Suction feeding preceded filtering in baleen whale evolution

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Abstract

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The origin of baleen, the key adaptation of modern whales (Mysticeti), marks a profound yet poorly understood transition in vertebrate evolution, triggering the rise of the largest animals on Earth. Baleen is thought to have appeared in archaic tooth-bearing mysticetes during a transitional phase that combined raptorial feeding with incipient bulk filtering. Here we show that tooth wear in a new Late Oligocene mysticete belonging to the putatively transitional family Aetiocetidae is inconsistent with the presence of baleen, and instead indicative of suction feeding. Our findings suggest that baleen arose much closer to the origin of toothless mysticete whales than previously thought. In addition, they suggest an entirely new evolutionary scenario in which the transition from raptorial to baleen-assisted filter feeding was mediated by suction, thereby avoiding the problem of functional interference between teeth and the baleen rack.

Keywords

Mysticeti; baleen whale; filter feeding; suction feeding; tooth wear; Aetiocetidae

Introduction

Baleen whales (Mysticeti) are the largest animals on Earth and owe their success to baleen, a unique feeding structure allowing them to filter vast quantities of small prey from seawater (Pivorunas, 1979; Werth, 2000b). The baleen apparatus of extant mysticetes consists of a series of keratinous plates suspended from the upper jaw, traditionally thought to be derived from the horny palatal ridges of extant artiodactyls (Werth, 2000b). More recent anatomical work, however, has shown that the basal tissue giving rise to baleen is innervated by the superior alveolar nerves, and is thus more likely homologous with the gingiva (Sawamura, 2008).

Baleen rarely fossilises (Esperante et al., 2008; Gioncada et al., 2016), but is thought to have originated early in mysticete evolution, during a transitional phase combining tooth-based raptorial feeding and baleen-assisted filtering (Deméré and Berta, 2008; Deméré et al., 2008). This transition is seemingly exemplified by the Aetiocetidae – a mostly Oligocene (34–23 Ma) family of archaic mysticetes which retained functional teeth alongside features commonly associated with filter feeding (Deméré et al., 2008). The underlying drivers, mechanics and accuracy of this scenario, however, remain contentious (Fitzgerald, 2010; Marx et al., 2015). Here we show that a new Late Oligocene aetiocetid fossil from Washington, USA, has a highly distinctive tooth wear pattern that is inconsistent with the presence of baleen, suggesting that this key mysticete adaptation emerged later and much closer to the origin of modern whales than previously thought. Our new fossil displays functional adaptations for suction feeding rather than filtering, casting doubt on the accepted ecomorphological context of chaeomysticete evolution. Based on this new information, we re-examine previous arguments in favour of a direct transition from raptorial to filter feeding, and propose an alternative model of baleen evolution more consistent with available evidence both from extant taxa and the fossil record.

Material and Methods

Except for the right p3, the teeth were found encased in soft sediment and washed out using water, with no mechanical or chemical preparation. The remainder of the specimen was prepared mechanically and using 10% acetic acid. All parts of the specimen in figs 1–3 were coated with ammonium chloride prior to photography. Where appropriate, photographs of the specimen were taken at varying foci and digitally stacked in Photoshop CS6. To visualise the gross wear features further, we scanned the two best-preserved teeth via micro-computed tomography using a Zeiss Xradia 520 Versa (Oberkochen,

Germany) at the Monash University X-ray Microscopy Facility for Imaging Geomaterials (XMFIG). The specimens were scanned with a source voltage of 140 kV and current of 70 μA, an exposure time of 2 seconds per image and a pixel size of 12.7 μm. 3D surface models were generated in Avizo v9.0.0 (Visualization Science Group) and are available as supplementary 3D figures (figs S1-S2).

Institutional abbreviations

AMP, Ashoro Museum of Paleontology, Ashoro, Hokkaido, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; NMV, Museum Victoria, Melbourne, Australia; UCMP, University of California Museum of Paleontology, Berkeley, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UWBM, Burke Museum of Natural History and Culture, University of Washington, Seattle, USA.

Results

Description of NMV P252567

The new fossil specimen (NMV P252567) comes from the upper part of the Pysht Formation (Clallam County, Washington State, USA; Late Oligocene) (Prothero et al., 2001), and comprises much of the cranium, both mandibles, and postcranial elements. Overall, the morphology of the skull is intermediate between that of *Aetiocetus* and *Fucaia* (Barnes et al., 1995). A detailed systematic analysis of NMV P252567 is currently under preparation, but it is confidently assigned to Aetiocetidae based on the presence of (i) an enlarged lacrimal incising into the lateral border of the ascending process of the maxilla (Deméré and Berta, 2008; Marx et al., 2015); (ii) a laterally expanded premaxilla overhanging the adjacent portion of the maxilla (Barnes et al., 1995; Fitzgerald, 2010; Geisler and Sanders, 2003; Marx, 2011); (iii) a proportionally large, anterolaterally directed orbit (also present in Mammalodontidae) (Marx, 2011); (iv) a (presumably ligamentous) mandibular symphysis with attendant symphyseal groove (also present in chaeomysticetes) (Fitzgerald, 2012); (v) gracile cheek teeth with fused roots (Deméré and Berta, 2008; Marx et al., 2015); and (vi) lingually ornamented tooth crowns (Deméré and Berta, 2008; Marx et al., 2015) (figs 1–3).

Based on the right mandible, NMV P252567 has 11 lower teeth, similar to archaeocetes, mammalodontids and *Fucaia goedertorum* (Barnes et al., 1995; Fitzgerald, 2010; Uhen, 2004). There are at least nine preserved teeth, including: a left (I1 or I2) and a right upper incisor (I2 or I3); the left upper canine or P1; the *in situ* roots of right p3; and five double-rooted postcanines, including at least one upper and one lower (figs 1–3, S1–S2). The left incisor has a broken apex, but otherwise displays intact labial and lingual enamel surfaces with no obvious abrasive wear (fig. 3A). The right incisor is abraded along two thirds of its lingual surface, but intact labially (fig. 3B).

