Serrated teeth in a new species of the early diverging macrophagous dolphin *Ankylorhiza*

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Ankylorhiza tiedemani is a large agorophiid-grade toothed whale (Odontoceti) from the Oligocene Ashley and Chandler Bridge formations of Charleston, South Carolina; this species is further the largest Oligocene odontocete. Macrophagous adaptations in this extinct "killer" dolphin include large body size, large teeth, fluted enamel, thickened cementum, large temporal fossae, and similar range of motion at the occipital-atlantal joint as in *Orcinus orca*. A new species, *Ankylorhiza serratidens* sp. nov., is reported from the Ashley Formation of South Carolina (late Rupelian; 28–30 Ma) and is based on a skeleton preserving mandibles, distinctive dentition, atlas vertebra, and other postcrania. The dentition of this specimen has extensive serrations (measuring 0.9–1.3 mm) on the posterior postcanine teeth. Though similar in size to *Ankylorhiza tiedemani*, *Ankylorhiza serratidens* sp. nov. was even more highly specialized for macrophagy. Accessory cusps in archaic cetaceans are preliminarily defined as being separated by deep notches and large size (>10% of mesiodistal crown length), with serrations preliminarily defined as lacking deep notches and small size (<5% of mesiodistal crown length). The holotype specimen bears several bone modifications including bite marks from sharks and *Osedax* bioerosion.

Key words: Mammalia, Cetacea, Odontoceti, dentition, feeding ecology, Oligocene.

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Introduction

Widespread convergence in tooth and rostral morphology within marine tetrapods is considered to track parallel trends in feeding ecology among disparate groups of marine reptiles and marine mammals; convergent adaptations for a fish-eating diet (piscivory) include homodonty, longirostry, and the development of apicobasal ridges (Massare 1987; Ciampaglio et al. 2005; McCurry et al. 2019; Fischer et al. 2022; Bennion et al. 2023). Macrophagous predators adapted towards feeding on other tetrapods tend to evolve larger body size, robust skull proportions, larger, and, in some cases, serrated teeth (Massare 1987; Fischer et al. 2022; Bennion et al. 2023), paralleling sharks that feed on marine mammals like great white and tiger sharks (Abler 1992; Frazzetta 1988; Corn et al. 2016).

Modern macrophagous marine mammals are few, but include the killer whale (*Orcinus orca*), false killer whale (*Pseudorca crassidens*), and the leopard seal (*Hydrurga leptonyx*), though none today possess serrated teeth. Fossils of extinct "killer" sperm whales (Lambert et al. 2016), basilosaurid whales (Fahlke 2012; Voss et al. 2019), and the giant dolphin *Ankylorhiza* (Boessenecker et al. 2020) indicate that cetaceans of different groups have filled macrophagous apex predator niches in the past. While sporadic denticles are documented in the dentitions of some archaeocetes (Gingerich and Russell 1990; Cooper et al. 2009; Gingerich et al. 2019; McLeod and Barnes 2008; Uhen 2014), some toothed mysticetes (Boessenecker et al. 2023), and occasional stem odontocetes (Pilleri 1985; Velez-Juarbe 2017; Boessenecker et al. 2020; Nelson et al. 2025a, c), teeth with extensively serrated cutting edges (e.g., preserved throughout many teeth in the dentition) have not been previously reported within Odontoceti (toothed whales).

The Oligocene epoch is a key period in the evolution of cetaceans as it marks the diversification of Odontoceti and toothed and toothless baleen whales (Mysticeti), with a major increase in diversity and disparity relative to the middle and late Eocene (Marx and Fordyce 2015; Boessenecker et al. 2017a, b) and a peak in evolutionary rate (Coombs et al. 2022). This period of nascent evolution is characterized by increases in encephalization (Marino et al. 2004), the first appearance of baleen (Deméré et al. 2008; Boessenecker and Fordyce 2015a), the evolution of echolocation (Geisler

et al. 2014; Churchill et al. 2016), and an explosive diversification in feeding morphology (Fitzgerald 2006; Marx and Fordyce 2015; Boessenecker et al. 2017a, b; Geisler et al. 2017). Within only a few million years of the earliest odontocete fossils, the large-bodied dolphin *Ankylorhiza* evolved, interpreted as a macrophagous killer whale-like apex predator (Boessenecker et al. 2020). *Ankylorhiza tiedemani* possesses a number of adaptations for macrophagy including large body size, teeth with sharp carinae, thickened cementum, massive temporal fossae, and a range of neck mobility nearly identical to modern *Orcinus* (Boessenecker et al. 2020). This study reports a new specimen and species of *Ankylorhiza* from the lower Oligocene Ashley Formation of South Carolina which possesses extensive serrations on its postcanine teeth and further indicates rapid evolution of macrophagous feeding ecology among early odontocetes.

