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Alton C. Dooley, Jr.

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A middle Miocene beaked whale tooth (Cetacea: Ziphiidae) from the Carmel Church Quarry, Virginia, and implications for the evolution of sexual dimorphism in ziphiids

Alton C. Dooley, Jr.[1.]

ABSTRACT

An apparent right apical mandibular tooth from a beaked whale (Family Ziphiidae) was collected at the Carmel Church Quarry, Caroline County, Virginia in August 2009. The occurrence of this specimen in Bed 15 of the Calvert Formation marks only the second report of a ziphiid from the Calvert Formation. Moreover, this specimen represents, along with the Peruvian *Nazcacetus* and *Messapicetus*, the earliest known occurrence of an enlarged mandibular tooth in a ziphiid. The complete closure of the pulp cavity indicates that this tooth derived from a fully mature animal, while the lack of wear on the crown indicates that the tooth had not erupted from the gums, suggesting that the animal was a female. The presence of unerupted mandibular teeth in a fully mature female suggests that, even by the middle Miocene, ziphiids had already evolved modern behavioral patterns in which enlarged mandibular teeth are used exclusively for intraspecific combat between competing males.

INTRODUCTION

While there is a perception that beaked whales (Family Ziphiidae) are not especially common as fossils, numerous remains have been described worldwide. Ziphiid crania and rostra have been collected from the North Sea Basin for more than 150 years (Lambert 2005), with new taxa still being identified (e. g. Lambert 2005; Lambert and Louwye 2006). A number of specimens have been reported from the late Miocene and Pliocene of Italy, including *Tusciziphius* and *Messapicetus* (Bianucci 1997; Bianucci et al. 1992). The description of ten new taxa based on remains trawled off the coast of South Africa greatly increased the known fossil ziphiid diversity (Bianucci et al. 2007, 2008).

Ziphiids are less common in the Americas. From Peru, Muizon (1983, 1984) described the Pliocene *Ninoziphius*, and Lambert et al. (2009) named the Miocene *Nazcacetus*; both of these taxa are based on fairly extensive and well-preserved remains. Lambert, Bianucci, and Post (2010) and Bianucci et al. (2010) reported the remarkable discovery of eight specimens of *Messapicetus* from the middle to late Miocene of Peru. The only other reported ziphiid fossils from South America are undescribed remains from the Miocene of Argentina (Cozzuol 1996) and fragments from the Miocene of Ecuador (Bianucci et al. 2005).

The majority of ziphiid remains from North America have been reported from South Carolina. Cope (1869a,b) and Leidy (1877) described several ziphiids of uncertain age from South Carolina (Oligocene to Pliocene sediments are known from the area). Post et al. (2008) suggested that most or all of these taxa should be considered *nomina nuda*, while noting possible similarities between *Tusciziphius*, *Caviziphius*, and *Eboroziphius*. True (1907) and Muizon (1984) discussed *Anoplonassa* Cope 1869a, which was based on a partial mandible. Post et al. (2008) reported a cranium of *Tusciziphius* from South Carolina, probably from Pliocene deposits. Whitmore

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1. Virginia Museum of Natural History, 21 Starling Avenue, Martinsville, Virginia 24112

and Kaltenbach (2008) reported 15 ziphiid specimens from early Pliocene deposits at the Lee Creek Mine in North Carolina, which they referred to *Ninoziphius*, *Mesoplodon*, and *Ziphius*. Several ziphiid specimens have been reported from the early Pliocene of Florida by Morgan (1994), including rostral fragments referred to *Mesoplodon* and partial dentaries referred to *Ninoziphius*.

While the specimens mentioned above are demonstrably or likely from the Pliocene, a few specimens from the southeastern United States are thought to derive from Miocene sediments. Whitmore et al. (1986) reported a rostrum recovered by dredging in the Atlantic off the coast of Florida, which they referred to *Mesoplodon*. Morgan (1994) reported that this specimen was likely middle Miocene in age based on associated microfossils. Morgan (1994) also reported a single ziphiid periotic from the late Miocene of Florida. Whitmore and Kaltenbach (2008) reported two ziphiids from the late early Miocene Pungo River Formation at the Lee Creek Mine, a rostral fragment they referred to *Choneziphius*, and a mandible fragment they referred to *Anoplonassa*.

