MID-CENOZOIC MARINE MAMMALS FROM ALASKA

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ABSTRACT--Mid-Cenozoic marine mammals of Alaska were isolated from the Arctic Ocean by Beringia and were thus part of a far North Pacific ecosystem. The amphicynodontid ?*Kolponomos*, a neocete whale, and a desmostylian were found in the latest Oligocene or earliest Miocene (approximately 23 Ma) Dutch Harbor Member of the Unalaska Formation, Aleutian Chain, Alaska. The Unalaska desmostylian is more derived than *Cornwallius* but more primitive than *Desmostylus*. Derived desmostylians are known from the early middle Miocene (16-15 Ma) Bear Lake Formation on the Alaska Peninsula and the Narrow Cape Formation on Kodiak Island. The Miocene Yakatat Formation has produced sparse mammal remains but records the onset of montane glaciation in southern Alaska.

INTRODUCTION

The inadequacy of the vertebrate fossil record of Alaska has long been lamented (Dorr, 1964), but it has certain aspects that are informative and quite important. The knowledge of Late Cretaceous terrestrial vertebrates, most notably dinosaurs (Fiorillo, 2008), is vastly improved from only a few years ago. New discoveries and research techniques have revitalized study of the Arctic mammoth fauna (Barnes et al., 2007; Greenwood et al., 2001; Guthrie, 2006; MacPhee and Greenwood, 2007), and Canadian high Arctic Paleogene and Neogene mammals (Dawson et al., 1976; Tedford and Harrington, 2003; Rybcznski et al., 2009) titillate the desire for new discoveries in Alaska.

Our purpose in this contribution in honor of Michael O. Woodburne is to review the fossil record of marine mammals from Alaska, to report new occurrences, and to discuss their geological, chronological, and paleoenvironmental significance. To accomplish this task we have compiled data and evaluated sources at the Museum of the Aleutians (MOTA), the University of Alaska Museum in Fairbanks, the U.S. Geological Survey in Denver (USGS), and the U.S. National Museum of Natural History to supplement the fieldwork we undertook in Alaska. Matrix containing the specimens we studied is dense and harder than the bone it preserves. Traditional mechanical preparation was employed, as well as latex peels and laser-scans to better observe details. To help delineate areas for future fieldwork, we have included reference to a specimen in private hands and to one known only from a photograph. After a brief introduction on the geology of Alaska to establish the boundary conditions for North Pacific marine mammal biogeography and paleoecology, we present the occurrences of marine mammals region by region with preliminary interpretations of specimens, then close with a summary of the paleoecology of Alaskan fossil marine mammals in the context of paleoenvironmental change.

Fossil marine mammals from Alaska are known from Unalaska Island in the Aleutian Archipelago, from Bear Lake and Cape Aliaksin on the Alaska Peninsula, from Kodiak Island, and from Yakataga on the eastern coast of the Gulf of Alaska (Fig. 1). The geology of this region is extremely complex, involving subduction, large-scale strike-slip movements, and accretion (Plafker et al., 1994). A number of terrains comprise the eastern coast of the Gulf of Alaska. Notably, the Yakatat Terrane was displaced 600 km northwest from its original position along the Queen Charlotte-Fairweather transform fault during the late Cenozoic (Plafker et al., 1994). The complicated accretionary processes of this and other terrains, and the subduction of the Pacific Plate, jammed the North American continent, created the distinctive sharp structural bend of the Alaska Peninsula, and uplifted mountains, including Denali, the highest peak in North America (6193 m).
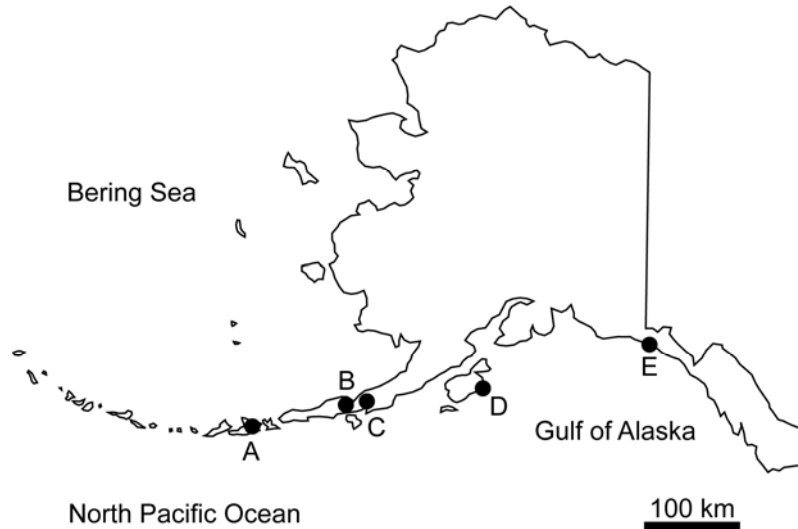
Figure 1. Distribution of marine mammal-bearing localities in Alaska. **A**, Unalaska Island; **B**, Cape Aliaksin and Beaver Bay, Alaska Peninsula; **C**, Bear Lake, Alaska Peninsula; **D**, Narrow Cape, Kodiak Island; **E**, Yakatat, eastern Gulf of Alaska.

