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from the Pliocene of the Western North Atlantic Ocean**

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## *BOHASKAIA MONODONTOIDES*, A NEW MONODONTID (CETACEA, ODONTOCETI, DELPHINOIDEA) FROM THE PLIOCENE OF THE WESTERN NORTH ATLANTIC OCEAN

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**ABSTRACT**—Here we describe *Bohaskaia monodontoides*, a new taxon of beluga-like odontocete cetacean from the early Pliocene Yorktown Formation of Virginia and North Carolina. Among odontocetes, *Bohaskaia* shares key characteristics of the rostrum and face with belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and *Denebola brachycephala* from the late Miocene of Baja California, thus placing it as a member of the Monodontidae. It also displays autapomorphies that merit its placement in a new genus and species. Both *Denebola* and *Bohaskaia* occurred in warmer latitudes than those of extant monodontids, even accounting for extralimital records. Such data from the fossil record of Monodontidae indicates that putative cold climate adaptations of living monodontids might have appeared under different environmental conditions and that their Holarctic and sub-Arctic distribution is a relatively recent phenomenon.

### INTRODUCTION

The only extant members of Monodontidae Gray, 1821, include two iconic Holarctic cetaceans: narwhals (*Monodon monoceros*) and belugas (*Delphinapterus leucas*). Both species have been documented in Arctic and sub-Arctic waters (Stewart and Stewart, 1989; Heide-Jørgensen et al., 2002), with occasional extra-limital occurrences recorded in temperate latitudes (e.g., Gladden et al., 1999). The fossil record of monodontids, however, indicates that this group was represented by extinct lineages that were distributed in lower, warmer latitude environments (Barnes, 1984; Barnes and Deméré, 1991), challenging panselctionist interpretations of monodontid specializations as adaptations to Arctic climate (e.g., Noren and Williams, 2000; Williams et al., 2011). The oldest fossil monodontids date to at least the late Miocene, with *Denebola brachycephala* Barnes, 1984, from the late Miocene Almejas Formation of Baja California, Mexico (Barnes, 1984). A *Denebola*-like form has been reported from the late Miocene San Mateo Formation of California, but it remains undescribed (Barnes and Deméré, 1991). This distribution suggests that monodontids belonging to lineages other than extant ones had ranges that extended to temperate latitudes at least by the late Miocene. With the exception of a putative monodontid occurrence based on a single periotic from the early Pliocene of Peru (Muizon and DeVries, 1985), other early Pliocene and Pleistocene remains referable to monodontids are known from the east coast of North America and the North Sea Basin (Whitmore, 1970, 1994; Post, 2005; Lambert and Gigase, 2007; Whitmore and Kaltenbach, 2008). Some of the remains from the North Sea Basin consist of cranial material that shares some similarities with *Delphinapterus*, although they are too incompletely preserved for identification below the family level (Lambert and Gigase, 2007). Reported fossils from the east coast of North America have been collected from the Yorktown Formation in North Carolina and Virginia; the most notable of

these finds includes material from the Lee Creek Mine, in North Carolina, which consists of an associated collection of isolated periotics, a fragmentary mandible, and skull fragments (Whitmore and Kaltenbach, 2008). Here we describe a new genus and new species of monodontid based on a nearly complete skull from the Yorktown Formation in Virginia, U.S.A., and refer some of the aforementioned Lee Creek material to this new taxon.

**Geological Setting**—The type specimen USNM 25819 was collected from the Rice's Pit locality of the Morgarts Beach Member of the Yorktown Formation, in Hampton, Virginia, U.S.A. Hazel (1971) recorded that USNM 25819 was collected from Locality 11 (now known as Rice's Pit), approximately 45–75 cm below a Pleistocene shell bed (dominated by the marine bivalve *Ensis* sp.) in a clayey sand. Rice's Pit is an extensive open excavation pit, about 13.2 m deep, which exposes marine sediments from the Pleistocene Tabb Formation, overlying the thicker Yorktown Formation, whose uppermost section is relatively fossiliferous and has previously yielded a monachine seal, *Pliophoca etrusca* (Koretsky and Ray, 2008), and the type specimen of *Balaena ricei* Westgate and Whitmore, 2002. It is unclear if these latter occurrences share the same precise stratigraphic provenance as USNM 25819, although it is likely, given that the marine mammal-bearing horizons at Rice's Pit are restricted to the uppermost, exposed horizons (Westgate and Whitmore, 2002).

Nearly all of the Yorktown Formation exposed at Rice's Pit belongs to the Mogarts Beach Member (Dowsett and Wiggs, 1992), based on the dominant presence of the planktic foraminiferans *Globigerina bulloides* and *Neogloboquadrina acostaensis*. Also, Hazel (1971) placed Rice's Pit in the *Orionia vaughani* Zone, based on that ostracode's presence at the locality. Dowsett and Wiggs (1992) reported an age estimate of 4.0–3.0 Ma, a range that largely concurred with Cronin et al. (1984)'s placement of Yorktown Formation localities from southeastern Virginia in standard planktic foraminifer zones N19–21 and Blackwelder (1981)'s M5 molluscan zone for the Morgarts Beach Member of the Yorktown Formation. Collectively, these biostratigraphic indicators point to Piacenzian age for this new monodontid.

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**Institutional Abbreviations**—**IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **M**, Fossil mammal collection of types and figured specimens of the IRSNB; **UCMP**, Museum of Paleontology, University of California, Berkeley, California, U.S.A.; **UCR**, Department of Geological Sciences at the University of California, Riverside, California, U.S.A.; **USNM**, Department of Paleobiology and Department Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

**Specimens Observed**—*Delphinapterus leucas* (USNM A21051, A21052, A22433, A23208, 238105, 275068, 572014); *Monodon monoceros* (USNM A22983, A23455, A267957–267961).

#### SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762  
ODONTOCETI Flower, 1867  
DELPHINOIDEA Gray, 1821  
MONODONTIDAE Gray, 1821  
*BOHASKAIA*, gen. nov.

