An Intraoral Thermoregulatory Organ in the Bowhead Whale (*Balaena mysticetus*), the Corpus Cavernosum Maxillaris

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ABSTRACT

The novel observation of a palatal retial organ in the bowhead whale (*Balaena mysticetus*) is reported, with characterization of its form and function. This bulbous ridge of highly vascularized tissue, here designated the corpus cavernosum maxillaris, runs along the center of the hard palate, expanding cranially to form two large lobes that terminate under the tip of the rostral palate, with another enlarged node at the caudal terminus. Gross anatomical and microscopic observation of tissue sections discloses a web-like internal mass with a large blood volume. Histological examination reveals large numbers of blood vessels and vascular as well as extravascular spaces resembling a blood-filled, erectile sponge. These spaces, as well as accompanying blood vessels, extend to the base of the epithelium. We contend that this organ provides a thermoregulatory adaptation by which bowhead whales (1) control heat loss by transferring internal, metabolically generated body heat to cold seawater and (2) protect the brain from hyperthermia. We postulate that this organ may play additional roles in baleen growth and in detecting prey, and that its ability to dissipate heat might maintain proper operating temperature for palatal mechanoreceptors or chemoreceptors to detect the presence and density of intraoral prey. Anat Rec, 00:000–000, 2013. © 2013 Wiley Periodicals, Inc.

Key words: bowhead whale; mysticete; rete; vasculature; thermoregulation; sensation; palate; corpus cavernosum

Bowhead whales (*Balaena mysticetus* Linnaeus 1758) are well-insulated marine mammals. Although blubber thickness (the layer between epidermis and fascia of underlying muscle, including dermis and hypodermis; Parry, 1949; McClelland et al., 2012) has been reported more than 40 cm, it typically ranges from 20 to 35 cm over much of the body, averaging 28 cm for 13–18 m long adults (Fetter and Everitt, 1981; Haldiman et al., 1981; Haldiman and Tarpley, 1993; George, 2009), far exceeding that of other whale species. In addition to the exceptionally thick blubber, the rotund body form limits surface area, aiding in retention of metabolic heat. The combined effects of size, shape, and heavy insulation presumably make cold stress unlikely even in the bowhead's arctic habitat. Hokkanen (1990) suggests this

TABLE 1. Bowhead dissection specimens used in this study (all measurements postmortem)

Specimen ID code	Body length (cm)	Snout-blowhole length (cm)	Rete length (cm)
90B2	(Previously harvested organ only]		?
90B3	1,170	?	375
90B4 (H)	?	?	?
90B4F (H)	390	71	83.5
93B6	1,499	379	463
93B12	1,010	260	303
93B16 (H)	1,105	315	294

Specimen 90B4F was a near full-term fetus. Specimens marked with (H) were used in the histological analysis.

TABLE 2. Dimensions of the palatal organ of specimen 93B16, cut transversely into 12 serial sections

Section	Length (cm)	Width (cm)	Depth (cm)
1	60.7	7–14	1.5–12.4[a]
2	25	11	21
3	25	11	9.5
4	22	9	13
5	15	6.9	10
6	15	6.5	10
7	21	6.4	11.7
8	30.2	?	9
9	26	?	4
10	25	?	?
11	29	4	5
12	122	?	?

[a]Least depth from center fold to periosteum of maxilla, greatest depth for paired lobes. Damage during butchering by native hunters explains unknown values and varying lengths of sections.
Section 1 was most rostral (starting at tip of rostrum) and included the paired lobes (Figs. 1, 6); section 12 was most caudal.

species may face hypothermia at low exercise levels. However, there is no direct evidence of this. Most cetaceans dissipate heat through skin covering the flukes, flippers, and dorsal fin (Hokkanen, 1990; Costa and Williams, 1999), the latter absent in bowheads. Numerous thermoregulatory vascular adaptations have been described in musculoskeletal and internal organ (e.g., reproductive) systems of cetaceans (Rommel et al., 1992, 1993, 1998; Melnikov, 1997), including arteriovenous anastomoses (AVAs) in retia or other countercurrent heat exchange (CCHE) mechanisms that alternately preclude or facilitate heat loss depending on body temperature (Scholander and Schevill, 1955; Schmidt-Nielson, 1997). AVAs have been documented in the tongue of the gray whale, *Eschrichtius robustus* (Heyning and Mead, 1997, 1998); they are also found in the root of the tongue in bowhead whales (Werth, 2007). Given that the mouth of mysticete (filter-feeding baleen) whales is exposed to cold water for prolonged periods during feeding, and that the ambient temperature of this seawater is invariably below body temperature, it has been speculated that lingual retia and perhaps also palatal retia may be a universal feature of mysticetes (Heyning et al., 1993; Heyning, 1998). As the discrepancy between ambient and body temperature is great in polar species, and because the mouth is opened for long durations while skim feeding, it would be expected that thermoregulatory adaptation is an even greater priority for survival in *Balaena*.

