Morphological variation of the relictual alveolar structures in the mandibles of baleen whales

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Living baleen whales (mysticetes) are bulk filter feeders that use keratinous baleen plates to filter food from prey laden water. Extant mysticetes are born entirely edentulous, though they possess tooth buds early in ontogeny, a trait inherited from toothed ancestors. The mandibles of extant baleen whales have neither teeth nor baleen; teeth are resorbed *in utero* and baleen grows only on the palate. The mandibles of extant baleen whales also preserve a series of foramina and associated sulci that collectively form an elongated trough, called the alveolar groove. Despite this name, it remains unclear if the alveolar groove of edentulous mysticetes and the dental structures of toothed mammals are homologous. Here, we describe and quantify the anatomical diversity of these structures across extant mysticetes and compare their variable morphologies across living taxonomic groups (i.e., Balaenidae, Neobalaenidae, Eschrichtiidae, and Balaenopteridae). Although we found broad variability across taxonomic groups for the alveolar groove length, occupying approximately 60–80 percent of the mandible's total curvilinear length (CLL) across all taxa, the relictual alveolar foramen showed distinct patterns, ranging between 15–25% CLL in balaenids, while ranging between 3–12% CLL in balaenopterids. This variability and the morphological patterning along the body of the mandible is consistent with the hypothesis that the foramina underlying the alveolar groove reflect relictual alveoli. These findings also lay the groundwork for future histological studies to examine the contents of these foramina and clarify their potential role in the feeding process.

1   Morphological variation of the relictual alveolar structures in the mandibles of baleen whales

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11   **ABSTRACT**

12   Living baleen whales (mysticetes) are bulk filter feeders that use keratinous baleen plates to filter food

13   from prey laden water. Extant mysticetes are born entirely edentulous, though they possess tooth buds

14   early in ontogeny, a trait inherited from toothed ancestors. The mandibles of extant baleen whales have

15   neither teeth nor baleen; teeth are resorbed *in utero* and baleen grows only on the palate. The

16   mandibles of extant baleen whales also preserve a series of foramina and associated sulci that

17   collectively form an elongated trough, called the alveolar groove. Despite this name, it remains unclear

18   if the alveolar groove of edentulous mysticetes and the dental structures of toothed mammals are

19   homologous. Here, we describe and quantify the anatomical diversity of these structures across extant

20   mysticetes and compare their variable morphologies across living taxonomic groups (i.e., Balaenidae,

21   Neobalaenidae, Eschrichtiidae, and Balaenopteridae). Although we found broad variability across

22   taxonomic groups for the alveolar groove length, occupying approximately 60–80 percent of the

23   mandible's total curvilinear length (CLL) across all taxa, the relictual alveolar foramen showed distinct

24   patterns, ranging between 15–25% CLL in balaenids, while ranging between 3–12% CLL in

25   balaenopterids. This variability and the morphological patterning along the body of the mandible is

26   consistent with the hypothesis that the foramina underlying the alveolar groove reflect relictual alveoli.

27   These findings also lay the groundwork for future histological studies to examine the contents of these

28   foramina and clarify their potential role in the feeding process.

29

30   Key Words: Cetacea, filter feeding, Mysticeti, variation, mandibles, dentition,

31

32 **Introduction**

33   The diversity and ecological success of baleen whales (mysticetes) has been linked to dramatic

34 evolutionary transformations in their feeding mechanisms (Pyenson 2017; Slater et al. 2017). Living

35 baleen whales depart from the macroraptorial feeding of their toothed ancestors and instead bulk filter

36 feed using keratinous baleen plates (Marshall & Goldbogen 2015; Marshall & Pyenson 2019). Baleen

37 whales are born entirely edentulous, although fossil relatives have mineralized teeth as adults.

38 Embryological evidence demonstrates extant mysticetes briefly develop teeth *in utero* before resorbing

39 them prior to birth (Lanzetti 2019; Lanzetti et al. 2018; Peredo et al. 2017a).

40   Because teeth are resorbed *in utero* and baleen develops only on the palate, the body of the

41 mandibles of extant baleen whales lack any specialized feeding structure (Peredo et al. 2017b).

