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Gigantism precedes filter feeding in baleen whale evolution

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SUMMARY

Baleen whales (Mysticeti) are the largest animals on Earth, thanks to their ability to filter feed vast amounts of small prey from seawater. Whales appeared during the latest Eocene, but evidence of their early evolution remains both sparse and controversial [1, 2], with several models competing to explain the origin of baleen-based bulk feeding [3-6]. Here, we describe a virtually complete skull of *Llanocetus denticrenatus*, the second-oldest (ca 34 Ma) mysticete known. The new material represents the same individual as the type and only specimen, a fragmentary mandible. Phylogenetic analysis groups *Llanocetus* with the oldest mysticete, *Mystacodon selenensis* [2], into the basal family Llanocetidae. *Llanocetus* is gigantic (body length ca 8 m) compared to other early mysticetes [7-9]. The broad rostrum has sharp, widely-spaced teeth with marked dental abrasion and attrition suggesting biting and shearing. As in extant whales, the palate bears many sulci, commonly interpreted as osteological correlates of baleen [3]. Unexpectedly, these sulci

converge on the upper alveoli, suggesting a blood supply to well-developed gums, rather than to baleen. We interpret *Llanocetus* as a raptorial or suction feeder, revealing that whales evolved gigantism well before the emergence of filter feeding. Rather than driving the origin of mysticetes, baleen and filtering likely only arose following an initial phase of suction-assisted raptorial feeding [4, 5]. This scenario strikingly differs from that proposed for odontocetes, whose defining adaptation – echolocation – was present even in their earliest representatives [10].

RESULTS

Systematics

Cetacea; Mysticeti; Llanocetidae; *Llanocetus denticrenatus*

Holotype

National Museum of Natural History, Smithsonian Institution (Washington DC, USA; USNM), specimen no. 183022; virtually complete skull (Figs 1–3, S1–7), partial hyoid apparatus, and assorted postcranial material (Fig. S8).

Locality and horizon

Seymour Island, Antarctica; near the top of unit Telm 7 of the La Meseta Formation. Mollusc-based $^{87}Sr/^{86}Sr$ dating suggest an age of 34.2 ± 0.87 Ma, or latest Eocene [11].

Emended diagnosis

Differs from all known cetaceans in having markedly palmate, widely-spaced teeth, and a robust a mandibular crest [new term] immediately lateral to the lower tooth row. Differs from archaeocetes in having a supraoccipital that projects anteriorly well beyond the anterior border of the squamosal fossa. Shares with mysticetes, but not archaeocetes or odontocetes, the presence of a dorsoventrally flattened maxilla, and a transversely thickened basioccipital crest. Further differs from odontocetes in lacking a transversely expanded ascending process of the maxilla and a premaxillary foramen. Differs from all known mysticetes in having palatal sulci that converge on the alveoli. Further differs from all mysticetes except *Mystacodon* in having a sagittal trough on the parietals; from all mysticetes except mammalodontids, *Mystacodon* and *Morawanocetus* in having teeth with strong enamel ornament both

lingually and labially; from all mysticetes except *Mystacodon* and eomysticetids in having extremely elongate nasals; from all chaeomysticetes in retaining a functional dentition and unfused basi- and thyrohyals; and from *Mystacodon*, mammalodontids and aetiocetids in its larger size, and in having a lateral lamina of the pterygoid that underlaps the anterior process of the periotic.

Overview and phylogenetic placement

Llanocetus denticrenatus is the second-oldest described mysticete, exceeded in age only by *Mystacodon selenensis* from the Late Eocene of Peru (ca 36 Ma) [2]. Our new material, discovered by REF in 1987, is fragmentary but relatively complete, preserving fine details of the palate, dentition, and auditory region (Figs 1–3). It represents the same individual as the type and only specimen, a fragmentary mandible and cranial endocast originally described by Mitchell [1]. This identification is confirmed by two mandibular fragments that perfectly connect with the original holotype (Fig. 3). A full description of the combined specimen is included in the Supplementary Information.