All of the remaining teeth are heavily abraded with the consequent loss of all lingual enamel, except for a thin band along the base of the crown that was presumably located below the gum line (fig. 2). Between this basal band and the apex, the lingual surface of each crown is deeply excavated and polished. Where preserved, the centre of the polished surface bears several deep, horizontal striations, the edges of which are themselves polished and rounded (fig. 2). Anteriorly and posteriorly, the abraded surface wraps around the crown, resulting in an hourglass-shaped labial wear pattern. The extent of labial wear varies, but in at least one tooth all of the enamel has been removed except for a centrally located, vertical strip (fig. 2B). The most heavily worn teeth, which are likely also the most posterior, have lost most of their crowns and are reduced to a basal band of enamel and a lingually excavated, low remnant of dentine (figs 2C, 3C).

Comparisons with Aetiocetidae and other marine mammals

The pattern and intensity of tooth wear in NMV P252567 is unique among Aetiocetidae. Besides the present material, tooth wear has been described in some detail for three aetiocetids, namely, *Aetiocetus cotylalveus*, *A. weltoni* and *Fucaia buelli* (Deméré and Berta, 2008; Emlong, 1966; Marx et al., 2015). In addition, teeth are preserved but have not been properly figured in *A. polydentatus* and *Morawanocetus yabukii* (Barnes et al., 1995). The enamel covering the crowns in all of these species lacks the heavy abrasion characteristic of NMV P252567. Several of the premolars and molars in the holotypes of *A. cotylalveus* (USNM 25210) and *A. weltoni* (UCMP 122900) instead show attritional wear, which has removed much or all of the accessory denticles (Deméré and Berta, 2008; Emlong, 1966). In addition, relatively minor apical abrasion is evident along at least the anterior portion of the tooth row in *A. weltoni*, and on both the premolars and molars of *A. cotylalveus*.

Tooth wear in *A. polydentatus* has not been described in detail, but (presumably attritional) wear facets seemingly occur at least on the posteriormost mandibular teeth (Deméré and Berta, 2008). Both attrition and apical abrasion also occur in *Fucaia buelli*, with extensive attritional wear facets occurring on the lingual surfaces of the upper premolars and molars of the type specimen (UWBM 84024; Marx et al., 2015). Too little is known about *Morawanocetus* to be sure about wear patterns in this species. Nevertheless, based on photographs, at least one of the posterior molars preserved with the holotype (AMP 01) displays strong apical and, possibly, attritional wear.

In general, the dental wear of NMV P252567 most closely resembles that of the bizarre-looking archaic mysticete *Mammalodon colliveri* and the extant walrus, *Odobenus rosmarus*, both of which show lingual abrasion and (microscopic) striations, and are considered to be benthic suction feeders (Fitzgerald, 2010; Gordon, 1984). Unlike NMV P252567, however, *M. colliveri* has small, peg-like incisors displaying heavy abrasion, and its dentition is generally even more heavily worn (Fitzgerald, 2010). Other marine mammals known to show heavy dental wear include the killer whale *Orcinus orca*, the beluga *Delphinapterus leucas,* the porpoises *Phocoena phocoena* and *Semirostrum ceruttii*, and the archaic beaked whale *Ninoziphius platyrostris*. However, in orcas such wear generally consists of severe apical abrasion, possibly as a result of preying on sharks (Ford
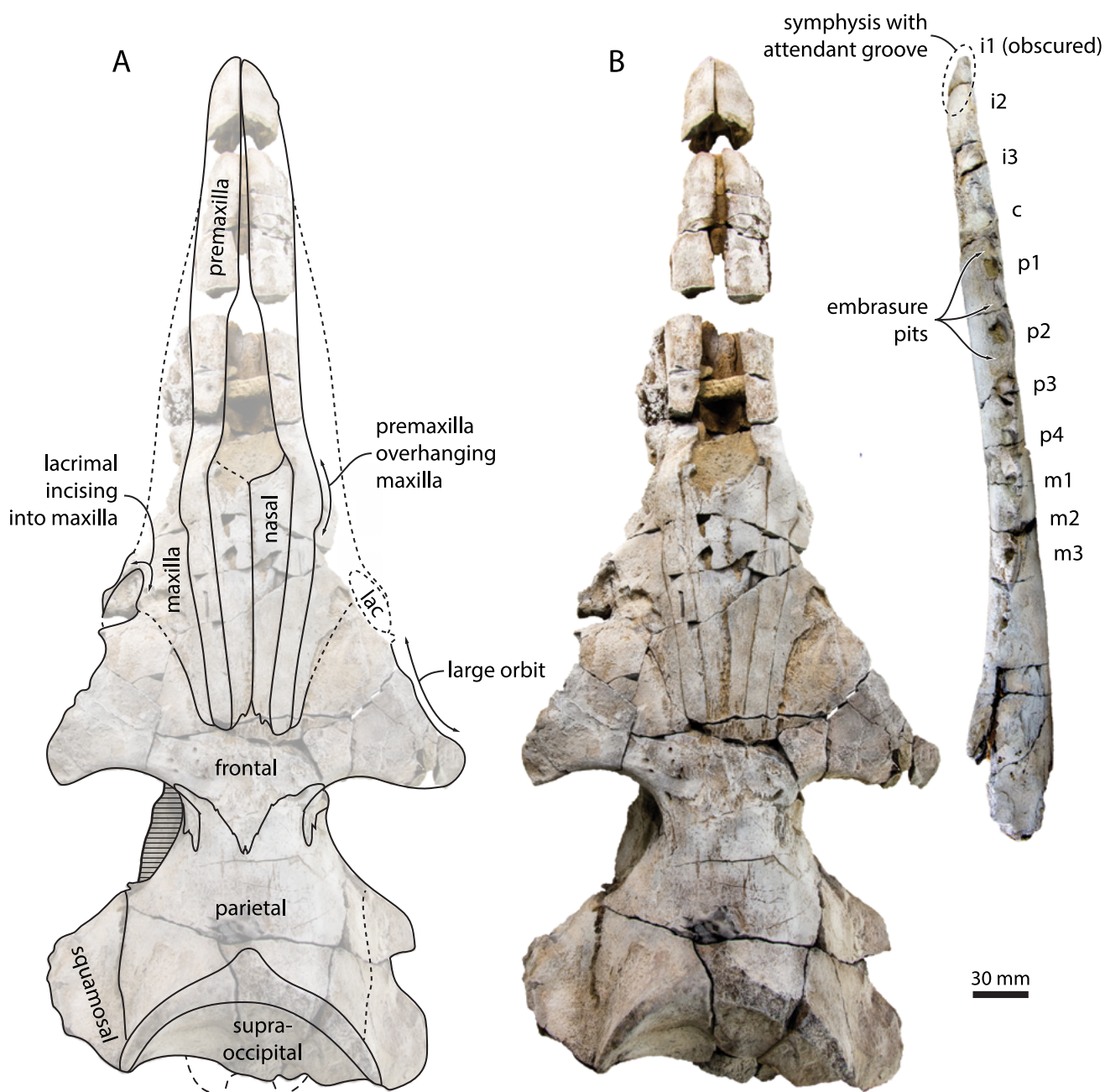
Figure 1. Diagnostic characteristics identifying NMV P252567 as an aetiocetid. A, explanatory line drawing of the skull; B, photograph of the skull (left) and mandible (right), both in dorsal view.