42 Nonetheless, the mandible is still essential to the feeding process (Goldbogen et al. 2017; Pyenson et al.

43 2013; Shadwick et al. 2017) and at least some mysticetes have evolved novel sensory organs that

44 facilitate feeding (Ford et al. 2013; Pyenson et al. 2012). Understanding how the edentulous mandible

45 facilitates mysticete feeding is crucial to understanding the ecological transitions associated with the

46 evolution of bulk filter feeding.

47   The mandibles of baleen whales preserve a series of dorsal foramina and associated sulci, often

48 in such close proximity that they form a shallow groove (Figure 1). These foramina have long been

49 considered vestigial homologues to the dental alveoli of the resorbed teeth and the shallow groove has

50 been termed the "alveolar groove" or "alveolar gutter". Mead & Fordyce (2009; page 42) consider

51 "alveolar groove" to be the preferred terminology and review several other synonymous names for the

52 structure. Recently, some authors have questioned this homology, and instead suggested that they

53 represent distinct branches of the inferior alveolar artery or nerve and thus may have a vascular or

54 nervous function (Peredo et al. 2017b). However, other authors have identified similar foramina in other

55   edentulous mammals (Ferreira-Cardoso et al. 2019), indicating that they may indeed be homologous to

56   alveolar structures, though leaving it uncertain if these structures are vestigial or have some function.

57   Understanding the homology and potential function of these structures has been hampered by

58   a lack studies detailing their morphology and variability. Here, we describe and quantify the observed

59   morphology of these structures across the diversity of extant mysticete taxa. We report the number of

60   foramina, the lengths of the alveolar region, and the lengths of the relictual alveolar foramen as defined

61   by Pyenson et al. (2012) (the expanded distalmost foramen) for representative taxa of all four extant

62   clades (including n = 34 specimens) and compare these values across taxonomic groups. Our results

63   provide the anatomical context necessary for subsequent histological studies to examine the contents of

64   these foramina and thereby elucidate their potential role in the feeding process.

65

66   **Materials and Methods**

67   We examined the mandibles of 34 baleen whales deposited in the collections of the Department

68   of Vertebrate Zoology's Division of Mammals at the Smithsonian Institution's National Museum of

69   Natural History. Our dataset includes members from all four major taxonomic groups. For each

70   specimen, we report six anatomical measurements from one mandible of a pair (Figure 1): the straight

71   length of the mandible (SL); the curvilinear length of the mandible (CLL); the number of mental foramina

72   (#MF); the number of alveolar openings in the alveolar groove (#AL); the length of the alveolar groove

73   (LAG); and the length of the relictual alveolar foramen (LRAF). We also report the length of the alveolar

74   groove and the length of the relictual alveolar foramen as percentages of the total curvilinear length

75   (Table S1). For smaller specimens, we took measurements using an anthropometer, and for larger

76   specimens we took measurements using a measuring tape directly on the mandibles. The

77   measurements for straight length (SL) and curvilinear length (CLL) follow (Pyenson et al. 2013, figure 2).

78   Additionally, we categorized each specimen based on its ontogenetic age: fetal, subadult, or adult based

79   on suture fusion of associated cranial material (Bisconti 2001; Walsh & Berta 2011). Specimens were

80   designated as fetal based on collection records and as subadult based on the degree of suture fusing in

81   the skull. The final dataset includes four fetal, three subadult, and 27 adult specimens spanning 11 total

82   species.

83

84

85   **Results**

86   Our dataset comprises 34 baleen whale mandibles including 5 balaenids, 1 neobalaenid, 5

87   eschrichtiids, and 23 balaenopterids, 7 of which are fetal or subadult specimens. For the entire

88   mysticete dataset, the number of mental foramina ranged from 4 (*Balaenoptera acutorostrata*) to 9

89   (*Balaenoptera physalus*). The number of alveolar openings in the alveolar groove ranged from 10

90   (*Eubalaena australis* and *Eubalaena glacialis*) to 26 (*Balaenoptera physalus*). Overall, both the number

91   of mental foramina and the number of alveolar openings in the alveolar groove varied within a species

92   and neither showed clear taxonomic patterns.

