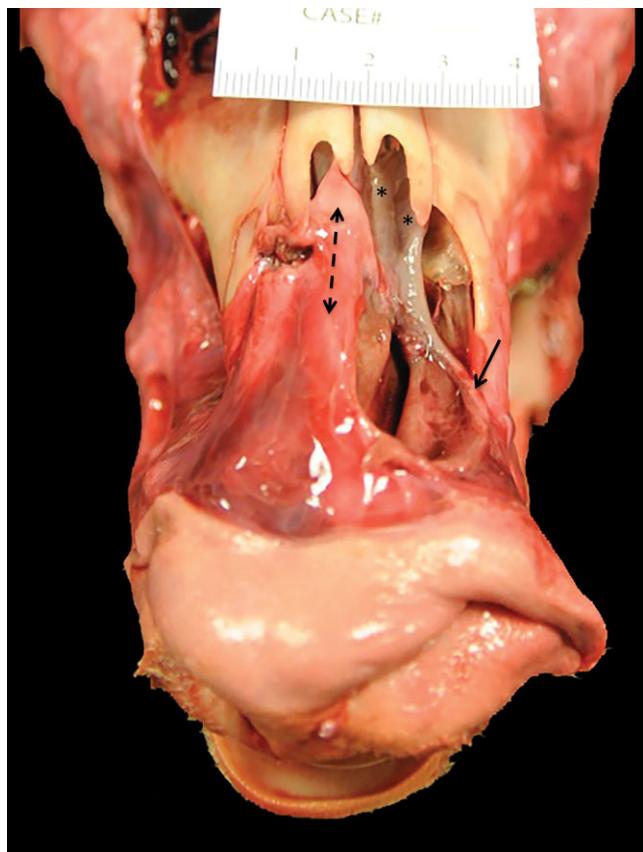


Fig. 22. A fan-shaped muscle takes origin from the ventral surface of the nasal bones and medial side of the premaxillary nasal processes (left, dashed double arrow) in *Dama dama*. They appear to function in the retraction of the alar fold externally. When dissected away, several deeper muscle tendons are revealed (solid arrow). These take origin from the distal tips of the maxilloturbinal and first and second ethmoturbinals (proximal attachments marked by asterisks). Such an anatomical configuration has been rarely described.

This likely assists in closing off the nasal cavity from influx of water when foraging for submerged aquatic vegetation. The re-orientation of the nasal apparatus has had the effect of modifying the function of these muscles permitting for the first time active constriction of the anterior naris.

The morphological configuration of the cartilages and muscle surrounding the moose nares may indeed be adaptations for diving behaviors as they retain the ability to close off the nasal cavity. Multiple ethological studies confirm that they engage seasonally in diving behaviors that are unknown among most other artiodactyls. As evidenced by other cervids, this family is extremely variable in nasal morphology with both *Alces* and *Dama* exhibiting unique autapomorphies, particularly in the anterior portion of the nasal cavity. *Alces alces* has a greatly expanded maxilloturbinal, which protrudes beyond the piriform aperture lateral rim, a derived trait not present in ancestral *Cervalces*. Its double-scrolled morphology may allow for efficient warming and humidifying of cold air as much of the skeleton of the anterior nasal cavity recedes posteriorly, necessitating support of the distal rostrum by large cartilages. The distinctive nasal

