

Archaeocete-like jaws in a baleen whale

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The titanic baleen whales (Cetacea, Mysticeti) have a bizarre skull morphology, including an elastic mandibular symphysis, which permits dynamic oral cavity expansion during bulk feeding. How this key innovation evolved from the sutured symphysis of archaeocetes has remained unclear. Now, mandibles of the Oligocene toothed mysticete *Janjucetus hunderi* show that basal mysticetes had an archaeocete-like sutured symphysis. This archaic morphology was paired with a wide rostrum typical of later-diverging baleen whales. This demonstrates that increased oral capacity via rostral widening preceded the evolution of mandibular innovations for filter feeding. Thus, the initial evolution of the mysticetes' unique cranial form and huge mouths was perhaps not linked to filtering plankton, but to enhancing suction feeding on individual prey.

Keywords: Cetacea; Mysticeti; Mammalodontidae; evolution; Australia; Oligocene

1. INTRODUCTION

Living baleen whales (Mysticeti) have bizarre skulls that enable dynamic oral cavity expansion and accommodation of vast volumes of sea water during filter feeding [1–3]. This is achieved with kinetic skull joints, including an elastic lower jaw joint (mandibular symphysis), which permits independent rotation of the jaws in two planes: on their long (α) and horizontal (Ω) axes [2,3]. This key innovation supported the evolution of titanic body sizes and the extraordinary success of mysticetes [1,4], but contrasts with the primitive rigid symphysis of early whales (archaeocetes) [5,6]. The transition from this morphology in raptorial feeding archaeocetes to the specialized jaws of baleen whales has been obscure: until now, all mysticetes were thought to possess an elastic symphysis [5,7]. Here, I report that the basal-toothed mysticete *Janjucetus hunderi* (Oligocene, Australia [7]) has an archaeocete-like sutured symphysis paired with a typically mysticete-like wide rostrum. Thus, rostral modifications for increased oral space preceded the evolution of mandibular innovations for filter feeding in early mysticetes. The initial shift to increasing oral capacity may represent skull-shape optimization for suction feeding, which was perhaps the first step towards the unique cranial form of baleen whales.

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2. MATERIAL AND METHODS

Museum Victoria, Melbourne (NMV) specimen P229455 and United States National Museum of Natural History, Washington, DC (USNM) specimen 534009 are casts of an incomplete pair of mandibles currently held in a private collection (figure 1*a–d*). The analysis, photographs and measurements (see the electronic supplementary material) are all based on the original fossils, which are from the Jan Juc Formation (Chattian, Late Oligocene, 24.2–27.9 Ma [8]) at Jan Juc Beach, southwest of Torquay, Victoria, Australia (near 38°21' S, 144°17' E). Additional institutional abbreviations: NMVC, Museum Victoria Mammalogy collection (Melbourne); UCMP, University of California Museum of Paleontology (Berkeley).

3. RESULTS

The pair of mandibles represented by NMV P229455 and USNM 534009 possess a suite of characters unique to the toothed mysticete clade Mammalodontidae: (i) short mandibular symphysis without a symphyseal groove (figure 1*a,d*); (ii) relatively large mental foramina; (iii) mandible has a salient lateral edge to the alveolar margin such that lower post-canine teeth are implanted within an alveolar groove (figure 1*a–c*); (iv) posterior half of the alveolar margin of the mandible forms an angle with the ventral margin of the mandible; (v) posterior half of the mandible with a straight ventral margin and no ventral expansion of the pan bone; (vi) teeth have salient longitudinal ridges developed on both the buccal and lingual surfaces of the crown enamel; (vii) posterior lower post-canines with two roots joined below the crown base by a transversely narrow isthmus; and (viii) lower post-canines closely spaced along the alveolar margin without elongated intervening diastemata or embrasure pits.

Within Mammalodontidae, the specimen represented by NMV P229455 and USNM 534009 differs from *Mammalodon colliveri* by having: (i) mandibles with externally concave profiles viewed dorsally (figure 1*a*); (ii) a robust alveolar portion of the mandible; (iii) seven lower post-canine teeth (*Mammalodon* has eight [6]); (iv) an anterior apex of the mandible that is not recurved medially; (v) a rugose symphyseal surface occupying the entire vertical diameter of the mandibular symphysis (figure 1*d*); and (vi) separate alveoli for i1 and i2. It unambiguously shares all but character (v) with the holotype specimen (NMV P216929) of *J. hunderi* (which is missing this region of the mandible [6,7]) supporting its referral to the latter species. Furthermore, measurements of the specimen represented by NMV P229455 and USNM 534009 closely approximate the equivalent measurements of NMV P216929 (see the electronic supplementary material).

4. DISCUSSION

Until now, all living and fossil mysticetes have been shown to possess a mandibular symphysis characterized by a smooth symphyseal surface and longitudinal symphyseal groove (figure 2*c,d*) [2,3,9]. These features, respectively, accommodate a fibrocartilage annulus, which allows mandible rotation while feeding, and a thickened periosteum, which strengthens the symphysis by counteracting the torque exerted during oral cavity expansion [2,9]. *Janjucetus* lacks these derived features, resembling basilosaurid archaeocetes in having a rugose symphyseal surface (figure 2*a,b*). This shows that *Janjucetus* had a sutured symphysis and could not deploy α or Ω mandibular rotation during feeding. Yet, *Janjucetus* shares with all mysticetes a short symphyseal surface and a wide rostrum,

