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Contributions to International Polar Year Science

Igor Krupnik, Michael A. Lang,
and Scott E. Miller
Editors

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Considerations of Anatomy, Morphology, Evolution, and Function for Narwhal Dentition

Martin T. Nweeia, Frederick C. Eichmiller, Cornelius Nutarak, Naomi Eidelman, Anthony A. Giuseppetti, Janet Quinn, James G. Mead, Kaviqanguak K'issuk, Peter V. Hauschka, Ethan M. Tyler, Charles Potter, Jack R. Orr, Rasmus Avike, Pavia Nielsen, and David Angnatsiak

ABSTRACT. Interdisciplinary studies of narwhal cranial and tooth anatomy are combined with Inuit traditional knowledge to render a more complete description of tooth-related structures and to propose a new hypothesis for tusk function in the adult male. Gross anatomy findings from computed tomography (CT) and magnetic resonance (MR) imaging and dissections of an adult male and female and one fetus, four to six months in development, were documented. Computed tomography scans rendered images of the tusks and vestigial teeth and their shared sources of innervation at the base of the tusks. Paired and asymmetrical tusks and vestigial teeth were observed in all three samples, and their relative positions reversed during development. Vestigial teeth shifted anteriorly during growth, and the developing tusks moved posteriorly as they developed. Examination of tusk microanatomy revealed the presence of a dentinal tubule network with lumena approximately 2 micrometers in diameter and 10–20 micrometers apart over the pulpal and erupted tusk surfaces. Orifices were present on the cementum surface indicating direct communication and sensory capability from the environment to the inner pulpal wall. Flexural strength of 95 MPa at mid tusk and 165 MPa at the base indicated resistance to high flexural stresses. Inuit knowledge describes a tusk with remarkable and combined strength and flexibility. Elder observations of anatomy are described by variable phenotypes and classified by skin coloration, sex, and tusk expression. Behavioral observations of males leading seasonal migration groups, nonaggressive tusk encounters, and frequent sightings of smaller groups separated by sex add to the discussion of tusk function.

INTRODUCTION

The narwhal is unique among toothed marine mammals and exhibits unusual features, which are described in the literature (Figure 1). A single 2–3 m tusk is characteristic of adult males (Tomlin, 1967). Tusks are horizontally imbedded in

*Martin T. Nweeia, Harvard University, School of Dental Medicine, Boston, MA, USA. Cornelius Nutarak and David Angnatsiak, Community of Mittimatilik, Nunavut, Canada. Frederick C. Eichmiller, Delta Dental of Wisconsin, Stevens Point, WI, USA. Naomi Eidelman, Anthony A. Giuseppetti, and Janet Quinn, ADAF Paffenbarger Research Center, National Institute of Standards and Technology, Gaithersburg, MD, USA. James G. Mead and Charles Potter, Smithsonian Institution, Division of Mammals, Department of Zoology, Washington, DC, USA. Kaviqanguak K'issuk and Rasmus Avike, Community of Qaanaaq, Greenland. Peter V. Hauschka, Smithsonian Institution, Division of Mammals, Department of Zoology, Washington, DC, USA. Ethan M. Tyler, National Institutes of Health, Clinical Center, Bethesda, MD, USA. Jack R. Orr, Fisheries and Oceans Canada, Arctic Research Division, Winnipeg, MB, Canada. Pavia Nielsen, Community of Uummannaq, Greenland. Corresponding author: M. T. Nweeia (martin_nweeia@hsdm.harvard.edu). *Accepted 19 May 2008.*

the upper jaw and erupt through the left side of the maxillary bone, while the smaller tusk on the right side, usually not longer than 30 cm, remains embedded in the bone. Narwhal thus exhibit an extreme form of dental asymmetry (Hay and Mansfield, 1989; Harrison and King, 1965). One and a half percent of narwhal exhibit double tusks. Such expression is marked by a right tusk that is slightly shorter than the left (Fraser, 1938) and has the same left-handed helix surface morphology (Clark, 1871; Gervais, 1873; Thompson, 1952). An expected tusk antemere would be equal in size and have a mirror-imaged morphology. Thus, narwhal dental asymmetry is uncharacteristic in size and shape. Only in rare instances, such as the fossil record of *Odobenoceptops peruvianus*, a walrus-like cetacean hypothesized to be in the Delphinoidae family and possibly related to Monodontidae, does such tusk asymmetry exist (de Muizon et al., 1999; de Muizon and Domning, 2002). Thus, narwhal dental asymmetry is uncharacteristic in size and shape.

Erupted tusks pierce through the lip, while the embedded tusk remains in bone. Tusk surface morphology is distinguished by a characteristic left-handed helix (Kingsley and Ramsay, 1988; Brear et al., 1990) rarely seen in other tusked mammals, with the exception of unusual examples like elephants that undergo trauma shortly after birth and develop spiraled tusks (Busch, 1890; Colyer, 1915; Goethe, 1949). Most male narwhal have a tusk, while only 15% of females have a tusk (Roberge and Dunn, 1990). When exhibited, female tusks are shorter and narrower than male tusks (Clark, 1871; Pedersen, 1931). Narwhal tusk expression is thus an unusual example of sexual dimorphism in mammalian teeth. Comparative findings are limited for other beaked whales that exhibit sexually dimorphic teeth (Heyning, 1984; Mead, 1989). Fetal narwhal develop six pairs of maxillary teeth and two pairs of mandibular teeth. Only two pairs of upper teeth form in the adult narwhal, the second pair being vestigial and serving no known function.

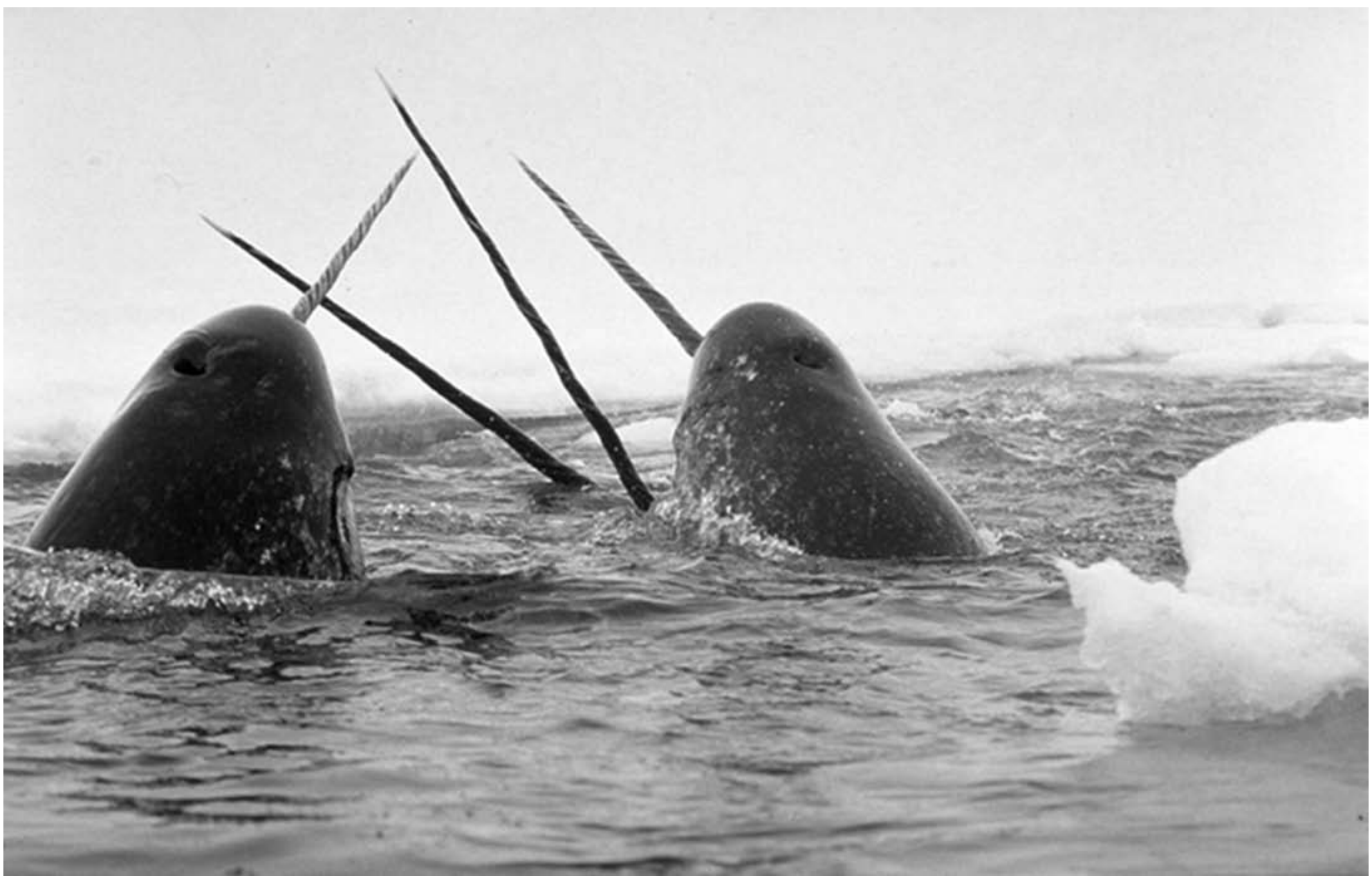


FIGURE 1. Male narwhal whales with their characteristic tusks.

Many theories have been hypothesized to explain the purpose and function of the erupted tusk. Proposed explanations include a weapon of aggression between males (Brown, 1868; Beddard, 1900; Lowe, 1906; Geist et al., 1960), a secondary sexual characteristic to establish social hierarchy among males (Scoresby, 1820; Hartwig,1874; Mansfield et al., 1975; Silverman and Dunbar, 1980), an instrument for breaking ice (Scoresby, 1820; Tomlin, 1967), a spear for hunting (Vibe, 1950; Harrison and King, 1965; Bruemmer, 1993:64; Ellis, 1980), a breathing organ, a thermal regulator, a swimming rudder (Kingsley and Ramsay, 1988), a tool for digging (Freuchen, 1935; Pederson, 1960; Newman, 1971), and an acoustic organ or sound probe (Best, 1981; Reeves and Mitchell, 1981).

Examination of tusk anatomy, histology, and biomechanics combined with traditional knowledge of Inuit elders and hunters has revealed features that support a new sensory hypothesis for tusk function (Nweeia et al., 2005). Narwhal tusk reaction and response to varying salinity gradients introduced during field experiments support this.