Ziphiids are particularly rare in the otherwise cetacean-rich deposits of the Oligocene-Pliocene Chesapeake Group in Maryland, Delaware, and Virginia. *Pelycorhamphus pertortus* Cope, 1895 includes a partial premaxilla for which exact locality is unknown, but which is thought to derive from the Chesapeake Group. Post et al. (2008) considered this taxon a *nomen nudum*. Specimens from the Chesapeake Group reported by Gottfried et al. (1994) as ziphiid were reinterpreted by Gerholdt and Godfrey (2010) as pathological rostra that are not demonstrably from ziphiids. Whitmore and Kaltenbach (2008) mentioned but did not figure two specimens (a mandibular fragment, and an associated rostral/mandibular fragment) that they referred to *Ninoziphius*, from Westmoreland County, Virginia. Sediments in this area range from middle Miocene to late Pliocene in age (Ward and Andrews 2008). Fuller and Godfrey (2007) reported a rostral fragment of *Messapicetus* from the late Miocene St. Marys Formation in Maryland. Lambert, Godfrey, and Fuller (2010) reported a partial ziphiid cranium from Maryland that has been the only reported ziphiid demonstrably from the middle Miocene Calvert Formation.

One of the remarkable features of the Ziphiidae is the enlargement of one or two pairs of mandibular teeth. These teeth are sexually dimorphic, and while present in both sexes they typically only erupt in males (True 1910; Moore 1968; Mead 1989a, 1989b, 1989c). Except in some species of *Mesoplodon*, the enlarged teeth are apically located (Dalebout et al. 2003). Among living genera, *Berardius* has two pairs of enlarged mandibular teeth (one of which is apical), while all other taxa have a single pair (Moore 1968). Almost all modern ziphiids exhibit reduction (and typically complete loss) of all other maxillary and mandibular teeth, although reduced teeth that are embedded in the gums (and occasionally protrude from the gums) occur with some frequency (Boschma, 1951). The exception among modern ziphiids is *Tasmacetus*, which retains a fully functional post-apical dentition (Oliver 1937; Moore 1968).

Given the nature of the ziphiid fossil record, with the most common remains being isolated rostra and partial crania often found out of context, reports of ziphiid teeth are exceptionally rare. Typically the presence of either enlarged mandibular apical teeth, or enlarged alveoli to accommodate such teeth, is used as a definitive character to refer mandibular remains to the Ziphiidae. The type mandible of *Anoplonassa* includes alveoli for two pairs of enlarged teeth, including an apical pair (True 1907; Muizon 1984). Two pairs of enlarged mandibular alveoli are also present in a fragmentary mandible from Belgium (IRSNB 3854-M.538, placed in Ziphidae *incertae sedis* by Lambert 2005). A mandibular fragment recovered from the seafloor off the coast of New Zealand, probably late Miocene in age, has enlarged apical alveoli (Fordyce and Cullen 1979). Bianucci (1997) figured casts of a right dentary fragment with an *in situ* tooth from the Pliocene of Italy, which he referred to *Mesoplodon* sp. This does not appear to represent an apical tooth, but rather is located more proximally, which is consistent with some modern species of *Mesoplodon*. A pair of enlarged apical mandibular alveoli is present in *Ninoziphius* (Muizon 1983, 1984). According to Morgan (1994:257) one of the Pliocene specimens from Florida that he referred to *Ninoziphius* included “two large, rounded, anteriorly directed teeth,” but unfortunately this specimen was not figured. One of the Pliocene specimens referred to *Ninoziphius* by Whitmore and Kaltenbach (2008) included large, circular, anterolaterally-oriented alveoli. Whitmore and Kaltenbach (2008) also reported two teeth (one *in situ* in a mandible fragment) from the Pliocene at Lee Creek Mine that they referred to *Ziphius*. These teeth have bulbous roots with small enamel crowns. Whitmore and Kaltenbach (2008) noted that, in addition to their similarity to *Ziphius*, these teeth also resembled the anterior teeth of *Tasmacetus*. The earliest known occurrences of enlarged mandibular teeth are in the middle Miocene *Nazcacetus* from Peru (Lambert et al. 2009), for which only the alveoli are known, and several specimens of *Messapicetus*, also from the middle Miocene of Peru (Lambert, Bianucci, and Post 2010; Bianucci et al. 2010). The *Messapicetus* sample includes at least six specimens with dentaries, including two with *in situ* apical teeth.

The new specimen reported here represents only the second record of a ziphiid from the Calvert Formation and, with the Peruvian specimens of *Nazcacetus* and perhaps *Messapicetus*, is the oldest record of an enlarged mandibular tooth in a ziphiid.

Institutional Abbreviations: **IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels; **MUSM**, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; **USNM**, United States National Museum of Natural History, Washington, DC; **VMNH**, Virginia Museum of Natural History, Martinsville, Virginia.