A palatal rete, deduced to function in thermoregulation, has been described previously (Ford and Kraus, 1992; Heyning et al., 1993) in the North Atlantic right whale, *Eubalaena glacialis*. This cavernous organ, which can be engorged with blood (Ford and Kraus, 1992), is presumed to be an important heat sink that can lower elevated body temperature during migration or other strenuous activity. Accordingly, gross and microscopic anatomical study of the palate and associated structures of *Balaena* (sister species of *Eubalaena*) captured during subsistence hunting by native Inupiat whalers was undertaken to ascertain and characterize the presence of similar thermoregulatory features in this species.

MATERIALS AND METHODS

The heads of seven bowhead whales (six adult, one fetal; Table 1) harvested at Barrow, Alaska, were examined during a four-year period (1990–1993). All animals were harvested by Inupiat hunters through their exemption to the U.S. Marine Mammal Protection Act in accordance with guidelines established by the Alaska Eskimo Whaling Commission and the International Whaling Commission. Initial work was done on site at the locations where each whale was landed and harvested on the ice sheet, typically 8–10 miles offshore at the edge of ice leads. One specimen (90B2) was studied solely from a palatal organ that had been removed from a whale during harvesting; the organ was frozen and later preserved with formalin prior to laboratory examination. Recording of gross anatomical analysis began with photography, VHS videotaping, sketching, and measuring of undisturbed structures *in situ* followed by superficial and deep dissection on site. Standard photographic images were taken in various views. Additional thermographic imaging of bowhead specimens using a forward-looking infrared or FLIR camera (FLIR Systems, Boston, MA) permitted visualization of the location and absolute and relative amounts of heat loss in the oral cavity, and of the rate of heat radiation/cooling.

In one specimen (93B16, Table 2), the palatal organ was cut via transverse sections into 12 serial segments. The segments varied in length to take advantage of postmortem lacerations incurred during butchering of the animal's baleen racks by Inupiat hunters. Tissue samples and selected gross sections were removed from this and

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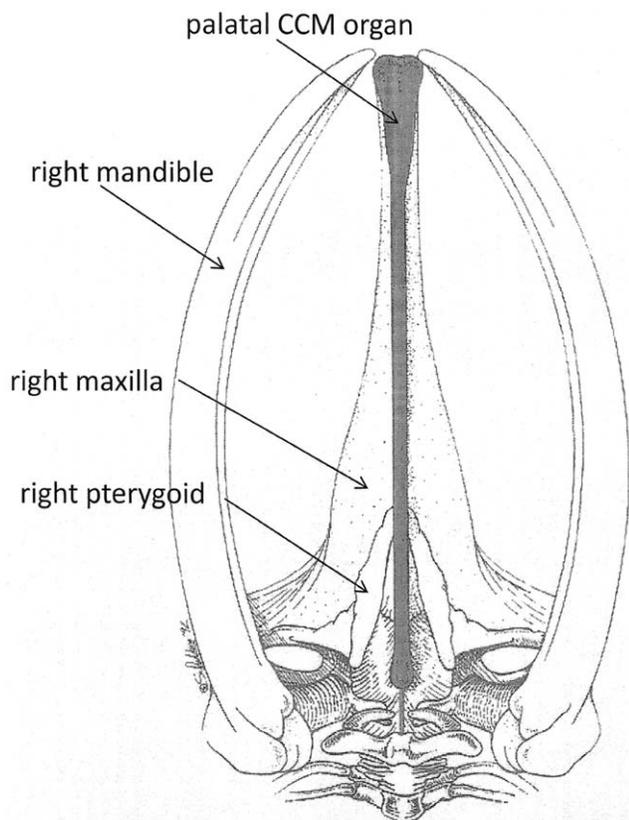
Fig. 1. The CCM is shown (central shaded area) in ventral view (rostrum at top) running along the palatal surface of the maxilla on the midline of the skull.

two other whales (Table 1) and immediately immersed in 10% buffered formalin solution. The samples were processed for paraffin histology at the Boston University School of Medicine. Tissue specimens were cut via microtome at 10 μm, and resulting sections were stained in hematoxylin and eosin for general tissue survey, using Gomori (trichrome) technique to highlight connective tissue, and the Bodian (silver) method to stain nerves.