The Aleutian Islands rise from a submerged mountain ridge that extends westward from the Alaska Peninsula. This arcuate feature stretches over 3 000 km from the Kamchatka Peninsula of Siberia, to the Russian Komandorsky Islands, then Alaska, and terminates at Cook Inlet near Anchorage. The Aleutian Arc forms the boundary between the Bering Sea, which is mostly continental shelf to the north, and the deeper Pacific Ocean to the south.

The Aleutian Arc and the over 6000 meter-deep Aleutian Trench on the Pacific side of the arc resulted from the subduction of the Pacific Plate under the North American Plate. Therefore, the Aleutian Ridge with its islands, the Alaska Peninsula, and Kodiak Island are segments of the Aleutian Arc that share similar histories from about 50 million years ago. The Alaska Peninsula and Kodiak Island have had more extensive uplift than the Ridge, but all three have produced marine mammals.

As outlined by Vallier et al. (1994), the Aleutian Ridge was built from widespread and voluminous igneous activity between 50 and 37 million years ago. After 37 Ma sedimentary processes dominated, although volcanic activity continued punctuated by episodic plutonic emplacement. The final phase of Aleutian Arc construction began at about 5.3 million years ago, around the Miocene-Pliocene boundary, with renewed igneous activity, accelerated rates of deformation, and the formation of extensional summit basins along the crest of the ridge. We are most concerned with the middle interval of Aleutian geologic history, that between 37 and 5 million years, when sedimentary processes dominated over igneous processes, because it is in that middle interval of arc construction, at 23 Ma, that desmostylians occur in the Aleutian Islands, and later in the Miocene when they occur along the Alaska Peninsula and Kodiak Island.

The Bering Strait lies north of the Bering Sea, forming its northern boundary with the Arctic Ocean. As a land bridge or an ocean gateway, Beringia has played an obvious and fundamental role in understanding vertebrate biogeography and dispersal among North America, Europe, and Asia (Heilprin, 1887; Hopkins, 1967; Hopkins et al., 1982; Hoffecker and Elias, 2007; Fiorillo, 2008). The Bering Strait now separates North America and Asia by a scant 100 km.

Although a few Cenozoic and Cretaceous freshwater fish localities are known in Alaska (Schlaikjer, 1937; Brown, 1946; Dorr, 1964; Rawlinson and Bell, 1982; Grande, 1986), the lack of relevant fossils surrounding the Bering Strait prevents a local analysis of terrestrial dispersal. The only record of terrestrial Cenozoic mammals older than Pliocene in Alaska is a mention of tracks from Wishbone Hill in the Matanuska Valley (Robinson et al., 2004), a site that is chronologically near the Paleocene-Eocene boundary (Triplehorn et al., 1984).

On the other hand, the foundering of the land bridge is important for marine biogeography. The Bering Strait controls the introduction of North Atlantic and Arctic Ocean species into the North Pacific. Beringia was emergent for most of the Late Cretaceous and Cenozoic (Fiorillo, 2008), as witnessed by numerous terrestrial dispersal events inferred from fossiliferous localities outside Alaska. It foundered between 5.4 and 5.5 Ma, allowing southward dispersal of marine invertebrates from the Arctic Ocean through the Bering Sea to the North Pacific (Marincovich and Gladenkov, 1999; Gladenkov et al., 2002). Then, at 3.6 Ma, the shoaling of the Central American Seaway and the uplift of the Isthmus of Panama precipitated a reversal of current. At that time dispersal of marine invertebrates was largely from the North Pacific, through the Arctic Ocean, into the Atlantic (Marincovich, 2000). The marine mammals reviewed in this paper all predate the final opening of the Bering Strait, which means they are part of a North Pacific fauna strictly defined, and they were subject to other oceanographic effects that influenced the Gulf of Alaska but not the Arctic Ocean. However, these oceanographic events are also relevant because the initial timing of tidewater glaciation and climate-related environmental change as interpreted through fossils is controversial (Marincovich 1988a, b, 1990; Lagoe et al., 1993) and bears on age estimates of marine mammals in the Gulf of Alaska.