**Type and Only Known Species**—*Bohaskaia monodontoides*, sp. nov.

**Diagnosis**—Same as that of the species.

**Etymology**—Honors David J. Bohaska, in recognition of his extensive contributions to understanding the Cenozoic geology and paleontology of the east coast of North America, and his life-long commitment to enhancing the quality and care of natural history collections in museums everywhere.

*BOHASKAIA MONODONTOIDES*, sp. nov.  
(Figs. 2–5; Table 1)

Delphinapteridae, Whitmore, 1970:A145.

Delphinapterid, Hazel, 1971:12.

*Delphinapterus* Whitmore, 1994:225.

*Delphinapterus* sp., Whitmore and Kaltenbach, 2008:228–229 (in part).

**Holotype**—USNM 25819, an incomplete skull, missing the left supraorbital process, both zygomatic processes, the entire basicranium, and both tympanopariotics; collected by B. Burdette and C. Carter in January, 1969.

**Type Locality**—Rice's Pit, Hampton, Virginia, U.S.A. (Hazel, 1971). See Figure 1.

**Formation**—Morgarts Beach Member of the Yorktown Formation.

**Age**—Early Pliocene (3.8–2.9 Ma; Dowsett and Wiggs, 1992).

**Referred Specimens**—USNM 182963 (Whitmore and Kaltenbach, 2008:fig. 71), anterior fragment of left maxilla associated with an incomplete right zygomatic process of the squamosal; collected at Lee Creek Mine, South Side of Pamlico River, near Aurora Bath, by C. E. Ray, 7 November 1974.

**Range**—Pliocene of North Carolina and Virginia, U.S.A.

**Diagnosis**—Monodontidae based on (1) the medial exposure of the maxillae surrounding the anterior and lateral margins of the external bony nares, forming a 'keyhole window' reflected in rectilinear exposure of the maxillae anterior of the nares and maxillary exposures rimming the anterolateral narial margins; (2) lack of fossae for the pterygoid sinus in the orbital region (also absent in *Denebola*); and (3) a lateral lamina of the palatine that passes anterior of the lateral edge of the frontal groove. *Bohaskaia* shares with *Denebola*: (1) a subcircular, blunt rostrum in dorsal view, which differs from the squared, dorsoventrally flattened rostral terminus of *Delphinapterus* and the broadly triangular rostral outline of *Monodon* (ignoring the enlarged maxillary alveolus for the tusk in males); (2) premaxillae that

TABLE 1. Measurements of holotype skull (USNM 25819) of *Bohaskaia monodontoides*, gen. nov., sp. nov., in mm (after Perrin, 1975).

Length of rostrum—from tip to line across hindmost limits of antorbital notches	259
Width of rostrum at base—along line across hindmost limits of antorbital notches	216 e
Width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches	151+
Width of rostrum at midlength	138
Width of premaxillae at midlength of rostrum	82
Width of rostrum at $\frac{3}{4}$ length, measured from posterior end	112
Distance from tip of rostrum to external nares (to mesial end of anterior transverse margin of right naris)	381
Greatest width of external nares	72
Greatest width of premaxillae	121
Projection of premaxillae beyond maxillae measured from tip of rostrum to line across foremost tips of maxillaries visible in dorsal view	15
Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest	50
Length of upper left tooth row—from hindmost margin of hindmost alveolus to tip of rostrum	154
Number of teeth—upper left	12
Number of teeth—upper right	11

**Abbreviations:** e, estimate; +, measurement on incomplete element.

dominate the anterior end of the rostrum, relative to the maxillae, in dorsal view, differing from *Delphinapterus*, which has rectilinear premaxillae and maxillae in equivalent widths, and differing from *Monodon*, whose premaxillae taper with the maxillae; (3) having the posterior end of the premaxillae reaching to about mid-level of the external nares; and (4) palatines that are separated in the midline by the maxillae.

*Bohaskaia* shares with both *Denebola* and *Delphinapterus*: (1) pinching of the dorsal profile of premaxillae by anteromedial-most dorsal infraorbital foramina, which undercut the lateral margins of the premaxillae (this feature is absent in *Monodon*); (2) shallow and planar premaxillary sac fossae, whereas those of *Monodon* are convexly inflated; and (3) teeth oriented anteroventrally. *Bohaskaia* exclusively shares with *Delphinapterus*: (1) a window-like exposure of the vomer on the posterior of the palate (unknown in *Denebola*); and (2) anteromedial sulci of the premaxillae that extend anterior of the level of the antorbital notches. It shares with *Denebola* and *Monodon*: (1) a narrow V-shaped outline of the anterior margin of the exposure of the maxilla medial to the premaxilla anterior to the external nares, differing from the U-shaped outline of *Delphinapterus*; and (2) apex of vertex composed of frontals.

*Bohaskaia* shares with *Delphinapterus* and *Monodon*: (1) an absence of premaxillary teeth; (2) a raised rostral portion of premaxilla, giving the rostrum a dorsally convex outline when viewed laterally; and (3) long anterolaterally oriented frontal groove. *Bohaskaia* exclusively shares with *Monodon* a vertex that is constricted at the base, forming a knob dorsally, and rounded dorsal outline of the nasals.

Lastly, *Bohaskaia* displays the following autapomorphies: (1) contact between the maxillae and vomer in the posterior palate; (2) open, or L-shaped, antorbital notches of the maxillae; (3) cardiform exposure of the premaxillae in the palate; and (4) proportionately wider external nares, relative to the breadth of the skull; (5) frontal groove more anteriorly oriented relative to the long axis of the skull ( $\sim 33^\circ$ ); and (6) posterior accessory foramen and sulcus, positioned much further anteriorly, relative to external bony nares, than in any other monodontid (although related to the posterior extent of the premaxillae, which *Bohaskaia* shares with *Denebola*, this character is unclear in the latter).