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
ZIPHIIDAE (Gray, 1850) Gray, 1865
Gen. et sp. indet.
(Fig. 1)

Referred specimen—VMNH 120025, right apical mandibular tooth.

Horizon and Locality—VMNH 120025 was collected *in situ* at the Carmel Church Quarry, Caroline County, Virginia, during August 2009. The specimen was removed along with large numbers of chondrichthyan teeth and osteichthyan bones during the excavation of a mysticete skeleton, and was not noticed until January 2010 during cleaning of this sample.

Ongoing excavations of the marine bonebed at Carmel Church since 1991 have yielded several thousand vertebrate fossils representing a minimum of approximately 50 taxa. The fauna is dominated by chondrichthyans and cetaceans (Dooley et al. 2004; Beatty and Dooley 2009) but other marine mammals, osteichthyans, and terrestrial mammals (Dooley 2007) are also present.

Diatoms present at the site (Trochim and Dooley 2010) indicate that the bone bed is located in Bed 15 of the Plum Point Member of the Calvert Formation (Ward and Andrews 2008) (East Coast Diatom Zone 6 of Andrews 1988). This is consistent with biostratigraphic correlation based on terrestrial mammals (Dooley 2007). This yields an age of approximately 13.4-14.4 Ma (Ward and Andrews 2008).

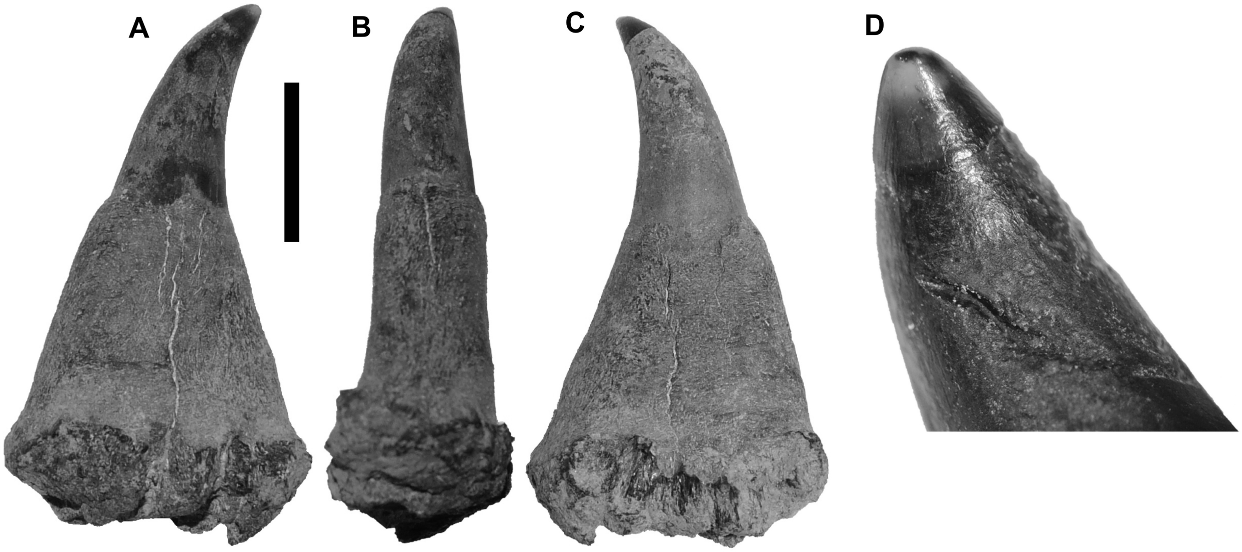

Fig. 1. Ziphiid right apical tooth, VMNH 120025. **A**, lingual view; **B**, anterior view; **C**, buccal view; **D**, closeup of crown showing details of enamel, and possible bite mark. Scale bar for A-C equals 1 cm.

DESCRIPTION

The tooth has a large, rectilinear base with a moderately curved crown with a total height of 33.7 mm. The crown has an approximately circular cross section at the apex, but becomes more transversely compressed proximally. In anterior view the lingual edge is straight to slightly convex but the buccal edge is somewhat sigmoidal, with the buccal side at the apex angled medially (Fig. 1B). The height of the crown is 15 mm.

The distal 2 mm of the crown is covered with relatively smooth enamel, ornamented with slight ridges on the proximal half. The remainder of the crown is enamel-free. There is a slight indentation at the base of the enamel. At the base of the crown the tooth is covered with a thick cementum sheath, marked by a slight lengthening of the tooth anteroposteriorly and a more rugose surface texture. The tooth becomes more bulbous and laterally compressed from this point proximally, until at the base of the root the anteroposterior length of the tooth (19.3 mm) is almost twice as large as the transverse width (10.5 mm). The basal 5 mm of the tooth is heavily rugose. There are two large grooves running transversely across the base of the root. The pulp cavity is completely closed.