RESULTS

A cavernous vascular organ nearly identical in external morphology to the previously reported intraoral rete of the right whale (Ford and Kraus, 1992; Heyning et al., 1993) was found in the same anatomical location in the bowhead whale, running longitudinally along the midline of the full length of the hard palate (Fig. 1). Its caudal-most limit is at the caudal end of the maxilla near the basioccipital bone, just above the fauces that open into the pharynx. This slightly enlarged but flattened caudal end of the vascular organ is associated with a notch in the suture line of the palatal plates. Cranially, the structure extends to the rostral-most limit of the upper jaw, at the subrostral gap between the paired racks of baleen, terminating in two large lobes (each one-fifth of the organ's total length) immediately caudal to what appear to be paired, vestigial depressions of nasopalatine duct openings, noted as bilateral pits on the ventral tip of the rostrum. The terminal rostral lobes

of the palatal organ are broader and flatter than those of the right whale (Ford and Kraus, 1992). The bowhead palatal organ retains a mottled pink and gray coloration, immediately postmortem and for many hours after death. When first sectioned (indeed, abraded or even trod upon during Inupiat butchering), its extensive network of perfusing vasculature and high blood volume is immediately apparent, from heavy blood flow, to the unaided eye.

Microscopic examination revealed a complex structure (Fig. 2A). The ventral (exposed) surface is covered with highly stratified, nonkeratinizing squamous epithelium. This is typical of normal oral gingival tissue. The integument has dermal papillae. Smooth muscle tissue is present in three orientations (transverse, dorsoventral, and longitudinal). Three to five bands of smooth muscle traverse the organ's width in the horizontal plane (left-right, lateral-to-lateral) for its entire length. Longitudinal muscle fibers also run the length of the organ at its lateral extremity. These longitudinal fibers are located dorsal to the horizontal bands. Small, scattered muscle fibers run radially in a dorsoventral orientation. They extend from the longitudinal groups to the dermis. Very little areolar tissue can be found near the ventral (exposed) surface. Diffuse, scattered elements of connective tissue support numerous blood vessels and myelinated nerves. Just below the surface are numerous free nerve endings and terminal bodies, along with general mechanosensory structures, including Meissner's and Pacinian corpuscles.

Deeper tissues display marked vascularization with, notably, centrally placed veins with large luminal openings (6–17 mm) and loose connective tissue elements (Fig. 2B). These cavernous spaces are separated by many fibrous trabeculae that extend in all directions, creating a sponge-like erectile tissue that resembles the corpus spongiosum of the penis. Veins dominate the entire organ with large vessels centrally located. These vessels are adjacent to an expansive network of venous spaces, with diameters decreasing to capillary size (averaging 9 μm in diameter, and one endothelial cell in thickness). Several veins of large diameter demonstrate marked degrees of elastic tissue in the outer tunic. Principal venous drainage appears to be through two large venous sinuses located lateral to the main body of the organ and between the maxillary periosteum and the organ proper. These sinuses derive from branches of the internal maxillary veins. Large, thick-walled arteries, terminal branches of the internal maxillary and sphenopalatine arteries (as described by Walmsley, 1938), are centrally positioned close to the periosteum of the maxilla. Small arterioles are found associated with nerve bundles throughout the organ. No venous vessels are found that exhibit an internal elastic membrane. Lymphatic vessels are loosely scattered throughout the organ, but no lymphoid nodules can be found here.

A notable histological feature of this organ is the marked innervation of the tissue. Myelinated nerves of varying diameter (0.01–0.6 mm; Fig. 2C) are present throughout the cavernous spaces (Fig. 2D). Given the position and origin of the palatal organ, these nerves (Fig. 2C) are likely to be branches of the second division of the trigeminal nerve, which innervates the maxilla in all mammals.