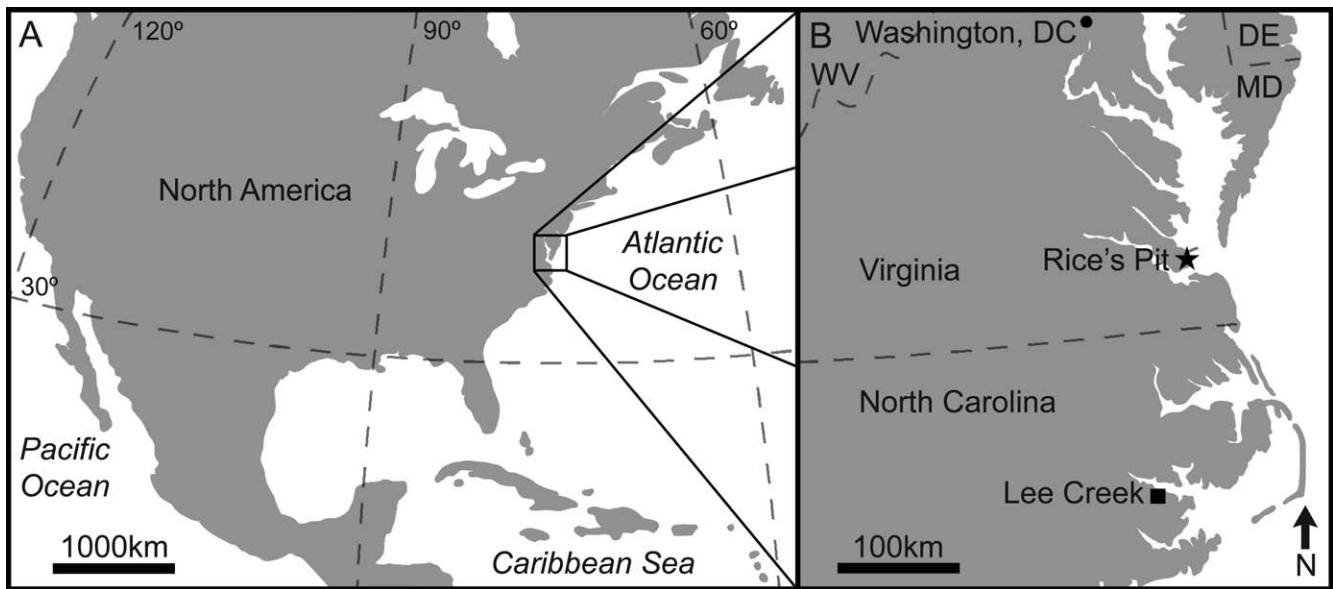


FIGURE 1. Locality map showing **A**, North America and **B**, the eastern Mid-Atlantic of the United States, showing the type locality (Rice's Pit, Virginia) and referred locality (Lee Creek Mine, North Carolina) for *Bohaskaia*. States of Delaware, Maryland, and West Virginia (DE, MD, and WV, respectively) are also shown.

**Etymology**—Monodontidae, the crown clade of living narwhals and belugas; *-oides*, likeness (Latin). Named for its similarities to both extant species of monodontids.

## DESCRIPTION

### Skull

The premaxillary sac fossae and vertex of the type specimen of *Bohaskaia* are asymmetrical relative to sagittal plane of the skull (as typical for many extant Delphinoidea) (Figs. 2–5). The rostrum is broad relative to the breadth of the skull, and the vertex is skewed sinistrally (Fig. 2). The external nares are nearly circular in outline. Ventrally, the alveolar margins of the rostrum are intact, but missing all dentition, and the palate is intact, except that it lacks the pterygoids (Fig. 3).

**Premaxilla**—The premaxillae dominate the apex of the rostrum both in the type and referred specimens (USNM 25819 and 182963, respectively). Dorsally, the premaxillae are constricted at the level just anterior to the antorbital notches, it then expands laterally towards the apex of the rostrum. When viewed laterally (Fig. 5), the rostral portion of the premaxilla is notable for its dorsally convex outline. A mesorostral groove separates the premaxillae for their length anterior of the level of the orbits; posterior of this level, the mesorostral groove is filled by the ossified mesethmoid. The anteromedial sulcus of the premaxilla has well-demarcated lateral margins. The premaxillary foramina are located slightly posterior to the level of the antorbital notches; the posterolateral sulcus of the premaxilla is shallow and continues for most of the length of the premaxilla posterior to the premaxillary foramina. The premaxillary sac fossae are flat with an elongate, oval outline. As the premaxillae diverge laterally posterior of the antorbital notches, they expose the underlying maxillae along their medial margins anterior to the external nares. The posterior ends of the premaxillae are located at the level of the middle of the external nares; a small foramen is roofed by the premaxilla at this level, and it is continuous with a deep sulcus extending posteriorly along a longitudinal crest in the maxilla.

*Bohaskaia* does not possess premaxillary teeth. Although the premaxillae dominate the apex of the rostrum in dorsal view, they are excluded from the alveolar row by the maxillae in both USNM 25819 (Fig. 4) and 182963. The palatal exposure of the premaxillae is fairly long, reaching to about the level of the 11th maxillary alveolus. Anteriorly, this exposure has a cardiform outline that pinches posteriorly (Fig. 5).

**Maxilla**—Dorsally towards the anterior part of the rostrum, the maxillae are nearly completely covered by the premaxillae. Mediolaterally, the dorsal transition between the maxilla to the premaxilla is more abrupt than in extant monodontids, especially in the raised portion of the premaxilla anterior to the antorbital notches. Only the antorbital notch on the right side is preserved, and it is wide, shallow and directed anterolaterally with an L-shape outline; in extant monodontids they are deeper, U-shaped, and oriented anteriorly. On the right side, USNM 25819 shows a total of four anterior dorsal infraorbital foramina; the left side is mostly missing, providing no commensurate information. The largest of these foramina rank as the largest dorsal infraorbital foramina in any monodontid, and it opens anterolaterally between the maxilla and premaxilla. The maxilla is expanded posteriorly, covering most of the supraorbital process of the frontal and temporal roof, except for a small portion posterolateral to the vertex. The maxilla is exposed medially anterior to the external nares, which has been considered as a synapomorphy for Monodontidae (Muizon, 1988), forming the anterior margins of the external nares. The continuation of the small foramen that exists posteriorly between the maxilla and the posterior-most extent of the premaxilla extends with a moderately deep sulcus in the maxilla. The medial border of this sulcus slightly overhangs the floor of the sulcus. This feature has not been named in the literature (e.g., Mead and Fordyce 2009), and we elect to term it the posterior accessory foramen and sulcus (Figs. 2, 5).