93   The mandibles in our dataset span the full range of mysticete body sizes, resulting in a wide

94   variation of mandible length. The smallest adult mandible (*Caperea marginata*) in our dataset is 126 cm

95   in curvilinear length (CLL) and the largest has a CLL of 723 cm (*Balaenoptera musculus*). Consequently,

96   the length of the alveolar groove varies widely across out dataset as well: the minimum recorded value

97   of the alveolar groove in an adult mandible is 86 cm (*Eschrichtius robustus*) and the maximum recorded

98   value is 513 cm (*Balaenoptera physalus*). However, this variation is relatively constrained proportional to

99   the mandible's CLL (Figure 2). Our results demonstrate that most taxa have alveolar groove lengths that

100 are approximately 60–80 percent of the mandible's total CLL. This pattern was true across all four

101 taxonomic families and in the fetal and subadult specimens as well. Only one whale in our dataset fell

102 notably outside these values: USNM 571340 (*Balaenoptera borealis*) has an alveolar groove that is only

103 41% of the mandible's CLL.This anomalous datapoint may be the result of an unobserved pathology,

104 ontogenetic variation, or linked to the unusual feeding biomechanics of sei whales (Segre et al. 2021).

105 Despite no taxonomic pattern in the proportional length of the alveolar groove, the proportional

106 length of the relictual alveolar foramen (RAF) does vary by taxonomy (Figure 2). Balaenids and the lone

107 neobalaenid in our study have an RAF that is approximately 15–25% of the total CLL. However, most

108 adult balaenopterids have an RAF that is only approximately 3–12% of the CLL. The proportional length

109 of the RAF in balaenids is on average twice as long, and in some cases as much as five times as long, as

110 the values observed in balaenopterids (Figure 2). Eschrichtiid mandibles have values roughly between

111 balaenids and balaenopterids, approximately 9–16% of the mandible's CLL.

112 This pattern does not, however, extend to the fetal and subadult samples in our study, all of

113 which are balaenopterids. Interestingly, the subadult balaenopterids exhibit higher values for the

114 proportional length of the RAF (13–17% of the CLL) and the fetal specimens preserve even higher values

115 still (18–28% of the CLL). A full comparison of the allometry of these structures across whale ontogeny is

116 beyond the scope of this project. However, our data indicate that fetal balaenopterids have RAF of

117 similar proportional length to those of balaenids and suggest that the restriction of the RAF to the distal

118 tip of the mandible may occur later in ontogeny.

119 Importantly, the variation in the proportional length of the RAF is not a function of overall

120 length of the mandible. The largest (*Balaenoptera musculus*) and smallest (*Balaenoptera acutorostrata*)

121 balaenopterids in this study both preserve some of the proportionately shortest RAF (approximately 5–6

122 and 3–9% of the CLL respectively). In contrast, *Caperea marginata*, which is comparable in size to

123 *Balaenoptera acutorostrata*, has an RAF that is nearly 20% of the CLL, and the largest balaenids (*Balaena*

124 *mysticetus* and *Eubalaena glacialis*) have RAF that are approximately 14 and 18% of the CLL. This

125 suggests that, although the RAF becomes proportionately shorter throughout ontogeny in

126 balaenopterids, the pattern is not being driven simply by ontogenetic growth to larger body size.

127

128   **Discussion**

129   The high degree of variability in the number of alveolar foramina present is noteworthy given

130   that it remains unclear if the alveolar foramina and the alveolar groove are actually vestigial remnants of

131   the dentition resorbed *in utero*. Peredo et al. (2017b) considered their homology with teeth uncertain,

132   in part because the mandibles of baleen whales exhibit evidence of bone remodeling similar to the

133   patterns observed during pathological tooth loss, where the alveoli are entirely resorbed, and the bony

134   surface becomes solid. However, recent authors (Ferreira-Cardoso et al. 2019) have identified similar

135   structures in other edentulous mammals and considered them vestigial remnants of the resorbed

136   dentition. Our findings suggest that the morphology of the alveolar groove and the relictual alveolar

137   foramen are constrained by developmental pathways early in ontogeny , supporting the hypothesis that

138   they are homologous with the resorbed dentition (see also below about anatomical patterning). If this is

139   the case, then it is noteworthy that these foramina and internal canals are not resorbed during the bone

140   remodeling process (Peredo et al. 2017b), and their morphological patterning remains consistent across

141   all four extant families. The consistency of this pattern across extant mysticetes suggests that these

142   foramina may have been co-opted to perform a novel function in specific lineages, as documented in the

143   case of the chin sensory organ in rorquals (Pyenson et al. 2012). However, the chin sensory organ is

144   notably absent in balaenids, suggesting that these foramina function may more simply be related to

145   simply innervate soft connective labial eminences (see references in Peredo et al. 2018).