Figure 3 shows the gross anatomical position of the organ in a dead whale. The organ was swollen and firm yet
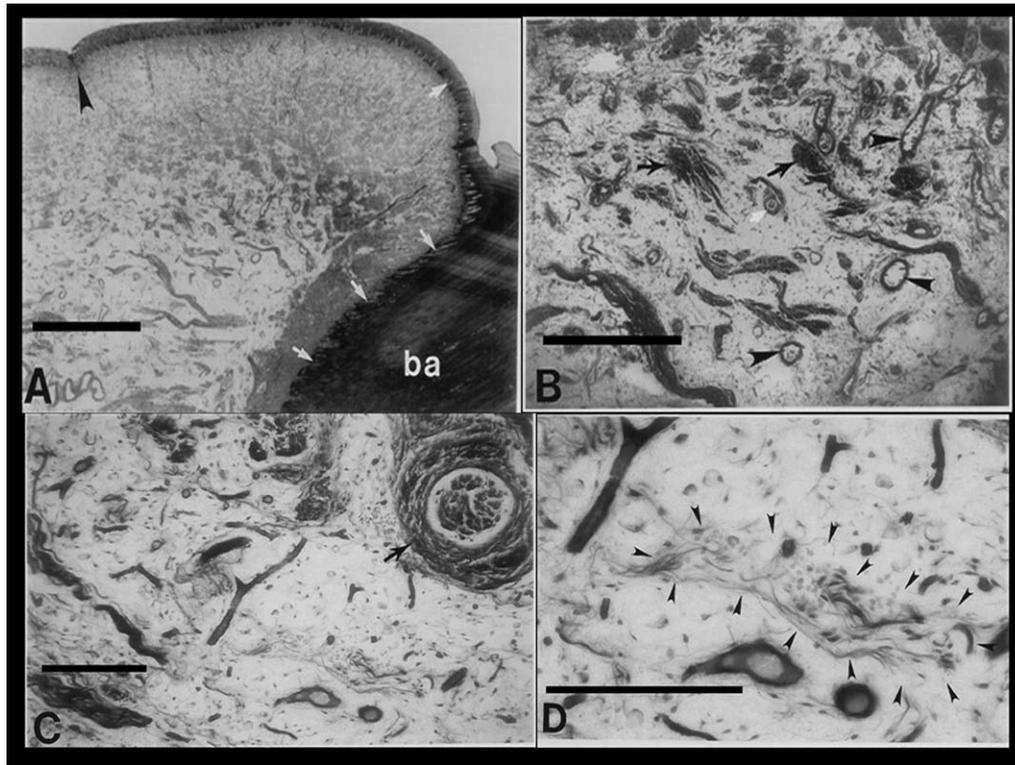
Fig. 2. A: Photomicrographic overview of the CCM, near the center of its length (scale bar = 1 cm). The large darkly stained area at right is baleen (labeled ba). White arrows indicate the basal layer of epithelium; note dermal papilla transition from gingiva to baleen plate. The dark arrow indicates the center line of the oral surface, at the depressed midline of the palatal organ. Deeper tissues are markedly vascular with centrally placed veins with loose connective tissue elements and cavernous spaces separated by many trabeculae extending in all directions to create a sponge-like erectile tissue. **B**: Photomicrograph of central tissue area (A) (scale bar = 1 cm), showing myelinated nerves (tailed arrows) and large arteries (plain arrowheads), circuitous vasculature, smooth muscle, and extravascular spaces. Trabeculae are composed of collagenous, elastic, and smooth muscle fibers. **C**: Arrow indicates myelinated nerve inside CCM (scale bar = 1 mm). Note also highly vascularized tissue, with small, meandering vessels and apparently collapsed spaces. **D**: The notable extravascular space delineated by arrows contains vascular elements, numerous erythrocytes, and a few lymphocytes (scale bar = 1 mm). Blood cells are extravascular. Engorgement of these sponge-like erectile tissue areas allows blood accumulation.

still soft to the touch. The animal shown in Fig. 3 died approximately 7 hr before the standard and infrared (FLIR) photographs were taken, indicating an extended capacity to hold and radiate heat. Temperatures measured from the palatal organ remained 6–8°C above other external body surfaces for up to 10-hr postmortem. Neither gross nor microscopic examination of the palatal organ revealed any adipose tissue or other insulating structures.