GROSS CRANIAL AND TOOTH ANATOMY

Three narwhal head samples, obtained during legal Inuit harvests in 2003 and 2005 were examined by computerized axial tomography and magnetic resonance imaging and then dissected. They included one adult male, one adult female, and one fetal specimen between four and six months in its development. The department of radiology at Johns Hopkins Hospital conducted computed tomography (CT) scans on all three specimens using a Siemens Medical Solutions SOMATOM Sensation Cardiac 64. The scanner generated 0.5-mm-thick slices on each of the three specimens. Original data from these scans has been archived at the Smithsonian Institution. Materialize Mimics 8.0 and Discreet 3D Studio Max 7 was used to create digital 3-D models of narwhal dental anatomy. Magnetic resonance imaging (MRI) was also used to investigate and visualize narwhal dental anatomy. Scientists at the National Institutes of Health MRI Research Facility conducted MRI on the thawed narwhal heads. Data from MRI assisted verification of known cranial anatomy and enabled examination of tooth vasculature. The narwhal heads were dissected at the Osteo-Prep Laboratory at the Smithsonian Institution, and digital photographs were taken to record anatomical landmarks and features of gross anatomy.

The skull of the fetus was 6.23 cm in length and 4.96 cm in width at the most distal points on its frontal bones (Figure 2). Computed tomography data were collected for the entire body of the fetus, though only the head was investigated for the purpose of this research. The total length of the specimen was 31.68 cm. Calcification of major bones of the skull was incomplete in the fetal narwhal specimen. The top of the skull was smoothly rounded, with a large anterior fontanelle, and there were lateral vacuities where ossification was incomplete. Most of the main membrane bones were present at this stage. The nasal bones were small elliptical bones positioned on the summit of the head dorsal to the tectum nasi; they did not make medial contact. The premaxillae were long, narrow shafts of bone medial to maxillae. The maxillae were large bones that were excavated anteroventrally to form two conspicuous pairs of tooth sockets, or alveoli. The maxillae overlapped the frontal bones. Pre- and postorbital processes were well developed. The parietal bones were small lateral bones that made contact with frontal

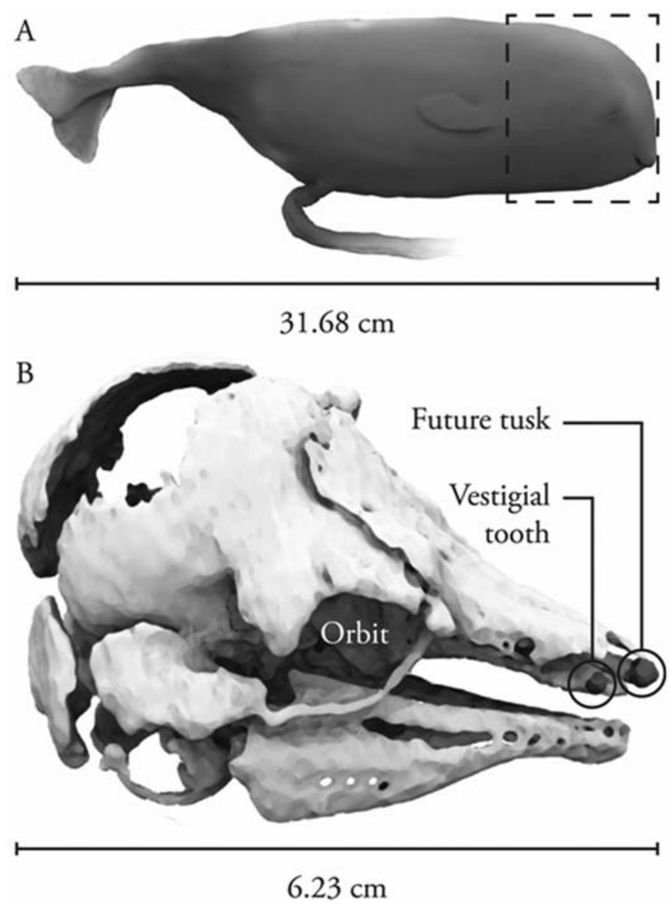


FIGURE 2. A drawing made from CT scans of the skull and teeth of a narwhal fetus showing the positions of the teeth.

bones on their anterior borders. As some of the bone was very thin and articulated with cartilage, digital models of the specimen had some minor artifacts.

Two pairs of teeth were evident in the upper jaw of the fetal narwhal specimen. Future tusks and vestigial teeth were located in their respective sockets in the maxillary bones. The future tusks were located anteromedially to the vestigial pair of teeth. These moved in a posterior direction during development, forming the two large tusks in the adult narwhal (Figure 3). In the male, the left future tusk usually becomes the erupted tusk, and the right tusk typically remains embedded in the maxilla. The future tusks exhibited asymmetry, with the right being 0.44 cm in length and 0.38 cm in width at its widest point and the left being 0.36 cm length and 0.36 cm in width at its widest point.

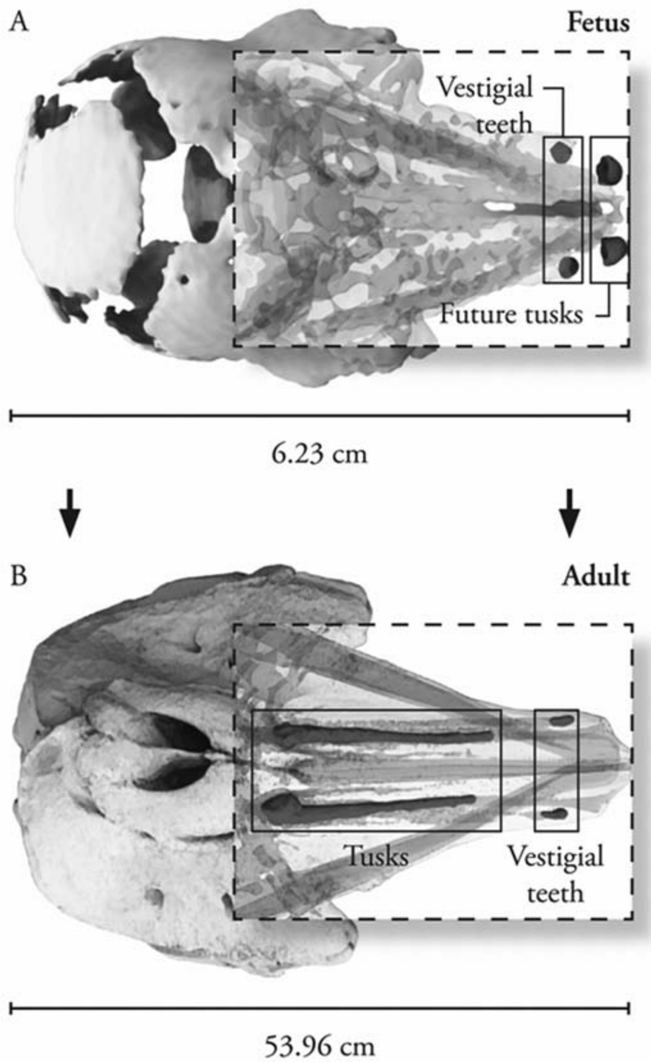


FIGURE 3. A drawing showing the migration and reversal of position of the teeth from fetus to adult that occurs during development.

The vestigial pair of teeth also exhibited asymmetry. The right vestigial tooth was 0.26 cm in length and 0.25 cm in width at its widest point, and the left vestigial tooth was 0.32 cm in length and 0.25 cm in width at its widest point. No teeth were evident in the mandible of this fetus, though dental papillae in the lower jaw have been documented in a report that describes up to six pairs of teeth in the upper jaw and two pairs in the lower jaw (Eales, 1950). The vestigial pair of teeth and their shared blood and nerve supply with the tusks suggest that the narwhal may have exhibited at least two well-developed pairs of teeth at some point in its evolution.

The head of the adult female narwhal was 55.82 cm in length and 47.90 cm in width at its base. The skull of the specimen was 53.96 cm in length and 35.08 cm in width at the level of the bases of the embedded tusks. Like most cetaceans in the family Odontoceti, the skull of the narwhal was asymmetrical, with bony structures skewed toward the left side of the head.

Two pairs of teeth were visible in the upper jaw of the female narwhal specimen (Figures 4 and 5). Both pairs, tusks and vestigial, were found in their respective sockets in the maxillae. The tusks were located posteromedially to the vestigial pair. In the female, the paired tusks typically remain embedded in the maxillae, as was the case for this specimen. The tusks exhibited asymmetry. The right tusk was 17.47 cm in length, 2.39 cm in width at its base, and 0.80 cm in width at its distal end. The left tusk was 18.33 cm in length, 2.06 cm in width at its base, and 1.07 cm in width at its distal end. In rare cases, the left tusk of the female erupts from the maxilla. Sockets for the tusks in the skull begin at the bases of the teeth and terminate in the most distal part of each respective maxillary bone.

The vestigial pair of teeth also exhibited asymmetry. The right vestigial tooth was 2.39 cm in length and 0.98 cm in width at its widest point. The left vestigial tooth was 1.90 cm in length and 0.98 cm in width at its widest point. Sockets for the vestigial teeth began near the bases of the tusks and, like the tusks, terminated in the most distal part of each maxillary bone. The right vestigial tooth slightly protruded from the bone. During dissection and preparation, vestigial teeth may be lost because they are not securely embedded in the bone. There is limited documentation on the presence and morphology of vestigial teeth. Evidence of developed sockets for the vestigial teeth in the narwhal is significant, as it suggests that this species may have exhibited at least two well-developed pairs of teeth

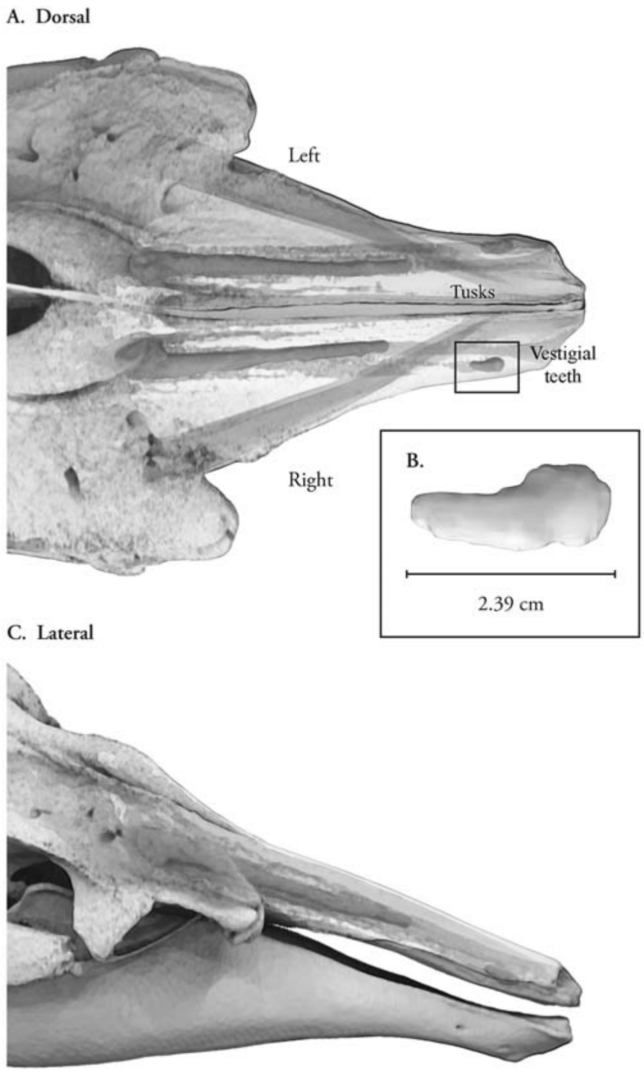


FIGURE 4. A three dimensional reconstruction made from CT data of the adult female dentition of *M. monoceros* showing (A) the dorsal view and (C) lateral view of the unerupted tusks with (B) detail of left vestigial tooth.