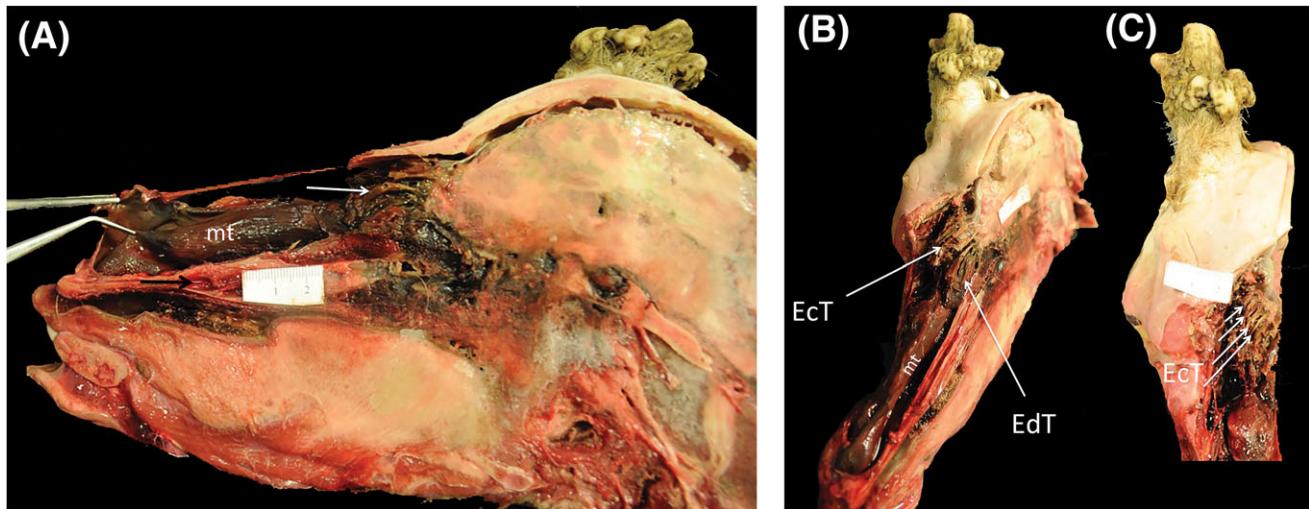


Fig. 23. **A.** The maxilloturbinal (mt) of *Dama dama* exhibits a long, narrow structure that dominates the entrance to the nasal cavity. Black arrow already reveals a pneumatized hard palate with white arrow pointing to an ethmoturbinal. **B, C.** Oblique dorso-rostro-medial views of *Dama dama*. This specimen exhibited a full complement of ectoturbinals (white arrows) and endoturbinals (EdT) to produce a labyrinthine ethmoturbinal morphology (see description on osseous nomenclature in Methods). Note the ectoturbinals are topographically positioned more laterally than the endoturbinals within the nasal cavity following Paulli (1900a).

morphology of moose appears to have been influenced by several factors including the evolutionary plasticity of the bones surrounding the piriform aperture (as evidenced by the diversity among living subspecies of *Alces alces*), the evolution of upper lip prehensility for browsing, and the

need to balance the opposing demands of terrestrial olfaction and respiration (warming and humidifying air) in arctic and subarctic climates while managing the functional stresses of seasonal diving behaviors. Once the evolutionary trend of shortened nasal bones and forward