DISCUSSION

The bowhead whale palatal vascular organ is a rete (Fawcett, 1942), though it lacks the typical CCHE network with periarterial venous "rosette" configuration characteristically seen in a retial AVA, particularly in cetaceans (Werth, 2007). Instead, a striking feature of this organ is the presence of a high number of irregular cavernous vascular spaces, together forming a large sponge-like region which comprises much of the organ's total volume. Red blood cells can be readily seen within these spaces, indicating the erectile nature of the organ, whose histology is highly reminiscent of the corpus cavernosum of the mammalian penis owing to the numerous fibrous trabeculae separating cavernous spaces

(Krstic, 1991; Fawcett, 1994; Kelly, 2000, 2002). Connective tissue fibers (including many elastin and some areolar fibers) are sparse and irregularly rather than uniformly arrayed. The bowhead whale palatal organ's extensive venous network, large cavernous spaces, and sponge-like trabeculae all suggest a structure that is alternately distended and collapsed. The highly stratified squamous oral surface of the organ strongly resembles transitional epithelium, as in the transitional epithelium of the urinary bladder or another space that is prone to contraction and expansion. This arrangement suggests tissues that can stretch to hold large volumes of blood.

These features of the organ, and its placement on the oral surface of the maxilla, have led to this newly described structure being named the corpus cavernosum maxillaris (CCM). This organ has not been described previously in general morphological accounts of this species (Reeves and Leatherwood, 1985; Haldiman and Tarpley, 1993) nor in publications that focus on bowhead oral anatomy (Pivorunas, 1979; Tarpley, 1985; Lambertsen et al., 1989, 2005). Although this organ was most closely investigated in the seven specimens examined for this study (Table 1), its presence and its relatively high
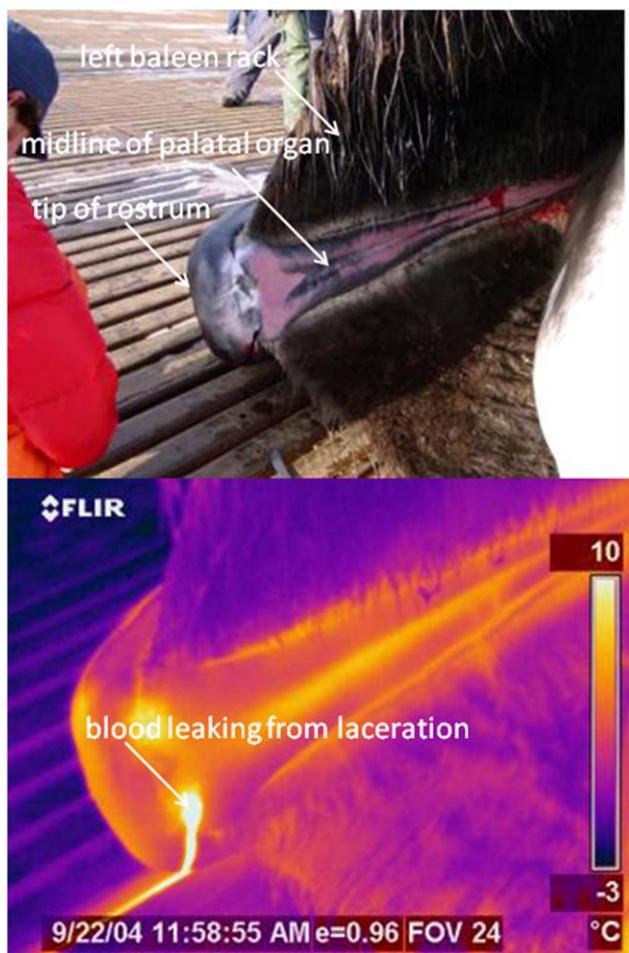
Fig. 3. The upper photograph shows the CCM organ in visible light, illustrating its gross anatomical position on the palatal midline (in oblique ventral view, looking into the mouth of a whale lying on its back and right side). The lower photograph was taken with a FLIR camera. Note that the organ continues to hold and radiate heat (indicated by bright orange color) in this animal, deceased for 7 hr when both photographs were taken. Thermal analysis indicates that the palatal organ remains 6–8°C above other external body surfaces for up to 10-hr postmortem.

blood volume has been observed and noted for many years in numerous bowhead whales of all sexes and ages (of the Beaufort-Chukchi Sea population) hauled out on ice or shore for butchering, as well as in stranded individuals. In all recorded cases, the dimensions, pigmentation, and other external aspects of the CCM were the same as in the specimens reported here. Several Inupiat people were consulted for traditional knowledge of this organ. They had noticed the structure previously but did not consider it to be of any anatomical or physiological significance. The organ is routinely cut up or otherwise destroyed by the process of harvesting the baleen from the upper jaw, and is of no food value.

