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Injuries in a Mysticete Skeleton from the Miocene of Virginia, With a Discussion of Buoyancy and the Primitive Feeding Mode in the Chaemysticeti

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ABSTRACT

A mostly complete skeleton of a mysticete from the Carmel Church Quarry displays some injuries, including a fractured and partially-healed left mandible, previously not reported in any fossil mysticete. The mostly healed nature of this non-union impaction fracture indicates that the animal died a significant amount of time after the injury. Additional injuries of the postglenoid process and left premaxilla, as well as the nature of the impaction fracture in the mandible suggest that the cause of this was some impact from the left anterior aspect. Possible scenarios for how this injury could have happened include intraspecific aggression and, more likely, impact with the seafloor during benthic feeding. The ribs of this individual are heavily osteosclerotic from dorsal to ventral ends, which would suggest that this taxon was a benthic feeder. In comparison with a sample of ribs from fossil mysticetes, it appears that *Diorocetus* may have been one of the last mysticetes with rib osteosclerosis, a feature possibly primitive to Mysticeti. Although this remains speculative, the presence of osteosclerotic ribs in primitive mysticetes suggests that the feeding mode employed by the earliest Chaemysticeti was one of benthic feeding.

Keywords: paleopathology, bone fracture, Cetacea, Mysticeti, Miocene, Calvert Formation, osteosclerosis

INTRODUCTION

“Whales are probably among the healthiest of living creatures”
Walter Ross Cockrill, 1960.

Modern cetaceans are susceptible to many of the same diseases as terrestrial mammals, although studies of the incidence of pathologies from years of data collecting from whaling ships and strandings have shown that they appear less susceptible to succumbing to natural injuries (Cockrill, 1960; Slijper, 1979). Cases do exist however, and include spondylitis that has been recognized in balaenids (Ledwell et al., 2007) and balaenopterids (Félix et al., 2007) and usually associated with bacterial infections spread among social animals. But the fossil record of disease and injury in marine mammals in general is not extensively studied, though many case reports exist (Bjotvedt and Turner, 1977; Pilleri, 1988; Dawson and Gottfried, 2002; Godfrey and Altman, 2005; Thomas et al., 2008), and recently more comprehensive studies of pathology utilizing more than strandings records have been brought to light (Moore et al. 2009). In a few cases, larger studies of their potential paleobiological meaning (Mulder, 2001) or more thorough studies of pathology frequencies in modern and fossil marine mammals have been reported (Beatty and Rothschild, 2008). The fossil record of such diseases and injuries is particularly interesting in marine mammals because of the extreme changes in their anatomy and physiology required of their lifestyles in water, particularly in terms of locomotor, respiratory, and cardiovascular physiology, which should presumably result in different susceptibilities to diseases than terrestrial organisms.

Excavations in the upper part of the Calvert Formation at the Carmel Church Quarry in eastern Virginia during 2006 resulted in the collection of a partial skeleton of a small baleen whale. The Carmel Church Quarry has been excavated for 19 years and has yielded a large Miocene fauna that includes numerous mysticetes, including new taxa (Dooley et al., 2004) and numerous other marine vertebrates, as well as terrestrial mammals (Dooley, 2007).. With a fauna this rich and well-preserved, it should not be surprising that some of the mysticete material would allow for detailed study of pathologies. This new specimen, VMNH 120000, tentatively identified as *Diorocetus hiatus* Kellogg, 1968, includes an essentially complete cranium, both dentaries, the first 24 vertebrae, and numerous ribs (Figure 1). Ribs from this specimen were first discovered

in March 2006, during the excavation of another nearby mysticete skeleton. Excavation of the ribs led to the discovery of the rest of the skeleton, which was collected during May and June 2006. Preparation of the specimen began in March 2007. The purpose of this report is to describe some unusual partially healed injuries visible on this specimen and what these injuries and other features of the skeleton suggest about this mysticete's paleobiology.

Paleopathologies in mysticetes are largely unreported except for cases of isolated vertebrae that cannot be identified beyond the suborder level (Thomas et al., 2008). Because behaviorally induced paleopathologies may occasionally lend insight into aspects of paleobiology that are otherwise unknowable (Beatty and Rothschild, 2008), it is hopeful that this specimen may allow us to gain some insight into fossil mysticete lifestyles. First we will describe these injuries, including the mandibular fracture, injuries to the postglenoid processes and premaxillae, and then discuss features of its skeleton that contribute to understanding this animal's paleobiology.

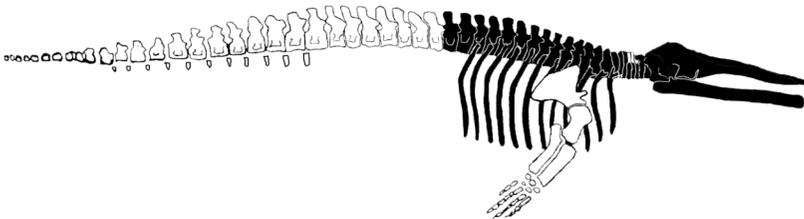


Figure 1. Skeletal reconstruction of VMNH 120000 with known elements indicated.

MATERIALS AND METHODS

Institutional abbreviations: **USNM** – United States National Museum of Natural History, Washington, DC; **VMNH** – Virginia Museum of Natural History, Martinsville, Virginia.

To aid visualization of these pathologies we generated x-ray images of these specimens using a VET-ATR Digital X-ray machine; when contrast of these images was digitally enhanced, the enhancement was applied uniformly across the image.

Cortical bone thickness in VMNH 120000 and NMNH modern and fossil cetaceans was measured with Mitutoyo digital calipers from broken or previously cut ends. Avoiding cutting or breaking specimens

for this study limited the sample available, but limited destructive sampling of unique specimens. In an attempt to make the data collected this way as comparable as possible, when possible these measurements were collected from ribs from the same position, and at the same location on each rib. Because future work may demonstrate that rib structure varies greatly depending on the rib or position within the rib, specifics of where data was collected for each rib is reported to allow for comparison of data once a larger dataset of this nature can be collected (see Table 1).