Institutional abbreviations.—CCNHM, Mace Brown Museum of Natural History, College of Charleston, USA; ChM, Charleston Museum, USA.

Other abbreviations.—b, postcanine (according to the dental numbering terminology of Dubrovo and Sanders 2000); C, cervical vertebrae; c, lower canine; i, lower incisor; L, lumbar vertebrae; pc, lower postcanine; T, thoracic vertebrae.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:1D030B6B-BDAC-42E7-B10F-C3676782D63D.

Systematic palaeontology

Mammalia Linneaus, 1758

Cetacea Brisson, 1762

Odontoceti Flower, 1867

?Agorophiidae Abel, 1914

Ankylorhiza Boessenecker et al., 2020

Type species: *Squalodon tiedemani* Allen, 1887; ?Ashley Formation, South Carolina, Oligocene.

Emended diagnosis.—*Ankylorhiza* is a large (bizygomatic width 350–405 mm; estimated body length 4.5–6 m) longirostrine stem odontocete (rostral proportion index 2.13–2.19) with moderate heterodonty, limited polydonty (13 upper teeth), and two fewer mandibular than upper teeth (11 lower teeth). *Ankylorhiza* differs from all other odontocetes in the extreme development of nuchal crests (nuchal crest depth 35% of the width of the supraoccipital shield at its anteroposterior midpoint), and differs from all other stem odontocetes in its larger size and the following combination of characters: most postcanine teeth single rooted (14% of postcanine dentition length is double rooted); postcanine dentition with triangular crowns lacking or possessing single large accessory denticle; inflated knob-like supramastoid crest on squamosal; possessing embrasure pits along the posterior 50% of the maxillary postcanine tooth row (also in *Squalodon* and most Xenorophidae); possessing a scalloped edge of the maxilla with thickened bone buttresses around the roots of teeth; and thickened cementum (1.8–4.3 mm at the gumline); mandible with moderately elongate symphysis (20–40% of mandibular length). Differs further from *Patriocetus* in possessing a triangular wedge of frontal separating nasals, and complete loss of the transverse parietal band at the vertex (though occupied by interparietal in CCNHM 103); differs further from *Agorophius* in its slightly narrower intertemporal constriction (22–24% of bizygomatic width vs. 26–32% in *Agorophius*), loss of parietal exposure in mature specimens, inflated tooth roots, rectangular outline of the occipital shield, and much larger and dorsolaterally flaring nuchal crests that overhang the exoccipital in dorsal view; differs further from *Squalodon* in its narrower intertemporal constriction, longer zygomatic process, fewer double rooted postcanine teeth (14% of tooth row double rooted vs. 40% in *Squalodon*); stronger degree of postcanine simplification (fewer accessory cusps, fewer teeth with accessory cusps, and smoother enamel with longitudinal striations, rather than rugose enamel); differs from *Phoberodon* in its narrower intertemporal constriction (22–24% of bizygomatic width vs. 54% in *Phoberodon*), more anteriorly placed premaxillary sac fossae, and less telescoped skull with nares and associated elements anterior rather than dorsal to the braincase. *Ankylorhiza* differs from all crown Odontoceti in possessing some double rooted teeth, deeply excavated embrasure pits, a prominent intertemporal constriction, and a widely open mesorostral gutter along the entire length of the rostrum. Modified from Boessenecker et al. (2020).

Ankylorhiza serratidens sp. nov.

Figs. 1–5.

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Etymology: From Latin *serratus*, serrate and *dens*, tooth; referring to the distinctive serrated teeth of this species.

Holotype: CCNHM 105, a partial skeleton including a nearly complete right mandible, partial left mandible, 12 mandibular teeth, atlas vertebra, C3? and C4?, four thoracic vertebrae including T8? and T10?, one lumbar vertebra, and seven ribs (collected by Ken Cloak and Andy Allen from the type locality).

Type locality: Edisto River, Dorchester County, South Carolina, USA. Detailed locality information available on request from CCNHM.

Type horizon: Ashley Formation, confirmed by adhering calcarenite matrix. Because two members of the Ashley Formation (Runnymede Marl and overlying Givhans Ferry Member) are present in the subsurface here (Weems et al. 2016), adhering matrix was examined to determine stratigraphic origin. Adhering matrix is richly quartzose and phosphatic, indicating derivation from the Givhans Ferry Member (Weems et al. 2016). The Ashley Formation typically consists of 10–15 m of yellow to olive calcarenite (Weems et al. 2016); it is typically sparsely fossiliferous, with common pectinids and ostreid bivalves, gastropods, barnacles, and the solitary coral *Balanophyllia*. Vertebrate remains are relatively scarce but include sharks, bony fish, sea turtles, sirenians, odontocetes, and mysticetes (Boessenecker et al.