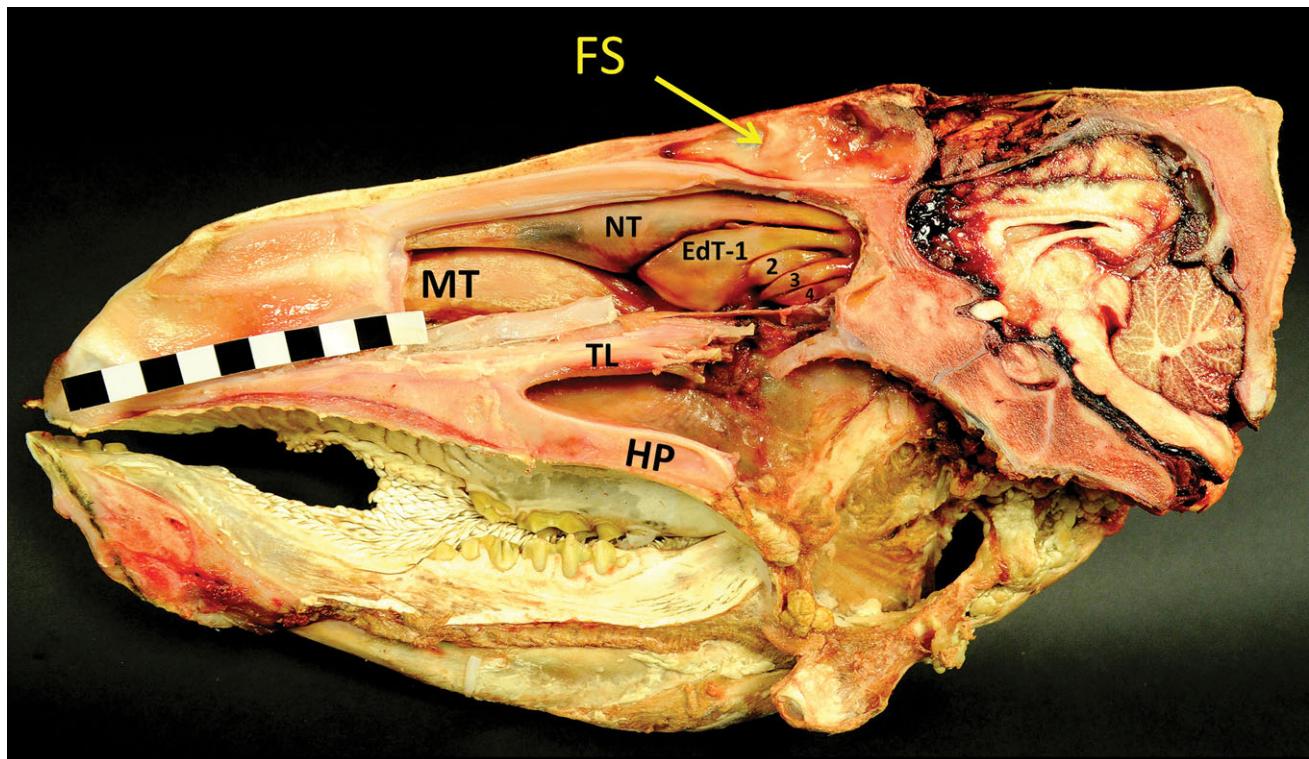


Fig. 24. *Bos taurus* (subadult specimen) exhibited a well-developed system of ethmoturbinals with the first being extremely large and club-like. A large nasoturbinal is also visible in this specimen. Note the enlarged frontal sinus. Note: FS, frontal sinus; MT, maxilloturbinal; NT, nasoturbinal; EdT-1-4, endoturbinals 1-4; TL, transverse lamina; HP, hard palate.

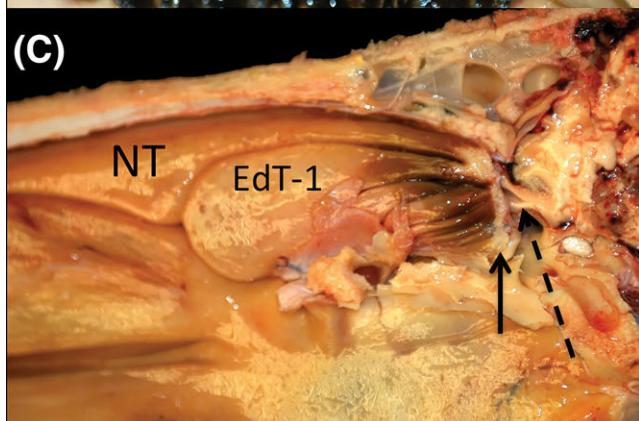
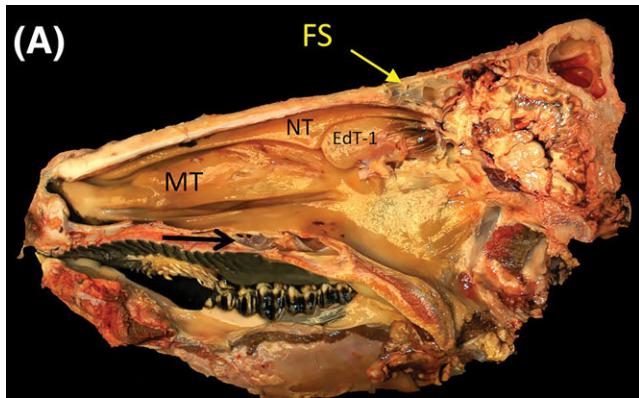


