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## 6 **Gigantism precedes filter feeding in baleen whale evolution**

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16

### 17 **SUMMARY**

18 **Baleen whales (Mysticeti) are the largest animals on Earth, thanks to their ability to filter feed**  
19 **huge volumes of small prey from seawater. Mysticetes appeared during the Late Eocene, but**  
20 **evidence of their early evolution remains both sparse and controversial [1, 2], with several**  
21 **models competing to explain the origin of baleen-based bulk feeding [3-6]. Here, we describe a**  
22 **virtually complete skull of *Llanocetus denticrenatus*, the second-oldest (ca 34 Ma) mysticete**  
23 **known. The new material represents the same individual as the type and only specimen, a**  
24 **fragmentary mandible. Phylogenetic analysis groups *Llanocetus* with the oldest mysticete,**  
25 ***Mystacodon selenensis* [2], into the basal family Llanocetidae. *Llanocetus* is gigantic (body**  
26 **length ca 8 m) compared to other early mysticetes [7-9]. The broad rostrum has sharp, widely-**  
27 **spaced teeth with marked dental abrasion and attrition suggesting biting and occlusal**  
28 **shearing. As in extant mysticetes, the palate bears many sulci, commonly interpreted as**  
29 **osteological correlates of baleen [3]. Unexpectedly, these sulci converge on the upper alveoli,**  
30 **suggesting a peri-dental blood supply to well-developed gums, rather than to inter-alveolar**

31 racks of baleen. We interpret *Llanocetus* as a raptorial or suction feeder, revealing that whales  
32 evolved gigantism well before the emergence of filter feeding. Rather than driving the origin of  
33 mysticetes, baleen and filtering likely only arose following an initial phase of suction-assisted  
34 raptorial feeding [2, 4, 5]. This scenario strikingly differs from that proposed for odontocetes,  
35 whose defining adaptation – echolocation – was present even in their earliest representatives  
36 [10].

37

## 38 RESULTS

### 39 Systematics

40 Cetacea; Neoceti; Mysticeti; Llanocetidae; *Llanocetus denticrenatus*

### 41 Holotype

42 National Museum of Natural History, Smithsonian Institution (Washington DC, USA; USNM),  
43 specimen 183022; virtually complete skull, partial hyoid apparatus, and assorted postcrania (Figures  
44 1–3, Table S1, Data S1).

### 45 Locality and horizon

46 Seymour Island, Antarctica; 64°14'51.09"S, 56°37'31.61"W; near the top of unit Telm 7 of the La  
47 Meseta Formation. Mollusc-based <sup>87</sup>Sr/<sup>86</sup>Sr dating suggests an age of 34.2 ± 0.87 Ma, or latest  
48 Eocene [11].

### 49 Emended diagnosis

50 Differs from all known cetaceans in having markedly palmate-denticulate, widely-spaced teeth, and a  
51 robust mandibular crest [new term] immediately lateral to the lower tooth row. Differs from  
52 archaeocetes, *Mystacodon* and mammalodontids in having a supraoccipital that projects anteriorly  
53 well beyond the anterior border of the squamosal fossa. Shares with mysticetes, but not archaeocetes  
54 or odontocetes, the presence of a dorsoventrally flattened and laterally expanded maxilla, and a  
55 transversely thickened basioccipital crest. Differs from all known mysticetes in having palatal sulci that  
56 converge on the alveoli. Further differs from all mysticetes except *Mystacodon* in having a sagittal  
57 trough on the parietals; from all mysticetes except mammalodontids, *Mystacodon* and  
58 *Morawanocetus* in having teeth with strong enamel ornament both lingually and labially; from all  
59 mysticetes except *Mystacodon* and eomysticetids in having extremely elongate nasals; from all

60 chaeomysticetes in retaining a functional dentition and unfused basi- and thyrohyals; and from  
61 *Mystacodon*, mammalodontids and aetiocetids in its larger size, and in having a lateral lamina of the  
62 pterygoid that underlies the anterior process of the periotic.

### 63 **Overview and phylogenetic placement**

64 *Llanocetus denticrenatus* is the second-oldest described mysticete, exceeded only by *Mystacodon*  
65 *selenensis* from the Late Eocene of Peru (ca 36 Ma) [2]. Our new material, discovered by REF in  
66 1987, is fractured but relatively complete (Figures 1–3). It is the same individual as the holotype, a  
67 fragmentary mandible and cranial endocast [1], as confirmed by two mandibular fragments that  
68 perfectly connect with the original specimen (Figure 3). The loss of both epiphyses on the single  
69 preserved cervical vertebra suggests a juvenile. A full description is included as Supplementary  
70 Information (Data S1).