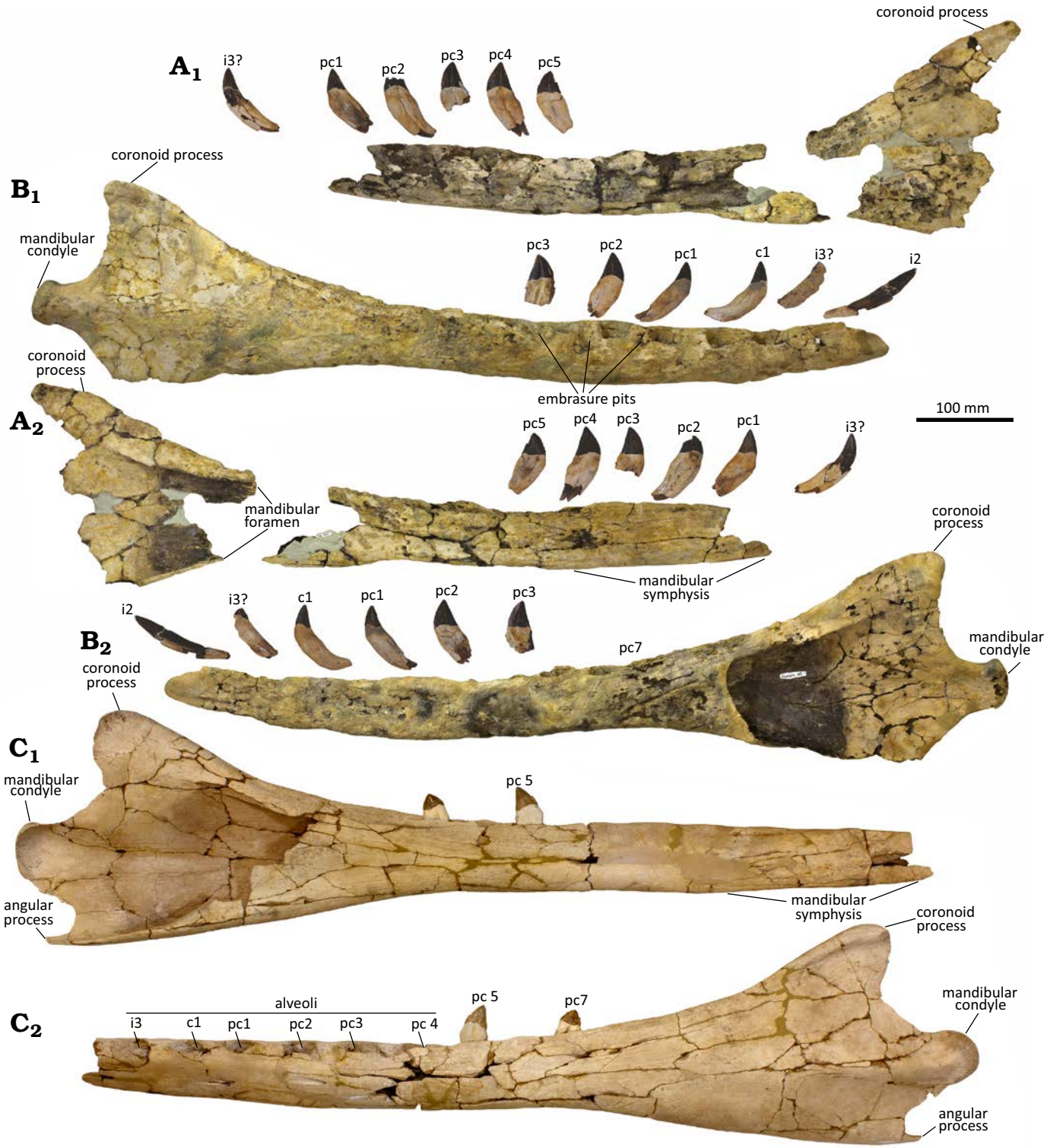

Fig. 1. Mandibles and teeth of the stem odontocete *Ankylorhiza* Boessenecker et al., 2020. **A**, **B**. *Ankylorhiza serratidens* sp. nov. (CCNHM 105) from lower Oligocene Ashley Formation of Charleston, South Carolina, USA. **A**. Left mandible and lower left dentition in lateral (A_1) and medial (A_2) views. **B**. Right mandible and lower right dentition in lateral (B_1) and medial (B_2) views. **C**. *Ankylorhiza* sp. (CCNHM 1075) from upper Oligocene Chandler Bridge Formation of Charleston, South Carolina, USA; left mandible in medial (C_1) and lateral (C_2) views.