The skeleton of *Llanocetus* is dominated by archaic traits, such as relatively minor cranial telescoping, teeth, an elongate temporal fossa, a weakly-developed antorbital notch, a well-developed superior process of the periotic, a non-rotated tympanic bulla that remains unfused to the periotic, a plate-like coronoid process of the mandible, unfused basi- and thyrohyals, a massive sternum, and cervical vertebrae with a round body (in anterior view) (Figs 1–3; S1-S8). As in basilosaurids, the dental formula appears to have been 3.1.4.2/3.1.4.3. Nevertheless, the broad rostrum of *Llanocetus* strikingly differs from the relatively narrow snout of archaeocetes (Fig. 1). Specifically, the elongate nasals suggest a lengthening of the basal portion of the rostrum, resulting in a wider palate and an anterior repositioning of the external nares that, temporarily, counteracted the long-term cetacean trend of facial telescoping [12]. A similar anterior shift of the nasal is apparent in *Mystacodon* and eomysticetids [2].

Our phylogenetic analysis groups *Llanocetus* with *Mystacodon* and a smaller, undescribed specimen (OU GS10897) from the Early Oligocene of New Zealand (Fig. 4). Diagnostic features of this clade, here equated with Llanocetidae, include the markedly elongate nasals, and a sagittal trough on the parietals (Fig. 1). Unlike all other basal mysticetes, llanocetids furthermore retain large teeth with two entirely separate roots, as well as strong labial and lingual enamel ornaments (uncertain in *Mystacodon*). Our results suggest Llanocetidae to be the basalmost mysticete lineage, with the exception of

Coronodon. Previous studies support the basal placement of *Coronodon* [6, 8, 13], but – with one exception [8] – interpreted *Llanocetus* as more crownward, and even as sister to Chaeomysticeti [6, 14, 15]. Crownward of Llanocetidae, our analysis recovered a ladder-like succession comprising Mammalodontidae, *Morawanocetus*, Aetiocetidae, and Chaeomysticeti. Unlike in analyses based on earlier versions of this data matrix [14, 16], mammalodontids and aetiocetids do not form a clade. This arrangement further contradicts another recent study [6], but is upheld by a variety of slightly older papers [3, 8, 17].

DISCUSSION

Feeding apparatus

The cheek teeth of *Llanocetus* are robust, notably emergent from the jaws, and, except for the first premolar, highly denticulate. The upper and lower teeth would have faced each other to occlude properly; the now-oblique upper teeth and adjacent rostral margin have been flattened by burial. Apical abrasion of the main and accessory denticles is evident throughout the tooth row, and particularly so in m1 and m2 (Fig. 2). In addition, p4–m2 bear pronounced attritional shear facets (Fig. 2), indicating occluding teeth capable of grasping and/or slicing prey. Prey processing, however, would have been impeded by the wide diastemata, of uncertain function, which prevent a continuous cutting surface. Likewise, the broad, flattened maxilla would likely be less resistant to large bite forces than the more tubular rostrum of archaeocetes.

Among cetaceans, a broad rostrum is typical of filter feeders [3]. Thus, the unusually long and palmate tooth crowns of *Llanocetus* could formed a lattice-like filtering sieve [6], as seen in extant leopard and crabeater seals [18]. Purely tooth-based filtering is unlikely, however, because the adjacent large diastemata would bypass such a filter. Furthermore, the pronounced dental wear implies biting of prey and tooth-on-tooth shearing, and the teeth are (quantitatively) sharp, with no obvious adaptations for water flow as seen in filter feeding seals [5].

Alternatively, filter feeding might be indicated by the presence of palatal sulci, which are widely considered as an osteological correlate of baleen [3]. Contrary to expectations [6], however, the sulci in *Llanocetus* converge directly on the upper alveoli, where baleen would be of little use, and there is no

vascularisation in the intervening diastemata (Fig. 2). Rather than baleen, we propose that the palatal sulci of *Llanocetus* supplied well-developed gums that supported the emergent teeth. This interpretation is consistent with the sulci being homologous with those of extant mysticetes, given that baleen develops from the gingiva [19].

The absence of baleen is further indicated by shear facets on the posterior cheek teeth, which suggest that the upper and lower jaws came into close contact during occlusion and approached each other vertically, rather than mediolaterally as in extant mysticetes [4]. In addition, vertical jaw movements are indicated by the high, straight coronoid process, which contrasts with the laterally bent structure facilitating longitudinal (alpha) rotation of the mandible in chaeomysticetes [20]. In extant baleen whales foetuses, teeth and baleen develop in approximately the same area of the maxilla, near the gingival edge of the rostrum [21]. Any baleen in *Llanocetus* would therefore have been at risk of being crushed by the interdigitating anterior teeth, or sheared between the posterior premolars and molars every time the jaws closed.