et al., 2011), while in belugas direct tooth-on-tooth occlusion results in a predominance of attrition (Fitzgerald, 2010; Struthers, 1895). By contrast, heavy wear in phocoenids and *N. platyrostris* may primarily reflect benthic foraging and the frequent ingestion of abrasive sediment (Lambert et al., 2013; Racicot et al., 2014), although more recent studies suggest that stem ziphiids may have foraged on epipelagic prey (Lambert et al., 2015).

Discussion and Conclusions

Feeding strategy of NMV P252567

The distinctive wear pattern of NMV P252567 provides insights into its likely feeding method. In particular, the pronounced lingual excavation of the crowns and attendant striations suggest that the insides of the teeth were subject to strong abrasive forces, such as repeated anteroposterior
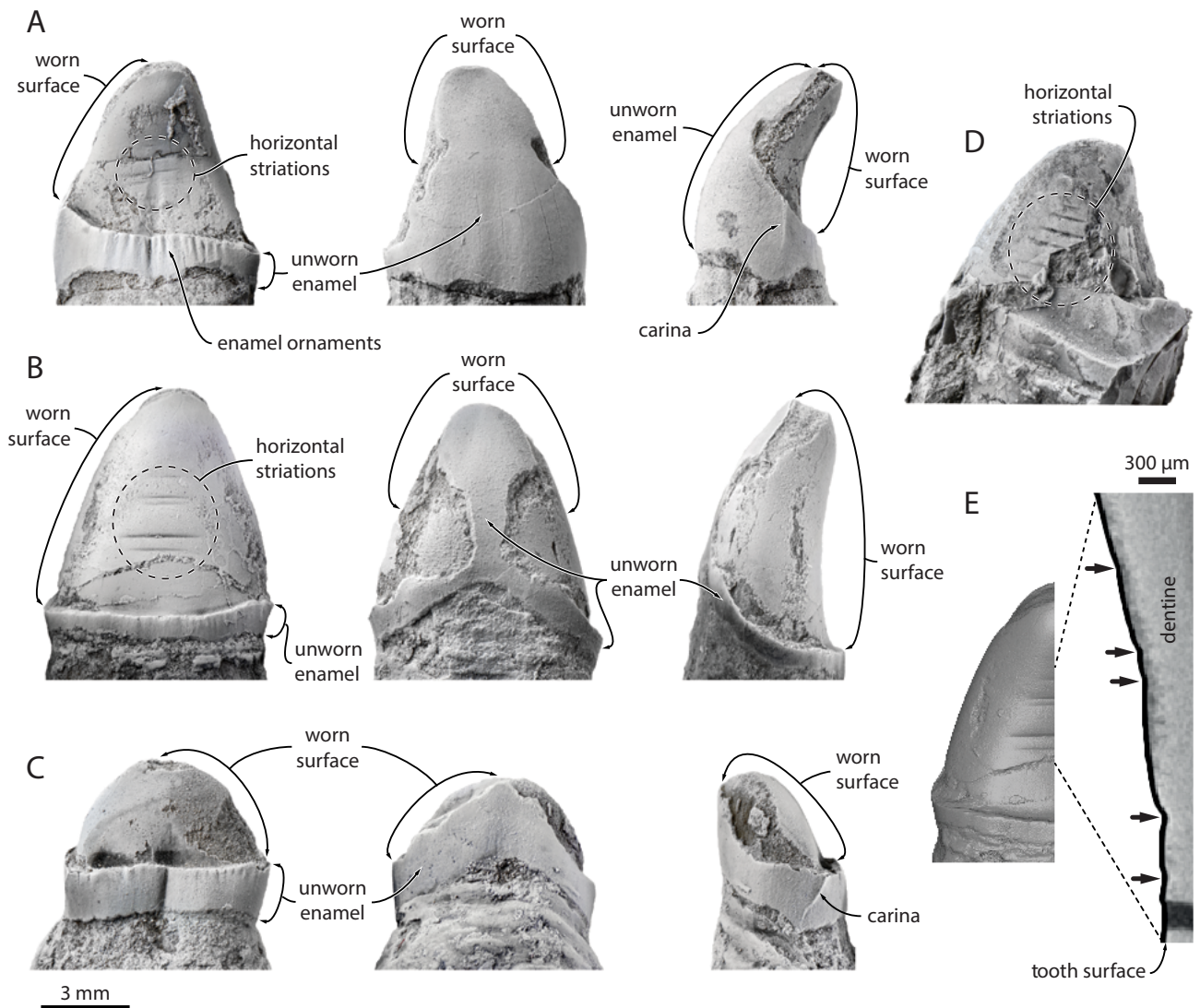
Figure 2. Wear patterns on representative teeth of NMV P252567, suggesting suction feeding in an aetiocetid. A, left upper canine or first premolar; B, double-rooted postcanine 1; C, ?lower double-rooted postcanine 2; D, ?lower double-rooted postcanine 3; E, micro-computed tomography cross section of postcanine 1, showing the depth and rounded edges of the horizontal striations (marked by large black arrows). A–C are shown in lingual, labial and anterior/posterior view, D in lingual view only.