Ventrally (Fig. 3), the maxillae form most of the palate, which is concave for most of its length, becoming flat to slightly convex posterior of the alveolar row. A total of 12 alveoli are present on the right maxilla and 13 on the left; most are separated by very shallow interalveolar ridges, except for the last alveolus on

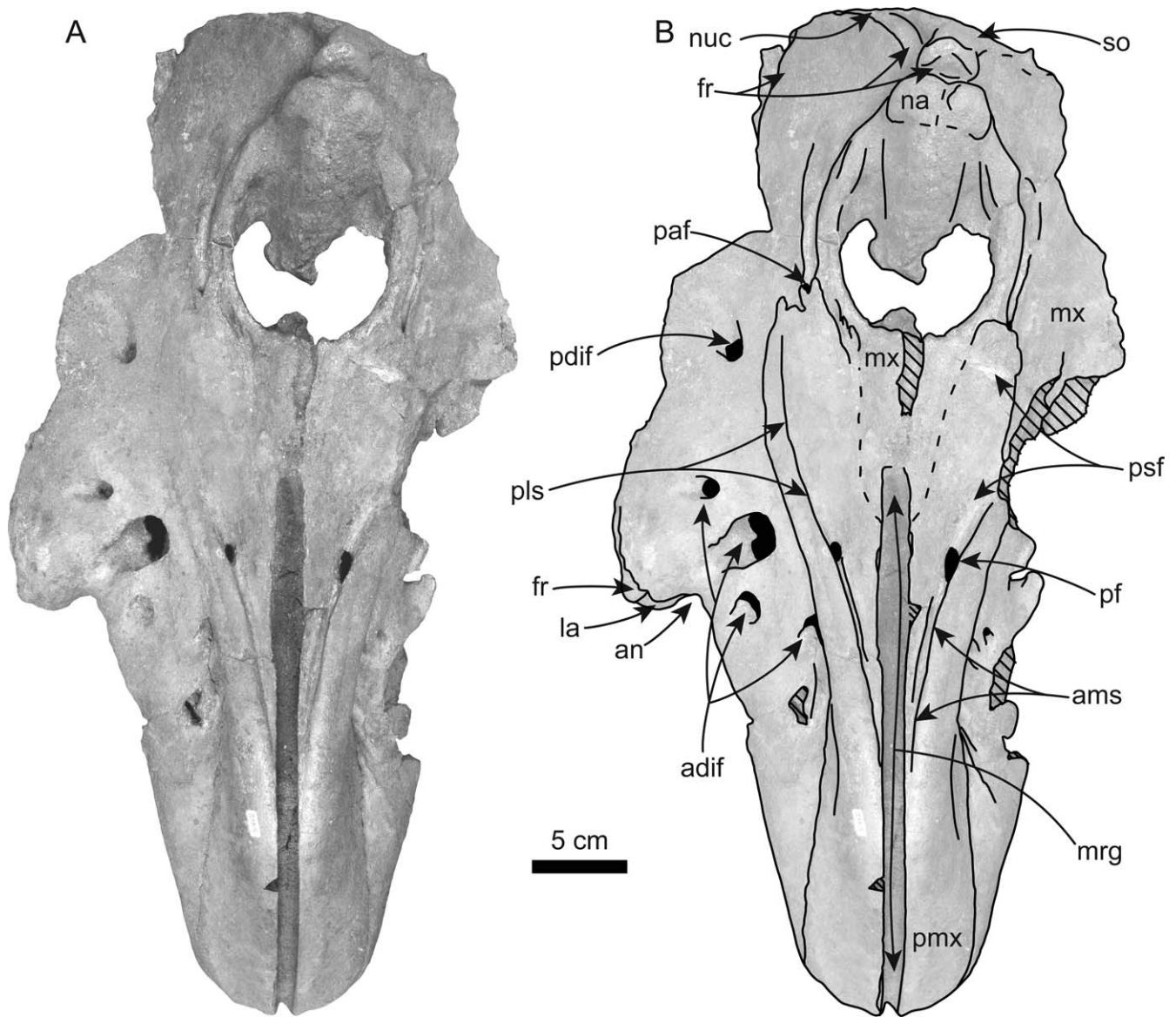


FIGURE 2. Dorsal views of the holotype skull of *Bohaskaia monodontoides* (USNM 25819), gen. nov., sp. nov. **Abbreviations:** *adif*, anterior dorsal infraorbital foramen; *ams*, anteromedial sulcus; *an*, antorbital notch; *fr*, frontal; *la*, lacrimal; *mrg*, mesorostral groove; *mx*, maxilla; *na*, nasal; *nuc*, nuchal crest; *paf*, posterior accessory foramen and sulcus; *pdif*, posterior dorsal infraorbital foramina; *pf*, premaxillary foramen; *pls*, posterolateral sulcus; *pmx*, premaxilla; *psf*, premaxillary sac fossa; *so*, supraoccipital. Diagonal lines indicate broken surfaces.

the right, which has a deeper ridge. Judging by the orientation of the alveoli, the upper teeth seemed to have been oriented anteroventrally as in *Delphinapterus* and *Denebola*. The palatine sulcus extends from the greater palatine foramen, at the level of the anteromedial edge of the maxilla-palatine suture, to about the level of the 9th maxillary alveolus; several other small foramina are present along the length of the groove. The maxillae contact the palatines posterolaterally, with two long median extensions that separate the palatines along the midline and contact the vomer posteriorly. These processes are asymmetrical, with the right one being wider and slightly longer.

**Lacrimal**—The lacrimals form most of the anterior edge of the supraorbital process, and then extend posteromedially towards the ventral infraorbital foramen (= maxillary foramen; Mead and Fordyce, 2009).