146   Moreover, if each alveolar foramen is the vestigial remnant of an individual alveolus resorbed *in

147   utero*, then we would predict the high degree of variability in the number of alveoli present (ranging

148   from 10 to 24) that we observed. Unfortunately, dental counts for embryonic mysticetes are rare,

149   making it difficult to test this prediction. Recent work by Lanzetti (2019) and Thewissen et al. (2017),

150   which builds on that of Ishikawa & Amasaki (1995) and Ishikawa et al. (1999), expands the histological

151   datasets of early ontogenetic variability in mysticete dentition, especially across a taxonomic breadth

152   that may elucidate an evolutionary framework to test the relationship between alveoli and tooth

153   identity. Additionally, many 19th and early 20th century anatomists report tooth counts for foetal

154   mysticetes, though this work is scattered across many languages and difficult to verify (see Peredo et al.

155   (2017a) for a review of embryological and histological data pertaining to mysticete tooth buds).

156   Traditionally, the ramus is defined as the vertical, non-tooth bearing portion of the mandible

157   (Mead & Fordyce 2009 and references therein). However, extant mysticete mandibles are single

158   elongated osteological elements that lack an obvious distinction between the body of the mandible and

159   the ramus. Our results demonstrate that proportional length of the alveolar groove is tightly constrained

160   around an average of 70% of the curvilinear length of the mandible. This suggests that although extant

161   mysticete mandibles have no obvious distinction between the body and the ramus, they retain the

162   distinct anatomical patterning of their terrestrial ancestors. Based on the fossil record of mysticetes, this

163   loss of a major distinction between the body and the ramus happened no later than the early Oligocene

164   (Peredo et al. 2018), after the origin of aetiocetids but prior to the lineage leading to *Maiabalaena+*

165   *Sitsqwayk*, eomysticetids, and crown mysticetes (Peredo & Pyenson 2018).

166   The co-option of the relictual alveolar foramen for novel functions in certain extant lineages

167   (e.g., Pyenson et al. 2012) appears to be part of a longer trend in bone remodeling that has occurred in

168   stem lineages leading to crown Mysticeti (Figure 3; and see Peredo et al. 2017b). Although stem

169   mysticetes with fully mineralized adult teeth (e.g., *Salishicetus*, Figure 3A) display no unusual patterns in

170   this regard, the stem mysticete *Maiabalaena* shows extensive cortical remodeling in the dorsal margin

171   of the mandible that is homologous with the alveolar groove in extant mysticetes (Figure 3B, 3C).

172   Interestingly, the complexity of the relictual alveolar foramen morphology in *Maiabalaena* is a trait that

173   appears in crownward eomysticetids, such as *Waharoa ruwhenua*, which may have possessed

174   mineralized teeth (Boessenecker & Fordyce 2015). The diversity of relictual alveolar foramina in these

175   stem lineages merits deeper examination to understand the range of alveolar morphology, any

176   associated dentition, and the distribution of internal structures related to the mandibular canal and

177   mental foramina (Peredo et al. 2017b).

178   Despite no taxonomic differences in the proportional length of the alveolar region for extant

179   mysticetes, we report substantial taxonomic differences in the proportional length of the relictual

180   alveolar foramen (Figure 2). This foramen is the distalmost opening on the dorsal margin of the

181   mandible and is elongated to as much as 20% of the CLL in balaenids and neobalaenids but constrained

182   to only about 5% of the CLL in balaenopterids. Previous authors have reported that in balaenopterids,

183   the relictual alveolar foramen is the opening through which the lunge feeding sensory organ in the chin

184   is innervated (Pyenson et al. 2012). This sensory organ facilitates lunge feeding in balaenopterids and is

185   absent in balaenids, but it remains unclear if a homologous structure is present in other mysticete

186   groups. If the relictual alveolar foramen has been coopted to innervate the chin sensory organ, then this

187   may constrain the length of the relictual alveolar foramen in balaenopterids.