Origin of filter feeding

Several models compete to explain the origin of mysticete bulk feeding, ranging from tooth-based filtering as seen in extant crabeater and leopard seals [1, 6], to a transitional morphology combining teeth and baleen [3], to an intermediary phase of suction feeding that gave rise to filtering only later [4, 5]. Previous studies relied on palatal sulci to hypothesise the concurrent presence of teeth and baleen in another archaic mysticete family (Aetiocetidae), and, consequently, argued for a direct evolutionary transition from raptorial to baleen-based filter feeding [3, 22]. The peculiar rostral and dental morphology of *Llanocetus* questions this idea, and instead suggests that mysticetes may have passed through an intermediate stage involving neither filtering (sharp teeth, no evidence for baleen) nor purely raptorial feeding (widely spaced teeth, flattened maxilla). Following earlier suggestions [4, 23-25], we propose that this intermediate phase may have involved suction-assisted raptorial feeding or, possibly, pure suction feeding, as seen in *Mammalodon* [8], an unnamed aetiocetid [4] and, possibly, *Mystacodon* [2].

Suction is widespread among extant marine mammals [23, 26], many of which may use this ability to transport prey intraorally [27]. In *Llanocetus*, suction would have been facilitated by both the broad rostrum and the presence of a strong sternohyoideus muscle, as inferred from the large sternum

(Fig. S8). In addition, suction plausibly accounts for the apparent decrease in effectiveness of the dentition, relative to archaeocetes, as well as the presence of a mandibular crest immediately lateral to the lower tooth row (Fig. 3). In lateral view, this crest partially obscures the teeth, and in life may have supported a slightly raised lower lip that aided in reducing the lateral gape during suction. A similar bony support is absent among extant right whales and rorquals, but occurs in the pygmy right whale, *Caperea marginata*, beaked whales (precoronoid crest) and, arguably, the grey whale, *Eschrichtius robustus*.

Gigantism precedes filtering

Llanocetids markedly differ from each other in their overall size, feeding apparatus, and dental wear. *Llanocetus*, in particular, is unusually large: at an estimated body length of nearly 8 m, its size is comparable to that of extant minke whales, and exceeds that of any other toothed mysticetes [28], eomysticetids [28], and – until the Late Miocene – even most crown mysticetes [9]. Notably, *Llanocetus* is also larger than a *Morawanocetus*-like aetiocetid from Japan, which was previously reported as reaching 8 m [7]; this estimate seems to have been erroneous, with the real length being approximately 6 m.

Unlike *Llanocetus*, *Mystacodon* only reaches about 4 m, and is characterized by relatively closely spaced teeth that have been obliterated by wear. At ca. 3 m, OU GS10897 is even smaller than *Mystacodon*, yet has large teeth marked by shear facets. Such pronounced intrafamilial disparity is consistent with comparable variation in mammalodontids (macroraptorial vs suction feeding) [8] and aetiocetids (variable degree of homodonty, suction vs raptorial feeding, wide range of body sizes) [4, 7, 24], and supports earlier suggestions of a short-lived phase of morphological and behavioral ‘experimentation’ early in mysticete evolution [14].

Overall, *Llanocetus* demonstrates that mysticetes have, at least sporadically, tended towards gigantism since their very origin [28]. Crucially, neither llanocetids [2, 5] nor mammalodontids [8, 29] seem to show any signs of filtering, and evidence for bulk feeding in *Coronodon* [6] and aetiocetids [3] has been questioned on grounds of tooth function, dental wear, and stable isotope data [4, 5, 24, 30]. Together, these insights suggest that both the emergence of mysticetes in general, and the origin of large body size in particular, preceded the origin of the key adaptation of modern whales: baleen and bulk feeding (Fig. 4). This scenario markedly differs from that of odontocetes, whose major hallmark – echolocation – appears to be as old as themselves [10, 31, 32].

AUTHOR CONTRIBUTIONS

Conceptualization, R.E.F and F.G.M.; Formal Analysis, F.G.M.; Investigation, all authors; Resources, R.E.F.; Writing, all authors; Funding Acquisition, all authors.