**Frontal and Parietal**—The lateral margin of the supraorbital process is straight-edged and arched dorsally. The frontals form a pyramidal knob at the highest point of the vertex. This base of the frontal portion of the vertex is constricted and pedestaled, with a slight posterior tapering in dorsal view. On the ventral surface of the supraorbital process the frontal groove is relatively long and anterolaterally oriented, with an angle of about 33° from the sagittal axis of the skull. There are no fossae for the pterygoid sinus in the orbital region. Only a small portion of the left parietal, where it contacts the frontal, is present.

**Nasal**—The nasals are subequal in size, and rounded (button-like) in outline when viewed dorsally.

**Palatine, Vomer, and Pterygoid**—In ventral view (Fig. 3), the palatomaxillary suture is posteriorly concave, and the palatines are separated in the midline by long interpalatine processes of the maxillae. The lateral lamina of the palatines are not preserved,

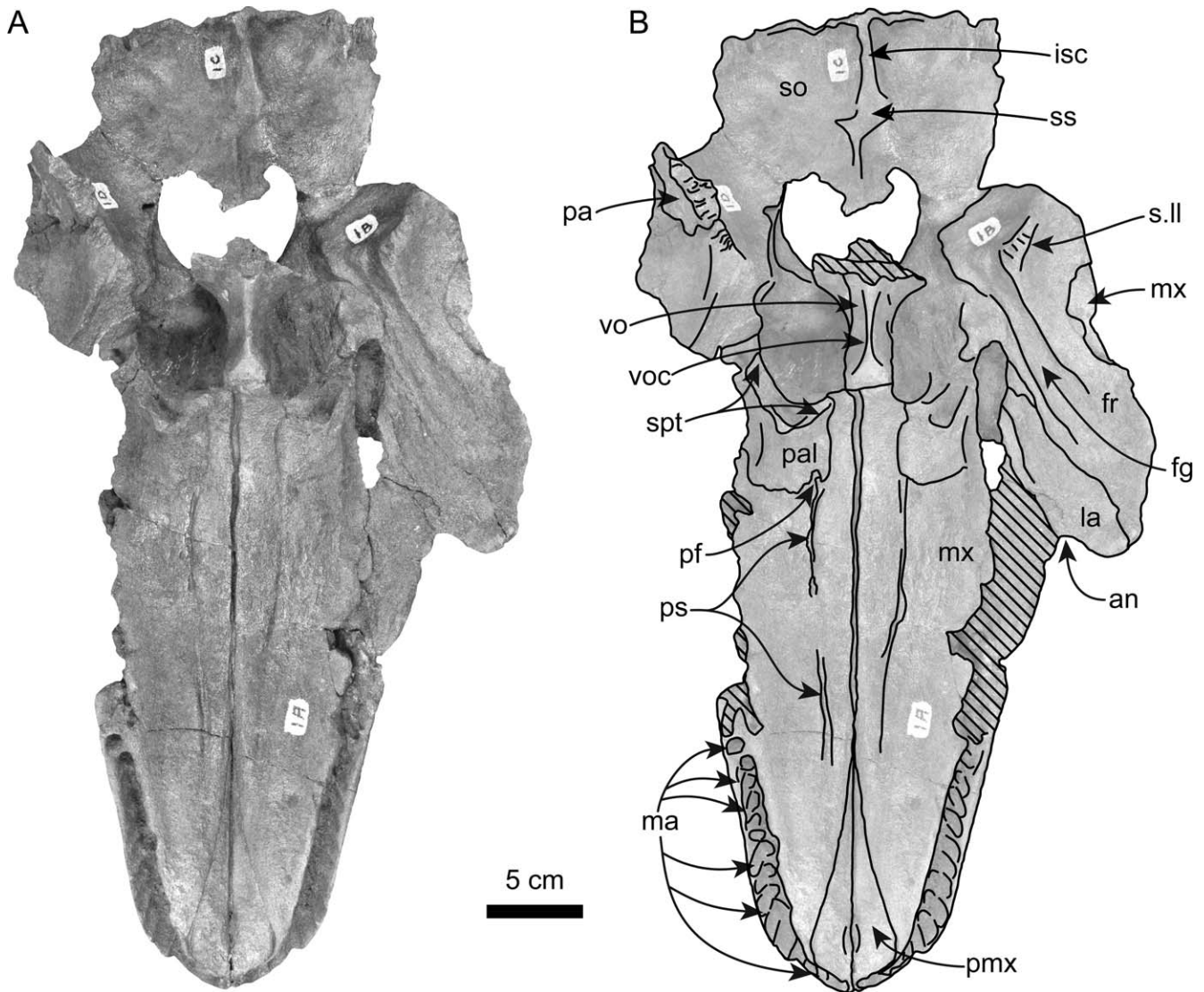


FIGURE 3. Ventral views of the holotype skull of *Bohaskaia monodontoides* (USNM 25819), gen. nov., sp. nov. **Abbreviations:** an, antorbital notch; fr, frontal; isc, internal sagittal crest; la, lacrimal; ma, maxillary alveoli; mx, maxilla; pa, parietal; pal, palatine; pmx, premaxilla; ps, palatal sulcus; s.ll, sutural surface for lateral lamina of the palatine; so, supraoccipital; spt, sutural surface for pterygoid; ss, sagittal sinus; vo, vomer; voc, vomerine crest. Diagonal lines indicate broken surfaces.