71 The skeleton of *Llanocetus* is dominated by traits generally considered archaic for mysticetes,  
72 including minor cranial telescoping, heterodont teeth, an elongate temporal fossa, a well-developed  
73 superior process of the periotic, and unfused basi- and thyrohyals (Figures 1–3; Data S1). Assuming  
74 the presence of three incisors and one canine, the dental formula would have been 3.1.4.2/3.1.4.3, as  
75 in basilosaurid archaeocetes. Nevertheless, the broad rostrum and wide palate of *Llanocetus* differ  
76 strikingly from the relatively narrow snout of archaeocetes (Figure 1). The elongate nasals may be  
77 developmentally linked to the lengthened basal portion of the rostrum, resulting in a wide palate and  
78 anterior external nares that contrast with the long-term cetacean trend of facial telescoping [12]. A  
79 similar prolongation of the basal rostrum is apparent in *Mystacodon* and eomysticetids [2] and, in the  
80 absence of pronounced polydonty, could explain the presence of variably-sized diastemata in archaic  
81 mysticetes.

82 Our phylogenetic analysis groups *Llanocetus* with *Mystacodon* and a smaller, undescribed  
83 specimen (Otago University Geology Museum, OU GS10897) from the Early Oligocene of New  
84 Zealand (Figure 4). Diagnostic features of this clade, the Llanocetidae, include the markedly elongate  
85 nasals and a sagittal trough on the parietals (Figure 1). Unlike all other basal mysticetes, llanocetids  
86 also retain large cheek teeth with two entirely separate roots, as well as strong labial and lingual  
87 enamel ornament (uncertain in *Mystacodon*). Our results, albeit with low support, suggest  
88 Llanocetidae to be the basalmost mysticete lineage, with the exception of *Coronodon*. Previous  
89 studies support the basal placement of *Coronodon* [6, 8, 13], but – with one exception [8] –

90 interpreted *Llanocetus* as more crownward [6, 14, 15]. Crownward of Llanocetidae, there is a ladder-  
91 like succession comprising Mammalodontidae, *Morawanocetus*, Aetiocetidae, and Chaeomysticeti.  
92 Unlike in several previous studies [6, 14, 16], mammalodontids and aetiocetids do not form a clade.

## 93 **DISCUSSION**

### 94 **Feeding strategy**

95 Several models compete to explain how baleen whales derived their signature filter feeding strategy  
96 from a raptorial ancestry, ranging from tooth-based filtering as seen in extant crabeater and leopard  
97 seals [1, 6], to a transitional morphology combining teeth and baleen [3], to an intermediary phase of  
98 suction feeding that gave rise to filtering only later [4, 5]. *Llanocetus* combines a basal phylogenetic  
99 position with well-developed teeth and, crucially, osteological features usually correlated with baleen.  
100 As a result, it provides a perfect opportunity to test alternative origins for mysticete filter feeding.

101 *Raptorial feeding.* The cheek teeth of *Llanocetus* are robust, notably emergent from the jaws,  
102 and highly denticulate. Attrition on p4–m2 indicates shearing occlusion, and thus the ability to slice  
103 through food. In addition, most teeth (and especially m1 and m2) show pronounced abrasion of the  
104 main and accessory denticles (Figure 2), suggesting their use in grasping prey. Nevertheless, prey  
105 processing would have been impeded by the wide diastemata, which separate the cutting surfaces  
106 along the posterior tooth row. Likewise, the broad, flattened maxilla would likely be less resistant to  
107 large bite forces than the more tubular rostrum of archaeocetes.

108 *Tooth-based filter feeding.* Extant crabeater and leopard seals use intricate postcanines as a  
109 lattice-like sieve [17]. Unlike in other carnivorans, the teeth of these seals are notably blunt, with  
110 broad, rounded intercuspal notches that facilitate water flow [5]. Tooth-based filtering has furthermore  
111 been hypothesized in the archaic toothed mysticete *Coronodon* (but see [5]), based on its intricate  
112 and largely unworn dentition [6]. The teeth of *Llanocetus* are broad and palmate-denticulate, and thus  
113 superficially consistent with filtering; however, they are also quantitatively sharp, with no obvious  
114 adaptations for water flow [5]. Purely tooth-based filtering furthermore seems unlikely given the large  
115 diastemata, which show no prey-trapping mechanism. This is especially true along the posterior tooth  
116 row, where the opposing teeth occlude, rather than interdigitate. Loss of small prey in the absence of  
117 a continuous filter has been demonstrated experimentally in California sea lions, whose teeth are far  
118 more closely spaced than in *Llanocetus* [17]. Finally, the pronounced dental wear implies biting of

119 prey and tooth-on-tooth shearing, unlike in both *Coronodon* [6] and extant filter feeding seals [17, 18].  
120 Together, these observations suggest that *Llanocetus* did not employ its teeth as a filter.

121 *Baleen-based filter feeding.* *Llanocetus* shares with extant mysticetes the presence of a broad  
122 rostrum, typical of both suction and filter feeders [3, 19], as well as palatal sulci, widely considered as  
123 an osteological correlate of baleen [3]. The sulci in *Llanocetus* do not enter the diastemata, however;  
124 rather, they are grouped into peri-dental bundles converging directly on the upper cheek teeth, where  
125 baleen would be of little use (Figures 1, 2). This pattern is particularly pronounced in P3, where the  
126 sulci terminate immediately medial to the alveoli, implying that any baleen did not extend beyond the  
127 margins of the tooth (Figure 2).