(piston-like) movements of the tongue and/or flows of water laden with prey and sediment. The horizontal orientation of these forces is consistent with some form of (presumably benthic) suction feeding, as in *Mammalodon* and *Odobenus*, with the presence of lingual abrasion as far anteriorly as the incisors suggesting that suction was used for prey capture.

This interpretation holds irrespective of the age of the individual, as mature ontogeny would have exaggerated enamel wear without producing a heavy lingual bias or, particularly, the characteristic deep horizontal striations. Nevertheless, the intact enamel on the left upper incisor demonstrates that at least some of the anteriormost teeth were protected from wear, e.g. by being largely covered by gum tissue or by being located far

away from the main flow of prey and water. Baleen and tooth-assisted filter feeding can almost certainly be excluded, given that (i) baleen was most likely absent (see below) and (ii) the highly worn teeth would have been exceedingly poor at retaining small food particles. There is also no clear evidence for raptorial feeding, such as pronounced apical wear or dorsoventral shear facets, although such features may have been obliterated by heavy abrasion. At least facultative raptorial feeding may therefore have been possible.

We are not aware of a modern marine mammal showing a pattern of labial 'hourglass' wear that resembles that of NMV P252567. Nevertheless, the anterior, posterior and labial wear of the individual teeth is consistent with water and abrasive
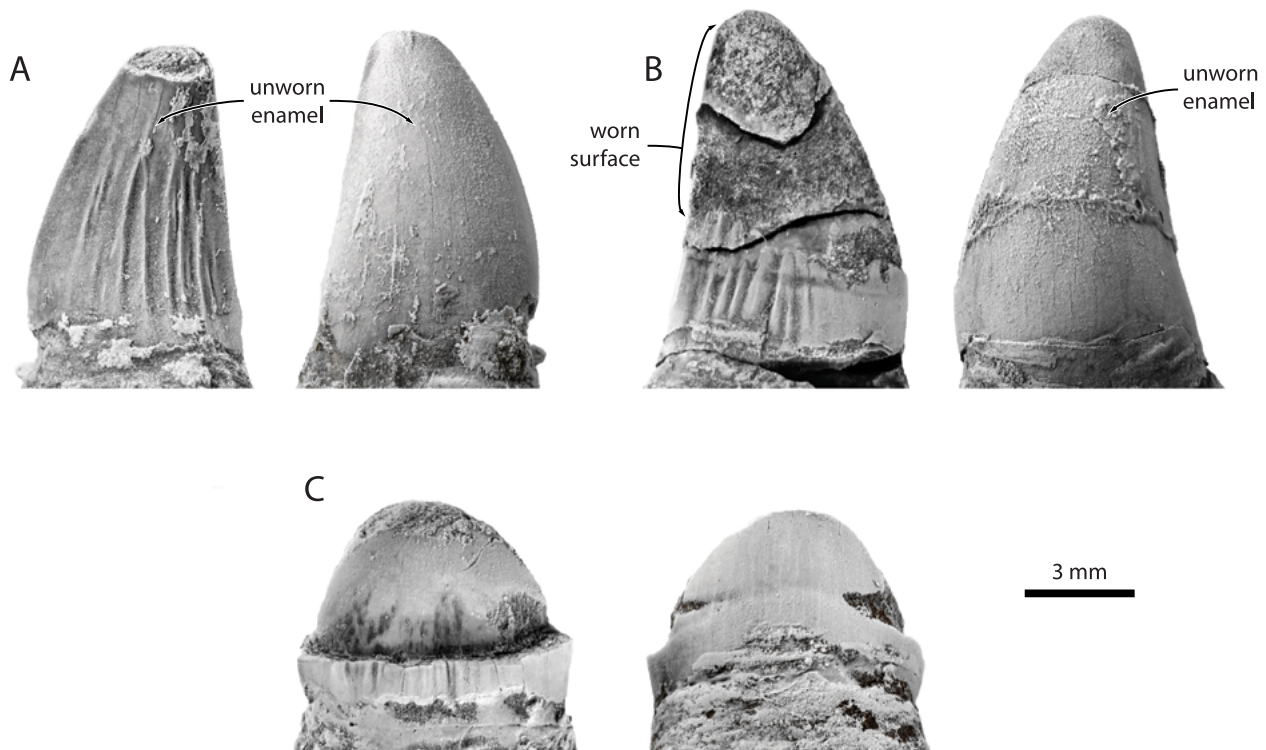
Figure 3. Additional teeth of NMV P252567. A, left upper incisor; B, right upper incisor; C, double-rooted postcanine 4. All teeth are shown in lingual (left) and labial (right) views. The lack or comparatively small degree of wear on the incisors suggests they may have been largely (left upper incisor) or partially (right upper incisor) enclosed within the gingiva, protecting them from the abrasive wear that affected the other teeth. A fifth double-rooted postcanine closely resembles postcanines 2 and 4 in terms of its wear, but is still partially encased in sediment and hence not shown here.

particles being forcibly expelled from the oral cavity through the diastemata. Similar water expulsion behaviour following suction has been observed in living species, such as pilot whales, belugas, leopard seals and Australian fur seals (Hocking et al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000a). During water expulsion, the jaws would likely have been held slightly open, causing the nearly occluding, interdigitating tooth rows to form a series of small gaps defined by the rims of the individual diastemata and the tips of the occluding upper or lower teeth. Sediment-laden water forced through these gaps would have abraded the enamel both along the rim of each diastema and on the immediately adjacent, labial portions of the tooth crowns. Over time, the labial wear surfaces would have enlarged into the hourglass wear observed here, possibly aided by the accidental, temporary retention of some sediment particles inside the lips after each water expulsion event.