Rib cross sections are rarely circular, making total thickness measures a matter of two measures, one of the cranial/caudal thickness as well as the superficial/deep thickness. The nature of rib morphology usually causes the cranial/caudal thickness to be greater than the superficial/deep thickness because of the oval-shaped cross section of most ribs. For fragmentary specimens where we could not be absolutely certain about which axis was cranial/caudal or superficial/deep, it was assumed that the longer axis was cranial/caudal and the shorter axis of the cross section was superficial/deep.

Aside from complex cross-sectional area analyses outside the scope of this study, no methods currently exist for comparison of rib cortical bone thickness and how it may scale, so only raw measurements of cortical bone thickness compared to total rib thickness are reported, along with simple averages of the composition of cortical bone to overall rib thickness.

INJURY DESCRIPTION

This whale shows evidence of injuries not previously described in any fossil mysticete. The left dentary was broken completely in half at approximately its midpoint during the life of the animal. The fracture occurred 68.5 cm from the rostral end of the dentary, and 61 cm from the caudal end of the dentary, at approximately half the length of the mandible (Figures 2, 3). The wound was apparently beginning to heal, but the two halves of the dentaries never fused back together. New bone growth (callus) is evident in abundance near the edges of the break. The mandibular canal can be seen open in both ends, although the edges of them near the break and callus formation show some evidence of narrowing due to endosteal bone growth. This can be seen in X-rays (Figure 3), as can the larger displacements of bone in the fracture itself. We can be sure that these fractures occurred at the time of injury because

this endosteal bone growth appears to cover and encompass part of these fractures near the broken ends, indicating that they occurred in life. The fracture appears to have displaced both broken ends considerably, much like what would be seen in an impaction fracture. When the broken halves of the left dentary are articulated, the overall length of the dentary (129.5 cm) is considerably shorter than the right dentary (133.8 cm). Together, the bony callus and displacements due to the fracture have made this region of the mandible 89 mm in height (compared to nearby healthy dentary height of 77 mm) and 67 mm in width (compared to nearby healthy dentary width of 44 mm).

Impaction fractures are not commonly seen in the mandibular body of most mammals, primarily because the morphology of their mandibles makes this region one of the least likely to experience compression along its long axis (Tams et al., 1997). Impaction fractures are most common in postcranial long bone elements of terrestrial animals as a result of sudden excess loading along the long axis of the bone. Most mandibles are dorsoventrally taller than they are mediolaterally broad, presumably to increase their resistance to bending in the sagittal plane. Mysticete mandibles are also dorsoventrally taller than mediolaterally broad, but are also much longer and their dorsoventral height is relatively far less. This could be because of the lack of dentition and surrounding alveolar bone, but is probably also due to the bowed mandibles and complex mechanics of feeding employed by modern mysticetes (Lambertsen et al., 1995). At present nothing quantitative is known about how differences in feeding modes employed by modern mysticetes (such as ram-feeding by balaenids) is reflected or influenced by the morphology and mechanical differences seen in their mandibles, although rostral curvature might be considered a means of differentiating skim-feeders from engulfment feeders.

What is perhaps most curious is that despite this evident healing, the two portions of the dentary appear to have never united. Non-union fractures are difficult to narrowly define, as they are simply fractures that persist in not uniting for various reasons, usually because of persistent edema to the site of fracture (Ray et al., 1964). Because most callus formation in mandibular breaks depends on the delivery of blood to regions affected (Rhineland, 1968; Nilsson and Granström, 1987), it is probable that either the inferior alveolar artery escaped being severed by

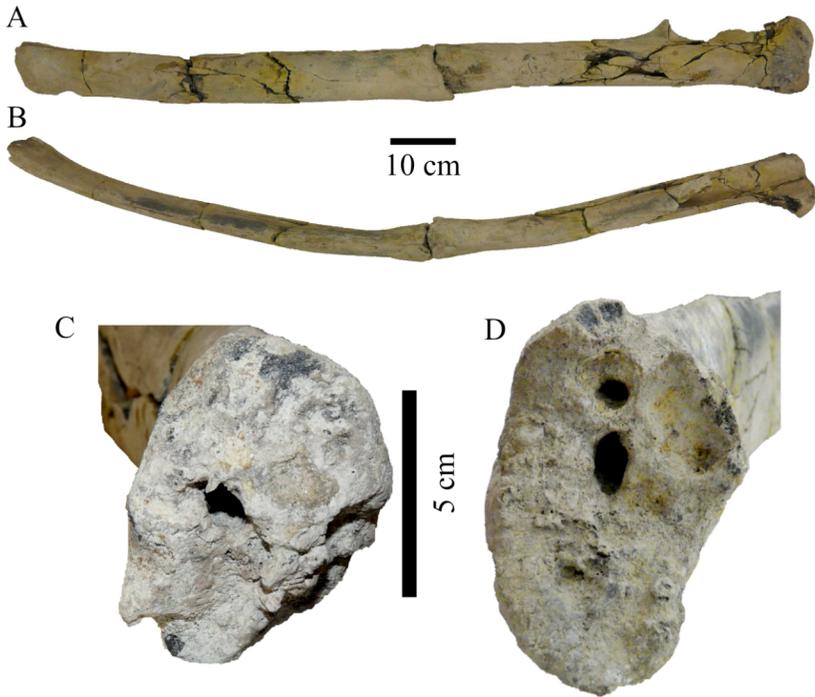


Figure 2. Broken left dentary of VMNH 120000 in A) lateral view, B) dorsal view, C), end-on view of broken surface of posterior portion, and D) end-on view of broken surface of anterior portion.