The first published report of a fossil marine mammal from Alaska of which we are aware was that of a *Desmostylus* upper third molar described and illustrated by O. P. Hay in 1924. Because the specimen had been purchased from a dealer in curiosities, the record of its provenance was deemed undependable at least, and certainly imprecise. This mention of a desmostylian tooth from Alaska was noted by Vanderhoof (1937) and was shown with a question mark on his map of desmostylian distribution.

The desmostylian fauna from Unalaska Island in the Aleutians was reviewed by Jacobs et al. (2007). The only other vertebrate fossils reported from Unalaska Island to date are mammoth tusks and molars found in 1801 (Stein, 1842; Ray, 1971). The record of marine mammal fossils other than desmostylians in Alaska is also depauperate. Fossil whales from Alaska are virtually unknown prior to the Pleistocene (Hopkins and Marincovich, 1984), and the same can be said of seals (Repenning et al., 1979).

LOCALITIES AND SPECIMENS

Unalaska Island

The occurrence of marine mammals, specifically desmostylians, from Unalaska Island was reviewed by Jacobs et al. (2007) who concluded that the age of the fossiliferous deposit lay between 24.1 and 13 Ma, but more likely at or just after the Oligocene-Miocene boundary (23.03 Ma). This locality, in the Dutch Harbor Member of the Unalaska Formation near Unalaska Lake, presents the oldest record of marine mammals in Alaska yet known.

Desmostylia, new taxon--At least four individuals of a new taxon of desmostylian, including one juvenile with dp4 beginning to erupt (Fig. 2), are known. Preparation has continued since the initial publication of Jacobs et al. (2007) and the specimens are more fully visible. Full description and phylogenetic analysis of this taxon is in progress and involves the digital reconstruction of the skull. The Unalaska desmostylian is more derived than *Cornwallius* but appears more primitive than *Desmostylus*, *Vanderhoofius*, or *Kronokotherium*. Younger desmostylian remains from Alaska reported below are more derived than the Unalaska taxon. In addition to the desmostylian material, two other mammals have been identified from the collections made on Unalaska Island.

Neoceti, indeterminate (MOTA 2004.009.10)**--**A whale is represented by a posterior fragment of a left mandible in sagittal section, exposing its lateral portion in medial view (Fig. 3). It is missing the ventral area below the lower limit of the tooth roots and the base of the coronoid process. The coronoid process is almost complete. Much of the bone is missing in the posterior portion of the jaw. The coronoid process is vertical, broad, lobate, and well defined with little distal overhang. It arises well posterior to the ultimate cheek tooth. The mandible below the coronoid is missing but the mold in the matrix shows a lateral curvature, indicating that there would be space for an enlarged mandibular foramen and canal. Approximately one cm of bone is missing at a gap that extends without displacement diagonally in a posteroventral direction from the junction of the ascending and horizontal rami. The angle between the posterior margin of the coronoid process and the dorsal margin of the mandibular neck (i.e., the mandibular notch) is perpendicular to obtuse.
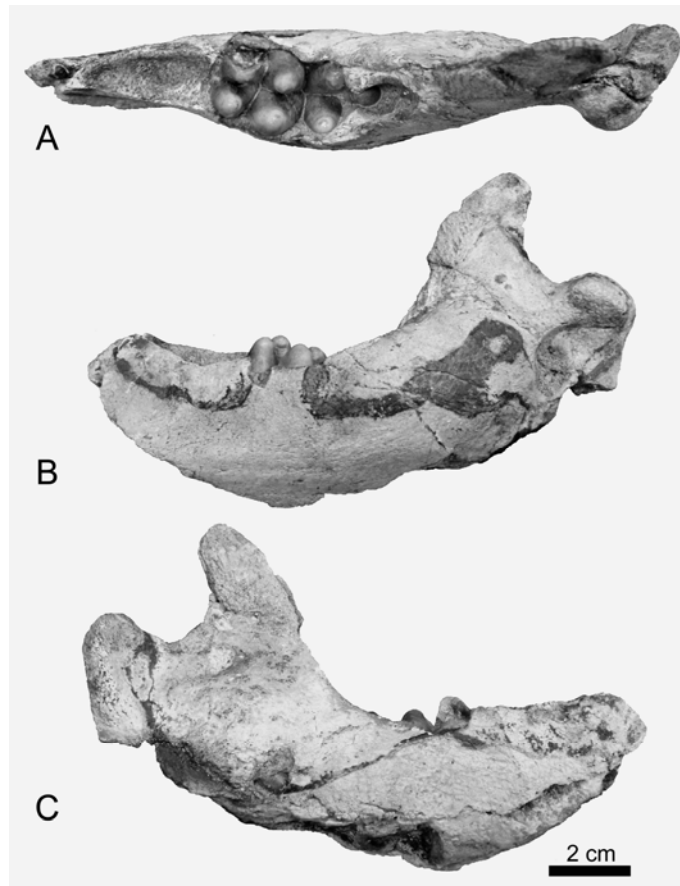
Figure 2. Juvenile desmostylian right dentary (MOTA 2004.009.06) from Unalaska Island. **A**, occlusal view; **B**, lingual view; **C**, buccal view.