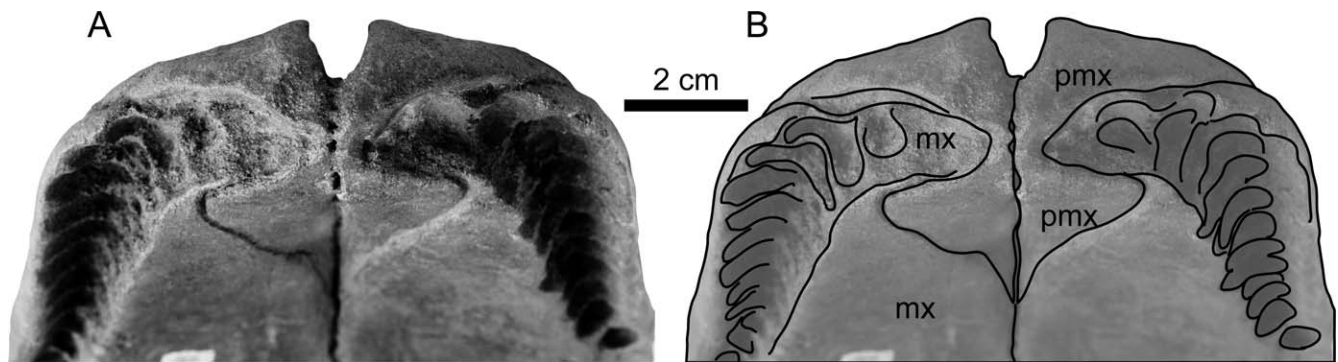


FIGURE 4. Anterovenral views of the rostrum of holotype skull of *Bohaskaia monodontoides* (USNM 25819), gen. nov., sp. nov. **Abbreviations:** mx, maxilla; pmx, premaxilla.

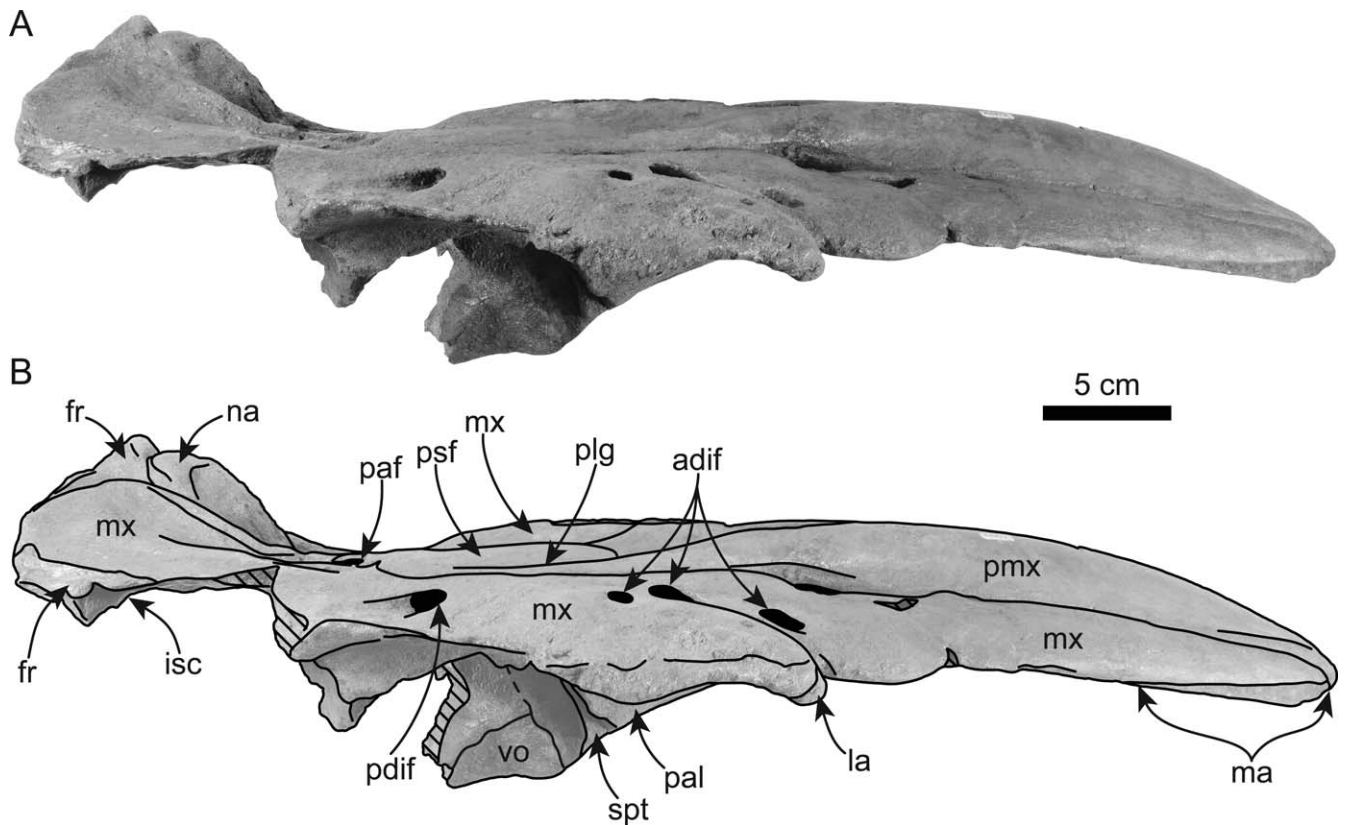


FIGURE 5. Lateral views of the holotype skull of *Bohaskaia monodontoides* (USNM 25819), gen. nov., sp. nov. **Abbreviations:** *adif*, anterior dorsal infraorbital foramen; *fr*, frontal; *isc*, internal sagittal crest; *la*, lacrimal; *ma*, maxillary alveoli; *mx*, maxilla; *na*, nasal; *paf*, posterior accessory foramen and sulcus; *pal*, palatine; *pdif*, posterior dorsal infraorbital foramina; *pls*, posterolateral sulcus; *pmx*, premaxilla; *psf*, premaxillary sac fossa; *spt*, sutural surface for pterygoid; *vo*, vomer. Diagonal lines indicate broken surfaces.

although a sutural surface on the frontal, posterior to the lateral edge of the frontal groove, seems to indicate that the lateral lamina was expanded, as it is in other monodontids (Muizon, 1988). The vomer is exposed in the posterior palate as a thin, elongate window, as observed in *Delphinapterus*. The pterygoids are not preserved.

**Supraoccipital**—Only a small portion of the supraoccipital is preserved. It is concave and seems to have been nearly vertical. The nuchal crest is unremarkable.