Did aetiocetids have baleen?

Aetiocetids have previously been proposed as the most basal mysticetes to possess baleen, the key adaptation of modern whales. More specifically, the widespread occurrence of palatal nutrient foramina (in *Aetiocetus*, *Fucaia* and *Morawanocetus*), which in extant mysticetes supply the baleen rack, has been used to infer the existence of an incipient baleen structure between or just lingual to the teeth (Deméré and Berta, 2008; Deméré et al., 2008). While such an interpretation is possible, it also remains untested: just as the origin of feathers in non-avian dinosaurs does not mark the beginnings of flight, so the appearance of palatal foramina in mysticetes need not indicate the presence of baleen. Instead, the foramina of aetiocetids could, for example, have supplied its immediate predecessor – namely, well-developed gums, the presence of which is indicated both by the strongly emergent teeth of early mysticetes (Deméré and Berta, 2008; Fitzgerald, 2010) and, possibly, the largely unworn incisor of NMV P252567.

The presence of palatal foramina in NMV P252567 cannot be determined owing to post-mortem breakage of the rostral margin. Nevertheless, this specimen is the first aetiocetid preserving clear evidence of its feeding strategy, and thus also the first test of the idea that baleen occurred in members of this family. In the case of NMV P252567, extreme lingual wear indicates that the teeth were directly exposed to strong abrasive forces uninhibited by adjacent keratinous tubules or plates. The deep horizontal striations in particular suggest that the teeth were affected by continuous, linear movements of the tongue and/or prey-laden water, which would have been hindered if baleen had shielded the inside of the tooth row.

The presence of baleen is made even less likely by the interdigitating dentition, as judged from the mandibular alveoli alternating with similarly-sized embrasure pits for the upper teeth (fig. 1). Interdigitating teeth also occur in *Fucaia goedertorum* (Barnes et al., 1995) and *Aetiocetus weltoni* (Deméré and Berta, 2008), and suggest a lack of space and risk of functional interference (i.e. teeth potentially damaging or disorganising the baleen rack) that speaks against the presence of functional baleen. Overall, we therefore conclude that NMV P252567 did not possess baleen and was hence incapable of filter feeding in a manner similar to modern mysticetes.

The condition of NMV P252567 reinforces previous, less decisive evidence against baleen in several other aetiocetids, such as the well-developed shear facets on the teeth of *Fucaia buelli* and the large size of the teeth in both *F. buelli* and *Morawanocetus* (Marx et al., 2015; Sawamura, 2008; Sawamura et al., 2006). Specifically, shearing in *F. buelli* would likely have posed a considerable risk of damage to the baleen rack after each bite, while the relatively elongate teeth of *Morawanocetus* (and, probably, *F. buelli*) result in short diastemata, abrogating the need for a baleen filter. Both of these observations rely on indirect evidence, but the difficulties in explaining how baleen could have functioned in these taxa are suggestive.

In extant baleen whales, tall lower lips, marked lateral bowing and longitudinal (alpha) rotation allow the mandibles to occlude on to the labial (rather than the ventral) surface of the baleen plates, thereby preserving the integrity of the rack (Lillie, 1915) (fig. 4). In *Aetiocetus* and *Fucaia*, essentially straight mandibles, a tall, straight coronoid process, embrasure pits, and the presence of attritional wear on the teeth (Deméré and Berta, 2008; Emlong, 1966) demonstrate that the lower jaw moved largely vertically and was positioned close to the upper jaw to enable tooth occlusion (fig. 4). An aetiocetid baleen rack would have been closely associated with the teeth, as judged from the position of the palatal foramina in *A. weltoni* and the juxtaposition of the rudimentary teeth and developing baleen in extant mysticete foetuses (Deméré et al., 2008; Ishikawa and Amasaki, 1995). As a result, aetiocetid baleen would have been constantly disturbed by mandibular contact.

Teeth could conceivably have acted as protective spacers between the jaws, allowing baleen to grow between or just medial to the upper teeth. However, the interdigitating dentition would still have resulted in considerable disturbance of the rack. It is also possible that the inherent flexibility of baleen would have allowed it to withstand compression, e.g. by folding away posteriorly as in extant bowhead whales (Werth, 2001; Werth, 2004). Unlike in bowhead whales, however, the presence of teeth in aetiocetids – both adjacent to the rack and coming from below – would likely have interfered with the folding process. We therefore suggest that, contrary to past proposals (Deméré and Berta, 2008; Deméré et al., 2008), the evolution of baleen likely only became feasible after the appearance of a laterally bowed mandible capable of clearing the baleen rack during mouth closure, and likely following the reduction or loss of emergent dentition (fig. 5).

Current model of baleen evolution

Current ideas on the origin of baleen argue for a direct transition from raptorial to bulk filter feeding, as seemingly exemplified by aetiocetids in their retention of functional teeth alongside features generally associated with filtering (Deméré et al., 2008). Besides the presence of (i) palatal foramina, these features include (ii) thin lateral margins of the maxillae; (iii) a relatively broad rostrum; and (iv) an unsutured, ligamentous mandibular symphysis. Laterally bowed mandibles, another feature claimed to be present in aetiocetids (Deméré et al., 2008), is not apparent in any of the specimens we examined (NMV P252567, fig. 1B; *Aetiocetus weltoni*, UCMP 122900; *Fucaia goedertorum,* LACM 131146), all of which instead possess effectively straight lower jaws.