188

189   **INSTITUTIONAL ABBREVIATIONS**

190   USNM PAL and VZ: Departments of Paleobiology and Vertebrate Zoology (Division of Mammals),

191   National Museum of Natural History, Smithsonian Institution, Washington DC, USA; UWBM: Burke

192   Museum of Natural History and Culture, University of Washington, Seattle, WA, USA.

193

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210

COMPETING INTERESTS

212   Nicholas D. Pyenson is an Academic Editor for PeerJ.

213

AUTHOR CONTRIBUTIONS

215   Both authors conceived and designed the experiments, performed the analyses, drafted and

216   edited the manuscript, prepared figures, and approved the final draft. CMP measured the mysticete

217   mandibles.

218

DATA AVAILABILITY

220   The following information was supplied regarding data availability:

221   The full raw data file is available in the Supplemental Files.

222

223   **SUPPLEMENTAL INFORMATION**

224   Supplemental information for this article can be found online at:

225

226

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295
296

297 **Figure Captions**

298 **Figure 1:** (A) Left mandible of *Balaenoptera acutorostrata* (USNM VZ 571487) in medial view with

299 selected regions enhanced in panel (B). (B) Enhanced view of the selected regions on panel (A),

300 specifically highlighting the alveolar groove, associated sulci, the relictual alveolar foramen at the distal

301 terminus of the mandible, and the symphyseal groove, using CT data. (C) Left mandible of *Balaenoptera*

302 *acutorostrata* (USNM VZ 571487) in dorsal view demonstrating the curvilinear length (CLL) and the

303 straight length (SL) measured in this study. (D) Left mandible of *Balaenoptera acutorostrata* (USNM VZ

304 571487) in medial view demonstrating the length of the alveolar groove (LAG) and the length of the

305 relictual alveolar foramen (LRAF) measured in this study.

306

307 **Figure 2**: Length of the alveolar groove (orange) and the length of the relictual alveolar foramen (blue)

308 as proportions of the total curvilinear length of the mandible. This graph includes all adult specimens in

309 our study but excludes the subadult and fetal specimens reported in Table S1.

310

311 **Figure 3**: Mandibles of a toothed stem mysticete (A) UWBM 50004: *Salishicetus meadi*; an edentulous

312 stem mysticete (B) USNM PAL 314627: *Maiabalaena nesbittae*; and an extant mysticete (C) USNM VZ

313 571847: *Balaenoptera acutorostrata*. Mandibles are figured in oblique view and in cross sectional slices

314 from CT scans to demonstrate the morphological variability of the distal alveolus or associated foramina.

Figure 1

Figure 1

Figure 1: (A) Left mandible of *Balaenoptera acutorostrata* (USNM VZ 571487) in medial view with selected regions enhanced in panel (B). (B) Enhanced view of the selected regions on panel (A), specifically highlighting the alveolar groove, associated sulci, the relictual alveolar foramen at the distal terminus of the mandible, and the symphyseal groove, using CT data. (C) Left mandible of *Balaenoptera acutorostrata* (USNM VZ 571487) in dorsal view demonstrating the curvilinear length (CLL) and the straight length (SL) measured in this study. (D) Left mandible of *Balaenoptera acutorostrata* (USNM VZ 571487) in medial view demonstrating the length of the alveolar groove (LAG) and the length of the relictual alveolar foramen (LRAF) measured in this study.