128 Steep attritional facets suggest that the posterior cheek teeth occluded, and that the upper  
129 and lower jaws approached each other vertically, rather than mediolaterally as in modern mysticetes  
130 [4]. In extant baleen whale fetuses, teeth and baleen develop in approximately the same region of the  
131 maxilla, near the gingival edge of the rostrum [20]. Any peri-dental baleen in *Llanocetus* would  
132 therefore have been at risk of being crushed by the interdigitating anterior teeth, or sheared between  
133 the posterior premolars and molars. Together, these observations suggest that *Llanocetus* lacked  
134 baleen, and we propose that its palatal sulci instead supplied well-developed gums (see below).

135 *Suction feeding.* Overall, the rostral and dental morphology of *Llanocetus* suggests a feeding  
136 strategy that involved neither filtering (sharp teeth, large diastemata, pronounced wear, no baleen)  
137 nor purely raptorial feeding (widely spaced teeth, flattened maxilla). By process of elimination, and in  
138 the absence of evidence to the contrary, we therefore propose that *Llanocetus* was a suction-assisted  
139 raptorial feeder. Alternative strategies no longer employed by living marine mammals could perhaps  
140 also be envisaged, but are necessarily speculative and, thus, less parsimonious.

141 Suction is widespread among marine mammals [21, 22], many of which may use it to  
142 transport prey intraorally [19]. Suction feeding leads to a decrease in prey size [23], which abrogates  
143 the need to process food [21, 22] and may have allowed the evolution of large diastemata in early  
144 mysticetes [6]. In *Llanocetus*, suction would furthermore have been facilitated by the broad rostrum  
145 [19]; the presence of a strong sternohyoideus muscle [24], as inferred from the large sternum (Data  
146 S1) [8]; and the presence of a mandibular crest (Figure 3). In lateral view, this crest partially obscures  
147 the lower teeth, and in life may have supported a raised lower lip that narrowed the lateral gape  
148 during suction [19]. A similar bony support occurs in suction-feeding odontocetes such as beaked

149 whales and *Australodelphis* (precoronoid crest) [25, 26], the pygmy right whale, *Caperea marginata*,  
150 and, arguably, the grey whale, *Eschrichtius robustus*.

151 Like *Llanocetus*, other llanocetids [2, 5] and mammalodontids [8, 27] also show no signs of  
152 filtering, and evidence for bulk feeding in *Coronodon* [6] and aetiocetids [3] has been questioned on  
153 grounds of tooth function, dental wear, and stable isotope data [4, 5, 28, 29]. Conversely, evidence for  
154 various degrees of suction has emerged in *Mammalodon* [8], an unnamed aetiocetid [4], and  
155 *Mystacodon* [2]. Together, these observations are consistent with a suction-based intermediary phase  
156 in mysticete evolution that smoothed the transition from raptorial to filter feeding [4, 21, 28, 30].

### 157 **Origin of baleen**

158 Palatal sulci in whales are widely assumed to be a direct correlate of baleen [3]. In extant mysticetes,  
159 these sulci carry a well-developed blood supply to the gums, which in turn ontogenetically give rise to  
160 baleen racks [31, 32]. Enhanced palatal vascularization is a distinct feature of mysticetes, and we  
161 agree that it and baleen are concomitants. Nevertheless, the directionality and timing of this  
162 association remain unclear. Because baleen growth is mediated by the phylogenetically older gingiva,  
163 its association with an enhanced palatal blood supply is indirect: blood vessels supply the gums,  
164 which *in turn* support the baleen [32-34].

165 There are three equally parsimonious origins for palatal sulci and baleen: both structures  
166 originated at the same time, as implied by previous papers arguing for the coexistence of baleen and  
167 teeth in archaic mysticetes [3, 35]; enhanced palatal vessels preceded baleen, and even may have  
168 been a prerequisite for its evolution, as assumed by recent studies arguing for an intermediary phase  
169 of suction feeding [4, 5]; or rudimentary baleen arose before an enhanced palatal blood supply, with  
170 the latter appearing only as the filtering apparatus became larger and more nutritionally demanding.

171 Given our phylogenetic hypothesis, and the poor preservation of the palate in *Mystacodon*  
172 and OU GS10897, it is not clear whether the palatal sulci of *Llanocetus* are homologous to those of  
173 later mysticetes. Nevertheless, the feeding morphology and basal position of *Llanocetus* imply that  
174 enhanced palatal vascularization in whales is possible *without* the presence of baleen. The only  
175 alternatives to this scenario are (i) that *Llanocetus* evolved baleen independently from  
176 chaeomysticetes; (ii) that baleen evolved near the base of Mysticeti, but was independently lost in  
177 *Mystacodon* and mammalodontids; or (iii), baleen was – contrary to all morphological evidence –  
178 present in *Mystacodon* and mammalodontids. We deem all of these alternatives equally unlikely.