While it is true that these traits facilitate bulk filter feeding in modern mysticetes (e.g. Lambertsen et al., 1995), their condition and function in archaic mysticetes is much less clear. As argued above, evidence from NMV P252567 and other aetiocetids speaks against the presence of baleen in this family, with the palatal foramina – the prime evidence for baleen – more likely supplying enlarged gums. Likewise, we see no direct link between thin lateral maxillary margins and filtering, and instead suggest that they may be a consequence of rostral broadening. The resulting increase in oral capacity would benefit both suction performance and filter feeding, so cannot be attributed to filtering alone (Fitzgerald, 2012; Werth, 2006). In any case, broad rostra are not characteristic of all filter-feeding whales: those of skim-feeding right whales are narrow and elongate, as essentially are those of the extant pygmy right (*Caperea marginata*) and even grey whales (*Eschrichtius robustus*).

Finally, the exact dental occlusion and tall, straight coronoid processes of *Fucaia* and *Aetiocetus* imply that longitudinal (alpha) rotation of aetiocetid mandibles was minimal compared with extant mysticetes, despite a ligamentous symphysis (Kimura, 2002; Lambertsen et al., 1995; Marx et al., 2015). Among extant mysticetes, a ligamentous mandibular symphysis enables extant balaenopterids to rotate their bowed mandible along its long axis, thereby increasing oral volume during engulfment feeding (Lambertsen et al., 1995). By contrast, the mandible of aetiocetids is straight and constrained to largely dorsoventral rotation, rendering a mobile symphysis ineffective for increasing oral capacity (Arnold et al., 2005; Marx et al., 2015).

Alternatively, mandibular rotation may initially have enhanced control of the lower lip. In right whales, lateral lip rotation serves to create a flow channel lateral to the baleen rack during skim feeding (Lambertsen et al., 2005; Werth and Potvin, 2016). This feeding strategy requires a large filtration area, which in right whales is created by the arched rostrum and elongate baleen plates. Given its short, flat rostrum and erupted teeth, space limitations in the aetiocetid skull would have precluded this feeding mode. In grey whales, lip rotation appears to assist lateral suction feeding by creating an aperture for prey and water to be sucked into the oral cavity (Ray and Schevill, 1974). A similar behaviour in aetiocetids is conceivable, but the tall coronoid process would likely have prevented the opening of a wide enough gap.
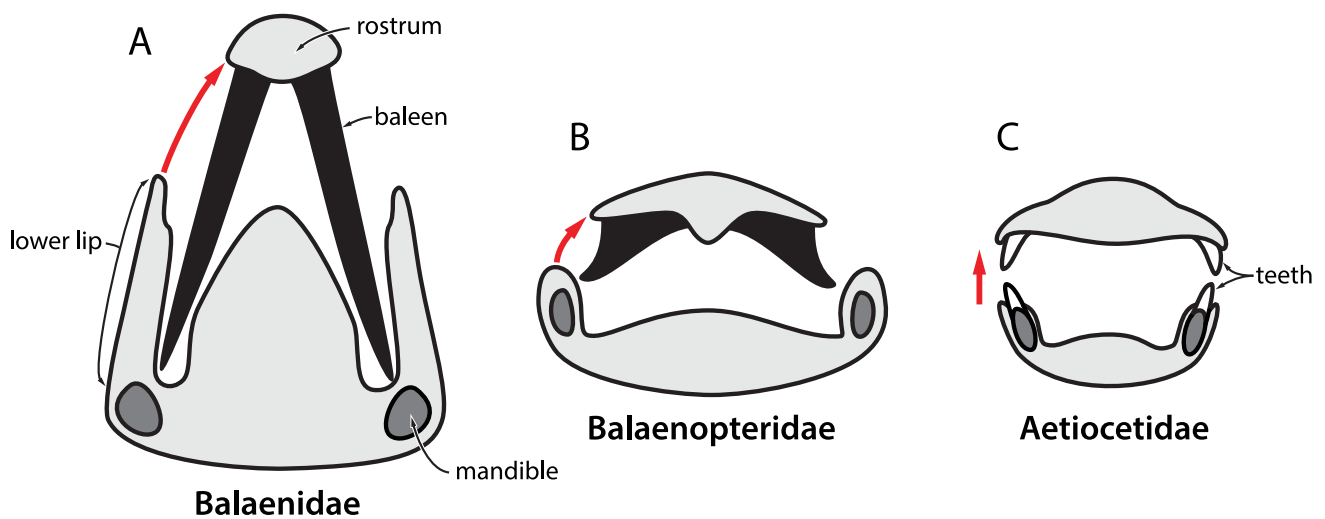
Figure 4. Cross section of the rostrum and lower jaws of A, a balaenid, B, a balaenopterid, and C, an aetiocetid, illustrating the relative movement of the mandible during jaw closure (red arrows). All drawings show the mouth slightly open. In right whales (A) and rorquals (B), the laterally bowed mandibles and/or tall lower lips rotate inwards on to the labial surface of the baleen plates, thereby leaving the rack intact. In aetiocetids (C), the movement of the mandible is mostly vertical and the upper and lower jaws need to approach each other enough to allow the teeth to occlude, thereby risking interference with any baleen present. A and B are adapted from Pivorunas (1979: fig. 3).
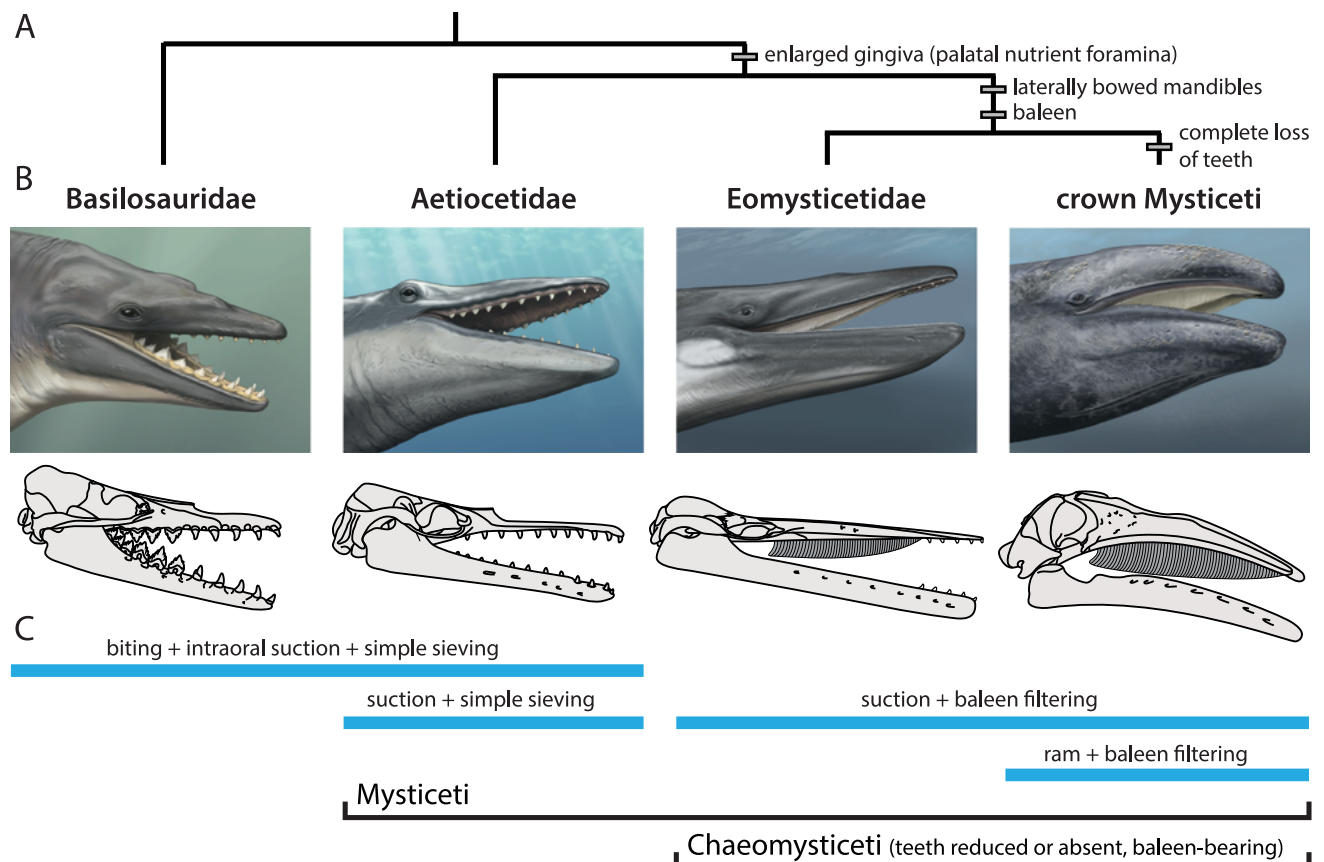