The bowhead tongue may remain a major source of oral heat loss in this species, particularly during long bouts of continuous filter feeding although it has manifest vascular adaptations (viz. CCHE retia) for heat con-

servation and large deposits of lingual adipose tissue (George, 2009). The amount of fat in the bowhead tongue varies seasonally, likely for energy storage in addition to thermal insulation (Werth, 2007). However, the palatal CCM appears, unlike the highly insulated tongue, ideally suited to shed heat to the environment. The thermal conservation or loss evident through the organ's relatively warm surface (via infrared photography, Fig. 3) reveals its exceptional vascularization. The thermoregulatory capacity of this uninsulated organ is largely owing to the fact that it extends nearly one-third of the animal's total body length, in a prime location of direct contact with flowing water.

The CCM's total surface area when engorged, estimated from direct measurements and photographs to be 0.48 m^2 in a 15-m whale with total surface area of 130 m^2, is small compared to that of the flukes (~4% of fluke area), which may also play a role in radiating excess body heat (Elsner et al., 2004). Unlike the skin and tongue and uniquely among bowhead thermoregulatory structures, the CCM has no blubber or other fat layer. The CCM also lacks conspicuous arteriovenous retia for organized countercurrent blood flow. Its dermal papilla configuration would aid in heat transfer, which is dependent on temperature differential, and the CCM has the highest heat flux measured anywhere on the bowhead's body surface (George, 2009). Given the bowhead's lack of a dorsal fin and the stout, rotund body shape, especially relative to the slender forms of balaenopterid whales, this species has less relative surface area available for cooling than other mysticetes. The metabolic rate of *Balaena* is not known but is often presumed to be fairly low, allowing this species to have an exceptionally long lifespan (George et al., 1999; George, 2009). However, the high drag generated by the continuous ram filtration of balaenid (bowhead and right) whales, in which the mouth is held open and pushed forward by muscular propulsion from the tail (Baumgartner and Mate, 2003; Werth, 2000, 2004, 2012), likely leads to the production of substantial metabolic heat. Digital acoustic recording tag data published by Simon et al. (2009) reveal high fluking rates during bowhead whale feeding dives off the coast of Greenland, signifying the high drag encountered while foraging. Strenuous swimming during dives and long distance migrations, also common in *Balaena* (Nowacek et al., 2001), similarly can be presumed to generate significant body heat that must be lost to prevent hyperthermia.

Owing to its location in the center of the mouth, the CCM is ideally positioned to radiate excess body heat, even with its small surface area (~0.48 m^2). The organ is largest at its rostral terminus, where water flowing into the whale's open mouth, at the subrostral gap between baleen racks, is coldest and most turbulent. The paired, enlarged terminal lobes of the CCM would allow full exchange of heat from engorged vessels with cold ambient seawater. Engorgement of the CCM is not presumed to involve change in shape or notable change in size except for slight increase in depth (ventrally) and width (laterally) although this was not measured. The main change from its flaccid state involves greater stiffness, especially of the paired anterior lobes, which become swollen and turgid.

Tissue examination of the CCM reveals terminal bodies and rich innervation, likely relating to control of

blood vessels, although it is possible that the profusion of nerves relate to sensory function. Both the anatomical position and the histological composition of this organ suggest a facultative thermoregulatory function. The heat shown in Fig. 3 (6–8°C higher at the CCM than in other external body surfaces) could be residual or owing to decomposition; nonetheless, it indicates a prime location for thermal exchange, whereas the remainder of the bowhead's body, being covered with blubber or avascular keratinous baleen, is unsuitable for heat transfer.

The caudal end of the CCM is associated with a groove in the center line of the pterygoid plate of the skull. The organ's vasculature, which was observed to traverse this groove, may link with the basicranial rete (Albert, 1980; Haldiman and Tarpley, 1993) at the base of the skull external to the foramen magnum. This would allow preferential cooling of blood entering the calvaria, protecting the brain from potential damage owing to hyperthermic blood flow (Albert, 1980). Overheating of the brain is a major concern for all mammals, particularly those whose core body temperature is subjected to major fluctuations. However, there is no apparent direct connection between the CCM and its vessels with vertebral arteries and anastomotic branches from the dorsal intercostal arteries which together form the rete mirabile (Walmsley, 1938) that delivers blood to the brain.

