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Abstract

Beaked whales, Family Ziphiidae, occur in deep offshore and oceanic seas, where they are very difficult to study, so that much of our knowledge about them is derived from stranded animals. Most beaked whales (e.g., genera *Mesoplodon* and *Ziphius*) have only one pair of mandibular teeth. A reduced dentition is widely regarded as an adaptation to suction feeding, primarily on squid. However, vestigial maxillary and mandibular teeth have been recorded in some species. Here, we describe new records of vestigial teeth in 12 Sowerby's beaked whales, *M. bidens,* and one Cuvier's beaked whale, *Z. cavirostris,* from a total 14 animals of these species, which stranded in 2019 to 2021 in Scotland. In nine *M. bidens* some tooth crowns were erupted and mild occlusal wear was visible, whereas pathological teeth were seen in ten individuals. The occurrence of vestigial teeth in Sowerby's beaked whale appears to be significantly under-recorded, suggesting that vestigial teeth form as part of the normal development of the dentition. The reasons for the under-recording of the occurrence and the possible functionality of vestigial teeth in ziphiids are discussed.

Introduction

Beaked whales, Family Ziphiidae, have a worldwide distribution and are usually found in deep pelagic waters up to the margins of continental shelves (Heyning 1989; Mead 1989; MacLeod et. al. 2006; Jefferson et al. 2015; Ellis and Mead 2017; Baird, 2018; Pitman 2018). They are very difficult to study at sea, because of their cryptic behaviour, so that opportunities for increasing our understanding of their anatomy and biology rely largely on examination of stranded animals (Ellis and Mead 2017; Pitman 2018). Twenty-four species are currently recognized in six genera (*Berardius*, *Hyperoodon*, *Indopacetus*, *Mesoplodon*, *Tasmacetus*, and *Ziphius*) (Ellis and Mead 2017; Yamada, et al. 2019; Carroll et al. 2021). All species except for Shepherd's beaked whale, *Tasmacetus shepherdi,* are characterised by a much-reduced dentition of either two (*Mesoplodon, Hyperoodon, Indopacetus, Ziphius*) or four (*Berardius*) mandibular teeth (Boschma 1951, Reeves et al. 2003, Dalebout et al. 2004). The reduced dentition is thought to be an adaptation to suction feeding (Werth 2006, Johnston and Berta 2011) mainly on squid and smaller deep-sea fishes, which have been recorded as the primary prey items in the stomachs of stranded animals (Santos et al. 2001; Tyack et al. 2006; West et. al. 2017; GH pers. obs.).

Vestigial teeth have been recorded infrequently in several beaked whale species, including Sowerby's beaked whale, *M. bidens*, Gray's beaked whale, *M. grayi*, Longman's beaked whale, *I. pacificus*, bottle-nosed whales, *Hyperoodon* spp. and Cuvier's beaked whale, *Z. cavirostris* (Harmer 1924, Fraser 1936, Boschma 1951, Kenyon 1961, Azzaroli 1968, Robson 1975, Reyes 1990, Gomerčić et al. 2006, Groom et al. 2014, Loch and van Vuuren 2016). Supernumerary tusks are also reported from True's beaked whale, *M. mirus, Berardius* spp. and *Hyperoodon* spp. (Robbins et al. 2019). Rows of regularly spaced small, homodont teeth (15-22 per quadrant) are commonly found in *M. grayi* (Robson 1975), but in other beaked whale species they appear to be recorded rarely and incidentally (Boschma 1951). In this paper we focus on the presence of vestigial teeth in two species of beaked whale.

Sowerby's beaked whale, *Mesoplodon bidens*, occurs in the North Atlantic Ocean including the North and Baltic Seas (Kükenthal 1914; Moore 1966; Kinze 1993; Reiner et al. 1993; Carlström et al. 1997, Martín et al. 2011; Wenzel et al. 2013; Waller 2014). Like all *Mesoplodon* species, *M. bidens* is characterised by two teeth (tusks), which in this species are each situated mid-way along the mandible. Both sexes have tusks, although these are usually only erupted in adult males, which use them primarily in intrasexual aggressive encounters (Mead 1989). Normally the males' tusks are flattened laterally and erupt vertically on either side of the rostrum, so that they are visible externally when the jaws are closed.

Cuvier's beaked whale, *Ziphius cavirostris,* has a global distribution (Jefferson et al. 2015; Ellis and Mead 2017) and has one pair of tusks situated at the distal end of the mandible. Similar to *M. bidens* the tusks are usually only erupted in males for use in aggressive encounters between males, which are often scarred as a result, although it has been argued this species also uses its tusks in visual displays (Gol'din 2014).