Figure 5. Suction feeding precedes baleen filtering in mysticete evolution. A, consensus tree of aetiocetid evolutionary relationships, based on all cladistic studies published to date (e.g. Deméré and Berta, 2008; Deméré et al., 2008; Fitzgerald, 2010; Geisler and Sanders, 2003; Marx and Fordyce, 2015; Steeman, 2007), showing major feeding-related synapomorphies; B, life reconstructions (top) and skulls (in lateral view) of a representative archaeocete (*Dorudon atrox*), aetiocetid (NMV P252567), eomysticetid (*Yamatocetus canaliculatus*) and extant suction feeding mysticete (grey whale, *Eschrichtius robustus*); C, inferred behaviours and feeding strategies. Life reconstructions by Carl Buell.

Overall, the function of the ligamentous symphysis in aetiocetids remains unclear. In particular, there is little evidence to suggest it was a specific adaptation to filter feeding. This point is emphasised further by the observations that, even among extant mysticetes, jaw rotation can be associated with suction feeding rather than filtration, and that an unsutured symphysis also occurs in a variety of other mammals, including – possibly – *Mammalodon* (Fitzgerald, 2010; Lieberman and Crompton, 2000).

An alternative model of baleen evolution

NMV P252567 makes a crucial contribution to the question of how baleen and bulk filtering first evolved. It is one of a limited number of fossil whales documenting the transition from raptorial to filter feeding; its cranial morphology disputes prior conjecture about the widespread presence of baleen in aetiocetids; and it provides the first reported evidence of suction feeding at the pivotal mysticete transition towards filter feeding and giant size. The ability to generate suction is fundamental to most marine vertebrates, and widespread among extant marine mammals, including pinnipeds and cetaceans (Hocking et al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000b; Werth, 2006). Nevertheless, up to this point it has rarely been associated with mysticete evolution, other than in reference to the highly unusual mammalodontids (Fitzgerald, 2010; Fitzgerald, 2012).

Suction is necessary when feeding underwater, where it enables the transport of food towards the back of the mouth for swallowing even in raptorial species that still employ teeth in prey capture (Werth, 2000b; Werth, 2006). This was likely already the case in archaic whales, soon after their initial transition to an aquatic environment. However, suction behaviour – whether for prey capture or intraoral transport – is generally difficult to demonstrate in fossils, since relevant osteological correlates, such as blunt, wide jaws (Werth, 2006) or a large hyoid apparatus (Bloodworth and Marshall, 2007; Heyning and Mead, 1996), are often either not preserved, or not always clearly developed, such as in the grey whale, *Eschrichtius robustus* (Kienle et al., 2015).