A

mandibular foramen

coronoid process

B

alveolar gutter

mental foramina

relictual alveolar foramen

alveolar gutter

symphyseal groove

C

CLL

SL

D

LAG

LRAF
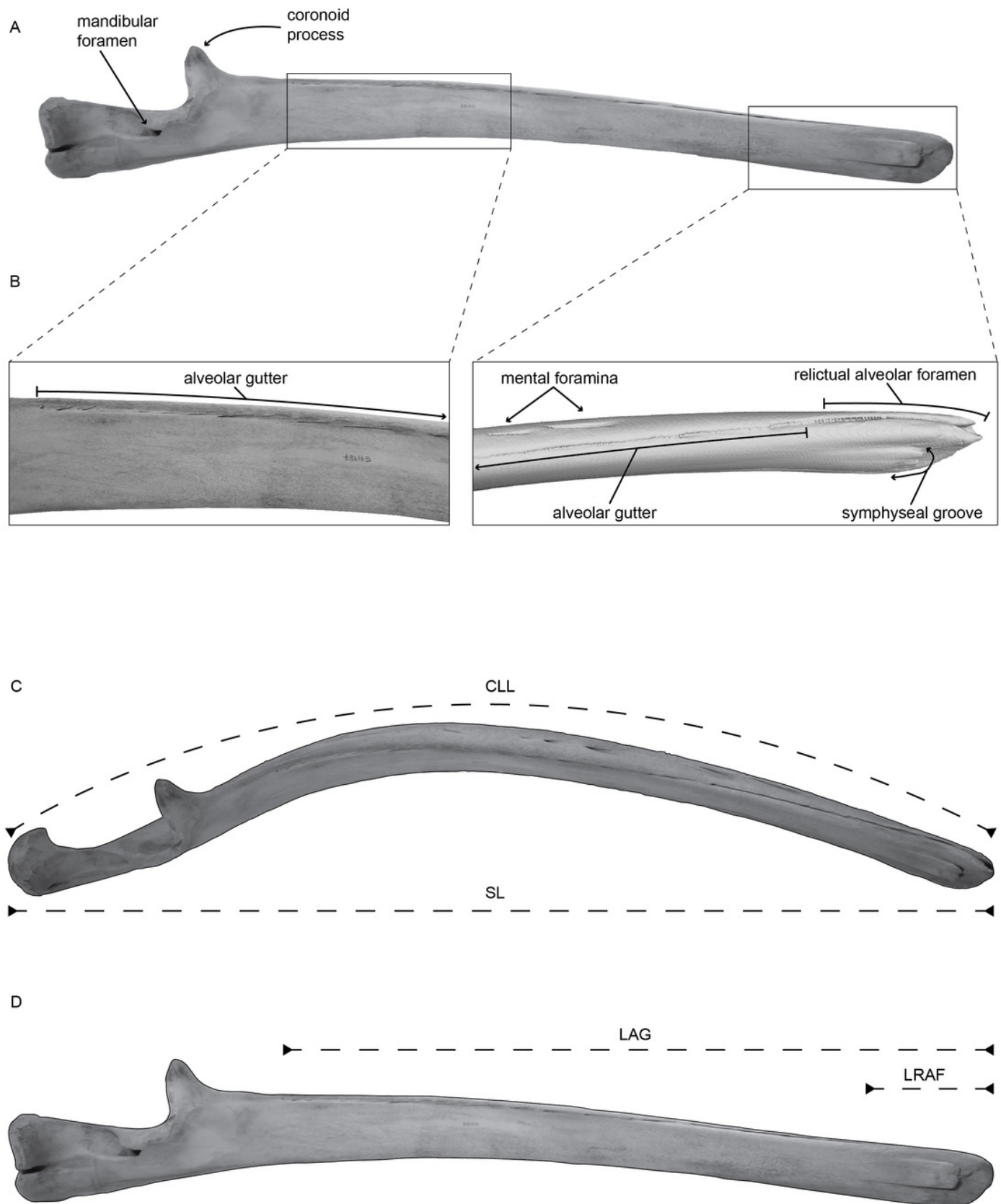
Figure 2

Figure 2

Figure 2: Length of the alveolar groove (orange) and the length of the relictual alveolar foramen (blue) as proportions of the total curvilinear length of the mandible. This graph includes all adult specimens in our study but excludes the subadult and fetal specimens reported in Table S1.