this fracture, or enough periosteal circulation remained to allow for the rostral end of the break to heal as well. The periosteum is one of the primary sources of osteogenic cells in callus formation in mandibular breaks, so any disturbance of it should have delayed healing or prevented it altogether (Rasubala et al., 2004). Without histological data for the bone, let alone the soft tissues that are long lost to time, it is impossible to get a more complete view of the stage of repair of this fracture. Studies of fractures in mysticete mortalities today require more complete analysis of soft tissues and histopathology to determine causes of fractures and whether they occurred antemortem, perimortem, or postmortem (Campbell-Malone et al., 2008), but the status of the fracture in this fossil mysticete shows enough healing that we can confidently claim that it occurred antemortem. This individual may have died prior to

completion of healing, although some healing was certainly ongoing and a future union may have been incipient. With only this moment in time of the healing of this fracture it is impossible to determine if periosteal and/or endosteal healing has ceased, and whether any soft tissues acted in any way to cause structural stiffness that would allow more precise classification of this fracture as normal, delayed union, or non-union fracture (Marsh, 1998). Still, in trauma-associated mandibular body fractures that fail to unite (non-union fractures), osteomyelitis is commonly associated and a likely secondary cause of the failed union, probably due to pyogenic bacteria that enter the injury from the mouth (Mathog et al., 2000). Although it is hard to imagine bacteria proliferating in a mouth awash in seawater so regularly, chronic lesions of this sort are known in the oral mucosa of balaenids (Albert et al., 1980; Philo et al., 1990).

In experimental work on displaced closed fractures in dogs, it appears that callus formation may be visually noted by the third week after a fracture (Rhineland et al., 1968). Even though data on the rate of bone growth in cetaceans is lacking, this rate of callus formation is fairly common in mammals and at least indicates that callus formation of this sort indicates that the fracture occurred at least a week or more prior to the time of death. So, though the details of surrounding soft tissues cannot be assessed here, it can be fairly confidently stated that this was something comparable to an impaction fracture one would see in a long bone, that maintained enough circulation (either from the inferior alveolar artery or periosteal circulation) that growth on both ends had begun to form a callus, and that this animal had persisted to live for some time, perhaps weeks after the injury occurred. Baleen whales have huge energy reserves in the form of blubber, which has been used to explain how they are able to migrate between large expanses of ocean that have little food, and may even explain why among some species females are often bigger than males (Brodie, 1975). Modern cases of rope entanglements of right whales have shown that they may be able to survive for months on their fat reserves with ropes entangling their baleen and/or rostrum, probably hindering their ability to feed (Moore et al., 2006). Indeed, this individual fossil mysticete may have lived for weeks or months with this injury, even if it hindered feeding success and led to a long, drawn-out starvation.

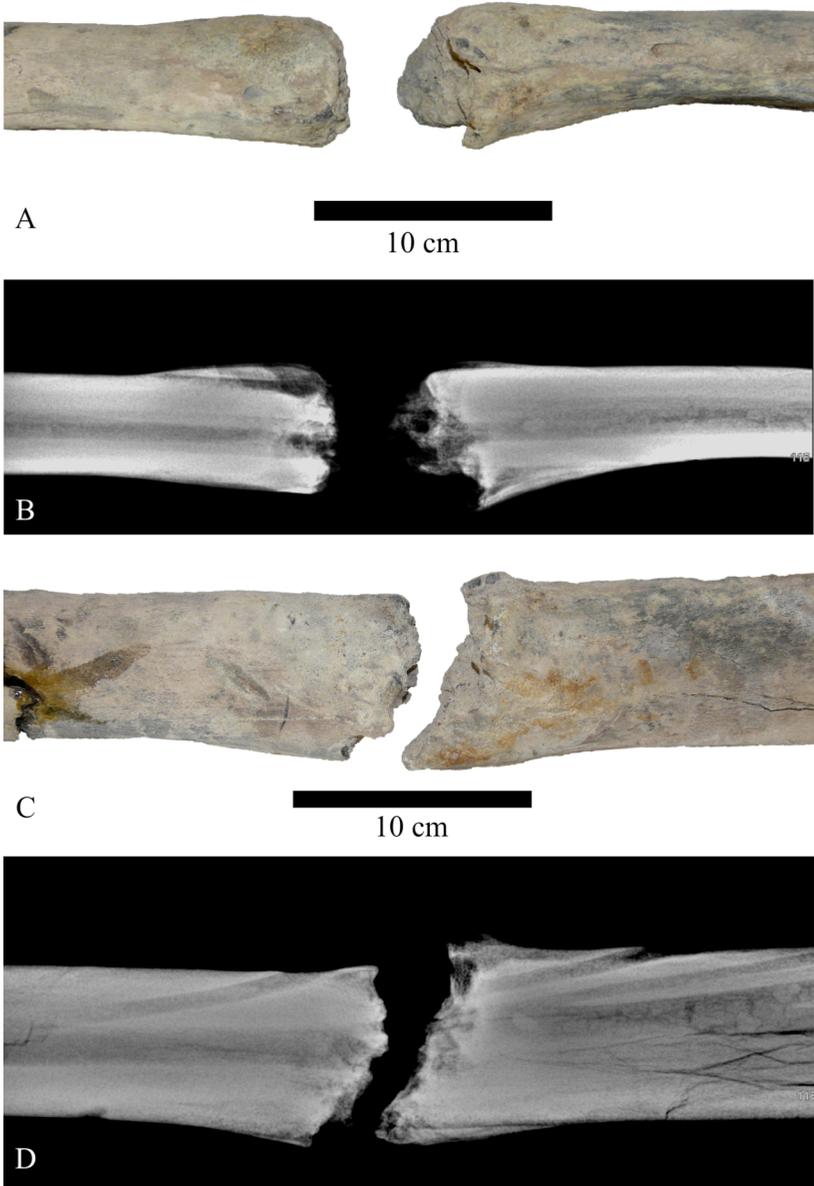


Figure 3. Broken portion of left dentary of VMNH 120000 in A) photographic dorsal view, B) x-ray dorsal view, C) photographic medial view, D) x-ray medial view.