NMV P252567 offers an extremely rare insight into the evolution of suction behaviour and, along with *Mammalodon*, demonstrates a tendency for early mysticetes to evolve suction-based feeding strategies. There is currently no evidence that other aetiocetids relied on suction to a similar degree, although such a behaviour may be less apparent in animals that feed higher in the water column, and hence ingest less or no abrasive (i.e. wear-inducing) sediment. Nevertheless, given the apparently high degree of specialisation of NMV P252567 and the widespread occurrence of suction behaviour among extant marine mammals, it seems highly likely that aetiocetids were at least able to use suction for intraoral transport.

Use of suction and lack of baleen in aetiocetids suggests an alternative model – briefly hinted at by Arnold et al. (2005) – of how and why filter feeding first arose (fig. 5). Archaic mysticetes, including aetiocetids, likely inherited both a functional dentition and the ability to use suction for intraoral transport from their archaeocete ancestors (Werth, 2000b). Water ingested as a result of suction was expelled prior to swallowing (Hocking et

al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000a), with the prey either being physically held in place, or the teeth, jaws and surrounding soft tissues acting as a barrier, or simple sieve, retaining food items inside the mouth (Bloodworth and Marshall, 2005; Hocking et al., 2013). Some of these early whales, including NMV P252567, *Mammalodon* and the ancestor of modern mysticetes, honed their suction capabilities to the point where they became able to capture prey, and we suggest that it was this transition, not filter feeding, that ultimately initiated tooth loss in the chaeomysticete lineage.

Among both extant (sperm whales, beaked whales and certain delphinids) and extinct odontocetes (e.g. *Australodelphis*, *Odobenocetops*), capture suction feeding strongly correlates with a reduced dentition (Werth, 2000b; Werth, 2006), and the same may plausibly have been the case in mysticetes. This scenario avoids potential problems of functional interference between a working dentition and incipient baleen (Marx et al., 2015), and explains how teeth could have been lost without impacting on foraging success. Further, a loss of functional teeth prior to the origin of baleen coincides with evidence of foetal development from extant mysticetes, which shows that baleen growth only initiates once the tooth buds have already started to degrade (Ishikawa and Amasaki, 1995; Karlsen, 1962). It is possible that teeth and baleen nonetheless co-occurred in some archaic chaeomysticetes, as shown by eomysticetids bearing shallow alveoli and, possibly, teeth (Boessenecker and Fordyce, 2015); however, the dentition in these taxa was already reduced. We also note the similar anterior positioning of teeth in eomysticetids and extant suction-feeding odontocetes like the beluga, and the delphinids *Grampus* and *Globicephala*.

Suction for capture limited the maximum size of prey that could be taken, and furthermore would have enabled the ancestors of modern mysticetes to gather small prey items in bulk; however, the absence of specialised filtering teeth, such as those of the extant crabeater (*Lobodon*) and leopard seals (*Hydrurga*), would have permitted the inadvertent expulsion of small food particles prior to swallowing, as observed in trials with California sea lions (*Zalophus californianus*) (Hocking et al., 2013). This problem was eventually solved by the elaboration of the gingiva, first potentially as a grasping (Miller, 1929) and, ultimately, a filtering apparatus – i.e. baleen. A similar condition exists in the extant Dall's porpoise *Phocoenoides dalli*, which supplements its rudimentary dentition with a series of 'gum teeth' that are structurally similar to the early growth stages of baleen (Miller, 1929). As Miller (1929: 4) himself observed: "These resemblances are so important that we are probably justified in regarding the gingival and dental structures of *Phocoenoides* as representing anatomical stages closely parallel to those through which the corresponding parts in the toothed ancestors of the Mysticeti must have passed."

The feeding strategy of the earliest baleen-bearing whales would initially have been a form of intermittent or continuous suction filter feeding, as inferred for a range of extinct cetotheriids (El Adli et al., 2014; Gol'din et al., 2014), and still observed in the extant grey whale, *Eschrichtius robustus* (Ray and Schevill, 1974). However, with baleen now in place, other methods of filtering no longer reliant on suction also became

possible, including the highly specialised skim (Werth and Potvin, 2016) and lunge feeding (Lambertsen et al., 1995) strategies of extant right whales and rorquals, respectively.

Our new model is consistent with all available palaeontological, developmental and behavioural evidence, but will benefit from further research effort. This might include an investigation of dietary stable isotopes, to determine at what trophic level aetiocetids were feeding (e.g. Clementz et al., 2014); an increased focus on the oldest (Late Eocene–Early Oligocene) mysticetes, to test for evidence of suction feeding in early chaeomysticetes (e.g. tooth wear), or further evidence regarding baleen in aetiocetids, e.g. in the form of actually preserved traces (e.g. Esperante et al., 2008; Gioncada et al., 2016); and further studies of the feeding strategies of extant marine mammals, to determine possible modern analogues of archaic mysticetes. Overall, our findings suggest that suction behaviour was fundamental to the evolution of baleen and filtering, and thus a crucial early innovation that helped to trigger the rise of the largest animals on Earth.

Acknowledgements

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Figure S1. Upper left canine or first premolar of NMV P252567.

- **Custom View 1:** Lingual view showing horizontal striations.

- **Custom View 2:** Labial view showing hourglass wear eroding the enamel surface.

- **Custom View 3:** Anterior view showing erosion of the lingual surface above the gum line.

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Figure S2. Double-rooted postcanine 1 of NMV P252567.

- **Custom View 1:** Lingual view showing horizontal striations.

- **Custom View 2:** Labial view showing hourglass wear eroding the enamel surface.

- **Custom View 3:** Profile view (anterior or posterior) showing erosion of the lingual surface above the gum line.

- **Custom View 4:** Close-up view of the horizontal striations showing polished edges.