Fig. 25. **A.** The maxilloturbinal dominates the entrance and much of the nasal cavity matching the approximate length of the hard palate in this adult *Bos taurus*. **B.** Palatal pneumatization was also observed in this specimen and is in communication with the maxillary sinus (marked by asterisk). **C.** Cribriform plate (black arrow) serves as the interface between the posterior tips of ethmoturbinals and olfactory bulb via olfactory filaments (dashed arrow).

migration of the premaxillae began, the maxilloturbinals appeared not to have grown anteriorly but, instead, the piriform aperture retreated posteriorly to leave them bound only by the cartilaginous proboscis at their anterior-most extremities. It is thus in addition to these derived features that moose also exhibit a primitively macrosmatic pattern of posterior nasal morphology, characterized by a large surface area within the olfactory

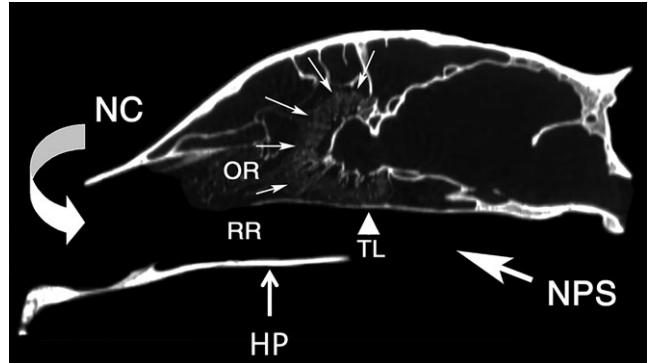


Fig. 26. Parasagittal view of *Ursus americanus* through the mid-portion of the ethmoid bone, shows the transverse lamina (TL), which divides the nasal cavity into an olfactory (OR) and respiratory region (RR); NC, nasal cavity; NPS, nasopharyngeal space. The series of radiating white arrows indicate the assembly of ethmoturbinals surrounding the cribriform plate, which is not straight but curvilinear in its conformation thereby maximizing the available surface area for communication with the ethmoturbinals.

recess for cover by olfactory epithelium of numerous, highly complex ethmoturbinals. These are set in contradistinction to microsmatic groups such as anthropoid primates that lack such features (although skeletal morphology should not be conflated directly with olfactory acuity; see Smith *et al.*, 2004). Moose exhibit a well expressed lamina transversalis of the ethmoid bone, full complement of endo- and ecto-turbinals arrayed in posteroinferior orientation within the olfactory recess, and close contact of these elements with a long, straight cribriform

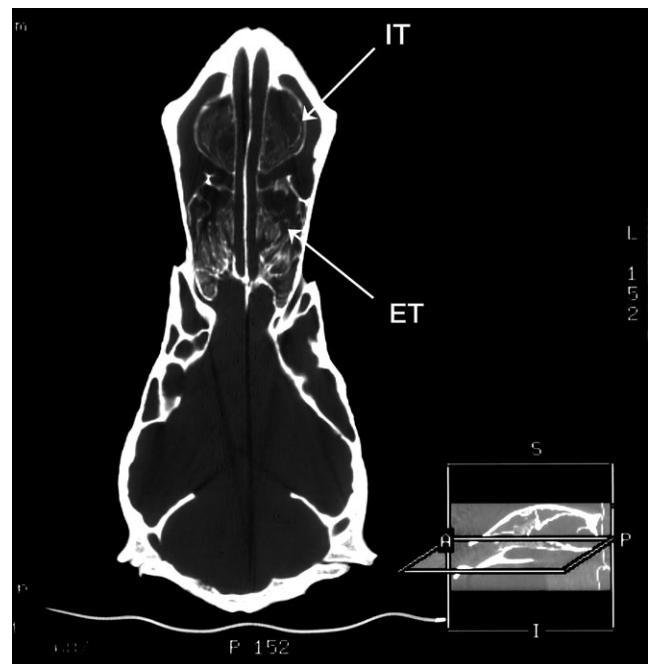


Fig. 27. An axial view of *Ursus americanus* above the level of the transverse lamina (see reference window) showing independent nature of maxilloturbinals (IT) and ethmoturbinals (ET).