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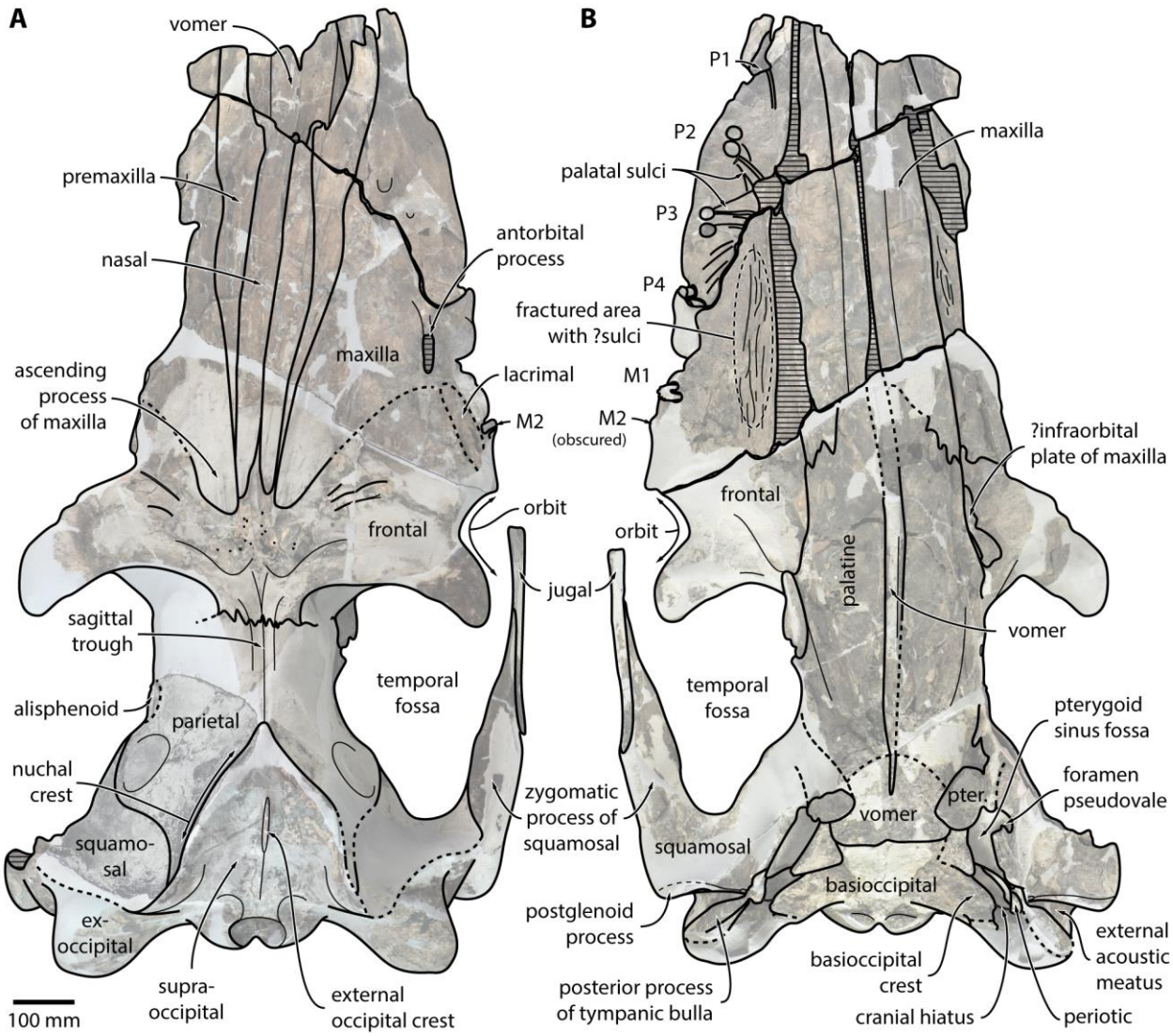

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183 **Fig. 1 Skull of *Llanocetus denticrenatus* (USNM 183022).** (A) dorsal view, (B) ventral view. See also