Elsewhere in the skull there is also evidence of an injury to the rostral end of the left premaxilla (Figure 4). The rostral end of the premaxillae in this animal are laterally expanded as compared to most other mysticetes. This can be clearly seen in both the injured (left) and healthy (right) sides, although on the injured side it can be seen that the rostral tip is damaged, shorter, and indented. This surface appears to have some remodeled bone, indicating that it too occurred some time before death and was healing to some degree. This injured tip lies at the same point as the tip of the left mandible would be in a slightly open position. Both of these edges are not as perfectly preserved as they are posteriorly, but enough reparative bone allows us to confirm that they suffered injury prior to death.

Lastly, though erosion cannot be counted out here, the left postglenoid process appears broken and unusually porous in comparison with the right postglenoid process. The ventral part of the left postglenoid process is missing, and although this edge seems too damaged to determine if the broken edge occurred in life or after fossilization, the whole postglenoid process appears more dominated by vacuities, making it radiographically lighter (Figure 4). The damaged nature of this postglenoid, however, makes this diagnosis extremely speculative.

DISCUSSION

What causes fractures in mysticetes?—Other than ice-breaking-related abrasion around the blowholes of balaenids (George et al., 1989), injuries to the rostrum and/or mandible in modern mysticetes are most well-known from boat collisions (Wiley et al., 1995; Laist et al., 2001) although such collisions can be found in many regions of the body and be found as blunt traumas or propeller cuts (Douglas et al., 2008). Even more than rope entanglements, ship collisions appear to be the major cause of *Eubalaena glacialis* mortalities in the Atlantic, and are often associated with massive fractures that, in at least some cases, the animal died from after a period of time that allowed for necrosis and some fracture remodeling (Moore et al., 2004). One case report of a *Balaena mysticetus* harvested off the coast of Alaska showed evidence of long-term necrosis after a mandibular break with no evidence of reduced body condition (Philo et al., 1990), suggesting that mandibular breaks in at least some mysticetes might not result in death for prolonged periods of

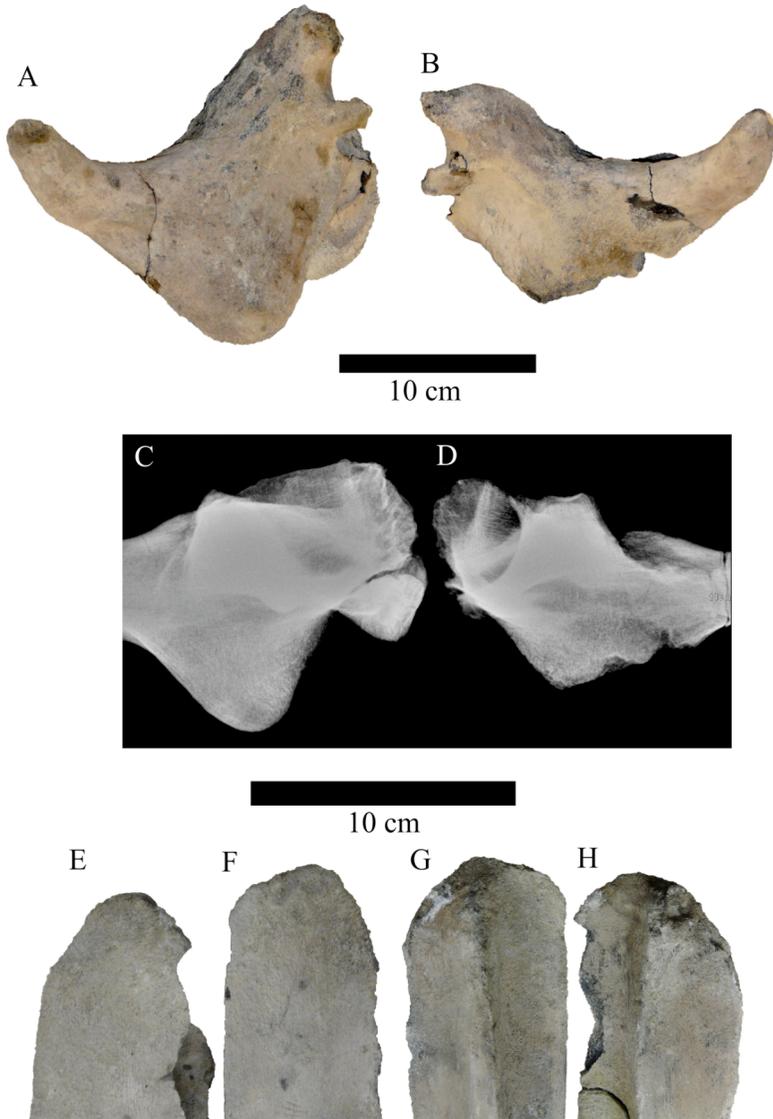


Figure 4. Squamosals and premaxillae of VMNH 120000. Right squamosal in A) photographic ventral view and C) x-ray ventral view. Left squamosal in B) photographic ventral view and D) x-ray ventral view. Left premaxilla in E) dorsal view and H) ventral view. Right premaxilla in F) dorsal view and G) ventral view.

time. In that individual's case, it was apparent that the inferior alveolar artery was severed (and probably the periosteum as well) and the resulting avascularity reduced the degree of healing. This fossil mysticete, on the other hand, must have maintained its vascular supply despite the break, as it can be clearly seen that both anterior and posterior broken ends show signs of healing.