The medial surface of the mandible is missing, exposing the internal portion of the bone, including teeth in sagittal section. The posterior-most three teeth are present. The specimen's anterior termination occurs at the first preserved tooth at the anterior portion of the crown and distal root. The second and third preserved teeth are double rooted and fully erupted. Teeth are spaced approximately 8 mm apart along the jaw. Tooth crown enamel terminates approximately 1 cm above the alveolar margin of the mandible, and the roots are emergent. The teeth are similarly shaped and of near equal size (distal tooth length = 16.2 mm; penultimate tooth length = 17.5 mm) with a central denticle, and as far as can be determined, accessory denticles along the distal and mesial margins. The most anterior tooth shows an acute central
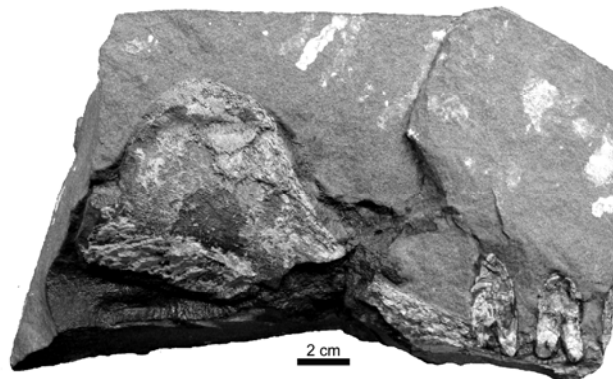

Figure 3. Basal neocete (MOTA 2004.009.10) from Unalaska Island, left mandible fragment in sagittal section, lingual view.

denticle and mesial and distal accessory denticles, with the apex of the mesial accessory denticle at a level just slightly lower than the distal accessory denticle. An impression in the matrix shows the enamel on the buccal surface of the crown to have fluted ornamentation, similar to the coronal ornamentation of basal Oligocene odontocetes such as *Simocetus rayi* (Fordyce, 2002) and *Xenorophus sloanii* (Kellogg, 1923), as well as stem Mysticeti in the families Llanocetidae (Mitchell, 1989) and Mammalodontidae (Fitzgerald, 2006; in press).

At least three accessory denticles can be seen on the distal edge of the second tooth, but none on the mesial margin, possibly due to the way it is broken. It is unclear how many accessory denticles lie on the mesial margin of the most distal tooth. Impressions of three accessory denticles lie along its distal margin.

We ruled out the affinities of this jaw with pinnipeds, which are hypothesized to have originated by the late Oligocene (Deméré et al., 2003). All pinnipedimorphs lack m3 (Berta and Wyss, 1994: their character 74), and all but *Enaliarctos* and *Pteronarctos* have lost the m2 (Berta and Wyss, 1994: their character 73). Those two genera retain a small m2. In addition, they have closely spaced teeth, retain a trigonid with a metaconid (although reduced), retain a talonid (albeit with only the hyponconid present; Berta and Wyss, 1994: their characters 71 and 72) on m1, and have a well-developed masseteric fossa (see illustrations in Berta, 1991, 1994).

The jaw fragment from Unalaska shows no sign of an alveolus for a smaller tooth behind the most distal preserved tooth (indicating that it does not have the primitive pinnipedimorph condition of retaining m2). In addition, unlike the condition in primitive pinnipedimorphs, the teeth are widely spaced and there is no evidence for a well-developed masseteric fossa.

On the other hand, possession of trenchant, double-rooted teeth with a central denticle and accessory denticles, and an inferred enlarged mandibular foramen, are features consistent with a cetacean identification. The coronoid process is more lobate, vertically oriented, and well defined than in crown group odontocetes, but resembles the more primitive anatomy of the coronoid seen in stem Odontoceti such as the xenorophid *Albertocetus meffordorum* (Uhen, 2008). The coronoid process of MOTA 2004.009.10 differs from that of mammalodontid mysticetes in being relatively shorter (dorsoventrally) and narrower (anteroposteriorly). Unlike the coronoid process in Aetiocetidae (e.g., *Aetiocetus weltoni*, Deméré and Berta, 2008), the coronoid of MOTA 2004.009.10 is not posteriorly reclined. Overall, the coronoid process of the mandible in MOTA 2004.009.10 most closely resembles that of the xenorophid *Albertocetus meffordorum*.