There are no obvious signs of wear on the enamel. Just proximal to the base of the enamel, the crown is somewhat rugose on the buccal surface, with a series of short grooves. It is possible that this wear is postmortem; an irregular, 5 mm long groove, interpreted here as a vertebrate bite mark, runs transversely across the posterior surface of the crown immediately adjacent to the rugose area (Fig. 1D).

DISCUSSION

The location of Carmel Church on the extreme western edge of the Atlantic Coastal Plain and the abundance of benthic diatoms in the deposit indicate that this was a shallow water setting, with a water depth of less than 20 m (Trochim and Dooley 2010). The presence of a ziphiid at this locality is somewhat surprising, given the shallow water depths associated with the site. The general shallow nature of Chesapeake Group deposits has been invoked as a possible explanation for the scarcity of ziphiids in these deposits (Gottfried et al. 1994; Fuller and Godfrey 2007; Lambert, Godfrey, and Fuller 2010).

The overall shape of a small conical crown with a large, laterally compressed root is consistent with apical teeth of many modern and fossil ziphiids. There is, however, considerable variation in tooth morphology among different taxa, in addition to intraspecific variation due to sexual dimorphism (True 1910; McCann 1962; Moore 1968; Lambert, Bianucci, and Post 2010). The overall shape of VMNH 120025 matches fairly closely the apical teeth from an adult female specimen of *Indopacetus pacificus*, figured by Dalebout et al. (2003:450), as well as juvenile teeth from the same species (Dalebout et al. 2003:440), but *Indopacetus* teeth are smaller and much less laterally compressed than the Carmel Church tooth. The *Indopacetus* tooth also has an open pulp cavity, even though it was recovered from an adult animal, while VMNH 120025 has a closed pulp cavity. VMNH 120025 also shows some similarity to female *Mesoplodon mirus* teeth figured by Moore (1968:241) (USNM 175019), although the *M. mirus* teeth are smaller and have a shorter crown, and also have an open pulp cavity.

The overall shape of VMNH 120025 is somewhat similar to juvenile teeth from *Hyperoodon ampullatus* figured by Moore (1968:234), particularly with respect to the rugose base of the tooth. As with the adult *Indopacetus* specimen, and in contrast with VMNH 120025, the *Hyperoodon* specimens all retained open pulp cavities.

While ziphiid teeth typically lack enamel, there are a number of exceptions. *Tasmacetus shepherdi*, the only extant ziphiid with an extensive dentition, has enamel crowns on all the teeth (Oliver 1937). Non-apical teeth associated with *Nazcacetus urbinai* appear to have small enamel crowns (Lambert et al. 2009); while this taxon had enlarged apical alveoli, no apical teeth were recovered with the type specimen. True (1910) mentioned a female specimen of *Ziphius cavirostris* with 2 mm of enamel at the tip of the crowns, but this does not appear to be typical for this taxon (True 1910; Moore 1968). Both teeth referred to *Ziphius* by Whitmore and Kaltenbach (2008) (USNM 392132 and USNM 182918) retained fairly large enamel crowns that comprise approximately one-fourth of the entire height of the tooth. Apical teeth from the Peruvian *Messapicetus* sample (MUSM 1037) appear to lack enamel, although the state of preservation of these specimens makes this uncertain (Lambert, Bianucci, and Post, 2010), but post-apical teeth associated with these specimens all have small enamel crowns (Bianucci et al. 2010).

With a maximum root length of 19.3 mm, the size of VMNH 120025 compares favorably with the alveoli of some other fossil ziphiids. In the type mandible of *Anoplonassa* the apical alveolus has a length of 23 mm (True 1907). The holotype specimen of the middle Miocene *Nazcacetus* has apical alveoli that are 20 mm in length (Lambert et al. 2009). VMNH 120025 is rather smaller than the alveoli of IRSNB 3854-M.538 from the late Miocene or Pliocene of Belgium, in which the anterior alveoli have a length of 28 mm according to Lambert (2005).