But ship collisions were certainly not occurring in the Miocene, so what sort of event could lead to a fracture? Blunt traumas can lead to fracture, although it seems as if the number of potential impacts that a whale is likely to encounter are few. Could a predator cause such an impact? The injuries in VMNH 120000 are limited to the midpoint of the left dentary, the anterior tip of the left premaxilla, and possibly the left postglenoid process; there are notably no injuries to the premaxilla nor to the maxilla adjacent to the site of the dentary break. Although *Carcharocles megalodon* teeth were found in close association, as well as several hundred teeth from smaller sharks, only bite marks suggesting post-mortem scavenging have been found. Predation and/or scavenging by sharks on whales is certainly documented, even in the fossil record (Deméré and Cerutti, 1982), but this is not the same as an injury that has subsequently healed. Secondly, the fact that this injury shows healing suggests that if it were a predatory event, it was unsuccessful. Most importantly, few if any marine predators attack prey in ways that would lead to a compressive fracture. It has been speculated that some fossil mysticetes with vertebral compression fractures were injured during shark attacks (Godfrey and Altman, 2005), but this sort of impact from below (or the flank) is not a feasible cause for an impaction fracture in the mandible. Scarring in mysticetes clearly show signs of how predators injure them, which is usually dominated by bites in the posterior of the torso and caudal region (Kraus, 1990; George et al., 1994) that result in blood loss, scarring, and sometimes death, not blunt impacts.

What about intraspecific interactions? Although odontocetes are known to have violent intraspecific interactions (Connor et al., 2000), the data for mysticetes is almost entirely focused on the odd lekking-like behaviors of *Megaptera* and only rarely involves serious bodily strikes that can lead to injury or death (Tyack and Whitehead, 1983; Baker et al., 1987; Weinrich, 1995; Pack et al., 1998; Craig et al., 2002; Spitz et al., 2002). The rostral callosities of *Eubalaena* are larger in males and have been implicated in male-male aggression and fighting (Payne and Dorsey, 1983), though the injuries resulting from this are usually cuts

and scrapes that lead to visible non-pigmented scars. Studies of testis size and behavioral observations of *Eubalaena* indicate that females mate with multiple males (Payne and Dorsey, 1983; Swartz, 1986; Payne, 1995), sometimes with simultaneous intromission (Brownell Jr. et al., 1986), suggesting that balaenid mating strategies are not dominated by male-male aggression (Connor et al., 2000). In studies comparing cetacean male aggression with that of other Cetartiodactyla (Lusseau, 2003) it has been assumed from these two taxa and ambiguous anecdotal records of *Eschrichtius* ramming whaling ships (Krupnik, 1993) that all mysticetes engage in head-butting behavior during intraspecific aggression. Head-butting has otherwise never been observed in modern mysticetes, despite years of observation and it seems possible that these cases are derived and not common among all mysticetes. Still, one cannot completely rule out intraspecific aggression as a potential cause for this injury. If it were, the nature of the fracture being one done by impaction may suggest that this individual was the one doing the head-butting. If so, the impact would have had to be from an oblique angle to only involve the left side.

How else could trauma occur? Aside from other animals, the only other solid object in these environments is the seafloor. But do mysticetes ever impact the seafloor? There is anecdotal evidence that scars on the head and rostrum in *Eubalaena* are likely caused by collision with a mud/gravel substrate (Kraus, 1990), and in these cases every individual with these scars and scrapes had mud on top of their rostra indicating a recent substrate interaction.

Among causes of death of 68 marine mammals found stranded along the Oregon coast in January 1973, grey whales (*Eschrichtius robustus*) most frequently had head trauma as their primary cause of death compared to odontocetes and pinnipeds (Stroud and Roffe, 1979). *Eschrichtius*, being a benthic feeder, forages in a complex coastal habitat and probably impacts the seafloor regularly. Obviously injurious impacts should be rare, but benthic feeding certainly multiplies the probability of an injurious impact.

Lateralization?—Perhaps most curious, but also the most speculative, feature of this specimen is that the left mandible is the injured one. Lateralized behaviors (“handedness”) has been observed in marine mammals (Marino and Stowe, 1997), especially among those feeding in a specialized way that interacts with the seafloor, such as in strand-

feeding *Tursiops truncatus* (Hoese, 1971), *Odobenus* (Levermann et al., 2003) and gray whales (Woodward and Winn, 2006). In at least some populations of gray whales, benthic feeding appears to be preferentially done with the right side of the mouth based on worn baleen and observed behaviors (Kasuya and Rice, 1970; Woodward and Winn, 2006). Humpback whales also show some signs of lateralized behaviors preferring the right side, although injuries resulting from their preferential direction of spin during benthic feeding only results in cutaneous scrapes and scars (Clapham et al., 1995), not bone fractures. Even though there is a clear population-level right-side preference in mysticetes, 10-20 percent of these populations seem to have a left-side preference (Kasuya and Rice, 1970; Woodward and Winn, 2006). If this break was the result of a benthic feeding event gone wrong, VMNH 120000 may have had a preference for feeding with its left side.

Feeding and the Ancestral Condition—Modern Chaemysticeti (baleen-bearing mysticetes) are mostly rather large animals. Most balaenopterids are the largest animals on the earth today, and even though the largest ones do not appear until the Plio-Pleistocene, most fossil baleen-bearing mysticetes are fairly large in comparison with their Eocene and Oligocene toothed mysticete cousins in the Aetiocetidae, Janjucetidae and Mammalodontidae (Barnes et al., 1994; Fitzgerald, 2006; Deméré et al., 2008). There have been some interesting hypotheses on the causes and role of body size extremes in mysticetes including pituitary specializations (Edinger, 1942), though at present the factor considered most influential has been the development of filter feeding that came with the development of baleen. Presumably filter feeding has allowed whales to shift away from the agility needed to pursue individual prey and instead focus on less agile means of filtering large amounts of water for more numerous smaller prey items. At large sizes baleen whales are less controlled by water viscosity and more controlled by inertial forces than their small prey items by virtue of their vastly different Reynolds numbers (Werth, 2000). Of course, no single adaptive role can be identified, and it is worth considering the role of body size in the ability of individuals to endure longer periods without food during parts of their migrations (Brodie, 1975), the benefit of body size as a means of deterring predation, and the role that migration enabled by body size might have on predator avoidance (Corkeron and Connor, 1999).