The tooth row of the Unalaska mandible terminates well in advance of the coronoid process and the teeth are openly spaced, both of which are derived characters relative to archaeocetes (e.g., Kellogg, 1936; Uhen, 2008). The presence of two roots is primitive for both mysticetes (e.g., *Janjucetus hunderi*, Fitzgerald, 2006) and odontocetes (e.g., *Xenorophus sloanii*, Kellogg, 1923), although the emergence of the roots above the alveolar margin is probably derived and is seen in both stem odontocetes (e.g., *Simocetus* and *Waipatia*, Fordyce, 1994, 2002), and stem mysticetes (Fitzgerald, 2006; in press). The lower cheek teeth of MOTA 2004.009.10 differ from those of most described aetiocetid mysticetes in bearing two distinct roots. The cheek teeth of aetiocetids, with the exception of *Morawanocetus yabukii*, are single-rooted (Barnes et al., 1995; Deméré and Berta, 2008). The teeth of MOTA 2004.009.10 differ further from those of aetiocetids in possessing strongly fluted enamel on the buccal surface of the crown. The buccal enamel of aetiocetid teeth is either smooth or only lightly fluted (Emlong, 1966; Deméré and Berta, 2008). The Unalaska specimen lacks the elongate palmate denticles seen in the cheek teeth of *Llanocetus* (Fordyce, 1989; Mitchell, 1989). Lastly, the relative size of the ultimate lower cheek tooth crown in MOTA 2004.009.10 differs from the condition in Mammalodontidae: both *Janjucetus hunderi* and *Mammalodon colliveri* have last lower tooth crowns that are distinctly smaller than the preceding crown (Fitzgerald, 2006; in press).

On balance, too few characters are present in the Unalaska specimen to determine precisely its phylogenetic affinities. Nonetheless, the mandibular and dental morphology is on the one hand more derived than that of archaeocetes, yet more plesiomorphic than crown odontocetes and mysticetes. We submit that MOTA 2004.009.10 represents an indeterminate example of basal Neoceti: either a toothed archaic mysticete of uncertain affinities or a stem odontocete. Below this level of classification, it cannot

be referred to any named clade. Conclusive determination of its systematic position must await the recovery of more complete cranial material associated with mandibular and dental remains.

　　Cf. *Kolponomos* (MOTA 2004.009.11)--A portion of a right maxilla with the lacrimal foramen and clear alveoli for two three-rooted teeth is identified as cf. *Kolponomos* (Fig. 4). The area for a more anterior alveolus is obscure but because of the width of the bone in that area, the preceding tooth would have been much smaller than that which followed. The bone is abraded, hindering accurate measurement. The anterior alveolus (L = 20 mm, W = 22 mm) lies under the posterior border of the large infraorbital foramen. The posterior alveolus is larger (L = 22 mm, W = 31 mm) and lies beneath the maxillary root of the zygomatic arch. The three-rooted condition and the roughly triangular shape of the alveoli indicate that the teeth filling them were broadly triangular in shape and quite large.

　　This maxillary fragment with alveoli for large teeth appears most similar in morphology and size to that of the ursoid amphicynodontid *Kolponomos*, sister taxon to pinnipedimorphs (Hunt, 1998; Tedford et al., 1994). Two species of the genus have been named, distinguished among other features by excavation of the maxillary anterior to the infraorbital foramen (Tedford et al., 1994). We are not certain how the Unalaska specimen compares to the two named species in that feature. *Kolponomos* has especially robust P4 and M1, which correspond to the large alveoli in the Unalaska specimen, with P4 beneath the infraorbital foramen and M1 at the maxillary root of the zygomatic arch. The described species of *Kolponomos* are limited to the early Miocene (Tedford et al., 1994). That age is consistent with and supportive of an earliest Miocene age for the Unalaska fossils.

Figure 4. Cf. *Kolponomos* (MOTA 2004.009.11) from Unalaska Island, right maxilla fragment with alveoli for three-rooted M1 and P4. Note infraorbital foramen.

Alaska Peninsula and Kodiak Island

　　There are three records of desmostylian dental remains, each from a separate locality, from the Alaska Peninsula. All three specimens are from the Bear Lake Formation of middle Miocene age based on mollusks and other invertebrates. The Bear Lake Formation crops out on both the north and south sides of the Alaska Peninsula. One of the teeth is represented by a cast, the other by a photograph, the third is a fragment of a tooth column. A desmostylian skull, currently in private hands, is known from the middle Miocene Narrow Cape Formation of Kodiak Island.