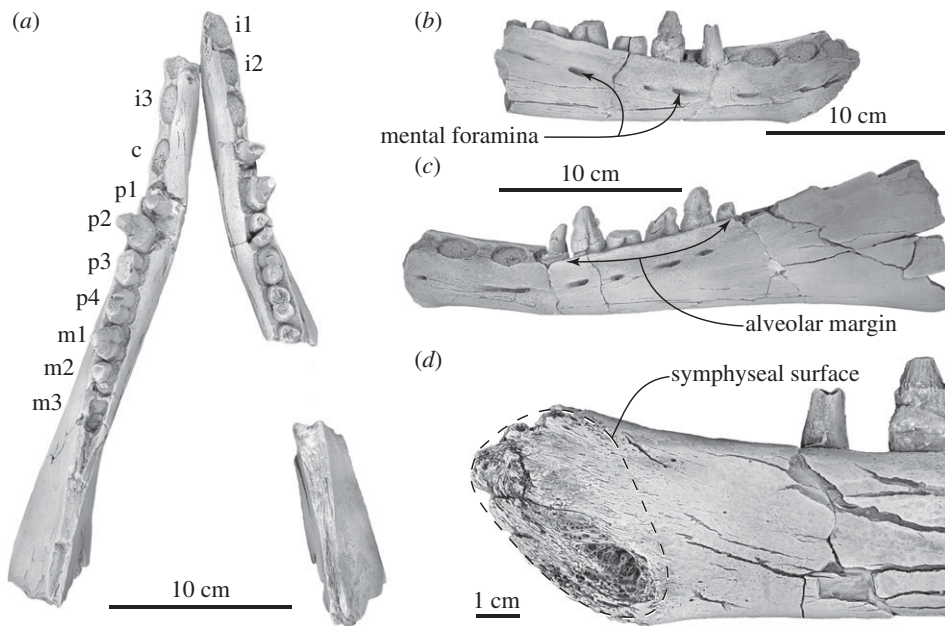


Figure 1. Mandibles of *Janjucetus hunderi*. (a–d) Original fossil specimen represented by NMV P229455 and USNM 534009, whitened with ammonium chloride. (a) Left and right mandibles in dorsal view; (b) anterior part of right mandible in lateral view (c) left mandible in lateral view; and (d) symphyseal region of right mandible in medial view. Anatomical abbreviations: c, canine; i, incisor; m, molar; p, premolar.

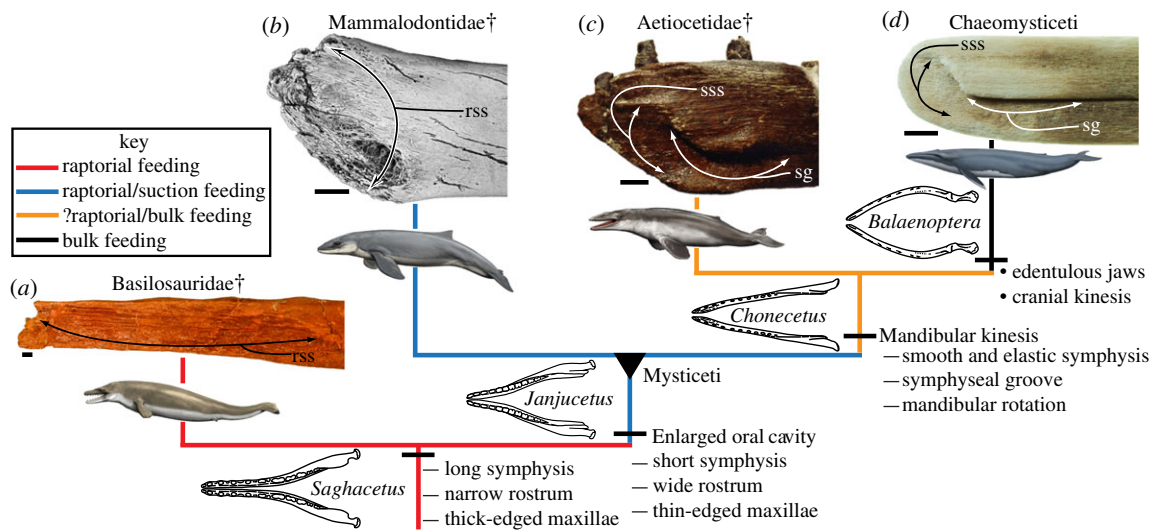


Figure 2. Evolution of mysticete skull features linked to feeding, based on the phylogeny in the study of Fitzgerald [6]. (a–d) Mandibular symphyses in right medial view: (a) *Zygorhiza kochii* (USNM 11962); (b) *Janjucetus hunderi* (specimen represented by NMV P229455 and USNM 534009); (c) *Aetiocetus weltoni* (UCMP 122900) and (d) *Balaenoptera acutorostrata* (NMV C24936). Dagger symbol (†) denotes extinct clades. rsg, rugose symphyseal surface; sg, symphyseal groove; sss, smooth symphyseal surface. Cetacean artwork by C. Buell.

specializations that in baleen whales increase palate surface area and oral cavity volume [2,6,7].

Janjucetus bridges the gap in jaw morphology between archaeocetes and more advanced baleen whales, showing that the earliest mysticetes lacked mandibular kinesis (figure 2). A non-sutured and kinetic mandibular symphysis has until now been considered a key synapomorphy of Mysticeti [5,7]. The absence of this unique innovation in *Janjucetus* suggests that the earliest mysticetes could not engulf and expel large volumes of water, which is a crucial prerequisite for bulk filter feeding [1–3].

Thus, evolution of bulk planktivory was decoupled from initial enlargement of oral capacity via rostral widening—a feature present in *Janjucetus* and other basal toothed mysticetes. Odontocete species with a wide and blunt head shape are capable of generating significantly greater negative pressures during suction feeding than those with elongate and narrow jaws [10–12]. The increased rostral width in basal mysticetes may therefore represent optimization of head shape for suction feeding, which, in tandem with mandibular kinesis, was later co-opted for bulk feeding in edentulous mysticetes.

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