184 Figs S1–S8. pter., pterygoid.

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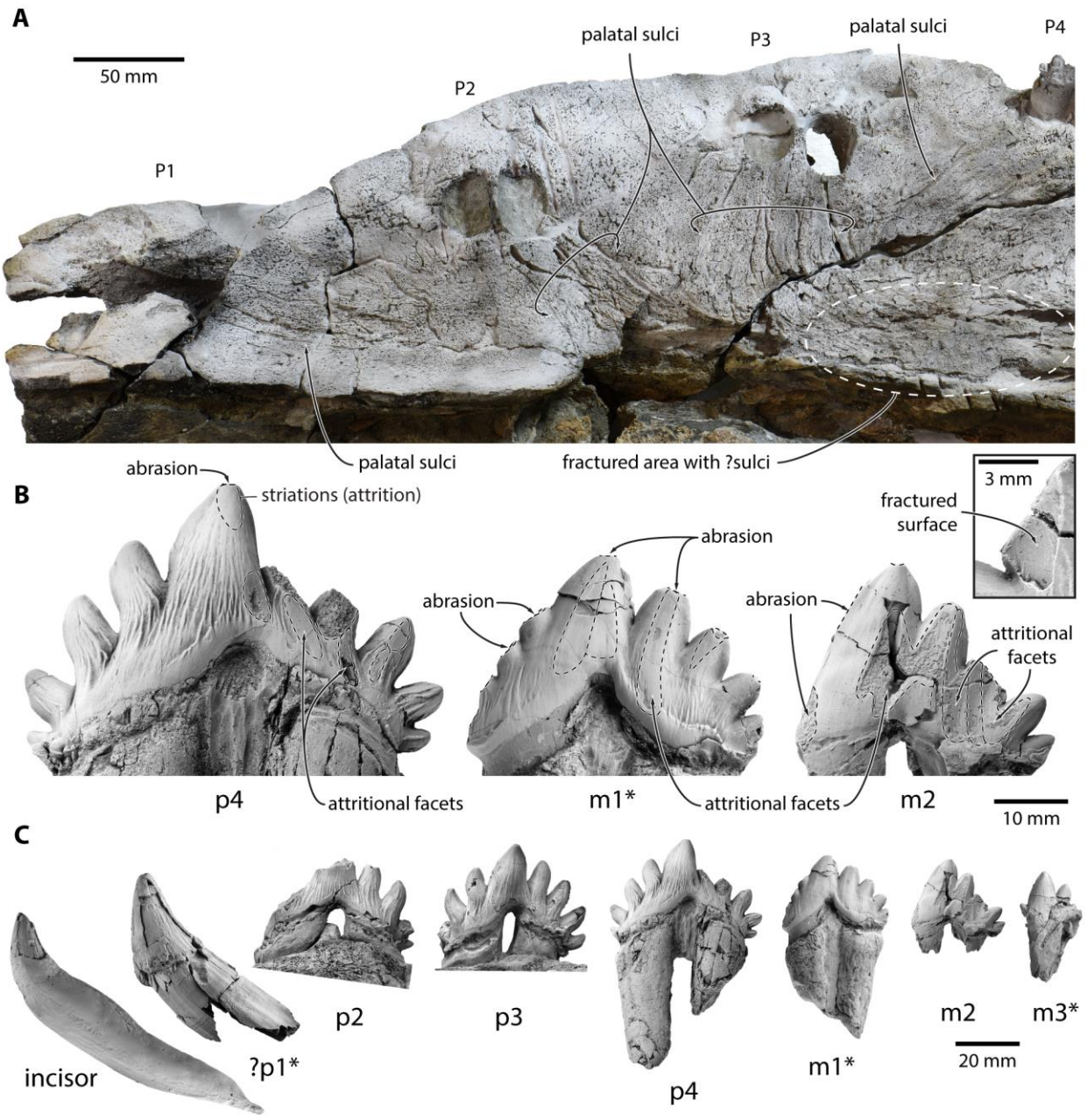
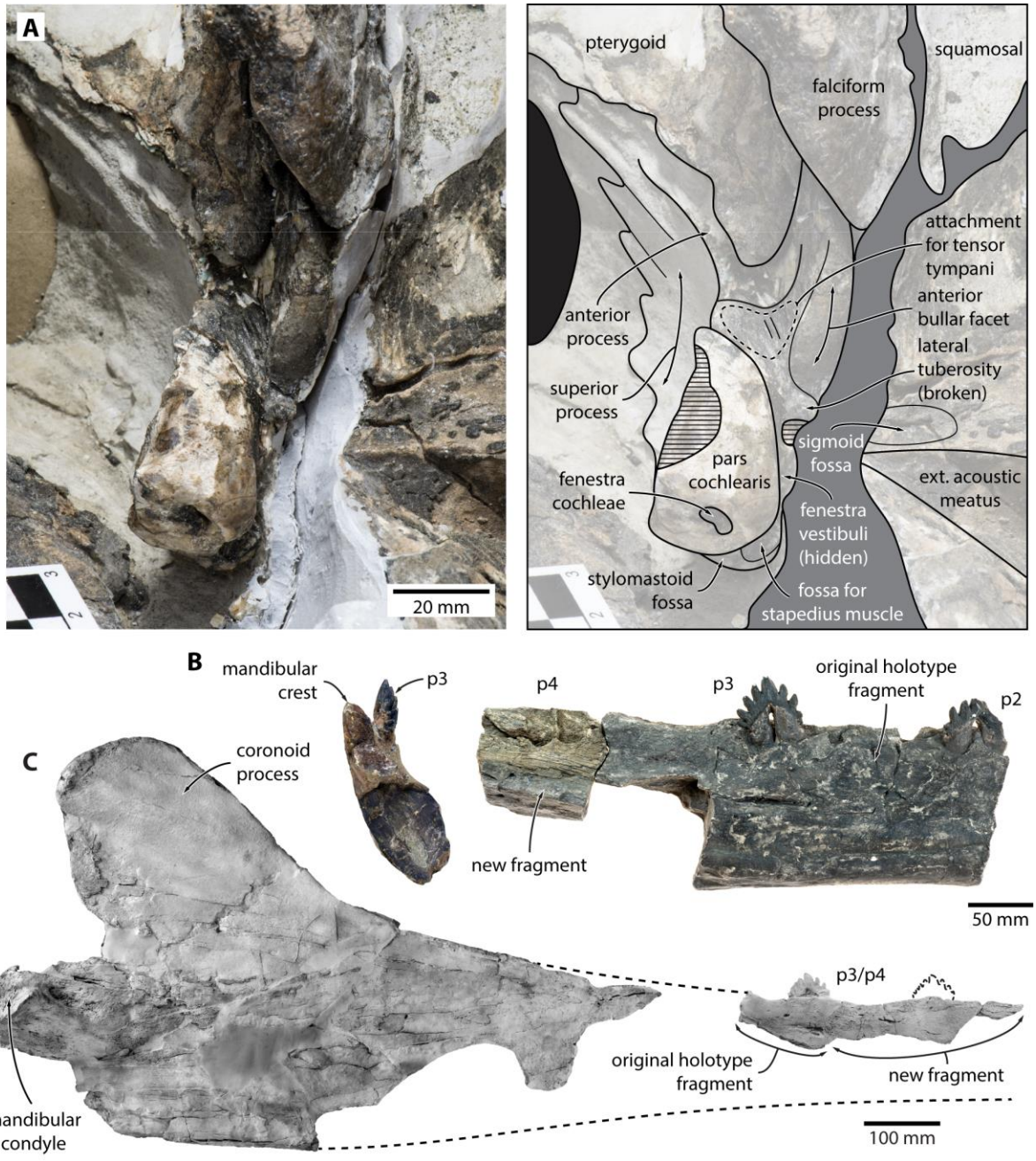