179           The situation in *Llanocetus* implies that palatal vascularization is not always a clear correlate  
180 of baleen. This conclusion holds irrespective of whether its sulci are homologous or analogous to  
181 those of chaeomysticetes, and casts doubt on the idea that palatal sulci and baleen arose  
182 concurrently in the ancestor of modern whales: even if the sulci of *Llanocetus* had arisen  
183 independently, the fact that strong palatal vascularization without baleen exists at all means that these  
184 two structures cannot be unequivocally linked. Because palatal sulci directly supply the gingiva, they  
185 are best interpreted as an osteological correlate of enlarged gums, such as those that give rise to  
186 baleen in modern whales. Well-developed gingivae have been inferred for virtually all archaic  
187 mysticetes [4, 6, 8, 28]. In *Llanocetus*, it seems that gingival enlargement eventually became  
188 integrated into the morphology of the palate, without this leading to the emergence of baleen. This  
189 situation is analogous to the evolution of flight feathers in birds: although they are undoubtedly  
190 correlated with flight, they originally evolved for a different purpose [36].

191           A similar scenario seems plausible for *Morawanocetus* and aetiocetids: as in *Llanocetus*,  
192 large gums may initially have induced an enhanced blood supply (i.e. palatal sulci), which  
193 foreshadowed, and predated, the emergence of baleen in functionally toothless chaeomysticetes.  
194 This idea avoids problems posed by a direct tooth–baleen transition, such as small diastemata  
195 offering little room for baleen in *Morawanocetus* and *Fucaia* [28, 33, 37], or the presence of dental  
196 abrasion consistent with suction feeding, but probably not filtering, in at least one aetiocetid [4, 6].  
197 Furthermore, it is consistent with developmental evidence, including the observation that mysticete  
198 fetuses start to develop baleen only once their tooth buds are already degrading [20, 38], and the  
199 guidance of baleen formation via a co-opted signaling pathway normally responsible for tooth  
200 development [39]. The latter leads to an extreme degree of fetal polydonty not seen in any mysticete  
201 fossil, and thus presumably postdates the disappearance of postnatal teeth [39].

## 202 **Gigantism precedes filtering**

203 Relative to most other cetaceans, *Llanocetus* is a giant: at an estimated minimum length of nearly 8  
204 m, for a presumed juvenile, its size is comparable to that of extant minke whales, and exceeds that of  
205 all other toothed mysticetes, eomysticetids, most odontocetes and – until the Late Miocene – even  
206 most crown mysticetes [9, 40]. Notably, in a previous study that modelled mysticete body size  
207 evolution based on 1000 Brownian motion simulations, *Llanocetus* was the only species besides blue  
208 whales that plotted beyond the upper 95% quantile [9: fig 1].

209           Across marine vertebrates, large body size is correlated with filter feeding, likely as a result of  
210 its individual and trophic efficiency [41-44]. Nevertheless, extreme gigantism, as characteristic of  
211 whales today, appears to be a relatively recent phenomenon: for much of the Oligocene and Miocene,  
212 whales rarely exceeded 6 m, and most stayed well below [9]. Toothed mysticetes, in particular, tend  
213 to be diminutive (2–5 m), and suggest that whales may have evolved from a relatively small ancestor  
214 [40]. Optimizing body size on our topology confirms this view, and indicates that, for the most part,  
215 large size only arose in the ancestor of chaeomysticetes (Figure 4). This pattern holds even if  
216 borderline taxa, such as *Coronodon*, *Eomysticetus* and *Tohoraata*, are treated as large instead of  
217 small, and suggests that bulk feeding indeed arose in chaeomysticetes, rather than their toothed  
218 ancestors [6].

219           In light of this general pattern, *Llanocetus* is exceptional, with its unusually large size perhaps  
220 related to its polar habitat or to long-distance foraging [45]. Nevertheless, *Llanocetus* demonstrates  
221 that large size in baleen whales need not always be related to bulk feeding. Further, our results  
222 support the notion that large body size may have originated multiple times in baleen whale evolution  
223 [40], and show that mysticetes themselves emerged well before the key adaptation of modern whales:  
224 baleen and bulk feeding (Figure 4). This scenario markedly differs from that of odontocetes, whose  
225 major hallmark – echolocation – appears to be as old as themselves [10, 46, 47].

226

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## 237 **AUTHOR CONTRIBUTIONS**