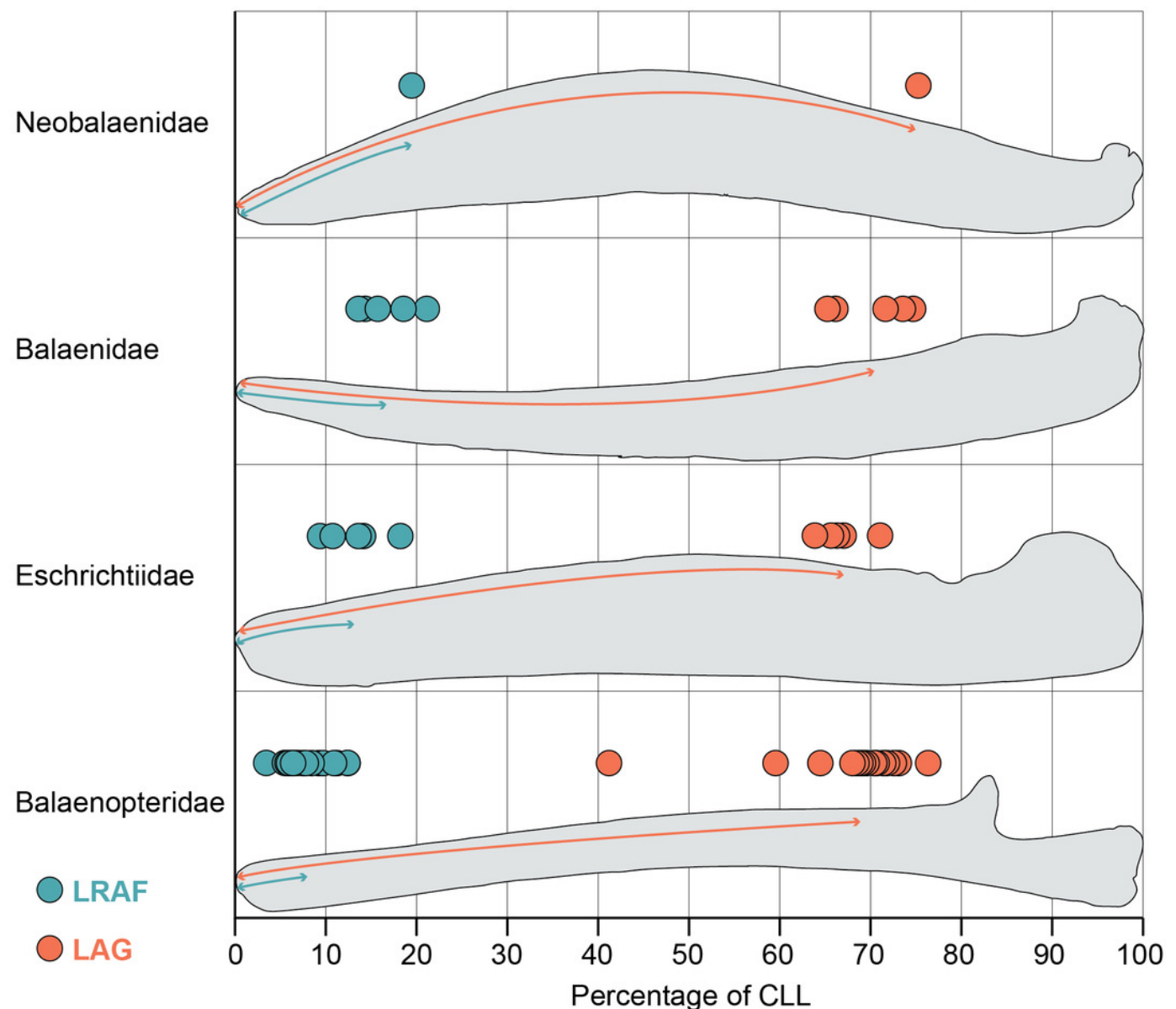
Figure 3

Figure 3

Figure 3: Mandibles of a toothed stem mysticete (A) UWBM 50004: *Salishicetus meadi*; an edentulous stem mysticete (B) USNM PAL 314627: *Maiabalaena nesbittae*; and an extant mysticete (C) USNM VZ 571847: *Balaenoptera acutorostrata*. Mandibles are figured in oblique view and in cross sectional slices from CT scans to demonstrate the morphological variability of the distal alveolus or associated foramina.