## DISCUSSION

**Comparisons**—Besides the extant genera of monodontids, the other available fossil comparisons with *Bohaskaia* are limited to the type specimen of *Denebola brachycephala* (UCMP 321245; formerly UCR 21245), described by Barnes (1984), and an indeterminate monodontid (IRSNB M. 1922) from the early Pliocene of Belgium, reported by Lambert and Gigase (2007). Although the type specimen of *Bohaskaia* is represented by a skull lacking the basicranium, the preserved skull length from the rostrum to the posterior surface of the vertex (~45 cm) makes it commensurate in size with the largest skulls of adult *Delphinapterus* and *Monodon*. This size is notably larger than the *Denebola* type specimen, which represents an immature individual, based on the lack of suture fusion between the basisphenoid and the basioccipital. Viewed dorsally, the rostrum of *Bohaskaia* is broad, compared to other monodontids, with laterally expanded anterior terminations of the premaxillae that dominate the apex of the rostrum, which differs from their anterior constriction

in *Denebola* and *Monodon*, and the rectilinear ones of *Delphinapterus*. The premaxillary sac fossae of *Bohaskaia* are flat, like *Delphinapterus*, and ovate, but not raised as in *Monodon*, nor forming the bosses observed in phocoenids, albireonids, and the Belgian monodontid (Barnes 1984, 2008; Fajardo-Mellor et al., 2006; Lambert and Gigase 2007). The antorbital notches of *Bohaskaia* are L-shaped, like *Pontoporia* (Pyenson and Hoch 2007), whereas most other monodontids possess U-shaped ones; the Belgian monodontid approaches this condition (Lambert and Gigase 2007:fig. 3). Viewed laterally, the rostrum of *Bohaskaia* exhibits a strongly convex profile, whereas it is less convex in extant monodontids and nearly flat in *Denebola* (Barnes 1984).

Viewing the rostrum anteriorly, the alveolar margin of *Bohaskaia* is devoid of premaxillary teeth (Fig. 4), as in other extant monodontids, with the exception of *Denebola*, which possesses one alveolus per premaxilla (Fig. 6) (Barnes, 1984). Despite the lateral expansion of the premaxillae on the dorsal surface in *Bohaskaia*, the maxillae pinch medially to exclude the premaxillae from the alveolar margin. Continuing in ventral view, the curvilinear outline of the window exposing the premaxillae is more laterally exaggerated in *Bohaskaia* than in *Denebola* (Fig. 4, 6), but it is dissimilar to extant monodontids, where the anterior portion of this outline is straight. In *Bohaskaia*, the posterior termination of this window pinches in an acute angle, whereas this pinching is more gradual and straight-edged in other monodontids. The vomer is exposed in the posterior palate in *Bohaskaia*, a condition similar to that seen in *Delphinapterus*; in *Monodon*, the pterygoids meet along the ventral midline, thus covering the vomer in that region; this area is



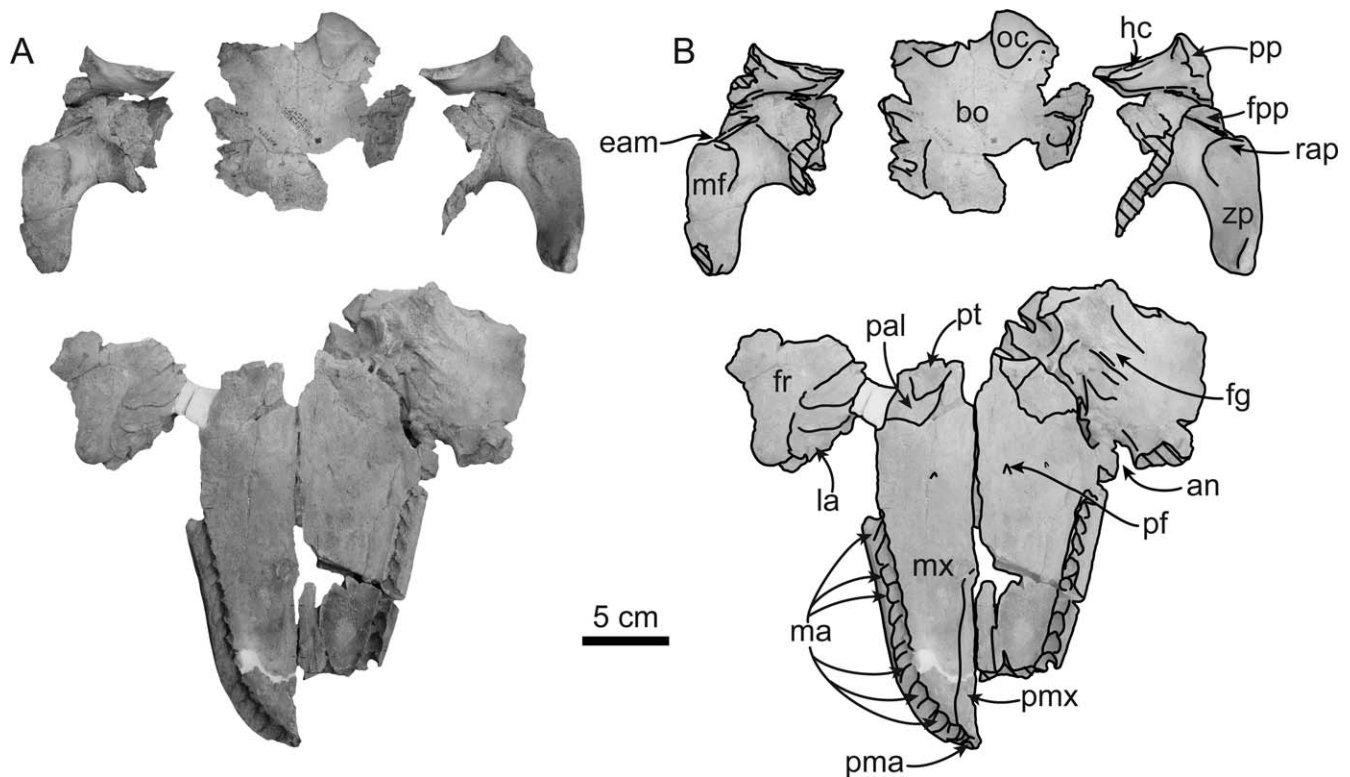


FIGURE 6. Ventral views of the holotype skull of *Denebola brachycephala* (UCMP 321245). **Abbreviations:** an, antorbital notch; bo, basioccipital; eam, external auditory meatus; fg, frontal groove; fpp, facet for posterior process; fr, frontal; hc, hypoglossal canal; la, lacrimal; ma, maxillary alveoli; mf, mandibular fossa; mx, maxilla; oc, occipital condyle; pal, palatine; pf, palatal foramen; pma, premaxillary alveoli; pmx, premaxilla; pp, paroccipital process; pt, pterygoid; rap, retroarticular process; zp, zygomatic process. Diagonal lines indicate broken surfaces.