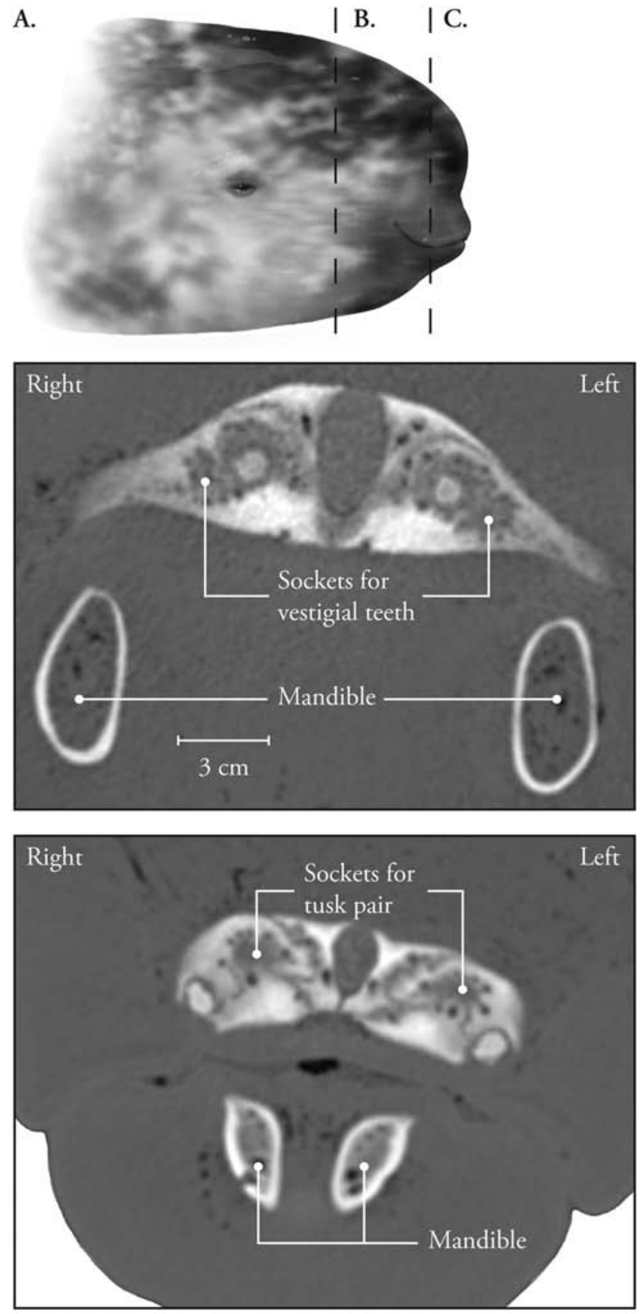


FIGURE 5. (A) Lateral view of the complete female head with coronal cuts (B) and (C). (B) shows the embedded tusks and vestigial teeth and (C) shows vestigial teeth with vascularized tusk sockets.

at some point in its evolution. The two pairs of teeth also effectively reverse positions during development.

On the basis of intracranial dissection of the trigeminal or fifth cranial nerve, the optic nerve branch passed through the superior orbital fissure (Figure 6). The maxillary branch, a sensory nerve, passed through the foramen rotundum, and the mandibular nerve branch, a motor and sensory nerve, passed through the foramen ovale.

The head of the male narwhal was 62.33 cm in length and 49.70 cm in width at its base. The skull of the specimen was 57.24 cm in length and 35.01 cm in width at the level of the base of the left tusk. Like the female narwhal, the skull of the male narwhal was asymmetrical, and bony structures skewed toward the left side of the head.

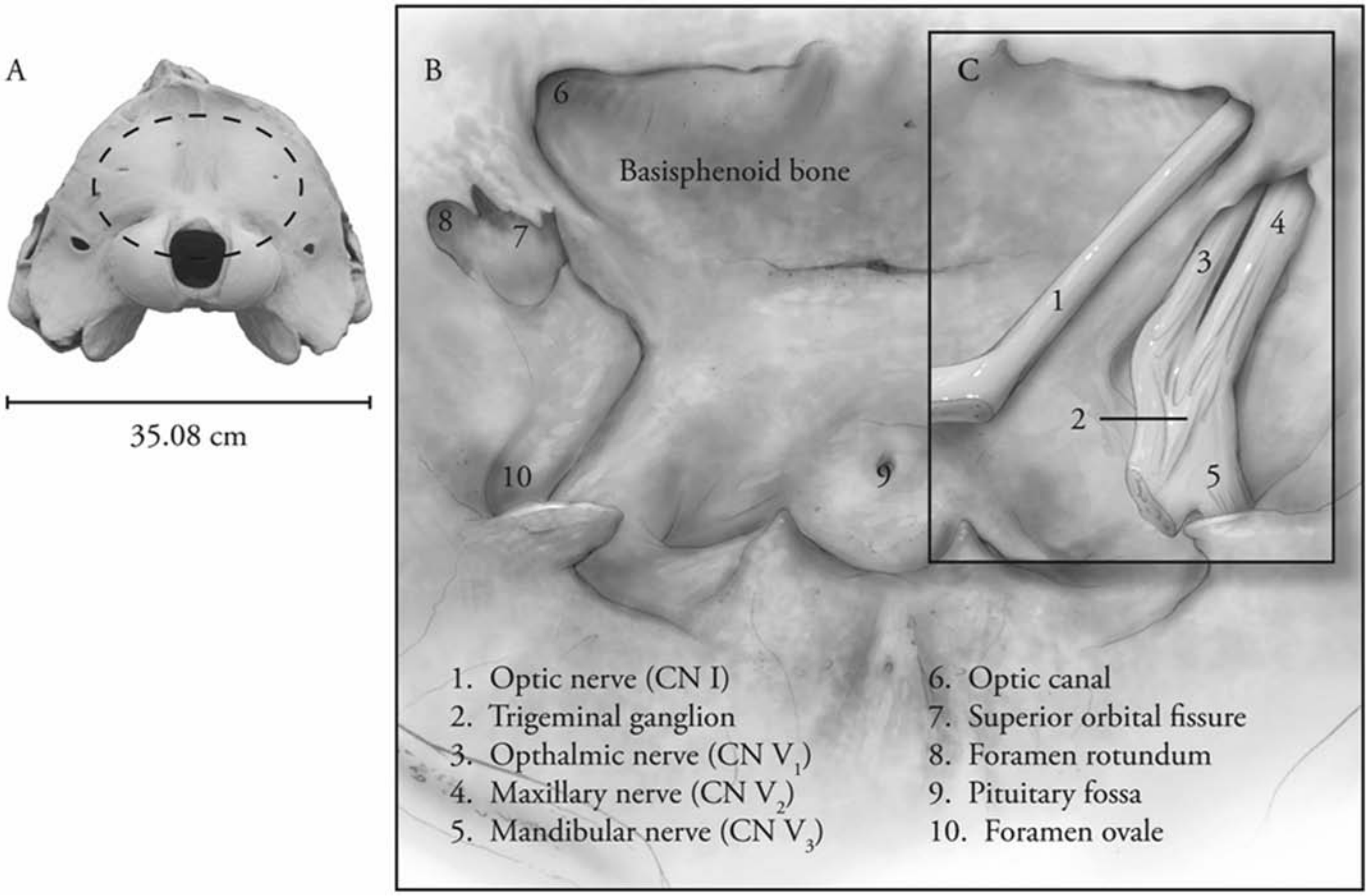


FIGURE 6. (A) Three dimensional reconstruction made from CT data showing the posterior view of the adult female *M. monoceros* skull with the access opening for intracranial dissection, and (B, C) a drawing from photographs taken during dissection showing the nerves and foramen at the cranial base.

Two pairs of teeth were visible in the upper jaw of the male narwhal specimen (Figure 7). The paired tusks were located posteromedially to the vestigial pair of teeth. As is typical with the species, the right tusk remained embedded in the skull, and the left tusk erupted from the maxilla. The right tusk was 20.81 cm in length and 2.51 cm at its base; it was 0.96 cm in width at its distal end. The left tusk was 89.62 cm in length and 4.33 cm in width at its base. It was 4.36 cm in width as it exited the maxilla, and 2.96 cm in width at the termination of CT data at 56.45 cm distal to the maxilla. Bony sockets for the tusks began at the bases of the teeth and terminated in the most distal part of each respective maxillary bone. The vestigial pair of teeth also exhibited asymmetry. Unlike the vestigial teeth of the female specimen, the vestigial teeth of the male narwhal were not embedded in bone; they were suspended in the tissue lateral to the maxillae. The right vestigial tooth was 0.59 cm in length and 0.21 cm in width at its widest point; the left vestigial tooth was 0.67 cm in length and 0.20 cm in width at its widest point.