But baleen does not restrict whales to a single mode of feeding, and many mysticetes employ different means of using baleen to their greatest potential. Coarse-fringed baleen-bearing mysticetes tend to be less specialized and eat more large prey items than mysticetes with finer-fringed baleen (Nemoto, 1970). Gray whales, which have the shortest and coarsest baleen of extant mysticetes, are primarily benthic feeders (Nemoto, 1970), sucking in mud and filtering out benthic invertebrates and fishes (Darling et al., 1998) and leaving significant changes to the benthic substrate and its community (Nerini and Oliver, 1983), although depending on prey availability they can also feed on planktonic prey (Dunham and Duffus, 2001). Balaenids, though often observed skimming food at or near the water's surface (Watkins and Schevill, 1979), are generally found feeding where prey is densest (Baumgartner and Mate, 2003), taking advantage of upwelling zones that concentrate prey (Rogachev et al., 2008). These prey concentrations can cause them to dive to significant depths and, based on stomach contents, rostral scrapes and mud on their heads, certainly must be skimming along the bottom as well (Carroll et al., 1987; Kraus, 1990). Balaenids, in contrast to gray whales and rorquals, have the longest and finest baleen plates and a larger area of filtering per body size than engulfment feeders (Nemoto, 1970). *Caperea* has baleen texture and filtering area similar to the balaenids, and is most likely a "skimmer" (Sekiguchi et al., 1992). Rorquals typically feed using an engulfment method, either horizontally or coming up from below prey, which usually keeps them free from interaction with the bottom (Watkins and Schevill, 1979). However, some evidence of bottom feeding has been noted for *Megaptera* in the western Atlantic, characterized by rostral scrapes known as "jaw scuffing" (Hain et al., 1995). When these feeding modes are optimized on a cladogram of the Mysticeti (Deméré et al., 2008), one can see that the most parsimonious assumption is that engulfment feeding is derived in the Balaenopteridae, and that the primitive state for the Chaecomysticeti (the "true" mysticetes (Mitchell, 1989)) is some mix of benthic and continuous ram filter feeding ("skimming").

Mysticetes evolved from toothed cetaceans that probably fed like many odontocetes do today, with interdigitating teeth used in capturing single prey items (Fitzgerald, 2006). Previous analysis of baleen evolution in mysticetes had suggested that some toothed mysticetes, particularly aetiocetids, represent a stage in which filter feeding utilized teeth and baleen together (Deméré et al., 2008). If the primitive state for

all of the Chaemysticeti can be inferred from optimizing the feeding modes of modern taxa, then these early baleen-bearing mysticetes probably fed much like modern balaenids and gray whales do today, optimizing oral morphology to allow prey to flow into the mouth (Werth, 2004) as well as feeding, at least occasionally, from the benthos.

The Role of Buoyancy in Feeding—Except for seals that exhale before diving (Scholander, 1940; Kooyman et al., 1970; Kooyman 1979), all other mammals dive with lungs full of air, including cetaceans (Ridgway et al. 1969), sea lions (Dormerer et al., 1977), and manatees (Scholander and Irving, 1941). If the primitive mode of feeding included benthic feeding as a component, the earliest Chaemysticeti would have needed some manner of becoming negatively buoyant, as reaching the benthos is a challenging task for an otherwise positively buoyant marine mammal with lungs at least partially full of air. A number of modern and fossil marine vertebrates that have osteosclerotic, pachyostotic, or pachyosteosclerotic bones are inferred to have been negatively buoyant and used this for feeding purposes (Stein, 1989; Domning and Buffrénil, 1991; Taylor, 1994; Ricqles and Buffrénil, 2001; Buffrénil et al., 2008). Yet, among the Cetacea the only reported pachyosteosclerosis has been reported in *Basilosaurus* and *Zygorhiza* (Buffrénil et al., 1990), which has been interpreted as an adaptation for maintaining trim during swimming. Modern odontocete ribs are thin with thin cortical bone compared to terrestrial mammals of similar size (Buffrénil et al., 1990). The osteoporosis-like state of the bones of odontocetes is argued to enhance maneuverability by making the skeleton lighter, although other factors may cause this skeletal lightening as well (Buffrénil et al., 1985). This skeletal lightening, in addition to the effect of blubber buoyancy, makes many odontocete carcasses positively buoyant post-mortem (Schäfer, 1972), and presumably pre-mortem. Among mysticetes, balaenopterids are generally considered to be negatively buoyant when deceased, although balaenids are positively buoyant (which is the reason right whales were considered the “right whales” to hunt) (Nowacek et al., 2001). It is still unclear whether the osteoporosis-like state found in odontocetes is universally found in all Neoceti. Skeletal histology in mysticetes is generally considered “spongy” (= osteoporosis-like) (Nowak, 2003), but published data on bone structure and/or histology in mysticetes is actually quite scarce (Klevezal and Mitchell, 1971) (almost

negligible) and has not received as much attention outside of the ear region (Ketten, 2000).