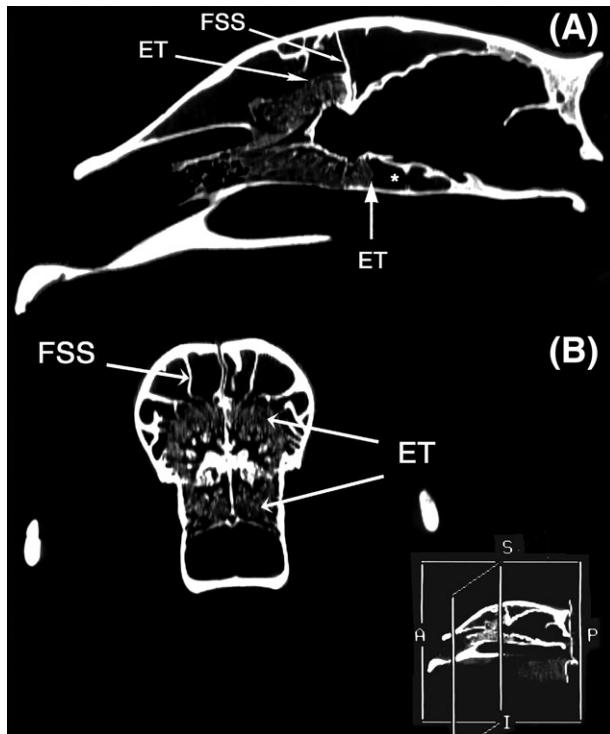
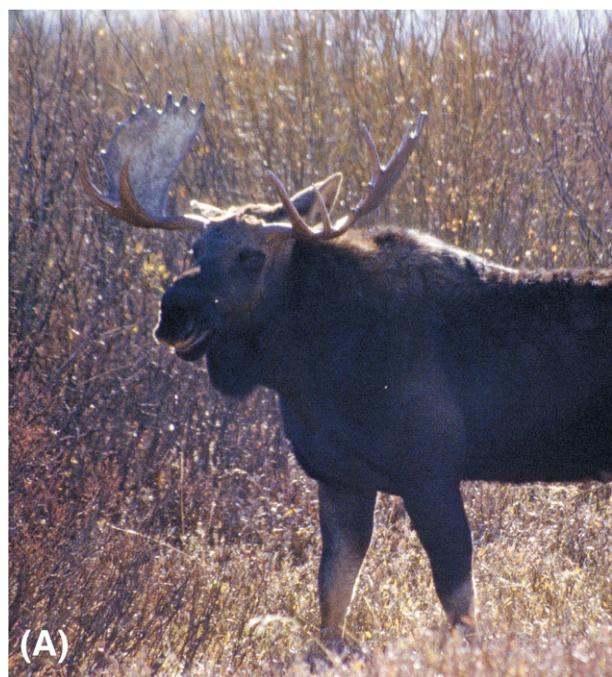


Fig. 28. **A.** A parasagittal view of *Ursus americanus* demonstrating no coronal septal division within the sphenoid sinus (white asterisk) but complete and incomplete septa in frontal sinuses (FSS). Note the intrusive nature of the ethmoturbinals (ET) invading both **(A)** sphenoid sinuses and **(B)** frontal sinuses.

plate. Similar morphology was found among all of the cervids (*Alces*, *Dama*, *Odocoileus*) and the one bovid (*Bos*), each exhibiting straight cribiform plates with some variation in lateral view.