The Inuit classify narwhal with separate names on the basis of skin color and tusk expression. For example, a male with black coloration is ᕿᓂᐊᒃᑐᖅ, and a male with white coloration is ᖃᑯᐊᒃᑐᖅ. Males with a shorter and wider tusk are called ᑐᒫᐃᑐᓐ, and those with a longer, narrower tusk and black skin coloration are ᑐᒪᓇᓐᓂᖅᓴᐃ. Several Inuit from High Arctic communities in northwestern Greenland are able to recognize and differentiate narwhal populations from Canada and Greenland by their body form and their behavior. They describe Canadian narwhal as being narrower through the length of their bodies and more curious and social, while the Greenlandic narwhal

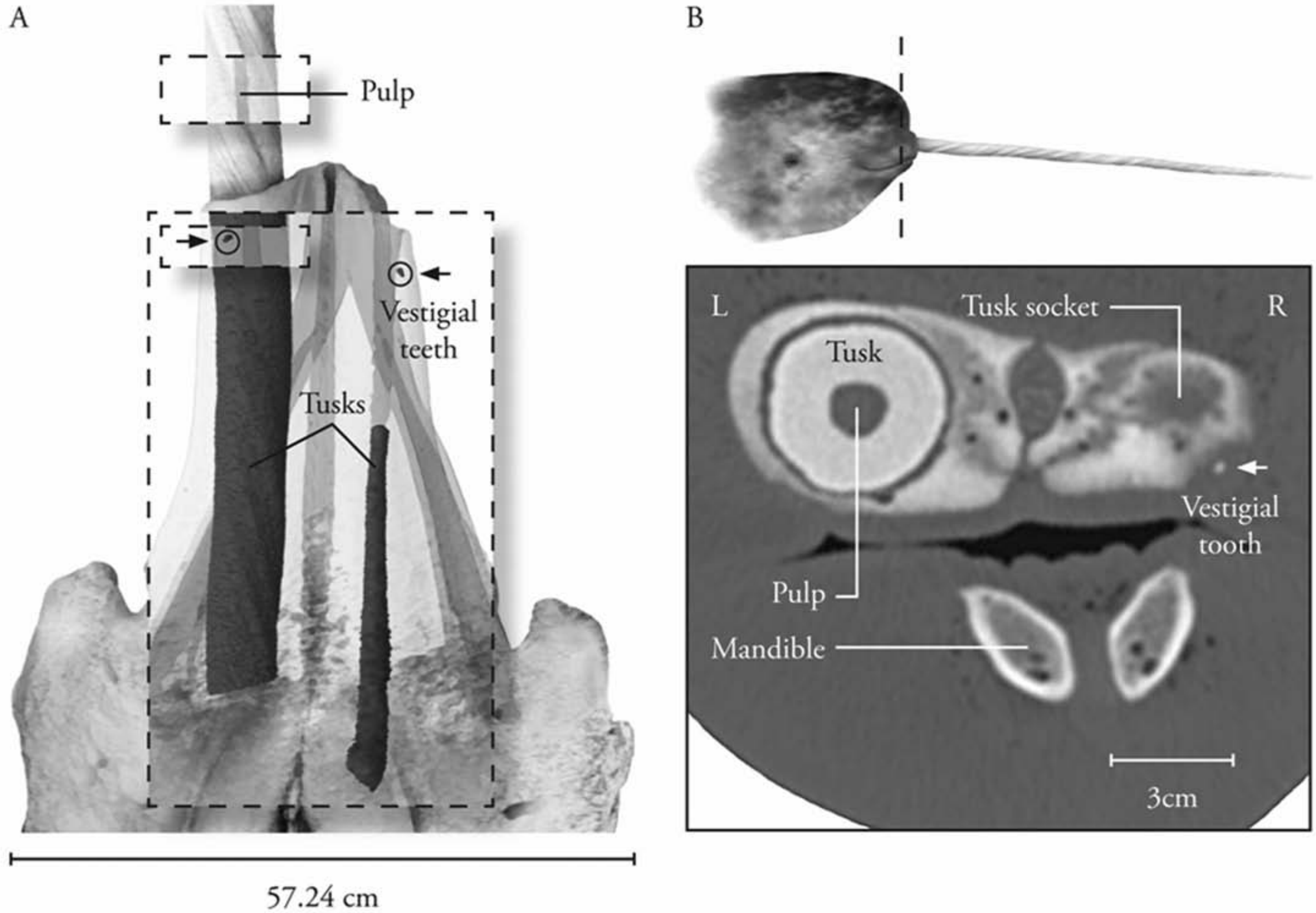


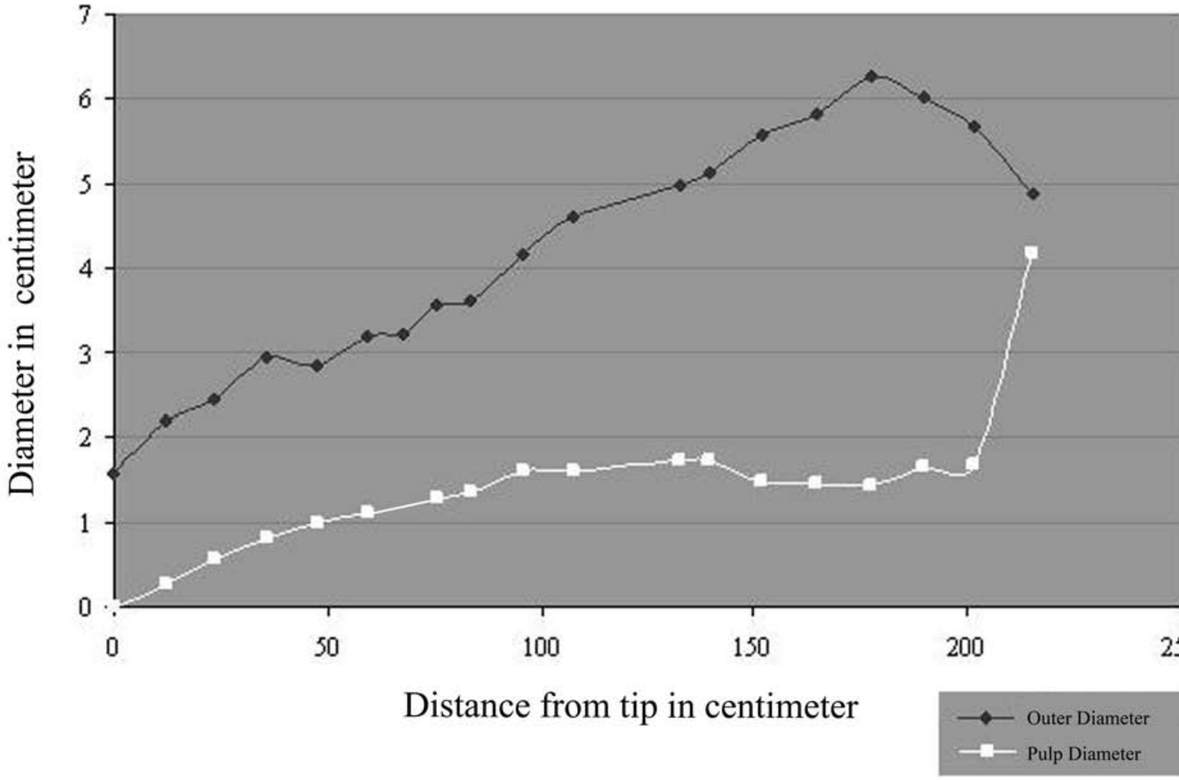
FIGURE 7. (A) Three dimensional reconstruction made from CT data of the adult male dentition of *M. monoceros* showing the dorsal view of the fully developed tusk, the unerupted tusk, and the vestigial teeth, and (B) a lateral view of the complete head illustrating the location of the coronal slice at the level of the right vestigial tooth.

are wider and more bulbous in the anterior two thirds of their bodies and taper at the tail. Their personalities are described as being shyer, and thus they are more elusive.

GROSS TUSK MORPHOLOGY

A 220-cm-long tusk harvested in 2003 at Pond Inlet, Nunavut, Canada, during the Inuit hunting season was sectioned in the field using a reciprocating saw into transverse slices averaging approximately 5 cm in length. Sectioning was started approximately 40 cm inside the skull from the point of tusk eruption and as close to the developing base as possible. The sections were immersed in an aqueous solution of 0.2% sodium azide and frozen in individual serially identified containers. The sections were first evaluated for gross features and dimensions while intact, and selected specimens were further sectioned for more detailed microscopy.

Gross section measurements revealed an outer diameter tapering evenly from approximately 6 cm at the base to 1.6 cm at the tip (Figure 8). The tusk diameter increased evenly to the point of eruption at approximately 175 cm from the tip and then decreased rapidly within the skull. A regression of average outer diameter to distance from the tip for the length of tusk starting at the point of eruption



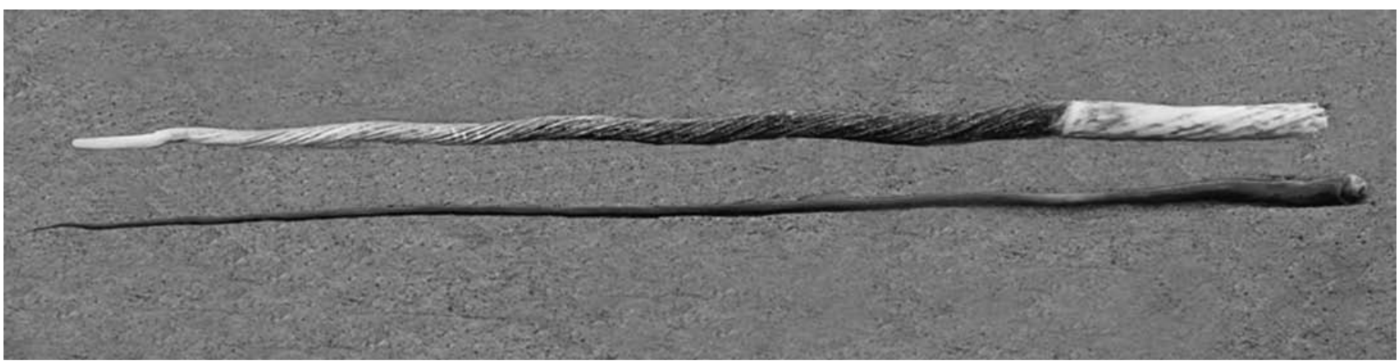


FIGURE 8. (top) A plot of the average cross sectional diameter in cm of the outer surface and pulp chambers of the sectioned tusk as a function of distance from the tip. (bottom) Photograph shows pulpal tissue removed from an intact tusk.

resulted in an equation yielding the average diameter in centimeters as follows: Diameter = 1.75 + 0.025 × (distance from tip), with an R^2 value of 0.989.

The average pulp chamber diameter is shown in lower plot of the graph in Figure 8 and does not mirror the linear trend of the outer diameter. The chamber tapers evenly for the first 100 cm from the tip and then reaches a plateau of approximately 1.75 cm for the next 50 cm and decreases in diameter slightly at 150 to 175 cm from the tip. The pulp diameter increases dramatically over the last 10 cm at base of the tusk. Soft tissue remnants were visible in the pulp chamber of all the frozen sections. A photo of an intact tusk with the entire body of pulp tissue removed is shown in the photograph in Figure 8.