One feature observed in this wonderfully preserved individual is the osteosclerotic nature of its ribs (Figure 5). The outer appearance of these ribs is not abnormally thick (hence, not pachyostotic), yet the medullary cavity is smaller and the cortical bone is thicker than in typical mysticetes (osteosclerotic). This is an example of osteosclerosis by means of endosteal filling of the medullary cavity (Ricqles and Buffr enil, 2001), presumably by appositional growth. Although comparative data for other mysticetes is limited, other mysticetes from Carmel Church, including *Eobalaenoptera* and cf. *Metopocetus*, have ribs that are not osteosclerotic to the same degree (Table 1). This cortical bone thickness occurs throughout the length of the rib, not just in the ventral ends like in archaeocetes (Buffr enil et al., 1990), indicating that this had a ballast function rather than a role in maintaining trim or preventing rolling like it is presumed to have had in basilosaurids. Compared to sirenians that have completely solid pachyosteosclerotic ribs, this mysticete's osteosclerosis may have only cancelled out the buoyancy of the blubber and allowed for more neutral buoyancy. Still, this probably would have eased regular benthic feeding.

To better assess whether or not rib osteosclerosis is primitive or derived for this taxon, we investigated ribs of modern and fossil mysticetes from the USNM collections that were previously broken or sectioned and available for study. Cross sectional dimensions and cortical bone thickness were measured using digital calipers for a selection of modern and fossil mysticetes (Table 1) and compared. This preliminary data indicates that cortical bone thickness in relation to total rib thickness is a primitive character for mysticetes, as is evident in the toothed mysticete *Aetiocetus cotylaveus* and the earliest known chaemysticetan (Uhen, 2007) (Table 1). Cortical bone thickness measures from the Carmel Church *Diorocetus* (VMNH 120000) are very close to those of *Aetiocetus*. Other chaemysticeti such as the balaenid *Balaena ricei*, as well as *Pelocetus*, and especially *Eobalaenoptera* and balaenopterids such as VMNH 120001 and *Megaptera*, have much smaller cortical bone thickness ratios than *Diorocetus* and *Aetiocetus*. *Metopocetus*, *Parietobalaena*, and the subadult holotype of *Diorocetus hiatus* (USNM 16783), have cortical bone thickness ratios closer to that of VMNH 120000 and *Aetiocetus*, but still reduced in comparison.

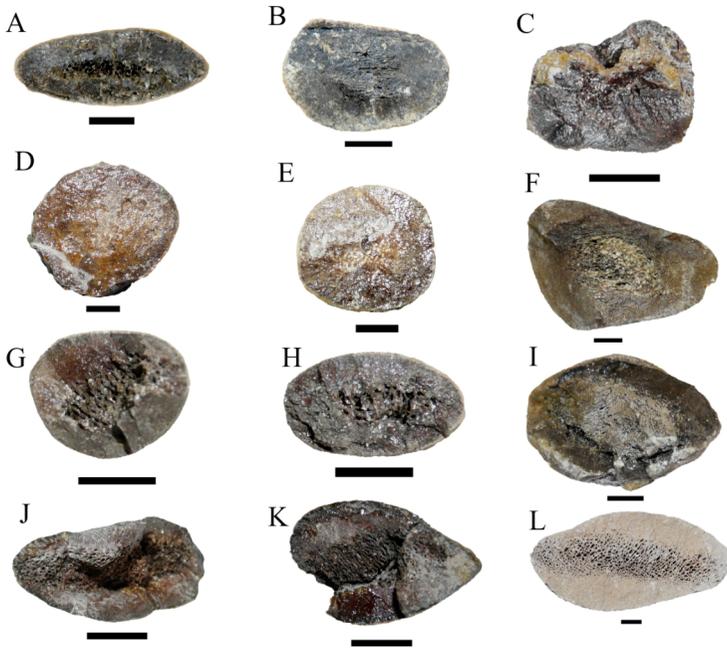


Figure 5. Cross-section of ribs of various mysticetes. A, B) *Diorocetus hiatus*, VMNH 120000. C) early chaemomysticetan, USNM 314627 (Uhen, 2007). D, E) *Aetiocetus cotylaveus* USNM 25210. F) Balaenopteridae, VMNH 120001. G, H) cf. *Metopocetus* sp., VMNH 1782. I) *Eobalaenoptera harrisoni*, VMNH 742. J, K) *Diorocetus hiatus*, USNM 16783. L) *Balaena ricei*, USNM 22553. All scale bars = 1 cm.

It is curious that osteosclerosis is found in *Diorocetus*, a member of the stem mysticetes that is considered the sister taxon to balaenids and eschrichtiids (Deméré et al., 2008). No mention of osteosclerosis is made in descriptions of fossil eschrichtiids (Ichishima et al., 2006), but no mention of rib internal structure is made in these at all, and no mention of unusual rib histology has been noted in any modern mysticetes among the few studies investigating the histology of various bones, including ribs (Klevezal and Mitchell Jr., 1971). If rib osteosclerosis were more commonplace in mysticetes, especially *Eschrichtius* and balaenids, then it would be a feature supporting the notion that the primitive feeding mode in the Chaemomysticeti was one of ram-feeding (“skimming”) and benthic feeding. However, in light of this small sample of data it appears as if *Diorocetus* may have either retained osteosclerosis

plesiomorphically from its pre-Chaeomysticeti mysticete ancestors, or alternatively, redeveloped it for adaptive reasons. Without a more thorough study of postcranial osteosclerosis in modern and fossil mysticetes, we may never know whether this trait and its functional consequences were arrived at once and lost, or repeatedly evolved in mysticetes that needed to achieve neutral buoyancy.

Likewise, among modern mysticetes, bodily features such as the large low aspect ratio of the flippers of balaenids appears to be optimized for low-speed maneuverability in complex coastal water habitats (Woodward et al., 2006). Perhaps further studies of flipper geometry in fossil mysticetes will enhance our understanding of how maneuverability and foraging strategies evolved in the Mysticeti. Unfortunately, no forelimb elements were preserved with VMNH 120000.

The idea that Chaeomysticeti started out as ram-feeding/benthic feeders is perhaps not so unbelievable. Among the toothed mysticetes, the degree of tooth wear seen in taxa such as *Mammalodon* appears indicative of benthic feeding (Fitzgerald, in press), primarily because of the role of benthic substrate in tooth wear in marine mammals (Beatty, 2007). Perhaps, with additional data on the distribution of bone histology, tooth wear (for toothed mysticetes), bodily dimensions useful for determining maneuverability, and further data on the distribution of pathologies in modern and fossil taxa, we can compose a more complete view of the individual lives and livelihoods of the early Chaeomysticeti.