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

## 240 DECLARATION OF INTERESTS

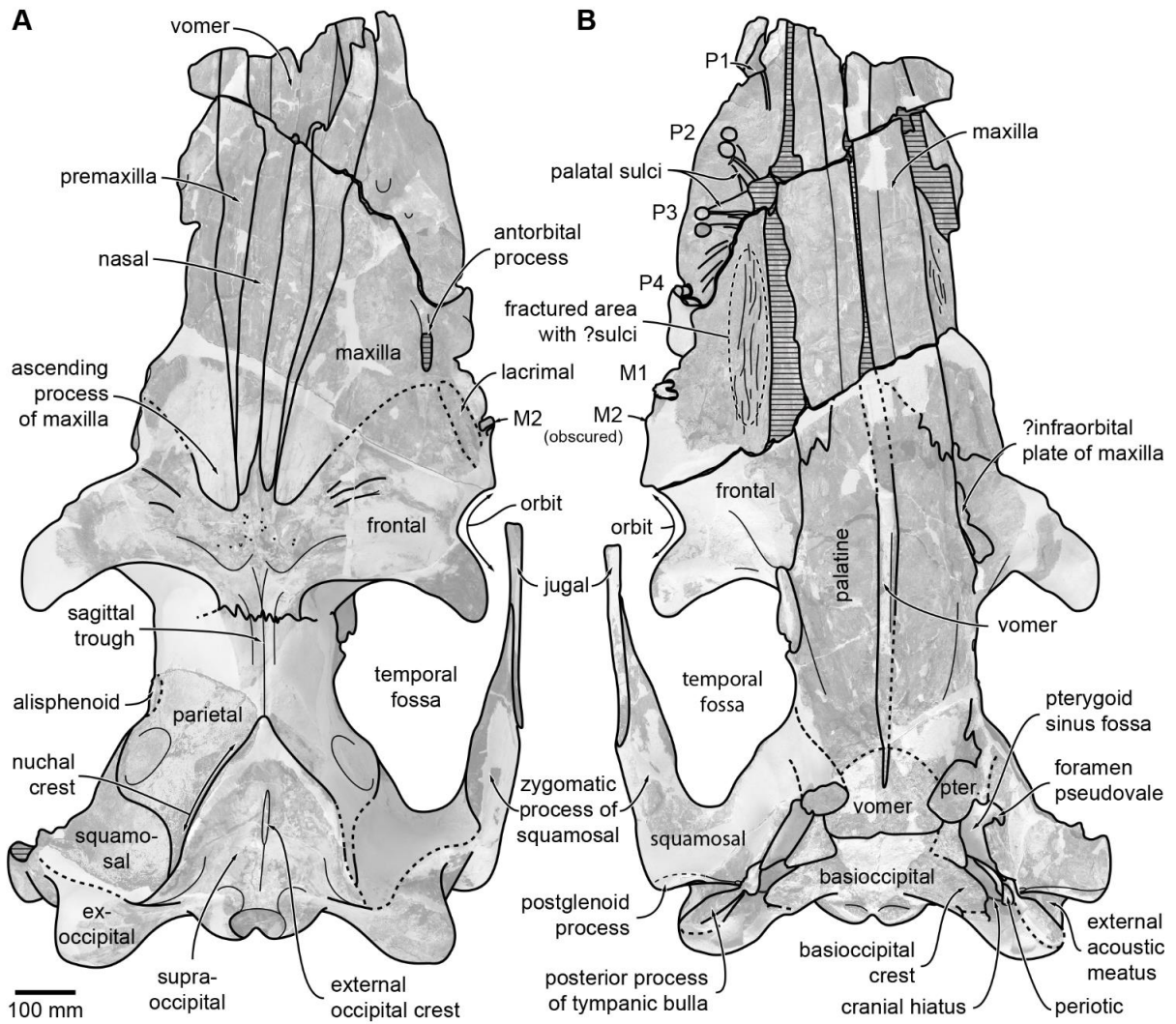
241 The authors declare no competing interests.