The tongue has a median sulcus that runs along the length of its dorsal surface (Lambertsen et al., 1989; Werth, 2004). Rostrally, this groove widens into a spoon shaped depression to accommodate the expansion of the bifid bulbs of the CCM. A fringe of epithelial lingual rugae rings the rostral dorsal margin of the tongue and may enfold the cranial end of the palatal organ. The tongue's dorsal surface is itself well insulated by subdermal fat deposits (Werth, 2007), but the underlying intrinsic and extrinsic lingual musculature afford substantial mobility for prey capture and removal from baleen fringes (Werth, 2001). Tongue movements could also restrict water flow to the immediate area of the palatal organ's surface, maximizing heat loss from the CCM while (at the same or different times) potentially shielding other intraoral tissues from the chilling effect of water. Under active control, the tongue can rise steeply in the caudal section and match the curved contour of the maxilla quite closely (Werth, 2004; Lambertsen et al., 2005). It is possible yet unlikely that the CCM warms the tongue.

Thermoregulation typically involves means both to radiate and to conserve heat for which CCHE structures are well suited. We surmise that the CCM acts mainly as a heat sink (a passive heat exchanger that lowers temperature by dissipating heat to the surrounding medium), with little if any heat conserving function although blood flow could be restricted and therefore reduce the heat flux described here. No evidence was seen of typical CCHE organization in the bowhead palatal rete, which is more aptly described as a corpus cavernosum, with a thin surrounding layer of areolar tissue and less elastic tissue yet more vascular and extravascular space than a corpus spongiosum. Engorgement of the CCM occurs when the internal muscularis relaxes and blood floods into vascular sinus spaces lined with true endothelium (as in the penile corpora cavernosa), extravascular spaces (not lined with endothelium), and

collapsed veins. Blood flowing in the CCM appears to be ordinarily from artery to capillary bed and on to veins. Erection of the organ apparently redirects vascular flow from arteries to vascular sinuses and extravascular spaces, then to veins. Collapse of the organ results when smooth musculature contracts, forcing blood into underlying venous sinuses. The consistent finding of blood cells in extravascular spaces (of various whales and histological sections) suggests this condition is not an artifact of paraffin histology preparation or owing to inflammation or other physiological response in living animals. It should be noted that adult whales examined for this study did not die of natural causes; it is possible that this extravascular blood results from agonal death although many whales harvested by Inupiat hunters die instantly (George, 2009). Nonetheless, the histological results shown in Fig. 2 are from a near full-term fetus that was not traumatized but died *in utero*.

Two mechanisms working in concert may govern heat loss by (1) control of water flow along the CCM's surface and (2) vascular engorgement or constriction of blood vessels internal to the organ. Control of water flow is apparently somatic, dependent on both gape angle and shape and position of the tongue relative to the CCM. If the mouth is not open, there is no possibility of heat loss. Control of the palatal organ's vascular engorgement may be strictly autonomic. The CCM's profuse innervation is presumably provided (it was not traced back directly) by the autonomic fibers of the second division of the trigeminal nerve, which innervates the maxilla in great whales (Jacobs and Jensen, 2004). Some part of this extensive innervation may relate to control of the vascular complex. Heavy myelination implies an active and rapid neural action (Barrett and Barrett, 1982), suggesting a high degree of control of the CCM's vasculature and musculature. It is possible that a temperature-sensing function may be involved although microscopic examination yielded no definitive proof of that capacity in this organ.

Bowhead whales seen swimming with open mouths during migration (Carroll and Smithhisler, 1980), when there is no indication of concomitant foraging, could be using the CCM to shed excess heat generated by long durations of locomotion. The organ could be employed intermittently depending on ambient water temperature and the need to discharge excess waste heat. Unlike foraging conditions, the mouth need not be fully opening under migratory conditions. A small gape would allow full exposure of the organ to cold water. No matter the gape, effluent water flowing past the CCM would pass along the orolabial sulci (the spaces lateral to the baleen racks and medial to the lips) and exit the oral cavity through the corners of the mouth behind the semicircular lower lips (Werth, 2001, 2004, 2012). Field observers of balaenid whales must be cognizant of the potential for open-mouthed behavior to be thermoregulatory in nature rather than for foraging. Unless plankton tow netting confirms the presence of food, it cannot be assumed that such behavior implies active feeding. Reassessment of previous conclusions regarding observed open-mouthed behavior of bowhead (and right) whales may be warranted.