In 2019 two juvenile *M. bidens* were stranded together in Scotland and during subsequent preparation of their skeletons, it was noticed that both had vestigial teeth. Subsequent strandings of beaked whales in Scotland during 2019-2021 were investigated for the presence of vestigial teeth, so that in this paper we describe 13 recent records of vestigial teeth in 12 out of 13 specimens of *M. bidens* and one specimen of *Z. cavirostris*. In comparison with previous reports of vestigial teeth in these species, we discuss their frequency of occurrence and to what extent they may be functional in ziphiids in relation to their ontogeny, feeding behaviour and evolutionary history.

Material and Methods

Thirteen Sowerby's beaked whales and a Cuvier's beaked whale were reported to the Scottish Marine Animal Strandings Scheme (SMASS) from July 2019 to September 2021 (Table 1). All were subjected to standard post-mortem examinations (IJsseldijk et al. 2019) and skeletons were prepared at National Museums Scotland (NMS). After the observation of vestigial teeth in two *M. bidens* specimens in 2019, subsequent specimens were dissected carefully to check for their presence. Five of the specimens that appeared to show vestigial dentition were subjected to computer tomography (CT) scanning (see details below) before dissection and maceration. For all collected specimens and prior to maceration of the skulls, any vestigial teeth were removed, cleaned, dried, and stored in pinned "Torpac Lock Ring Capsules", with a record of the order in which they were situated in each jaw.

Crown wear was evaluated, following Loch et al. (2011), under a high-power stereomicroscope (Leica M205 C) with a Canon EOS 7D camera attached. Any pathological lesions or wear were recorded for each tooth. The length and maximum diameter of each tooth were measured using dial callipers to an accuracy of 0.1mm. Pathologies were recorded for each tooth where present following Loch et al. (2011).

Five heads of the stranded whales were subjected to CT imaging, using a 64-row multidetector CT scanner (Somatom® Definition AS Siemens, Erlangen, Germany). The CT scans were collected and compiled using the following protocol: Collimator pitch of 0.55, tube potential of 120 kVp, reference tube current of 250–320 mA, slice thickness of 0.6mm, matrix 512 × 512image reconstruction interval of 0.3 mm and reconstruction algorithms with both low (iterative kernel J40f) and high (conventional kernel H70f) pass filters.

Results

A total of 444 vestigial teeth was recorded from 14 specimens of beaked whale, including 421 teeth in 13 Sowerby's beaked whales and 23 teeth in one Cuvier's beaked whale (Table 1). Only one *M. bidens*, an apparently very old male, did not have vestigial teeth, although it did have anomalous dentition that caused trauma to its rostrum (Plint et al. 2021). When present, numbers of teeth per individual varied from 18 to 72 in 12 *M. bidens* specimens (there were two in an incomplete specimen, but this was likely a minimum number, owing to its decayed state) (Table 1). Lengths of teeth from whales stranded in 2019 and 2020 are shown in Figure 1 and detailed measurements and observations on eruption, tooth wear and pathology from all specimens are in Supplementary Table 1.

Tooth lengths varied from 0.9 mm to 10.4 mm in *M. bidens* and 2.1 mm to 7.7 mm in the single *Z. cavirostris* (Figure 1, Supplementary Table 1). Erupted teeth were recorded in nine specimens of *M. bidens*, ranging from 4.2% to 46.2% of the total number of vestigial teeth in each specimen. There were almost three times (2.85) as many teeth in the mandibles compared with the maxillae in *M. bidens*.

The vestigial teeth of the two species differ greatly from each other (Figures 2 and 3). However, for both species these teeth are small, homodont, and mainly needle-shaped with or without a conical crown, so that they are very different to the mandibular tusks. The vestigial teeth vary both in number and serial length, and exhibit marked asymmetry in numbers between jaw quadrants within individuals (Figure 2, Suppl. Table 1). In some individuals the first and the last vestigial teeth are the shortest, but within each series the lengths of neighbouring teeth may differ.

Vestigial teeth in all *M. bidens* specimens are small, pointed and cylindrical, and many possess a distinct crown (Figure 2). In seven *M. bidens* specimens the teeth are mainly well formed, have a similar shape, are hard, composed largely of dentine and with a cementum crown in most cases. The mandibular vestigial teeth were always in a bony grove starting about 1cm behind the tusk (Figure 3). All were regularly spaced about 6 mm apart. In contrast, the vestigial teeth from the male *Z. cavirostris* were arranged randomly along the jaws and were located only in the gum, as opposed to being rooted in bony alveoli as in the Sowerby's beaked whales.