not preserved in *Denebola*. The posterior palate of *Bohaskaia* is similar to that of *Denebola*, with palatines separated in the midline (Fig. 4, 6), differing from extant monodontids in which these bones meet along a suture. In both extant monodontids and *Bohaskaia*, the pterygoids are excluded from contacting the maxillae by the palatines; in *Denebola*, the pterygoids contact both the maxillae and the palatines (Fig. 6). The frontal groove in *Bohaskaia* is long as in extant monodontids and *Denebola*. However, in *Bohaskaia* it is more anteriorly oriented, forming an angle of about  $33^\circ$  from the midline of the skull, which is less than in *Denebola* ( $\sim 50^\circ$ ), *Delphinapterus* ( $\sim 47^\circ$ ), and *Monodon* ( $\sim 51^\circ$ ).

Like all other monodontids, *Bohaskaia* exhibits a key monodontid character with the medial exposure of the maxillae anterior of the external bony nares. Posterolateral to the nares, the posterior terminations the premaxillae of *Bohaskaia* are perforated by a foramen, which extends into a sulcus on the maxillae, penetrating deeply enough to create a slight lip overhanging the sulcus. We have identified this accessory foramen and sulcus in extant and fossil monodontids, as well as in phocoenids (Barnes, 1984; Lambert and Gigase, 2007; Ichishima and Kimura, 2009; Figs. 2, 5), although we note that this structure was not identified in Mead and Fordyce's (2009) compendium. The exact relationship of this feature to other soft tissue structures in the cranium remains unknown to us. Towards the vertex, *Bohaskaia* shares button-like nasals with *Monodon*, which differs from the elongate, chevron-shaped nasals observed in *Denebola* or the more triangular ones of *Delphinapterus*. Also at the vertex, the frontals of *Bohaskaia* form a pyramidal knob at the highest point, similar to *Monodon* and *Denebola*. The base of the frontal knob is

constricted and pedestaled as in *Monodon*, with a slight posterior tapering in dorsal view.

*Bohaskaia* and the Belgian monodontid are of similar age (Lambert and Gigase, 2007) and they do share some similarities (i.e., outline of the exposure of the maxillae in front of the external nares and the shape of the antorbital notch). However, other comparable characteristics of the Belgian monodontid, such as its smaller size, as well as features of the premaxillae, are different. *Bohaskaia* and IRSNB M. 1922 could represent different species of the same genus, but the fragmentary nature of the latter prevents any further comparison.

Overall among monodontids, *Bohaskaia* exhibits features of the premaxillae on the dorsal and ventral surfaces of the rostrum that most closely parallel those of *Delphinapterus*, *Denebola*, and the Belgian monodontid, while possessing a vertex that shares more similarities with *Monodon*. This mosaic of features suggests that *Bohaskaia* represents a distinct lineage of monodontid, separate from existing genera. We view our detailed differential diagnosis presented herein as a basis for conducting a phylogenetic analysis of monodontid relationships, although we have eschewed this step of our analysis primarily because of the low number of ingroup taxa (four operational taxonomic units to date, represented by each genus), and uncertain interrelationships among potential outgroup taxa (e.g., Delphinidae, Phocoenidae, Albireonidae, and Odobenetopsidae).

**Biogeographic and Temporal Significance**—The presence of monodontids in the early Pliocene of the eastern coast of North America and the North Sea indicates a more widespread distribution of this group in the Atlantic region. There is postcranial evidence, of at least two, perhaps three, monodontids occurring



in the Yorktown Formation at Lee Creek (Kazár and Bohaska, 2008); we propose that at least one of these morphotypes likely belongs to *Bohaskaia*. Equally, one of the other Yorktown taxa could belong to the Belgian monodontid. In either or both cases, such a multispecies assemblage of monodontids would represent occurrences of monodontids well south of the published extralimital records for extant *Delphinapterus* (Reeves and Katona, 1980).

Under the assumption that USNM 25819 represented *Delphinapterus*, Whitmore (1994) argued that its presence in the Yorktown Formation represented winter immigration from higher latitudes, rather than a lineage of more temperately adapted species. Given that this occurrence represents a novel taxon (*Bohaskaia*), either included or separate from a multispecies assemblage of Pliocene age monodontids, we suggest an opposing view, arguing that these data represent faithful records of *in situ* occurrence data, at least at the regional scale. First, extant monodontids generally exhibit high latitudinal fidelity even when breeding (Stewart and Stewart, 1989), and their death assemblages likely have similarly high fidelity (Pyenson, 2011), a supposition supported by abundant Pleistocene *Delphinapterus* fossils from the former Champlain Sea covering southern Quebec, northern Vermont, upper New York State, and western Ontario (Harrington, 1977).

Unlike the Holarctic and sub-Arctic distribution of living monodontids, the geographic occurrences of their fossil relatives are temperate, and possibly tropical latitudes. Estimates of sea surface temperatures, based on planktic foraminifera, for the Rice's Pit locality range from 18.4°C to 27.3°C (Dowsett and Wiggs, 1992) during the Pliocene. Late Miocene sea surface temperatures in the eastern Pacific Ocean, near the type locality of *Denebola* on Isla Cedros, Baja California, Mexico, were approximately the same as today, if not slightly warmer during the summer (Moore and Lombardi, 1981). Such warm water geographic distributions for extant monodontid lineages suggest that putative cold-climate adaptations observed in extant monodontids may have evolved recently in individual lineages leading to *Delphinapterus* and *Monodon*, rather than reflecting ancestral cold water adaptive features Monodontidae.

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