The evolutionary and developmental origins of this apparently unique structure are unknown. Unlike the paired, adjacent corpora cavernosa of the penis, the

bowhead palatal organ is a single erectile body, surrounded by a single fascial layer although it is cleft rostrally. It may be derived from a bilaterally paired structure that partially fused, or from a midline structure that bifurcated anteriorly. It may be derived from the midline block of tissue that forms the hard palate and alveolar ridges of other mammals (Evans and Christenson, 1979; Haldiman and Tarpley, 1993) although there appears to be little histological similarity, given the lack of keratinizing epithelium of the bowhead. The palatal CCM organ of the lone fetus examined for this study (90B4F) had a structure identical to that of the juveniles and adults that were inspected (Table 1). Examination of younger fetal or embryological whale material could clarify this question.

Preliminary study suggests that additional mysticete species may possess some form of palatal rete though likely with a more typical CCHE organization as in the right whale, *Eubalaena*. The pygmy right whale (*Caperea marginata*, Neobalaenidae) has a similar oral structure. This species is much smaller than balaenid (bowhead and right) whales, with a different body form and little-known foraging ecology (Baker, 1985; Fordyce and Marx, 2013). van Utrecht (1958) described retial CCHE rosettes in "baleen beds" of balaenopterid whales. Cursory examination (previously unpublished) suggests a smaller, less extensive palatal organ may be present in at least four balaenopterid (rorqual) mysticetes: blue (*Balaenoptera musculus*), fin (*B. physalus*), minke (*B. acutorostrata*), and humpback (*Megaptera novaeangliae*) whales. The presence of a palatal organ in Balaenopteridae would suggest its evolutionary origin as a derived feature of crown Mysticeti; at the least it seems a derivation of Balaenidae.

Although conjectural, we speculate, based on the findings from balaenids, that if a similar palatal vascular organ is indeed present in rorquals, it likely has a function similar to that of the bowhead CCM. However, a balaenopterid vascular organ would probably have less erectile tissue and extravascular space and hence less ability to eliminate heat during hyperthermic conditions, yet possibly better heat conservation capacity. Given that many rorqual species spend at least part of the year in cold, high-latitude waters and generate significant drag and body heat during lunge feeding and locomotion (Goldbogen et al., 2007), intraoral thermoregulatory function would be highly adaptive. We further speculate that mysticete palatal organs aid in baleen growth, given their extensive, diffuse blood supply and proximity to extensive, dynamic, ever-growing baleen racks along both sides of the rostrum. However, there is no evidence that the vascular bed of the palatal organ supplies the baleen. Evidence that baleen growth is modulated by changes in vascular supply or temperature is equivocal (van Utrecht, 1965; Schell et al., 1989).

Finally, although speculative, we postulate, based on the CCM's location and high degree of innervation (as in the right whale rete), that it is ideally suited to serve as a sensory structure to detect temperature, water flow/pressure, contact with the tongue, or the presence, and abundance/density of planktonic prey within the mouth (Werth, 2012). Studies of other marine mammal cranial mechanosensory structures (seal mystacial vibrissae; Denhardt et al., 1998) have shown that sensitivity of mechanoreceptors is impaired by low ambient tempera-ture, and thus that effective sensory function depends on proper maintenance of suitable operating temperature via vasodilation. In addition, studies of manatee hairs (Reep et al., 2001) suggest that blood sinuses and ampullae surrounding tactile vibrissae amplify mechanical stimulation and aid mechanosensory reception. Both the dermis and the subdermis of the bowhead CCM were found to contain numerous scattered Pacinian and Meissner's corpuscles and free nerve endings. The CCM nerve endings are branches of the second division of the trigeminal cranial nerve, which is typically associated with mechanoreception. Clearly, this speculative hypothesis requires further study, particularly to discern the exact distribution of sensory cells and neural connections, yet it could explain the exceptional ability of this organ to dissipate heat, which therefore might serve not only to lower total body temperature but also to heat the organ and adjacent palatal tissues (including sensory epithelium) for optimal mechanosensory function.

The possibility of oral prey reception in whales has attracted much speculation, particularly in balaenids (continuous filter feeders of tiny planktonic prey); yet, no hard evidence exists either for such a ability or for a structure with which to effect it. Pyenson et al. (2012) have published strong evidence for a sensory organ in the mandibular symphysis of balaenopterid mysticetes, which they claim coordinates rorqual lunge feeding behavior by relaying sensory input from the mandibular symphysis and fibrocartilage associated with ventral groove blubber. Although supported by this initial histological study, the notion of the bowhead CCM as an intraoral sensory organ remains speculative and requires further analysis.

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