The crania of raoellids such as *Indohyus* lack the bony traits associated with possession of a large, fleshy proboscis as among *Alces* that exhibits foreshortened nasal bones and enlargement of the piriform aperture. The nares of *Indohyus* and early cetaceans such as *Pakicetidae* appear located primitively (relative to later cetaceans) at the distal end of the rostrum. The former also exhibited a tapering snout (on the non-broken portions of specimen RR 208; see Thewissen *et al.*, 2007) that likely lacked swelling of the premaxillae as in *Hippopotamus* (Dieulafoy, 1906), which supports transversely oriented nares for respiration just below above the surface of the water while remaining mostly submerged. Thus, *Indohyus* may not have engaged in long bouts of diving or sub-surface behavior as they likely lacked nasal specializations such as those of the moose or hippopotamus. Only among Protocetids and other later cetaceans is there evidence of the nares migrating posteriorly and superiorly.

It can be argued that the moose is the only non-cetacean artiodactyl to forage actively in aquatic habitats. Both *Hippopotamus* and raoellids such as *Indohyus* (a probable sister taxon to ancestral Cetacea; Thewissen *et al.*, 2007) may share the behavioral similarities of foraging on land and fleeing to aquatic environments when threatened by predators or to engage in social behaviors. *Indohyus* has been characterized by high levels of carbon isotope C¹³ and the presence of trigonid and talonid crushing basins on their molars as likely terrestrial foragers and that it was only later among early true



(A)



(B)

Fig. 29. A bull moose engaged in what is known as lip-curl behavior, or by its German name *flehman*, allowing males to expose the vomeronasal organ in the palate to assess sexual receptiveness of females. **A.** The bull moose is able to pull up its highly mobile upper lip due to the modified dorsal lateral nasal cartilage which acts as pulley for the levator labii superior muscle (Clifford and Witmer, 2004). **B.** The male will then raise its head with anterior naris rising above eyelevel and remaining still with its mouth open and breathing rapidly to maximize exposure of pheromones to vomeronasal organ (Photographs by author KHA).

cetaceans such as *Pakicetus* that an adaptive behavioral shift to primarily aquatic foraging was made (Thewissen *et al.*, 2007, 2011; Fahlke *et al.*, 2013). Thewissen *et al.* (2007) also suggested that *Indohyus* may have consumed fresh water invertebrates as part of an omnivorous diet. This scenario would render *Indohyus* behaviorally similar to moose as both engaged in mainly terrestrial foraging supplemented with some aquatic resources from fresh water lakes and rivers. However, the generalized cranial and nasal morphology of *Indohyus* would suggest its aquatic behaviors (and perhaps those of the common ancestor of cetaceans) did not include prolonged bouts of diving as they lack osteological indicators for narial adaptations such as those of the moose and hippopotamus.

Among raoellids, modern hippopotamids, and nearly all secondarily aquatic tetrapods, osteosclerosis or a thickening of the cortical bone with compression of the medullary cavity allows for neutral buoyancy by using the skeleton as a ballast (see Gray *et al.*, 2007). This adaptation assists living hippopotamids in bottom-walking behaviors and is mostly absent among moose (Amson and Kolb, 2016), likely as a function of the seasonality of their aquatic behaviors. Given that moose engage in aquatic foraging for only four months out of the year (Peterson, 1955; MacCracken *et al.*, 1993), there may not be a strong selective pressure for large scale aquatic adaptations such as osteosclerosis in its postcranial skeletal structure. However, *Indohyus* (the raoellid for whom there is the most complete record of postcranial morphology) has been reconstructed as engaging in a digitigrade form of locomotion (Thewissen *et al.*, 2007; Cooper *et al.*, 2012), resembling the long limbed morphology of the moose that uses its elongated metapodials for walking on soft, marshy ground (see above). *Indohyus* has also been found in fresh water riparian sediments in the Himalayan foothills with skeletal elements of many individuals washing into a large death assemblage, suggesting a similarity in habitat preference to moose. Thus, similarities and differences with raoellids may render the moose of use in reconstructing behavioral and ecological factors that may have influenced the evolution of early cetacean ancestors.

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