The cross sections of the tusk were often not symmetric, but rather slightly oblong, with a major diameter in many sections being several millimeters larger than the minor diameter. The shape of the pulp chamber generally mimicked the shape and profile of the outer surface. The walls of the inner pulp chamber were very smooth when observed after removing the soft tissue remnants.

The outer surface of the tusk demonstrated a series of major and minor ridges and valleys that progressed down the length of the tusk following a left-hand helix. The major ridges were anywhere from 2 to 10 mm in width and 1 to 2 mm in depth, while the minor ridges were approximately 0.1 mm in width and depth. Brown and green deposits covered the major valleys, while the tops of the highest and broadest ridges were clean and white, accentuating the helical pattern of these features (Figure 9).

The tip section was relatively smooth with an oblique, slightly concave facet approximately 3 cm in length extending backward from the rounded end (Figure 10). A small stained deposit was present in the deepest depression of the facet. Higher magnification did not reveal surface scratches indicating abrasive wear, and a small occluded remnant of the pulp chamber could be seen at the tip. The surface of the facet had what appeared to be many small grooves and smooth indentations on the surface that may be due to the exposure of softer areas in the layered tissue described later in the microanalysis. The lack of abrasion scratches, the concave profile, and these small depressions indicate that the facet is more likely due to a combination of abrasion and erosion from abrasive slurry, such as sand, rather than being caused by rubbing against a hard abrasive surface. Facets were found on many but not all tusks observed during the hunting season, while all exhibit the smoothly polished or clean tip section of approximately 10 cm in length. It was not possible to determine the anatomical orientation of the facet in the sectioned tusk, but field observations describe it as varying in orientation from right, left, and downward, with an upward orientation rarely being reported.

Inuit descriptions of gross tusk morphology are described by variations of form within each sex and dimorphic traits that differentiate tusk expression in females. Most hunters note that the blood and nerve supply in the pulp extends to the tip, and indeed, some hunters are experienced in the extirpation of the pulp to its entire length. They describe a receding pulpal chamber for older narwhal, which is a consistent finding with the increased age of most mammalian teeth. However, the female tusk is quite different in morphology. Female tusks are shorter, narrower, and evenly spiraled and denser, with little or no pulp chamber, even at an early age. Such an observation suggests a difference in functional adaptation as females

FIGURE 9. A photograph showing the helical staining due to surface deposits of algae that remain in the deeper grooves of the tusk.

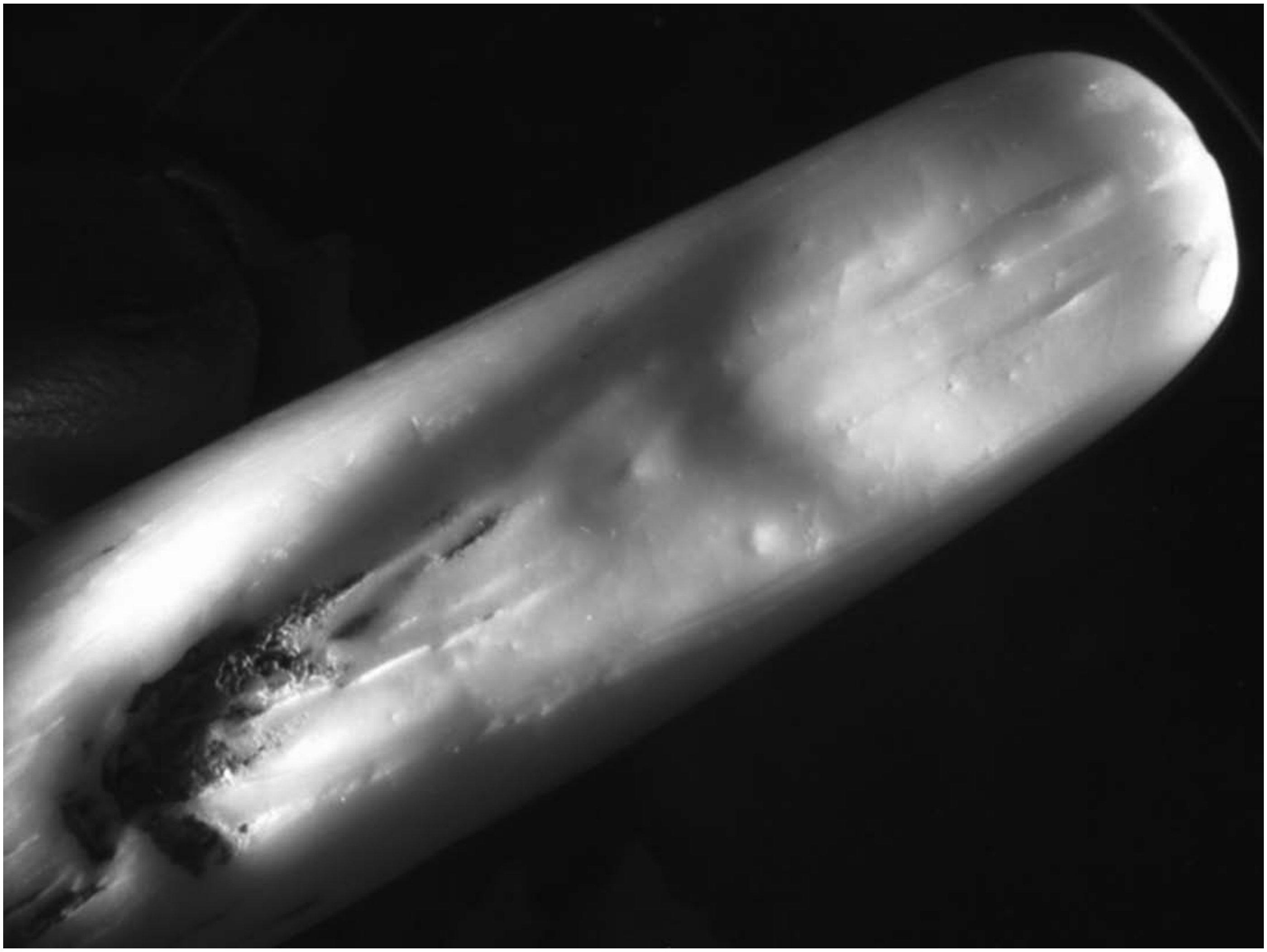


FIGURE 10. A close-up photograph of the flat facet on the tip of the tusk. A translucent remnant of the pulp chamber can be seen at the tip as well as many minor grooves and indentations.

would lack substantial tusk innervation to sense their environment.

TUSK MICROMORPHOLOGY

A mid-length section was chosen for visible and scanning electron microscopy (SEM). A 1-mm-thick slice was cut from the end of a section and polished using a metallographic polishing wheel and a series of abrasives down to 4000 grit size. Care was taken to retain the hydration of the section during processing and observation. The cross-sectional visual observation of this slice showed the tusk to be composed of several distinct layers (Figure 11). An outermost layer described as cementum was more translucent and approximately 1.5 to 2 mm thick. There was a distinct boarder between this outermost layer and the underlying dentin. The bulk of the section was made up of a relatively homogenous dentin that had numerous distinct rings, appearing much like the growth rings in a tree. The outermost rings were slightly whiter in color while the innermost ring adjacent to the pulp chamber appeared slightly darker opaque than the surrounding dentin rings. The dark lines radiating outward from the pulp chamber to the surface were associated with microtubules observable under SEM and are described later.

An additional pie-shaped section was cut from this polished slice to include both the pulpal and outer sur-

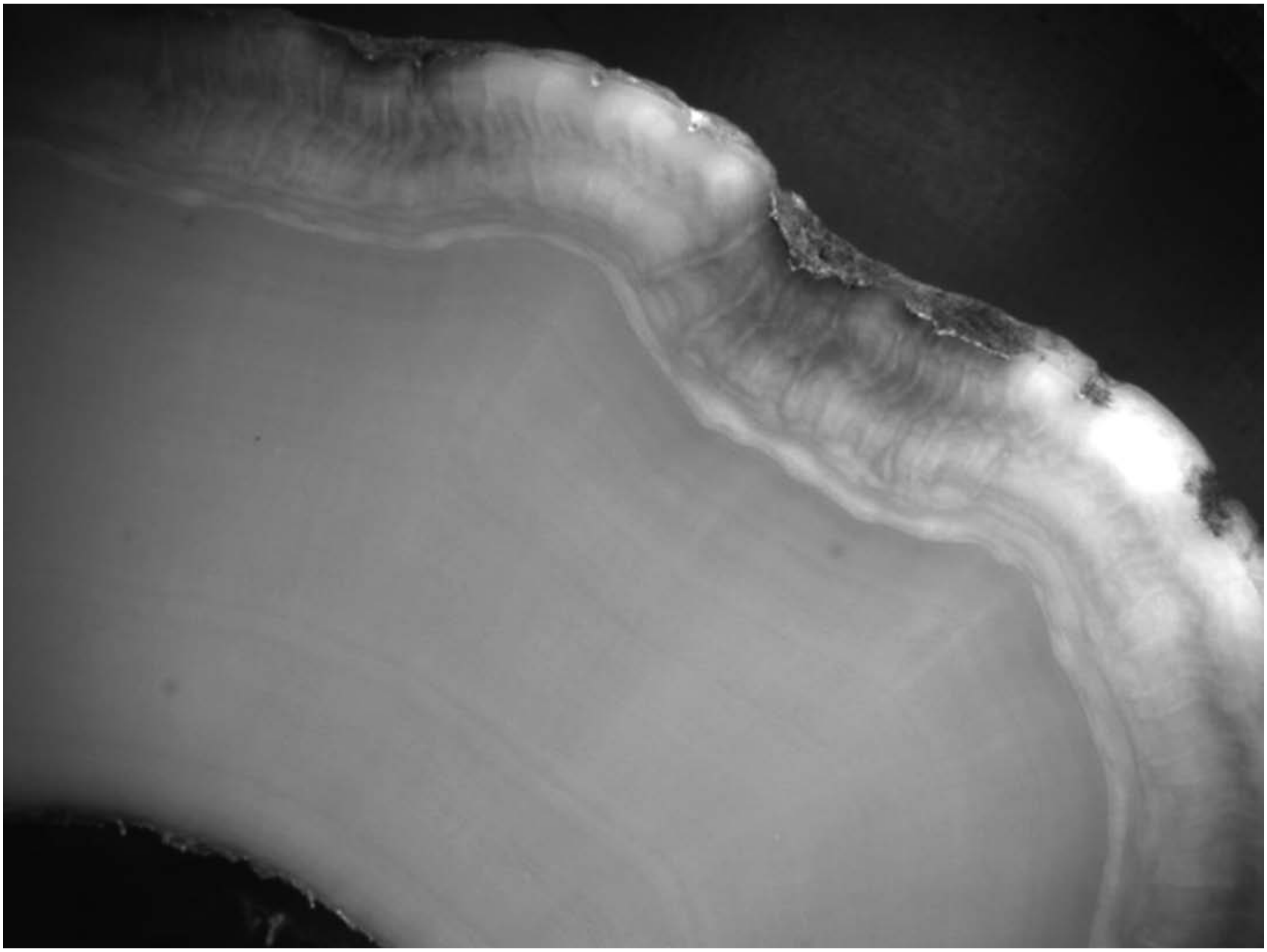


FIGURE 11. A transilluminated corner of a polished cross section showing the many distinct layer or rings within the tissue. The wide band of tissue making up the outer surface is described as "cementum."

faces for SEM observation. The specimen was cleaned to remove surface debris using a mild HCL acid etch followed by rinsing in dilute sodium hypochlorite. This piece was then dried in a vacuum dessicator and gold sputter coated for conductivity. The SEM images of the outer surface showed that the dark stain material found at the base of the grooves was made up of microscopic diatoms from algae deposits adhering in multiple layers to the surface (Figure 12).