All *M. bidens* specimens had vestigial teeth in the lower jaws, including many with open roots, indicating that they are either still growing or deciduous. The teeth situated towards both ends of their rows sometimes appear poorly developed and misshapen, so that no crowns are visible. In nine *M. bidens* some vestigial teeth were erupted. In three specimens the proportion of erupted teeth exceeded 45% and in six others it varied between 4.2% and 27% (Table 1, Supplementary Table 1). None of the teeth found in the remaining *M. bidens* individuals and the *Z. cavirostris* was erupted or showed signs of wear.

Seventy-six out of 421 vestigial teeth (18.0%) in ten out of 12 specimens of *M. bidens* and all teeth in a male *Z. cavirostris* showed evidence of pathology. The main pathologies included shape anomalies of the roots, alteration of the crown morphology and *amelogenesis imperfecta* (a genetic disorder affecting the development of enamel in teeth), which was found in all the teeth of the *Ziphius* individual. There is also partial resorption of the roots or of the entire tooth, as well as shape abnormalities, in almost all of the *Ziphius* vestigial teeth (Figure 4). As a result, these teeth were brittle, small and of variable shape, but most were needle- or rice-grain-shaped, with no distinctive crowns or roots. Six of the *Ziphius* teeth are almost spherical or have spherical crowns (Figure 4). In contrast, the vestigial teeth from the *M.*

bidens specimens show little evidence of resorption. Mean tooth length in males is significantly shorter than in females (male mean tooth length = 5.551 mm, female tooth length = 6.714 mm, $t_{192, 229}$ = 8.076, P<0.001), whereas there is no significant difference in tooth width. When plotted against body length, there is a suggestion that mean tooth length of females is greater than that of males at shorter body lengths (<3.8 metres), but sample sizes are too small for statistical testing.

Discussion and conclusion

In 12 specimens of Sowerby's beaked whale and one Cuvier's beaked whale we recorded vestigial teeth, ranging from 18 to 72 in *M. bidens* (Table 1) and 23 in a male *Z. cavirostris*. The juvenile female *M. bidens* (NMS.Z.2020.25.1) has the most vestigial teeth (72) recorded for this species, increasing by almost 50% the previous maximum of 50 reported in a juvenile female (Taylor 1900) (Figure 3). Percentage eruption of teeth varied from 0% to 46.2% per individual and tooth wear ranged from 0% to 33.3% of erupted teeth (16.8% total teeth) per individual in *M. bidens*. None of the teeth in the male *Z. cavirostris* were erupted. These findings appear to be in agreement with those of previous reports, suggesting that vestigial teeth are non-functional and that tooth wear is likely to be incidental owing to occlusion of the teeth in the upper and lower jaws or with prey (Boschma 1951).

In our study we have found vestigial teeth in 12 of 13 specimens of *M. bidens* that were stranded in a period of 27 months, giving a prevalence of 92.3%. This compares with only one specimen with vestigial teeth in 53 *M. bidens* in the NMS collection (1.9%) recorded prior to 2019. There are also only 13 records in the literature in the previous 183 years, so it is likely that their prevalence is under-reported, because they have been overlooked, possibly because they were unerupted (Table 2). The only *M. bidens* specimen without vestigial teeth that was examined during 2019-2021 was an adult male, which had anomalous dentition that caused trauma to its rostrum (Plint et al. 2021). Of the 11 specimens with vestigial teeth, for which we recorded sex and age class, 81.8% were subadults/juveniles and 72.7% were males. Vestigial teeth in beaked whales are likely to be under-reported, because they are often unerupted and rooted in soft tissue, so that they are easily lost owing to soft-tissue decomposition following stranding, or a lack of awareness of their possible presence. However, although the connective tissue in the gums makes these tissues more resistant to decay compared with other tissues, it can also impair dissection, especially where teeth are poorly calcified. Therefore, vestigial teeth, especially if unerupted, are most readily observed using CT scanning, even in decomposing specimens (Figure 3).