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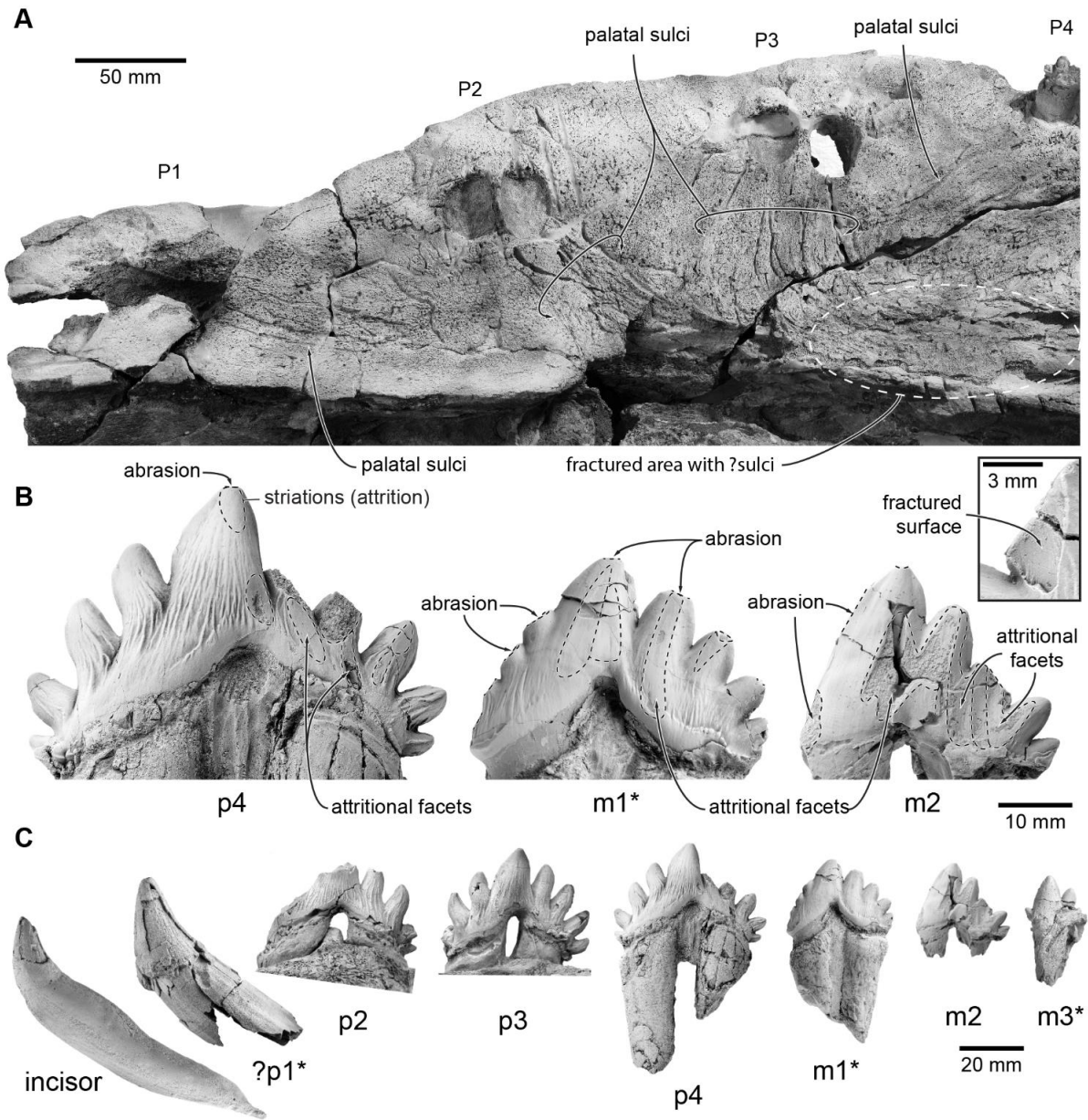
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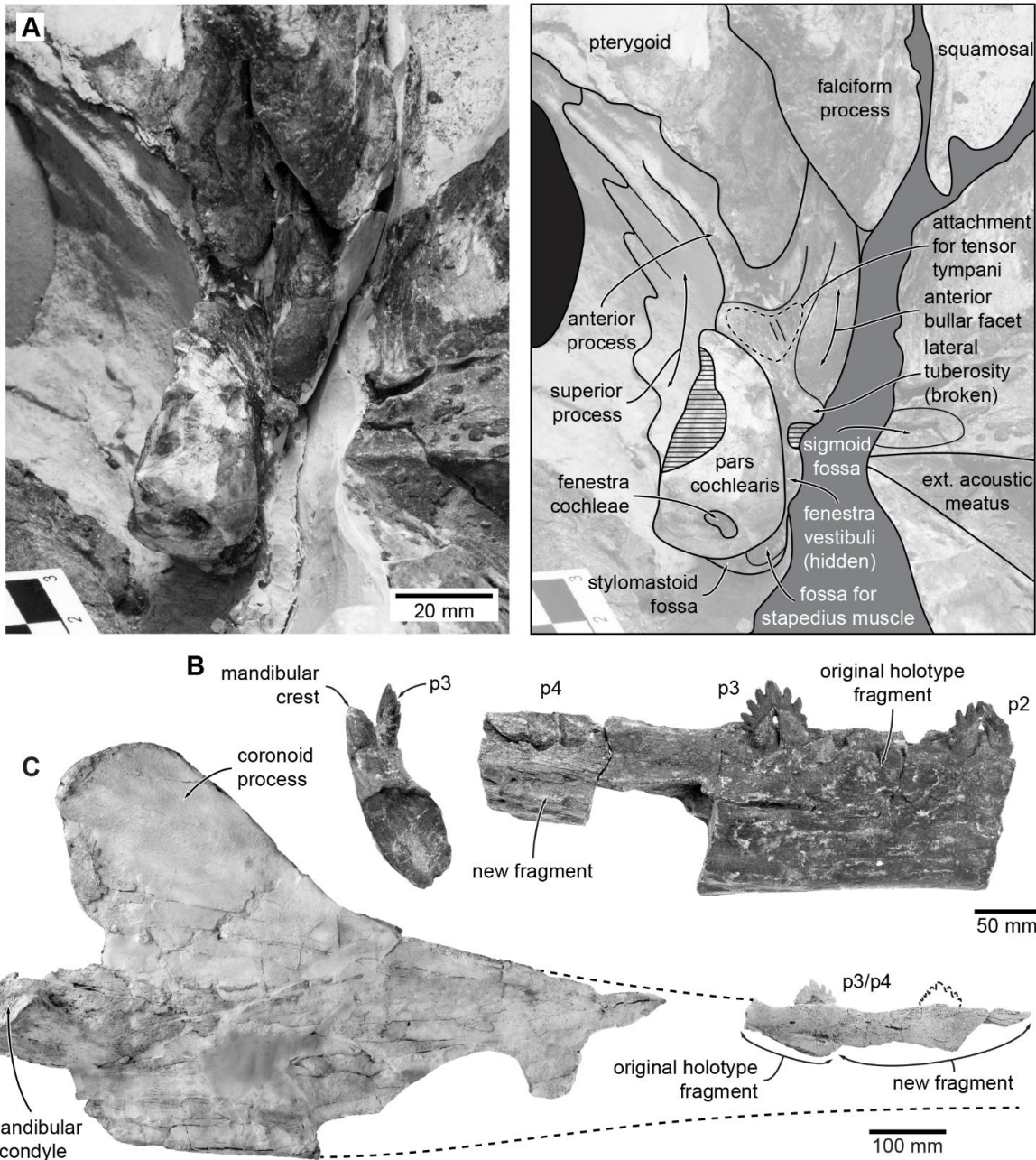


371 **Figure 1. Skull of *Llanocetus denticrenatus* (USNM 183022).** (A) dorsal view, (B) ventral view. See  
 372 Table S1 and Data S1 for additional details. pter., pterygoid.