　　Cape Aliaksin and Beaver Bay--A single tooth of a desmostylian was found at Cape Aliaksin, along the southern coast of the Alaska Peninsula, by Louie Marincovich, Jr., of the U. S. Geological Survey in 1977 (Louie Marincovich, pers. comm., June, 2004). The helicopter in which he was being transported was forced down due to bad weather. While waiting for a break, Marincovich examined exposures of the Unga Conglomerate Member of the Bear Lake Formation exposed along the beach. He discovered both a desmostylian tooth and an unusually large gastropod, which he named

Tyrranoberingius rex (*T. rex* for short, Marincovich, 1981). The Bear Lake Formation in this area is early middle Miocene in age (early Langhian Stage *fide* Gradstein et al., 2004:16-15 Ma) based on mollusks (Marincovich, 1988a, b).

The tooth is from USGS locality M1340, but the specimen is misplaced. A cast of the tooth (Southern Methodist University, SMU 76395, Fig. 5) shows it is a left m2 or m3 comprising six columns. It is considered a left molar based on the vertical orientation of the cleft between the posterior columns and the lingually inclined cleft from the occlusal surface toward the base of the crown between the two anterior columns. Oriented in this way, wear on the lingual cusps is slightly greater than on the buccal cusps, as would be expected. The buccal columns align slightly anterior relative to the lingual columns. A small swelling is present on the buccal side between the bases of the middle and posterior columns. The crown height is similar to *Desmostylus*. In size (L = 67 mm, W = 39 mm), it falls within the range of the *Desmostylus* m2 presented by Inuzuka et al. (1995).

2 cm

Figure 5. Cast of desmostylian tooth (SMU 76395) from Cape Aliaksin, Alaska Peninsula, left lower molar in occlusal view, anterior to top. Note anterior placement of buccal columns relative of lingual columns, as in *Kronokotherium*.

The two recognized species of *Desmostylus* and *Vanderhoofius* cannot be distinguished on shape of molars (Inuzuka et al., 1995). If we are correct that the tooth is from the left side, then the buccal columns are displaced anteriorly relative to the lingual columns, consistent with the distinguishing character of *Kronokotherium brevimaxillare* as reported by Inuzuka et al. (1995) from the middle Miocene of Kamchatka (Pronina, 1957; Dubrovo and Sinel'nikova, 1971). A skull fragment containing a molar from the latest Oligocene or earliest Miocene portion of the Pysht Formation, Washington, was identified as ?*Kronokotherium* sp. based on small size (molar apparently less than 5 cm in length), hypsodonty, and lack of accessory cusps on either side of the distal talon (Barnes and Goedert, 2001). These authors also referred a scapula from the Early Miocene Clallam Formation, Washington, to ?aff. *Kronokotherium* based on small size. If size is the determining generic feature, the Cape Aliaksin tooth is too large to be *Kronokotherum*.

The record of a desmostylian from Beaver Bay, adjacent to Cape Aliaksin, is documented by a photograph in the Bear Lake Lodge located at Port Moller. The label with the photograph reads, "Lower right molar tooth from the extinct *Desmostylus* sp., a late Oligocene-Miocene sirenian. Similar to a manatee or sea cow. These large teeth were used to crunch clams rooted up underwater. Found in Beaver Bay, Alaska Peninsula, July 1976."

The tooth, as shown in the photograph, is a desmostylian right upper molar. Three columns are arranged transversely across the anterior of the tooth, marking it as an upper. The anterior rank of columns is followed by two offset ranks of two and a medial posterior column. The columns are straight walled and closely appressed. There appear to be low swellings near the base of the columns on the labial

side. There are more columns than would be expected in *Cornwallius*, but fewer than in some specimens of *Desmostylus* (Inuzuka, 1988).

      Bear Lake--A desmostylian fragmentary column (Dallas Museum of Nature and Science, DMNH 18248) from Bear Lake on the Alaska Peninsula was collected by Karen Clautice in the course of fieldwork undertaken by the Alaska Division of Geological and Geophysical Surveys. According to Robert Blodgett (pers. comm., August, 2005), a member of the field party, the fossiliferous zone is restricted to an approximately 3 m thick interval of softer silty sandstone with harder, calcareous-cemented sandstone beds or lenses. In addition to the desmostylian tooth and marine invertebrate fossils, especially echinoderms, a lower first anterior tooth of a mako shark, *Isurus* sp. (identification by Robert Purdy) was also found.