Only one beaked whale species, *Tasmacetus shepherdi*, has a fully functional dentition, but it has morphological adaptations that indicate that it is a suction feeder like all other extant ziphiids (Heyning and Mead 1996, Johnston and Berta 2011). *Tasmacetus* is basal to all ziphiid genera in the phylogeny of living (crown) beaked whale species based on nuclear DNA, except for the genus *Berardius* (McGowen et al. 2020), although based on morphology, Lambert et al. (2015) placed *Tasmacetus* as basal to all crown ziphiids. Therefore, the absence of dentition is usually regarded as an indicator of suction feeding in crown ziphiids, but *Tasmacetus* and *Mesoplodon grayi* both have erupted teeth and are deep-diving suction feeders (Heyning and Mead 1996; Johnston and Berta 2011). In the fossil record of the Ziphiidae the dentition is complete in the most basal species, *Ninoziphius platyrostris* from the late Miocene of Peru, which is considered to have been adapted to raptorial snapping (cf. delphinids) rather than suction feeding (Lambert et al. 2013, 2015, Lambert et al. 2018). Members of the extinct *Messapicetus* clade also have full or partial maxillary and mandibular dentitions and were either not suction feeders or less specialised suction feeders (Lambert et al. 2015). Excluding *Tasmacetus,* the dentition of crown ziphiids is reduced to two or four mandibular tusks. The lack of maxillary teeth in most living beaked whales may be due to the obliteration of the basirostral groove (containing the dentary nerve and blood supply) on the underside of the rostrum during ontogeny (McCann 1976). Delayed or incomplete obliteration of this groove allows vestigial dentition to develop. It is unclear why the mandibular dentition does not develop, but this may be controlled in a different way, given that growth of tusks is part of normal dental development. However, the ability to develop maxillary and mandibular teeth has not been fully lost, even if the teeth are generally vestigial. *M. grayi*, appears regularly to develop both maxillary and mandibular teeth, which are similar in size to those of *Tasmacetus,* and these teeth are also considered functional (Boschma, 1951, Robson, 1975). Therefore, suction feeding evolved early in the adaptive radiation of crown ziphiids, which is dated to the Early to Middle Miocene, approximately 15.6 Mya (McGowen et al. 2020). Therefore, given that *Berardius* is basal to all other extant ziphiids, reduction of dentition may have occurred at least twice in the evolution of crown ziphiids or teeth re-appeared in *Tasmacetus*, but functional teeth do not prevent ziphiids from being effective suction feeders.

Boschma (1951) reviewed the literature for records of vestigial teeth in ziphiid whales and these were recorded principally in *M. grayi*, *M. bidens*, *Hyperoodon ampullatus*, *H. planifrons* and *Z. cavirostris*. We have reviewed the records of vestigial teeth in *M. bidens* and *Z. cavirostris* and found that several of those reported in Boschma (1951) have been reported incorrectly. Tables 2 and 3 summarise our findings based on the original literature cited by Boschma (1951), as well as more recent records. Modern records of vestigial teeth in extant specimens of *M. bidens* and *Z. cavirostris* are scant (Fordyce et al. 1979; Gomerčić et al. 2006, Loch and van Vuuren, 2016). Surprisingly, including the new records reported here, there appear to be only 39 records of vestigial teeth in these two species; 25 for *M. bidens* since Cuvier (1836) and 14 for *Z. cavirostris* since Gervais (1850) (Tables 2 and 3). Boschma

(1951) concluded that these vestigial teeth are poorly developed, often not erupted with fully closed roots, maybe partially reabsorbed and hence are not functional. They seem to occur most frequently in subadults and juveniles and hence may form part of the normal development of living ziphiids, but they mostly do not appear to occur in mature adults.

Vestigial teeth in beaked whales occur most commonly just posterior to the tusk in the lower jaws (Figure 3) and they are typically reported as being only loosely rooted in the soft tissue of the gums and are presumably lost as the animal ages (Kükenthal 1900; Boschma 1951). However, Cuvier (1836) and Gervais (1850, 1880) both show that teeth in their specimens were either in the mandibular groove or were in alveoli in *M. bidens* and *Z. cavirostris*, respectively. In the Scottish specimens reported here, the vestigial teeth were situated in mandibular grooves, but the maxillary teeth were situated only in the gums, except for two teeth, which were in bony alveoli in the maxillae. In contrast to Boschma (1951), we found open roots in 68 teeth from seven *M. bidens,* which suggests that either they are still growing, or were being reabsorbed, or that they are deciduous teeth, which are not replaced once they are shed.