The smooth white ridge areas were regions where these deposits were either very sparse or completely missing. The level of artifacts and debris on the surface made it difficult to observe the underlying tooth surface as cleaning did not remove the tightly adhered deposits in the grooves but did occasionally expose the ends of small tubule-like canals opening to the tusk surface. A more thorough cleaning removed more of the deposits and exposed the outer openings with regular frequency (Figure 13). These openings were approximately one to two micrometers in diameter and were similar in appearance to those found on the pulpal surface of the dentin.

Scanning electron microscopy observation of the pulpal surface of the section revealed the openings of multiple dentin tubules. These dentin tubules ranged from 0.5 to several micrometers in diameter and were evenly distributed with spacing of approximately 10 to 20 micrometers between tubules (Figure 14). This spacing was less dense than that observed on the pulpal surfaces of human or bovine teeth,

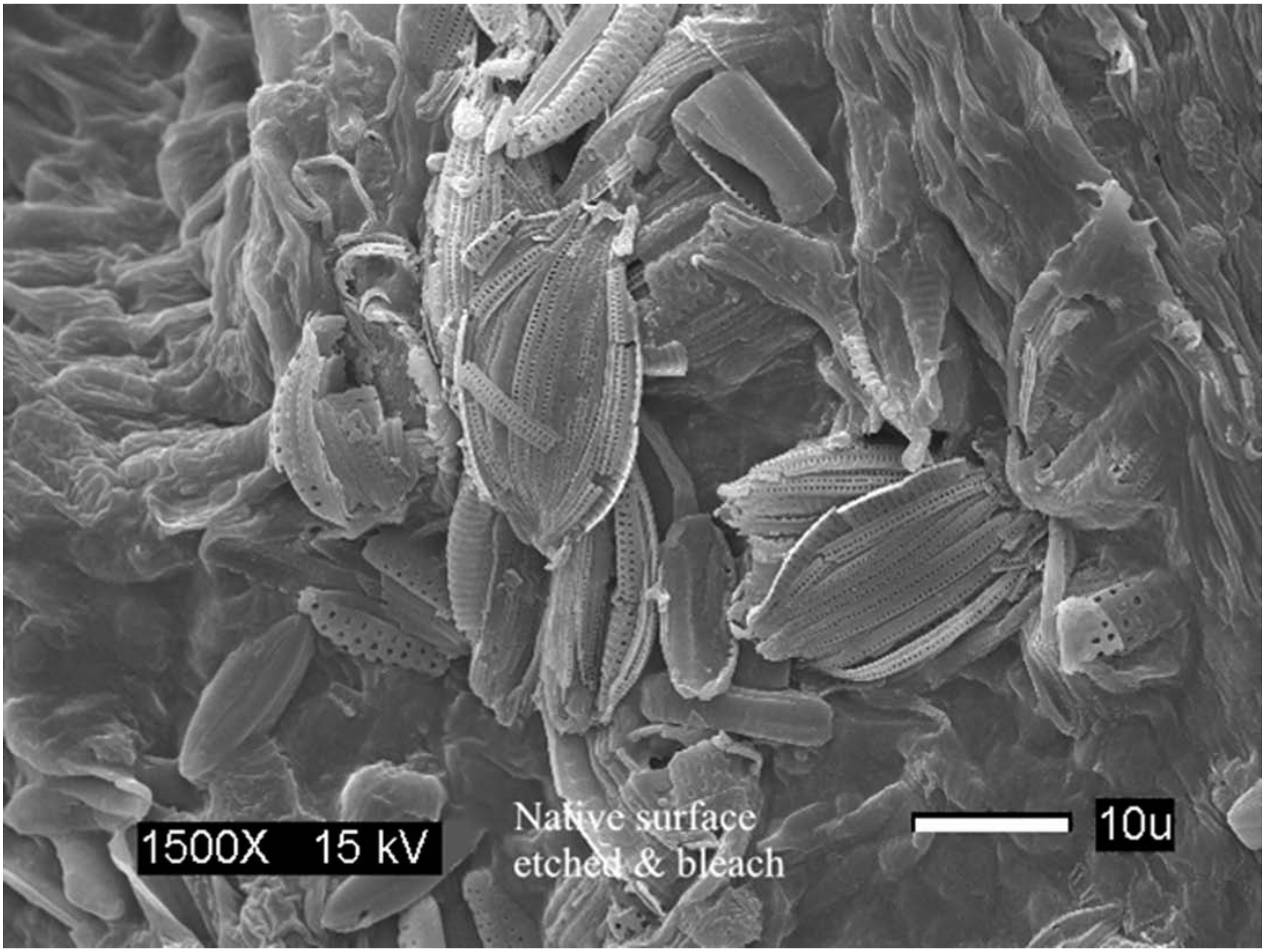


FIGURE 12. A scanning electron micrograph of the outside tusk surface showing stain deposits composed of diatoms and algae.

where spacing is approximately 3 to 5 micrometers between tubules. The appearance of the bell-shaped openings and lumen of the tubules was similar to that observed in the teeth of other mammals. The cross-sectional surface of one pie-shaped piece was acid etched to remove the collagen smear layer that forms as an artifact of polishing. This section and other serial sections taken across the tubules revealed that the tubules radiated outward from the pulpal surface through the entire thickness of the dentin and appeared to communicate into the outermost cementum surface layer (Figure 15). This observation is in contrast to what is found in masticating teeth of mammals, where tubules radiate through the body of the dentin but terminate within dentin or at the base of the outer enamel layer.

The flexural strength of the dentin from two fresh sections, one close to the base and one mid length down the tusk, was measured using $2 \times 2 \times 15$ mm rectangular bars cut longitudinally down the length of the tusk. These bars were loaded to fracture in a three-point bending mode over a 10-mm span using a universal testing machine. Nine specimens were cut from the midsection of the tusk and four from the base section. The transverse rupture strength at the midsection was 94.6 ± 7.0 MPa (mean $\pm$ standard deviation) and 165.0 ± 11.7 MPa near the base. The bars from near the base underwent much more deformation prior to fracture than those from the midsection with approximately twice the amount of strain occurring at fracture.

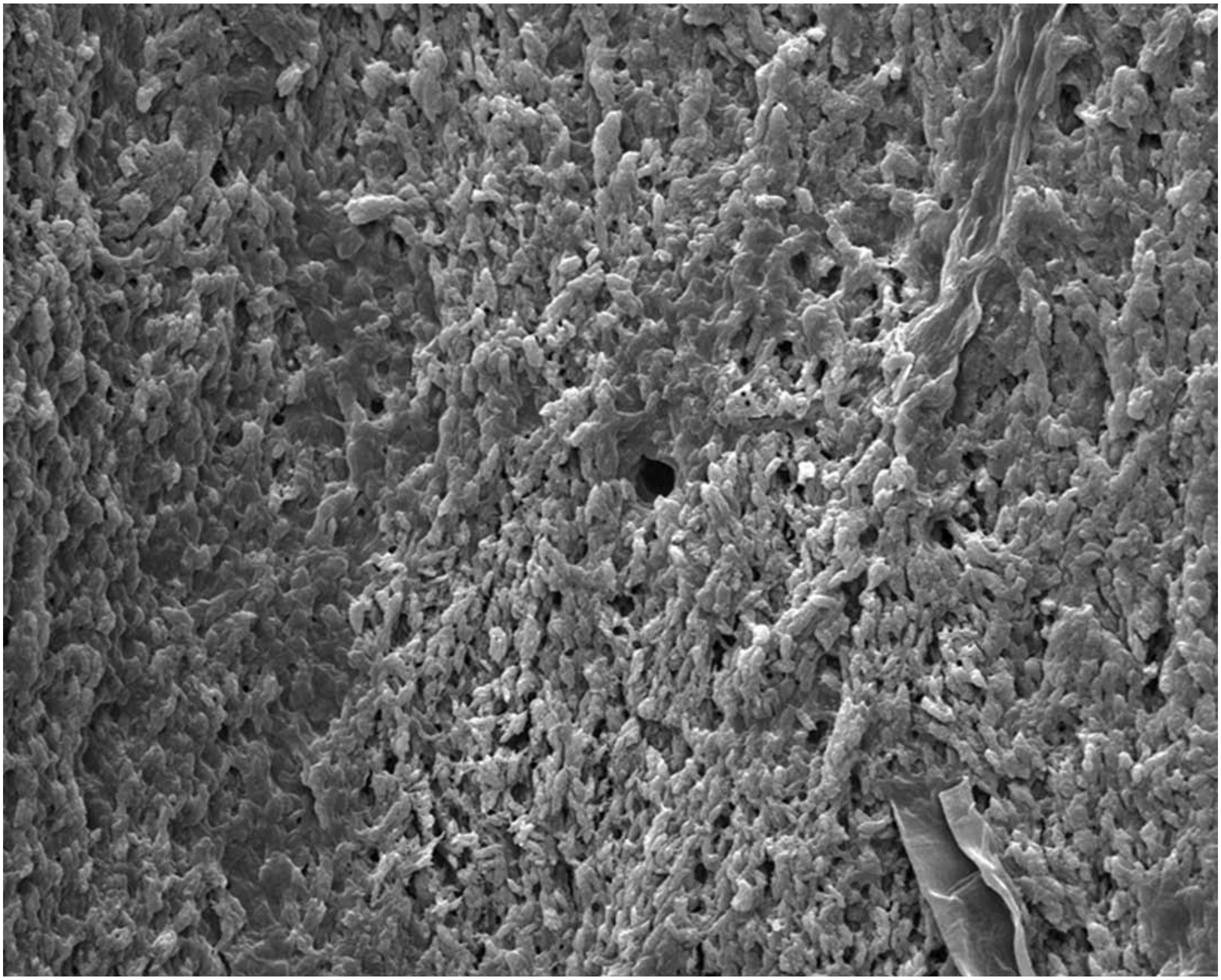


FIGURE 13. A scanning electron micrograph at 1000X magnification of the outer surface of the tusk after cleaning deposits from the surface. Tubule openings can be observed on the surface at a regular frequency. The large center orifice is approximately two micrometers in diameter.