      The desmostylian specimen, although but a scrap, is useful in documenting the presence of desmostylians on both sides of the Alaska Peninsula. The surface of the enamel is corroded, but the straight-walled column shows in section the increasing thickness of enamel from the base toward the occlusal surface, which is in relatively light wear. The crown height measured in this specimen is 31 mm.

      Given the variation seen in the teeth of desmostylian taxa and their fundamental similarity, little can be said of the identity of these specimens except that they are similar to some *Desmostylus* in crown height, straight walled columns, and general morphology, and that they are more derived than *Behemotops*, *Paleoparadoxia*, *Ashoroa*, or *Cornwallius*. It is not unlikely that all three specimens from the Alaska Peninsula pertain to the same species, but that supposition cannot be demonstrated at this time. Regardless of the number of species from the Alaska Peninsula, none is the same species as that found on Unalaska Island, which is lower crowned and has more rounded columns.

      Kodiak Island--The Narrow Cape Formation (Moore, 1969) on the southeastern coast of Kodiak Island has long been known to produce a rich Miocene molluscan fauna from its type area, firmly dated to the early middle Miocene (early Langhian Stage *fide* Gradstein et al., 2004), 16-15 Ma (Capps, 1937; Nilsen and Moore, 1979; Marincovich and Moriya, 1999). Repenning and Tedford (1977) reported an otarioid rib from Narrow Cape that may belong to *Desmatophoca*. The area is frequented by fossil enthusiasts, at least one of which has decorated his garden with stones enclosing whale bones from the Narrow Cape Formation.

      The formation at Narrow Cape is composed of gray fine sandstone and siltstone deposited under shallow marine conditions. Round calcareous concretions weather out of the cliffs at Narrow Cape and tumble to their feet, creating a boulder field in the modern intertidal zone. Bedding and other primary sedimentary structures are preserved in the concretions.

      In one such concretion, an outdoor enthusiast discovered a desmostylian skull weathered out of the Narrow Cape sea cliffs. Little can be said about the skull in its current state of preparation (Fig. 6),
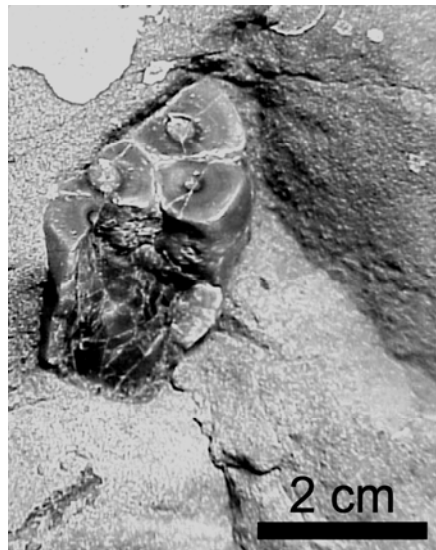

Figure 6. Desmostylian tooth in skull contained in concretion (private collection), Narrow Cape, Kodiak Island.

except that it is that of a derived desmostylian. A portion of an upper molar is exposed showing straight-walled, columnar cusps.

Yakataga

The eastern coast of the Gulf of Alaska is an important area because it contains a climatically significant set of rocks and it has produced a few incomplete marine mammal specimens, both seal and whale, but no desmostylians as yet. The record is scrappy and some unpublished specimens collected by Don Miller of the USGS are in the USNM. From the overlying Yakataga Formation, Repenning and Tedford (1977) reported a phocine radius (USNM 23876, their pl. 16) "most similar to that of *Pusa sibirica* among the radii of living phocids." The specimen is late Pliocene in age and was found about 1500 meters below the top of the Yakataga Formation in Malaspina District.

DISCUSSION AND CONCLUSION

The Alaska marine mammal fauna discussed in this paper lived in a North Pacific Ocean cut off from the Arctic Ocean by the Bering Land Bridge. In the Arctic, Eocene and younger climates were much less severe than today, supporting vertebrates and plants on Ellesmere and Axel Heiberg islands that could not tolerate today's conditions there. In the Aleutian Islands and the Alaskan Peninsula where the vertebrate and paleobotanical records are less extensive, marine mammal fossils have proven useful in age determination and paleoenvironmental interpretations that have relevance to both marine and nonmarine contexts.

The first published mention of a desmostylian from Unalaska was by Byers (1959) in his report on Umnak Island, west of Unalaska. No age-diagnostic fossils were discovered on Umnak, so Byers utilized lithostratigraphic correlations to tie sedimentary rocks in Umnak to desmostylian fossil-bearing strata on Unalaska. However, Byers did find "carbonized impressions suggestive of leaf fragments" on Umnak, although no plant fossils are known from Unalaska Island.