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Table 1. Measurements of cortical bone thicknesses and rib diameter from various cetaceans. All measurements in millimeters.

specimen	USNM 25210	USNM 25210	USNM 25210	USNM 314627	USNM 22553	VMNH 1782a	VMNH 1782b
taxa	<i>Aetiocetus coy/laveus</i>	<i>Aetiocetus coy/laveus</i>	Earliest Chaeomysticetid (Uhen, 2007)	<i>Balaena ricei</i>	<i>?Metopocetus</i> sp.	<i>?Metopocetus</i> sp.	<i>?Metopocetus</i> sp.
rib portion	left anterior rib, proximal shaft	left anterior rib, distal shaft	left middle rib, mid-shaft	left middle rib, mid-shaft	left middle rib, mid-shaft	posterior rib, near proximal end	posterior rib, near distal end
cortical thickness—cranial teran	7.37	6.22	4.65	1.74	4.8	5.2	
cortical thickness—caudal teaud	6.7	5.1	8.16	0.1	3.2	3.3	
total thickness—cranial/caudal C/C	22.56	24.2	27.64	80.87	22.9	21.3	
cortex % of total (teran + teaud)/(C/C)	62.37	46.78	46.35	2.28	34.93	39.91	
cortical thickness—superficial tsup	5.95	3.51	6.76	13.95	4.3	3.5	
cortical thickness—deep tdeep	3.85	3.07	4.86	11.79	3.6	3.2	
total thickness—superficial/deep S/D	14.31	12.83	17.35	42.44	12.4	13.2	
cortex % of total (tsup + tdeep)/(S/D)	68.48	51.29	66.97	60.65	63.71	50.76	
avg. cortex % of total $\{[(\text{teran} + \text{teaud}) / (\text{C/C})] + [(\text{tsup} + \text{tdeep}) / (\text{S/D})]\} / 2$	65.43	49.03	56.66	31.46	49.32	45.33	

Table 1. (continued)

specimen	VMNH 1782b	USNM 187316	VMNH 120001	VMNH 742	USNM 301636	USNM 23059
taxa	<i>?Metopocetus</i> <i>sp.</i>	<i>?Pariobalaena</i> <i>palmeri</i>	Balaenopteridae <i>sp.</i>	<i>Eobalaenoptera</i> <i>harrisoni</i>	<i>Megaptera</i> <i>novaeangliae</i>	<i>Pelocetus</i> <i>calvertensis</i>
rib portion	anterior rib, mid-shaft	right middle rib, mid-shaft	anterior rib, mid-shaft	posterior rib, mid-shaft	right posterior rib (#10), proximal shaft	left middle rib, mid-shaft
cortical thickness— cranial cran	3.1	5.36	7.2	3	6.08	5.45
cortical thickness— caudal tcaud	4.2	8.47	16.8	7.9	11.58	5.93
total thickness— cranial/caudal C/C	17.8	25.42	84.5	55.1	71.57	38.41
cortex % of total (cran + tcaud)/(C/C)	41.01	54.41	28.40	19.78	24.68	29.63
cortical thickness— superficial tsup	2.9	1.9	5.5	7.4	6.16	1.89
cortical thickness— deep tdeep	1.5	1.42	5.9	7.8	6.48	1.8
total thickness— superficial/deep S/D	16.7	14	33.4	33.3	37.53	24.65
cortex % of total (tsup + tdeep)/(S/D)	26.35	23.71	34.13	45.65	33.68	14.97
avg. cortex % of total {[(cran + tcaud) / (C/C)] + [(tsup + tdeep) / (S/D)]} / 2	33.68	39.06	31.27	32.71	29.18	22.30

Table 1. (continued)

specimen	USNM 550153	<i>Berardius bairdii</i>	USNM 16783	<i>Diorocetus hiatus</i>	USNM 16783	<i>Diorocetus hiatus</i>	VMNH 120000	cf. <i>Diorocetus hiatus</i>	VMNH 120000	posterior rib, mid-shaft	VMNH 120000	cf. <i>Diorocetus hiatus</i>	VMNH 120000	middle rib, proxima	USNM 22553	<i>Balaena ricei</i>
taxa																
rib portion		right anterior rib (#1), mid-shaft		left anterior rib, just past midshaft		posterior rib, mid-shaft		left anterior rib, just past midshaft		posterior rib, mid-shaft		cf. <i>Diorocetus hiatus</i>		middle rib, proxima		left middle rib, mid-shaft
cortical thickness— cranial tran	5.17		5.83		2.6		9.2		11.5		12.4		1.74			
cortical thickness— caudal teaud	2.41		1.34		5.83		9.7		11.1		10.2		0.1			
total thickness— cranial/caudal C/C	71.83		31.6		28.5		41.7		41.1		33.8		80.87			
cortex % of total (tr _{an} + te _{aud})/(C/C)	10.55		22.69		29.58		45.32		54.99		66.86		2.28			
cortical thickness— superficial tsup	4.41		5.4		6.2		6.2		6.2		6		13.95			
cortical thickness— deep tdeep	1.71		4.6		6.5		5.4		6.3		7.2		11.79			
total thickness— superficial/deep S/D	32.45		16.5		19.5		16.5		16.2		22.3		42.44			
cortex % of total (tsup + tdeep)/(S/D)	18.86		60.61		65.13		70.30		77.16		59.19		60.65			
avg. cortex % of total {[(tr _{an} + te _{aud}) / (C/C)] + [(tsup + tdeep) / (S/D)]} / 2	14.71		41.65		47.35		57.81		66.07		63.03		31.46			

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