Specimens of *Messapicetus gregarius* recently described from Peru have a significant size range, with apical alveoli lengths ranging from 23 to 35 mm (Lambert, Bianucci, and Post 2010). Ratios between the minimum and maximum alveolar diameters in *M. gregarius* range from 0.52 to 0.68 (Bianucci et al. 2010), compared to 0.54 for the root of VMNH 120025. These ratios indicate that the apical teeth are rather more strongly compressed than is typical for ziphiids. The adult female specimen of *Indopacetus* figured by Dalebout et al. (2003:450) has a ratio of approximately 0.72, while teeth from a female *Mesoplodon mirus* (USNM 175019) figured by Moore (1968:241) have ratios of 0.64 and 0.57. *Anoplonassa* has an alveolar ratio of 0.70 (True, 1907). However, while the degree of transverse compression of the roots is similar in VMNH 120025 and *M. gregarius*, the morphology of preserved apical teeth is quite different, with an apparently much shorter crown on a larger tooth in MUSM 1037 (Lambert, Bianucci, and Post 2010).

Several post-apical teeth are also known from *M. gregarius*, although it is unclear if these are derived from the maxilla or the dentary. These teeth show a great range of size and shape, although all have roots that are more strongly transversely compressed than in *M. gregarius* apical teeth or VMNH 120025, with minimum to maximum diameter ratios of 0.3 to 0.5 (Bianucci et al. 2010). These specimens have medially curved enamel crowns, and all but the smallest specimens show apical wear (Bianucci et al. 2010). While the presence of these specimens raises the possibility that VMNH 120025 could represent a post-apical tooth, the proportions and morphology are more consistent with an apical tooth.

The completely closed pulp cavity in VMNH 120025 suggests that this animal was an adult at the time of death. It seems that the pulp cavity remains open well into adulthood in many modern ziphiids (True 1910; Moore 1968), so, assuming growth patterns are comparable in fossil species, it is unlikely that VMNH 120025 represents a subadult or young adult individual.

The lack of any obvious wear on a tooth from an apparently fully mature ziphiid is also of some interest. The apical teeth are sexually dimorphic in all extant ziphiids (True 1910; Moore 1968; Mead 1989a, 1989b, 1989c). Even though there is at least one report of wear on the apical teeth from females of *Berardius bairdi* (Omura et al. 1955), the typical condition for ziphiids is that apical teeth only erupt and become functional in adult males. Enlarged mandibular teeth do develop in females but normally remain covered by soft tissue throughout the life of the animal. This is true even in *Tasmacetus*, in which both males and females have an erupted, functional dentition, yet the larger apical teeth are only emergent in males (Oliver 1937; Mead and Payne 1975;

Mead 1989a). Moreover, the emergent teeth in adult male beaked whales almost always show significant apical wear (True 1910; Moore, 1968). Given the lack of wear on VMNH 120025, combined with the closed pulp cavity indicating a fully mature adult, it seems highly unlikely that this tooth was emergent, and thus it most likely represents a female.

This has important implications for the evolution of sexual dimorphism in Ziphiidae. In modern ziphiids the dimorphism of mandibular teeth is not simply a sexual display feature, but rather has behavioral significance. In most modern taxa, male ziphiids use the mandibular teeth in intraspecific combat, raking the teeth across the bodies of competing males (McCann 1974; Mead et al. 1982; Heyning 1984; McLeod 1998).

While the functional significance of apical mandibular teeth for intraspecific combat in male ziphiids has been well established for modern ziphiids, it has been difficult to extend this to fossil ziphiids due to the paucity of mandibular remains. Lambert et al. (2009) noted that the presence of enlarged apical alveolae in *Nazcacetus* suggested the possibility that sexually dimorphic mandibular teeth extended back to at least the middle Miocene. With the availability of a large sample of *Messapicetus*, also from the middle Miocene, Lambert, Bianucci, and Post (2010) were able to establish a range of mandibular morphologies and apical alveolar sizes indicative of sexual dimorphism. One of the *Messapicetus* morphotypes includes a more robust mandible with larger apical teeth; Lambert, Bianucci, and Post (2010) interpreted this as the male morphotype, suggesting that males were engaging in intraspecific combat.

Given the fact that mandibular teeth are present but non-functional in most modern adult female ziphiids, it is plausible that these teeth may have served different or additional functions in both sexes in early ziphiids, with their use only later being restricted to male-male combat. Lambert, Bianucci, and Post (2010) did not report the recovery of any mandibular teeth in the *Messapicetus* female morphotype, so there is no direct evidence of the function (or non-function) of mandibular teeth in Miocene female ziphiids. The presence of an unworn, adult tooth at Carmel Church suggests that, even in the middle Miocene, apical teeth in some ziphiids were non-emergent and non-functional in females and that the function of apical teeth was restricted to their use in male-male combat.

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