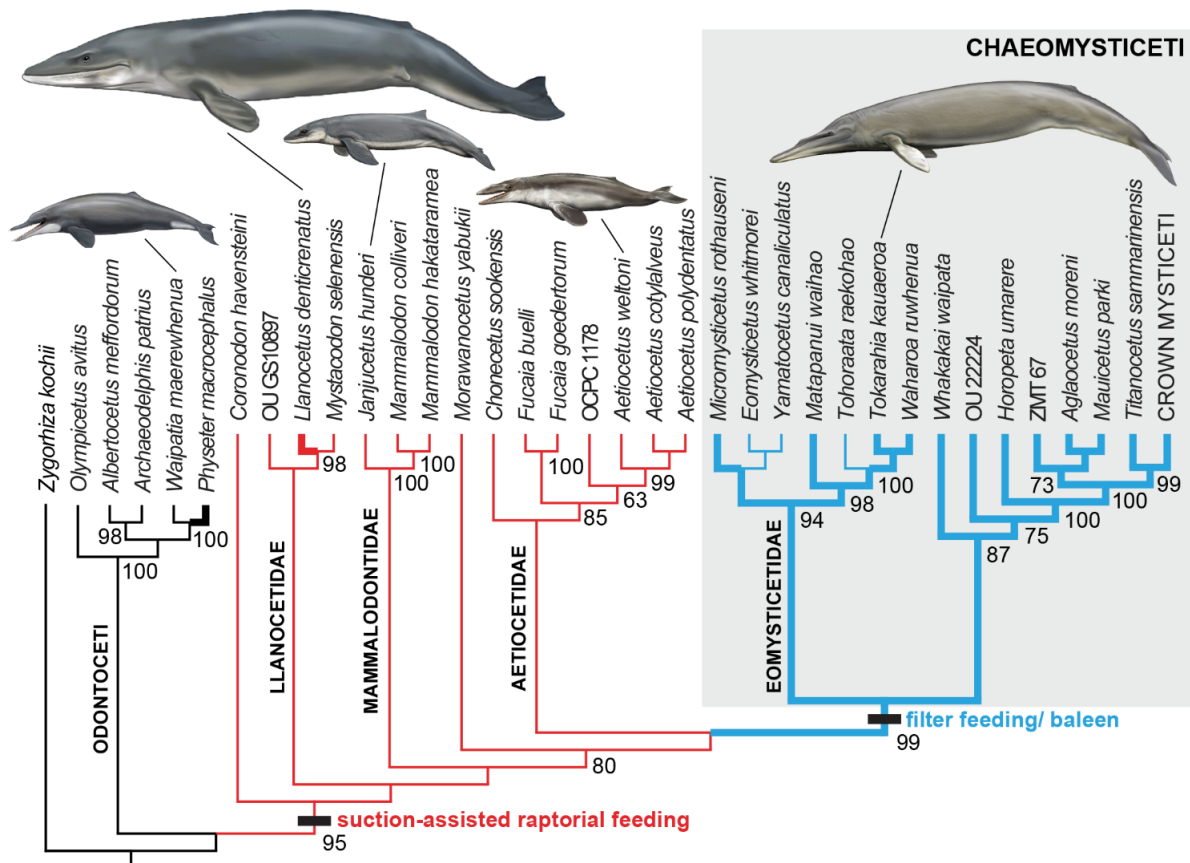
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374 **Figure 2. Feeding apparatus of *Llanocetus denticrenatus* (USNM 183022).** (A) left palate in  
 375 ventral view, showing alveoli and palatal sulci; (B) lower posterior check teeth, in labial view, showing  
 376 abrasion and attrition; (C) lower dentition, in labial view. Photographs marked by an asterisk have  
 377 been mirrored to facilitate comparisons. See Data S1 for additional details.



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379 **Figure 3. Periotic and mandible of *Llanocetus denticrenatus* (USNM 183022).** (A) left periotic, in  
 380 ventral view (*in situ*); (B) fragment of left mandible originally described by [1], in posterior (left) and  
 381 medial (right) view; note the previously undescribed fragment matching the original material; (C), right  
 382 mandible, in lateral view. See Data S1 for additional details.



383

384 **Figure 4. Phylogenetic relationships of *Llanocetus denticrenatus*.** Numbers next to nodes  
 385 represent posterior probabilities (only values  $\geq 50$  are shown). Thick lines indicate large body size (>5  
 386 m), with ancestral states reconstructed based on parsimony (likelihood yields equivalent results). Note  
 387 the markedly larger size of *Llanocetus* relative to other stem mysticetes. Reconstructions by Carl  
 388 Buell.