Fig. 2 Feeding apparatus of *Llanocetus denticrenatus* (USNM 183022). (A) left palate in ventral view, showing alveoli and palatal sulci; (B) lower posterior check teeth, in labial view, showing abrasion and attrition; (C) lower dentition, in labial view. Photographs marked by an asterisk have been mirrored to facilitate comparisons. See also Figs S1–S8.



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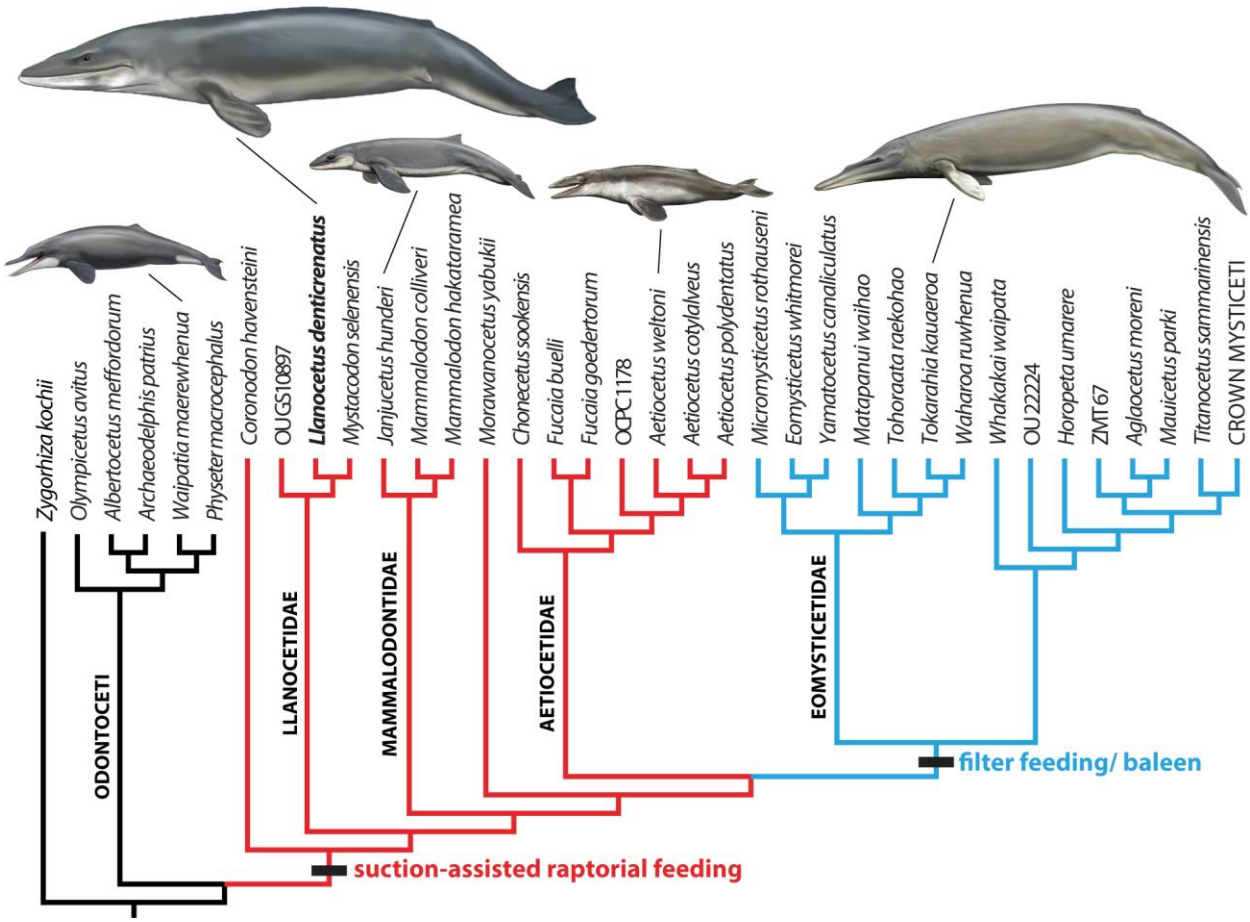
193 **Fig. 3 Periotic and mandible of *Llanocetus denticrenatus* (USNM 183022).** (A) left periotic, in ventral
194 view (*in situ*); (B) mandible fragment originally described by [1], in posterior (left) and medial (right) view;
195 note the previously undescribed fragment matching the original material; (C), right mandible, in lateral
196 view. See also Figs S1–S8.

197



198

199 **Fig. 4 Phylogenetic relationships of *Llanocetus denticrenatus*.** Note the markedly larger size of

200 *Llanocetus* relative to other stem mysticetes. Reconstructions by Carl Buell.

201

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STAR METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Morphological partition of the dataset	This paper; www.morphobank.org	P2044
Molecular partition of the dataset	[33]	N/A
Supermatrix used for analysis	This paper; www.morphobank.org	P2044
Software and Algorithms		
MrBayes 3.2.6	[34]	

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, R. Ewan Fordyce (ewan.fordyce@otago.ac.nz).

METHOD DETAILS

Phylogenetic Analyses

The phylogenetic analysis was based on a modified and somewhat enlarged version (106 taxa, 275 characters) of the total evidence matrix of Marx and Fordyce [14], fully illustrated with 6,340 individual specimen photographs. The analysis was carried out without any clock assumptions in MrBayes 3.2.6 [34], on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway [35] (20 million generations, first 25% of generations discarded as burn-in). All partitions and settings replicated those of Marx and Fordyce [14].

QUANTIFICATION AND STATISTICAL ANALYSIS

Estimates of Body Size

Body length estimates were calculated based on the following equations, where TL is total body length and BIZYG is bizygomatic width:

(1) $\log(TL) = 0.92 * (\log(BIZYG) - 1.72) + 2.68$ [36]

(2) $TL = 8.209 * BIZYG + 66.69$ [37]