The vegetation of the Aleutian Islands today is naturally devoid of trees and characterized by one-layered, low, grassy and shrubby vegetation (Shacklette et al., 1969). Eocene plants from Alaska, Kamchatka, and from Bering Island in the Komandorskys at the far western reach of the Aleutian chain indicate warmer conditions than today (Chelebayeva and Akhmet'eva, 1983) and more extensive vegetation at least on Bering Island, if not all of the Aleutians. Large trunks and stumps are found in Eocene to Miocene rocks at several localities along the Alaska Peninsula (Albanese and Goff, 1987). Conifer forests are not found on any Aleutian Island today, but during the middle Miocene (14-7 Ma) pollen records show conifer forest with *Lycopodium*, *Osmunda*, *Abies Larix/Pseudotsuga*, *Picea*, *Pinus*, *Tsuga*, *Alnus*, *Betula*, *Myrica*, Centrospermae, and Ericales, reminiscent of southeast Alaska today, growing on Atka Island, west of Unalaska (Hein et al., 1984). The forests of Atka were burned and buried by Miocene volcanic avalanches and debris flows (Hein et al., 1984). Based on pollen from northern East China and from south Central Alaska, Liu and Leopold (1994) determined that the temperature gradient during the early and middle Miocene between 35° and 65°N was less than half as steep as it is today, meaning that the North Polar region was warmer. The conclusion is that throughout the mid-Cenozoic, when desmostylians and ?*Kolponomos* frequented their shores, the climate of the Aleutian Islands and most of Alaska was milder than today.

With respect to desmostylians, Gingerich (2005) showed through principle components analysis that *Desmostylus* was a forelimb-dominated swimmer, and he considered polar bears to be a good general model for it. He also suggested that while adult desmostylians were large enough to be relatively safe from predators, the young would have benefited from the safety of island refuges during birthing and early development. In that regard, it is interesting that the Unalaska Island population includes a neonate. Clementz et al. (2003) interpreted isotopic values of *Desmostylus* teeth to indicate a diet ranging from marine seagrass to estuarine and even freshwater aquatic plants.

Along with the desmostylian, the beach-bear, *Kolponomos,* foraged the early Miocene coast of Unalaska Island. Its morphology and habits were discussed by Tedford et al. (1994). The few postcranial bones available indicate that *Kolponomos* was well capable of terrestrial locomotion but its occurrence in littoral deposits suggests an amphibious lifestyle. Its large well-worn teeth suggest a diet of hard-shelled

invertebrates. The enlarged infraorbital and mental foramina suggest sensitive vibrissae and lips. The muzzle and lips may have been enlarged based on the shape of the premaxilla. The head was carried downward relative to the vertebral column. These features, plus flexure of the palate, orientation of the eyes, large and firmly supported anterior teeth, and strong paroccipital and mastoid processes led Tedford et al. (1994) to consider that *Kolponomos* fed by prying epifaunal invertebrates off rocky nearshore substrate and crunching their hard shells to obtain the contents. While the sensitive muzzle may have been similar to walruses and the enlarged teeth were similar to sea otters, *Kolponomos* fed differently and had a different habitus from either.

Kolponomos has no record after the early Miocene. By the middle Miocene the Unalaska Island desmostylian was replaced by more derived forms. While there is considerable disagreement, Marincovich (1990) considers that uplift of the Chugach and St. Elias mountains due to interactions with the Yakatat terrain led to early middle Miocene montane glaciation and the initiation of a cold counterclockwise current in the Gulf of Alaska. Warm water incursions indicated by mollusks date the inception of the current to 15-16 Ma (Marincovich, 1990) and allow correlation of the desmostylian-producing Bear Lake and Narrow Cape formations. Lagoe et al. (1993) disagree and place the inception of tidewater glaciation at 5-6 Ma. At the heart of the issue is the age of the lower portion of the Yakataga Formation. While it is beyond the scope of this paper to delve into the issue fully, desmostylians contribute to the discussion because they are found with warm-water mollusks within cold water, early middle Miocene sections (15-16 Ma) in the Bear Lake and Narrow Cape formations, and to our knowledge there are no known desmostylians independently dated as young as 5-6 Ma.

The cooling of Alaskan waters may have played a role in the extinction of desmostylians. Domning (2001) suggested that competition with sirenians was a major factor and that the desmostylian fate was sealed as the hydrodamaline *Dusisiren* adapted to cool waters. There are no published records of sirenians in Alaska other than the Pleistocene occurrence of Steller's sea cow, *Hydrodamalis gigas*, on Amchitka Island in the Aleutian Islands (Gard et al., 1972; Whitmore and Gard, 1977; Domning and Furusawa, 1995). Steller's sea cow was hunted to extinction by humans in 1768 (Domning, 1972).

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