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405 **STAR METHODS**

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407 **CONTACT FOR REAGENT AND RESOURCE SHARING**

408 Further information and requests for resources and reagents should be directed to and will be fulfilled  
409 by the Lead Contact, Felix G. Marx (felix.marx@monash.edu).

410 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

411 The description is based on the holotype of *Llanocetus denticrenatus*, USNM 183022. Comparisons  
412 primarily focus on other toothed mysticetes, including *Mystacodon selenensis* (MUSM 1917), an  
413 unnamed skull from the Early Oligocene of New Zealand (OU GS10897), *Coronodon havensteini*  
414 (CCNHM 108), *Janjucetus hunderi* (NMV P216929), *Mammalodon colliveri* (NMV:P199986),  
415 *Aetiocetus* spp. (AMP 12, UCMP 122900, USNM 25210), *Fucaia* spp. (LACM 131146, UWBM  
416 84024), and *Morawanocetus yabukii* (AMP 01, AMP 14). A full list of specimens included in the  
417 phylogenetic analysis is available from MorphoBank ([www.morphobank.org](http://www.morphobank.org)), project P2044.

418 **Institutional abbreviations**

419 AMP, Ashoro Museum of Paleontology, Ashoro, Hokkaido, Japan; CCNHM, Mace Brown Museum of  
420 Natural History, College of Charleston, Charleston USA; LACM, Natural History Museum of Los  
421 Angeles County, Los Angeles, USA; MUSM, Museo de Historia Natural de la Universidad Nacional  
422 Mayor de San Marcos, Lima, Peru; NMV, Museums Victoria, Melbourne, Australia; OU, Geology  
423 Museum, University of Otago, Dunedin, New Zealand; UCMP, University of California Museum of  
424 Paleontology, Berkeley, USA; USNM, United States National Museum of Natural History, Washington  
425 DC, USA; UWBM, Burke Museum of Natural History and Culture, Seattle, USA;

426 **METHOD DETAILS**

427 **Phylogenetic Analyses**

428 The phylogenetic analysis was based on a modified and somewhat enlarged version (106 taxa, 275  
429 characters) of the total evidence matrix of Marx and Fordyce [14], fully illustrated with 5,617 individual  
430 specimen photographs on MorphoBank ([www.morphobank.org](http://www.morphobank.org); project 2044). The analysis was  
431 carried out without any clock assumptions in MrBayes 3.2.6 [49], on the Cyberinfrastructure for  
432 Phylogenetic Research (CIPRES) Science Gateway [51] (20 million generations, first 25% of  
433 generations discarded as burn-in). All partitions and settings replicated those of Marx and Fordyce



434 [14]. The supermatrix can be downloaded from the Documents section of the associated MorphoBank  
435 project.

### 436 **Body size**

437 Body size of extinct mysticetes was inferred from bizygomatic width, based on the equations provided  
438 by [52] and [53] (see Quantification and Statistical Analysis below). Body size was calculated for  
439 *Llanocetus* and its closest possible match, a *Morawanocetus*-like aetiocetid from Japan, which was  
440 previously reported as reaching 8 m [7]. Upon recalculating the length of the latter specimen, we  
441 found this estimate to be erroneous, with the real length being approximately 6 m, making *Llanocetus*  
442 the by far largest toothed mysticete described to date.

### 443 **Character Evolution**

444 We traced the evolution of palatal sulci and body size on our phylogeny, using the parsimony and  
445 likelihood options of Mesquite 3.11 [50]. The results of both were practically identical, and for  
446 convenience only the parsimony is presented here. Because we were primarily interested in archaic  
447 mysticetes, we subsumed all species crownward of eomysticetids into a single clade comprising  
448 crown Mysticeti and a small number of stem taxa. Sulci were coded as present or absent (present in  
449 crown Mysticeti), and body size classified into small ( $\leq 5$  m) and large ( $>5$  m; state scored for crown  
450 Mysticeti), following [40]. Three species – *Coronodon selenensis*, *Eomysticetus whitmorei*, and  
451 *Tohoraata raekohao* – are close to 5 m in length, and were thus coded twice (once as small and once  
452 as large) to determine the sensitivity of our results to our size threshold. A Nexus file comprising the  
453 simplified tree, palatal and size codings can be downloaded from the Documents section of the  
454 MorphoBank project associated with this study (P2044).

## 455 **QUANTIFICATION AND STATISTICAL ANALYSIS**

### 456 **Estimates of Body Size**

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

$$459 \quad (1) \log(\text{TL}) = 0.92 * (\log(\text{BIZYG}) - 1.72) + 2.68 \text{ [53]}$$

$$460 \quad (2) \text{TL} = 8.209 * \text{BIZYG} + 66.69 \text{ [52]}$$

461 **DATA AND SOFTWARE AVAILABILITY**

462 The fully illustrated cladistic matrix and associated 5,617 individual specimen photographs can be  
463 downloaded from MorphoBank, project 2044 ([www.morphobank.org](http://www.morphobank.org)).