Sowerby's and Cuvier's beaked whales catch their prey using suction feeding (Heyning and Mead 1996). Erupted maxillary and mandibular teeth could impede suction feeding by unnecessarily snagging the prey as it is swallowed, but they may also assist younger animals in grasping prey, where their suction-feeding technique has not fully developed. However, we have no knowledge of the behavioural development of suction feeding in ziphiids. Vestigial maxillary teeth have also been recorded in sperm whales, *Physeter macrocephalus*, of both sexes, which are also suction feeders, but with fully erupted mandibular teeth (Turner 1904; Ritchie and Edwards 1914, Matthews 1938; Gibbs and Kirk 2001; Toldeo and Langguth 2015). They occur in about half of individuals and are more prevalent in males

(Matthews 1938). They erupt in males at about 10 metres length and about 9 metres length in females (Matthews 1938). Wear on the erupted crowns of these teeth show that they have some functionality (Turner, 1904; Ritchie and Edwards 1914), but given that they are not present in all individuals, they are clearly not essential. This could be the same for beaked whales, where vestigial teeth are not universal.

It is likely that if vestigial teeth erupt in ziphiids*,* they are most likely shed (if deciduous), or pulled loose during prey capture. If the teeth remain unerupted, they may persist in the gums, or are gradually absorbed, as appears to be the case in *Z. cavirostris,* owing to the brittle porous nature of the poorly calcified teeth. The question remains as to whether these vestigial teeth could be functional, if erupted. Tooth wear in 33.3% of erupted teeth in a subadult female Sowerby's beaked whale suggests that they could offer an advantage in grasping slippery prey while perfecting suction feeding, but the low proportion of erupted and worn teeth amongst the specimens we examined, counters this suggestion. Therefore, tooth wear may be incidental rather than the consequence of function. This study, supported by CT scanning, has demonstrated that vestigial teeth may be much more prevalent than previous published records suggest and that their presence may be a normal part of the development of dentition, particularly in M. bidens. We urge others to take the opportunity to record further cases so that we can build a more complete picture of the prevalence, eruption, wear, and possible function of vestigial teeth in ziphiids.

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Author contributions

ACK and GH conceived the study. AB, MtD, NJD and GH collected the specimens. GH prepared and measured the teeth. TS carried out CT scanning on specimens. CCK and JSH contributed further records. All authors contriubuted to the writing of the paper.

Conflicts of interest

On behalf of all authors, the corresponding author states that there are no conflicts of interest.

Research ethics and best practice

This research was carried out on dead animals that had stranded on coasts in Scotland. Therefore, the specimens used in this study do not require institutional care approval and there are no international, national or institutional requirements for the consideration of the ethical treatment of the specimens of these taxa.

All specimens that were collected for this study are registered in the collections of National Museums Scotland and are fully accessible to all researchers.

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Table captions:

Table 1: Specimens of Sowerby's beaked whale and Cuvier's beaked whale that were stranded in 2020-2021 in Scotland that were examined for the presence of vestigial teeth.

Table 2: Historical records of the presence of vestigial teeth in Sowerby's beaked whales 1823-1992.

Table 3: Historical records of the presence of vestigial teeth in Cuvier's beaked whales 1849-2001.

Supplementary Table 1: Lengths and widths of vestigial teeth from each jaw quadrant of Sowerby's beaked whales, *Mesoplodon bidens*, and a Cuvier's beaked whale, *Ziphius cavirostris*, stranded in Scotland 2020-2021, along with informatuion on whether the teeth were erupted, worn and showed signs of pathology. *Tooth number and position are assigned from anterior to posterior of the jaw. **Teeth are considered "erupted" when they have penetrated the gumline and are visible at the surface of the gum. *** Teeth are considered worn if they show physical damage as a result of use.

Figure captions:

Figure 1: Tooth lengths (mm) of vestigial teeth in Sowerby's beaked whales *Mesoplodon bidens* stranded in Scotland 2019-2020. a. NMS.Z.2020.25.1, b. NMS.Z.2020.25.2, c. NMS.Z.2020.25.3, d. NMS.Z.2020.25.4, e. NMS.Z.2020.42, f. NMS.Z.2020.43. Blue = left jaw quadrant, red= right jaw quadrant.

Figure 2: Composite images of the vestigial teeth of a female Sowerby's beaked whale (NMS.Z.2020.25.1). a. Left mandubular tooth (tooth number 10, 8.8 mm long). b. Left

mandibular tooth (tooth number 11, 8.9 mm long). Crowns are at the top and roots below. © National Museums Scotland.

Figure 3: 3D rendering from a CT scan of the skull of a female Sowerby's beaked whale with 72 vestigial teeth (NMS.Z.2020.25.1). a. lateral view, b. dorso-frontal view. © National Museums Scotland.

Figure 4: Vestigial tooth from a Cuvier's beaked whale *Ziphius cavirostris,* right mandible, tooth number 1, tooth length 4.6 mm (NMS.Z.2020.25.5). Crown is at the top and root below. © National Museums Scotland.