DISCUSSION

Imaging and dissection of adult male, adult female, and fetal narwhal specimens recorded a detailed visual record of the cranial and dental anatomy. Among the findings were three new discoveries of the dental anatomy and one observation of growth and development for the tusks. The first major finding was the presence of paired vestigial teeth in all three specimens. Although a previous report in the literature found single vestigial teeth in a small collection of narwhal skulls (Fraser, 1938), this is the first study to document paired vestigial teeth. The lack of prior documentation on vestigial teeth may be due to their location, as they were embedded in bone in the female specimen and suspended in the tissue located lateral to the anterior third of the maxillary bone plate. Radiography and digital imaging provided an undisturbed view of these teeth in situ. The second discovery was linked to the anatomical location of all four maxillary teeth and their relative locations during growth and development as the two pairs of teeth reverse positions. In the fetus, the future tusks are located anteromedially to the vestigial teeth pair of teeth at four to

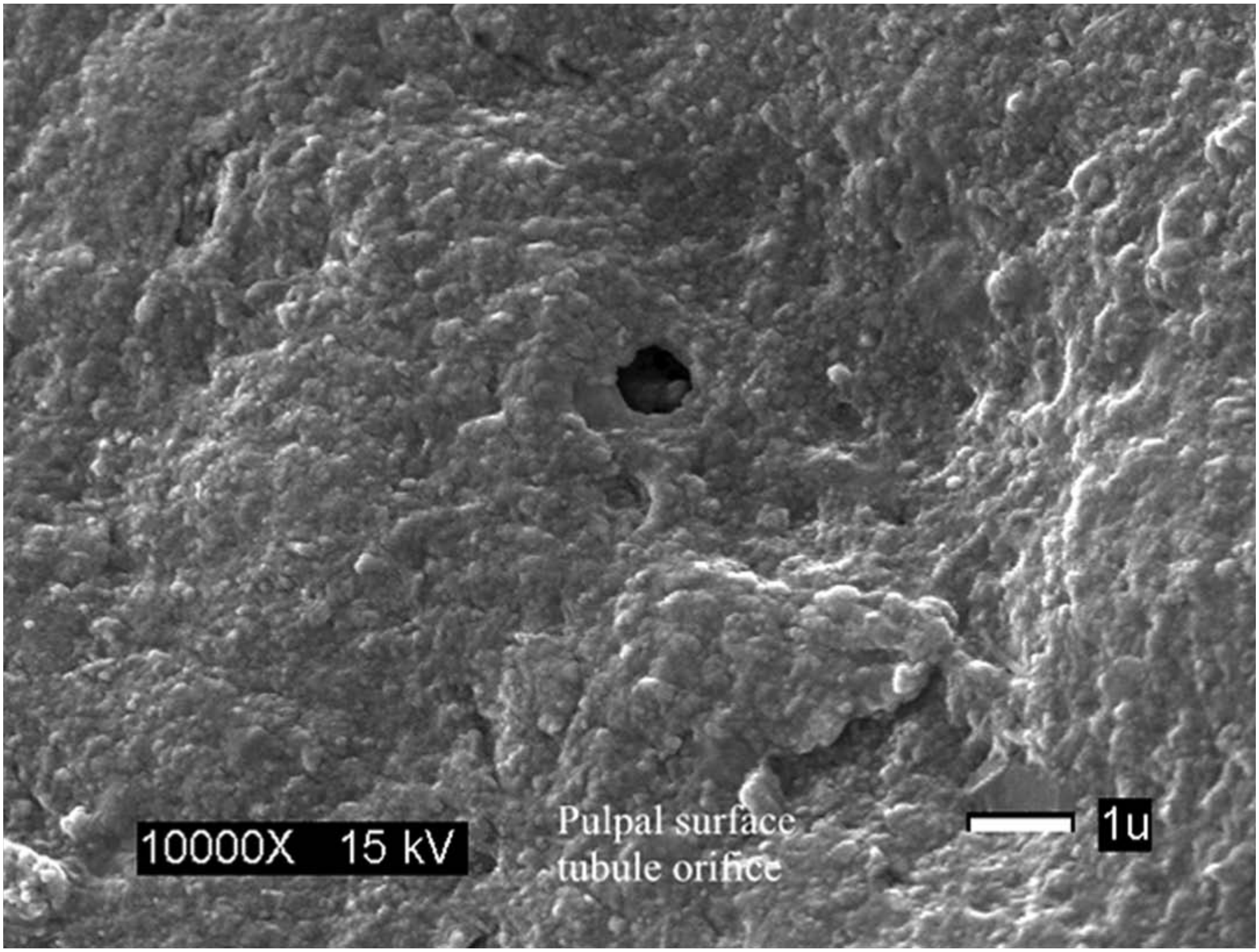


FIGURE 14. A scanning electron micrograph of the pulpal wall showing the opening of a dentin tubule. The tubule orifice is approximately 1 micrometer in diameter. The size and shape of the tubules is similar to those found in human and other mammalian teeth.

six months in development. The fully developed tusks are located posteromedially to the vestigial pair of teeth in the adult narwhal. The third finding was evidence of developed sockets for the vestigial teeth that extend posteriorly to the base of the developed tusks and communicate with their nerve and blood supply. Evidence of these developed vestigial tooth sockets suggests that this species may have exhibited at least two pairs of well-developed teeth at some point in its evolution. Likewise, if the vestigial teeth never existed beyond their current state, then well-developed sockets for these structures would not be expected as visualized in the fetal and adult female specimen. Intracranial dissection revealed fifth cranial nerve pathways that were consistent with other mammals, though there were some expected modifications based on the skull asymmetry.

The gross morphology of the male narwhal tusk showed a surprisingly unique feature by having a nearly full length pulp chamber. This observation is confirmed by most of the Inuit interviewed, though this feature has dimorphic characteristics, as traditional knowledge describes females with little to no pulp chamber, even at younger ages. This is much different from other tusked mammals, where the pulp chamber is often only a small proportion of the tusk length. It would also seem counterintuitive for a tooth evolving in a harsh and cold environment to contain vital vascular and nervous tissue through-

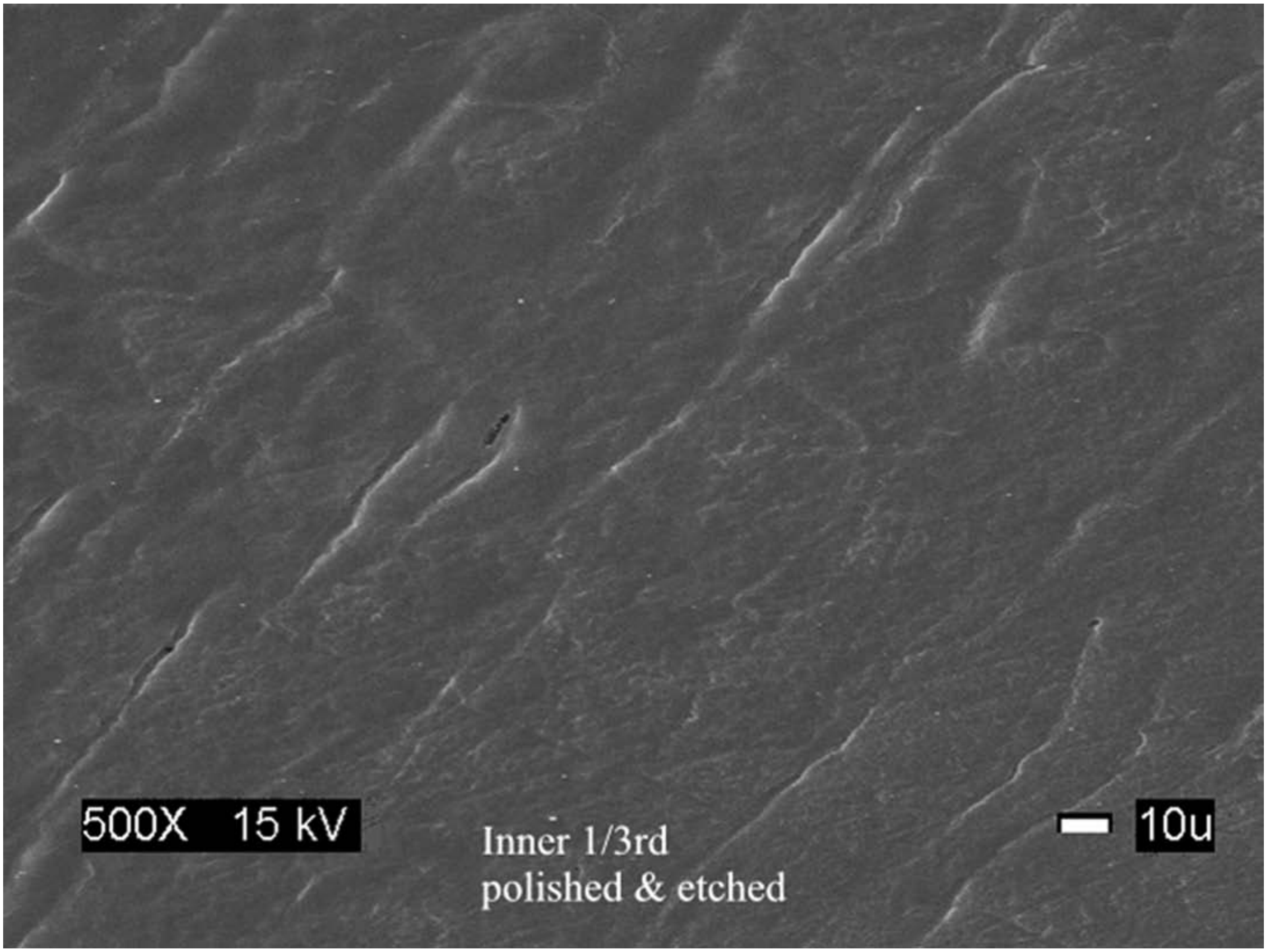


FIGURE 15. A scanning electron micrograph of a polished section of dentin shows the radiating and continuous nature of the tubules. Serial cross sections of tubules confirmed their presence throughout the tusk wall.

out its length. The pulp chamber also compromises the strength of this long and seemingly fragile tooth. The residual chamber seen at the tip of the tusk indicates that the chamber forms throughout tusk growth and development. One conversation with a broker of harvested tusks revealed that occasionally, a tusk is seen where the pulp chamber is very small and narrow and this usually occurs in larger and older tusks. It was not possible to verify the order or timing of dentin deposition using the methods of this study, but the possibility exists that the inner pulpal layer of dentin may be a feature of dentin formed at a later stage of tooth development or as a process of aging.

The left-hand helical nature of tooth development has been hypothesized to be a functional adaptation to maintain the overall concentric center of mass during growth. This hypothesis certainly makes a great deal of sense when one considers the hydrodynamic loads that would develop if the tooth were curved or skewed to one side. The clean smooth tip and facet observed in this specimen appears to be a secondary feature resulting from some form of abrasion and/or erosion. The lack of scratch patterns and the presence of large and small concavities across the facet indicate it is not formed by abrasion against a hard surface, but rather could result from gradual attrition by an abrasive slurry, such as sand or sediment. This cleanly polished tip appears on every tusk observed, regardless of the presence or absence of the facet. The behavior that causes this feature must be almost universal and is likely to be continuous, as the algae deposits that stain the surface would likely reappear if not continually removed. Water turbulence alone would probably not account for removal of these deposits from the tip and ridge areas of the tusk. The cleaned ridges are also smoothed, indicating that they could be cleaned by physically rubbing against a surface such as ice. There have also been traditional knowledge descriptions of "tusking," where males will gather in small groups and rub tusks in a nonaggressive manner. Hunters clean harvested tusks by rubbing them with sand to remove these deposits. Perhaps tusks come in contact with sand and sediment when narwhal feed close to the bottom.

The cementum layer on the outer surface of the tusk is also a rare feature for an erupted tooth. Cementum is generally found as a transitional layer between dentin and the periodontal ligaments that hold teeth into bone. These ligaments are able to attach to the cementum with small fibers, tying it to the surrounding bone. This appears to be consistent with the cementum observed in sections from the tusk base that were attached to segments of bone. In human teeth, however, if cementum becomes exposed to the oral environment, it is rapidly worn away, exposing the root dentin. In the tusk, the cementum layer appears to remain intact, even after long exposure to the ocean environment. The thickness of the cementum layer also appears to increase as the tooth increases in diameter. Cementum in mammalian teeth is generally a more proteinaceous tissue with greater toughness than enamel or dentin. A toughened outer layer that increases in thickness toward the tusk base would be consistent with the mechanics of fracture resistance, where tensile stresses would also be highest at the tusk surface and base. This toughened layer of tissue would resist cracking under functional stresses that could lead to tusk fracture.

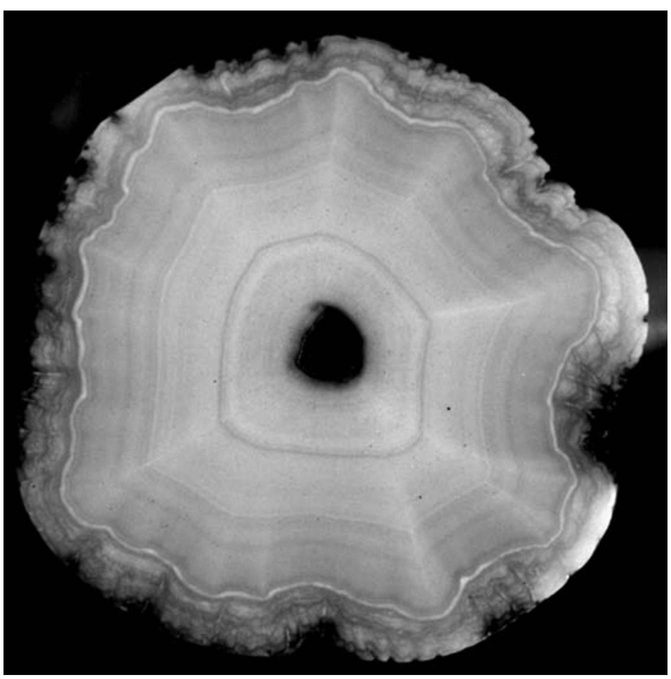


FIGURE 16. A section (2.0 cm corresponding to the third plotted point in Figure 8) cut near the tusk tip showing multiple dentin rings under transillumination.

It is impossible to tell from these studies what causes color changes that distinguish the rings observed within the dentin, but one possibility would be a change in developmental growth conditions, such as nutrition (Nweeia et al., in press) (Figure 16). The flexural strength and work of fracture both increased for dentin when comparing the tusk base to the midsection. The flexural strengths of 95 MPa at mid tusk and 165 MPa at the base compare to approximately 100 MPa for human dentin. These are adaptations for a tooth that must withstand high flexural stresses and deformation rather than the compressive loads of chewing.

The microanatomy of the tusk also provides insight into potential function. Scanning electron micrographs of the pulpal surface revealed tubule features that are similar in size and shape to the dentin tubules found in masticating teeth. The tubule diameters are similar to those observed in human teeth, but the spacing of these tubules across the pulpal wall is three to five times wider than that seen in human dentin. The polished cross sections show that these tubules run continuously throughout the entire thickness of dentin, just as they do in human dentin. A surprising finding, however, was the presence of tubule orifices on the outer surface of the cementum. This indicates that the dentin tubules communicate entirely through the wall of the tusk with the ocean environment. It is well established that dentin tubules in human and animal teeth provide sensory capabilities. Exposure of these tubules to the oral environment in human teeth is responsible for sensing temperature changes, air movement, and the presence of chemicals, such as sugar. An example of this phenomenon would be the pain one senses in a cavity when the tooth is exposed to sugar or cold air. The decay from the cavity removes the overlying protective enamel and exposes the underlying dentin, allowing the dentin tubules to communicate directly with the oral cavity. Changes in temperature, air movement, or osmotic gradient set up by the sugar cause movement of fluid within these tubules. This movement is detected by neurons at the pulpal end of the tubule, and these neurons send the pain signal to our brains. Narwhal teeth have similar physiology to human teeth, having both pulpal neurons and dentin tubules. The most distinguishing difference is that the tubules in the narwhal tusk are not protected by an overlying layer of enamel. This raises the distinct possibility that the tusk could provide a variety of sensory capabilities. Any stimulus that would result in movement of fluid within these tubules could possibly elicit a response (Figure 17). These include ion gradients, such as water salinity, pressure gradients caused by dive depth or atmospheric pressure changes, air temperature and movement, or possibly other chemical stimuli specific to food sources or environment. Field experiments on three captive male narwhal completed during August 2007 in the Canadian High Arctic provided evidence that water salinity is one stimulus that can be sensed by this tusk. Introduction of a high salt ion solution (approximately 42 psu), immediately after freshwater exposure, within a fixed gasket isolating a 35-cm portion of tusk surface, produced a marked movement of the head region and coordinated respiratory response. Two separate salt ion solution stimuli in two males and one stimulus in the third male were witnessed by twelve team members. Responses subsided immediately after freshwater was reintroduced to the tusk gasket. Though monitoring equipment was attached to the whale during experimentation, physiologic data recordings (EEG and ECG) were hindered by difficult field conditions.

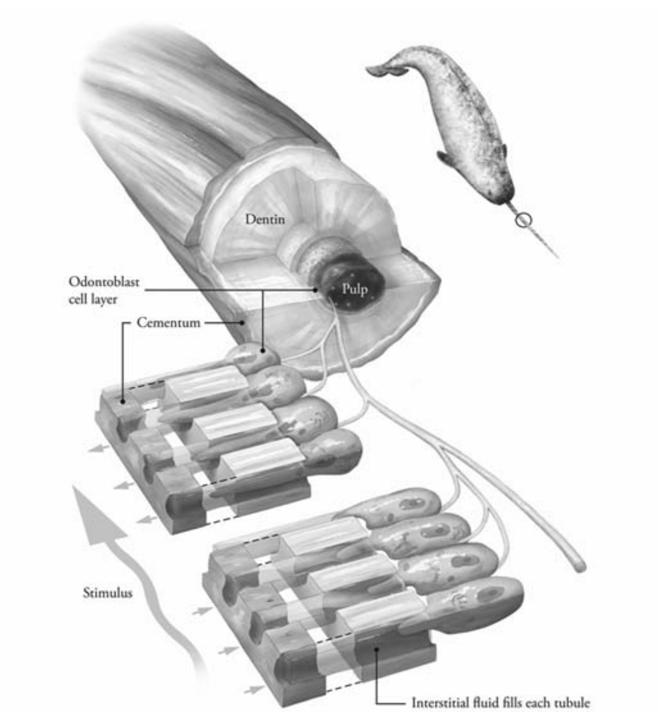


FIGURE 17. Tusk of male *M. monoceros* as a hydrodynamic sensor. The anatomic features of the narwhal tusk provide the potential for sensing stimuli that would result in movement of interstitial fluid within the dentin tubules. This fluid movement stimulates neurons located at cellular odontoblastic layer found at the base of each tubule.

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Expanded Author Information

Martin T. Nweeia, Harvard University, School of Dental Medicine, 188 Longwood Ave, Boston, MA 02115, USA; also Smithsonian Institution, Division of Mammals, Department of Zoology, 100 Constitution Avenue, Washington, DC 20056, USA. Cornelius Nutarak and David Angnatsiak, Community of Mittimatilik, Nunavut X0A

0S0, Canada. Frederick C. Eichmiller, Delta Dental of Wisconsin, 2801 Hoover Road, Stevens Point, WI 54481, USA. Naomi Eidelman, Anthony A. Giuseppetti, and Janet Quinn, ADAF Paffenbarger Research Center, National Institute of Standards and Technology, 100 Bureau Drive, Gaithersburg, MD 20899-8546, USA. James G. Mead and Charles Potter, Smithsonian Institution, Division of Mammals, Department of Zoology, 100 Constitution Avenue, Washington, DC 20056, USA. Kaviqanguak K'issuk and Rasmus Avike, Community of Qaanaaq, Greenland 3980. Peter V. Hauschka, Children's Hospital, Department of Orthopaedic Surgery, Boston, MA 02115, USA. Ethan M. Tyler, National Institutes of Health, Clinical Center, 9000 Rockville Pike, Bethesda, MD 20892, USA. Jack R. Orr, Fisheries and Oceans, Canada, Arctic Research Division, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada. Pavia Nielsen, Community of Uummannaq, Greenland 3962.

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