2017). Sedimentology, ichnology, micropaleontology, and fish remains suggest deposition from nearshore to outer shelf depths and warm temperate climate (Hazel et al. 1977; Weems and Lewis 2002; Edwards et al. 1997; Fierstine and Weems 2009). Strontium isotope ratios from the Runnymede Marl and Givhans Ferry members correspond to ages of 29.0 and 28.75–28.43 Ma, respectively, indicating a late early Oligocene or Rupelian age (Weems et al. 2016).

Diagnosis.—A species of *Ankylorhiza* differing from *Ankylorhiza tiedemani* in absolutely and proportionally larger

postcanine teeth (e.g., pc5 26% larger in absolute size than in *A. tiedemani* despite similar skull/mandible length), coarsely serrated carinae on postcanine teeth, strong apicobasal ridges (longitudinal flutes/facets in *A. tiedemani*), possession of a large distal accessory cusp on middle postcanine teeth (pc5), and proportionally smaller vertebrae. *Ankylorhiza serratidens* sp. nov. differs from the unnamed species of *Ankylorhiza* represented by ChM PV 2764 and CCNHM 1075 in its smaller size (90–92% of mandibular size of CCNHM 1075), proportionally longer mandibular symphysis (40% of mandibular length vs. 20% in CCNHM 1075), possession of an acutely triangular coronoid apex (lobate in CCNHM 1075), possession of large distal accessory cusps further anterior in the dentition (beginning in pc5, as opposed to pc8–9 only in CCNHM 1075), and possession of coarsely serrated carinae on postcanine teeth.

Description.—*Mandible*: The mandible is large for an Oligocene odontocete (estimated total mandibular length 90 cm), and dorsoventrally shallow; about 60% of its length is occupied by the tooth row (Fig. 1A, B; Table 1). The mandibular symphysis is long, extending posteriorly to the position of pc4, about 40% of mandibular length. The symphyseal surface is flat and slightly rugose (Fig. $1A_2$, B_2). The right mandible is slightly upturned in its anterior 20%, likely an error introduced in reconstruction, and does not seem to be replicated on the less reconstructed (but less complete) left mandible (Fig. 1A). The section including the right i1 alveolus is missing and was not reconstructed; the anteriormost natural alveolus appears to be i2. The left mandible is dorsoventrally deepest around pc3–4 and the posterior part of the symphysis. Within the symphyseal region, the mandible has a teardrop-shaped cross section as it is thickest dorsally and tapers ventrally; the lateral side faces ventrolaterally. Though the right mandible seems quite straight in dorsal outline (Fig. $2A_1$), the fragmentary left mandible (Fig. $2B_1$) is slightly sinuous as in CCNHM 1075 (*Ankylorhiza* sp.; Fig. 2C), suggesting that the straight outline of the right mandible is a result of inaccurate reconstruction.

The i2–c1 alveoli are somewhat procumbent; preserved incisor alveoli are circular, and the c1–pc3 alveoli become more oval in shape. Postcanine alveoli are vertical. Deep embrasure pits are present within the postcanine tooth row, beginning between pc2–3 and posteriorly to between pc6–7. They become shallow anteriorly and are positioned laterally (e.g., pc2–3 pit) and developed as a vertical trough. The pits between pc3–4 and pc4–5 are deep, positioned slightly lateral to the tooth row and slightly below the alveolar margin. The posteriormost pits (between pc5–6 and pc6–7) are deep but in line with the tooth row and positioned along the dorsal surface of the mandible.

The mandible deepens posterior to pc7 and leads to a triangular coronoid process (Fig. 1A, B; Table 1). The anterior margin is gradually sloped; the posterior margin is concave and the apex of the coronoid overhangs the posterior margin. Although the right coronoid process is damaged, the left coronoid process preserves a posterodorsally oriented finger-like apex. The ventral margin of the mandible is concave along its length and posteriorly it descends gradually, giving the posterior end a fan-shape in lateral view; the entire posterior end of the mandible is dominated by the cavernous mandibular fossa. The shape of the mandibular foramen is uncertain owing to breakage, but the dorsal margin was higher than the tooth row and approximated the entire depth of the mandible. The dorsal edge of the fossa is a low ridge rising posterodorsally above the level of the condyle. The mandibular condyle is transversely narrow and posteriorly convex; it is excavated medially by the mandibular fossa. The condyle is positioned at approximately the level of the tooth row. The angular process is not preserved.

Dentition: The anteriormost alveolus in the right mandible (Fig. $2A_1$) is most likely the right i2 alveolus, based on comparison with CCNHM 1075 (*Ankylorhiza* sp.; Fig. 2C). This indicates a total of 11 teeth are present, with postcanines pc1–7. Curiously, rather than possessing similar upper and lower dental counts, one undescribed specimen of *Ankylorhiza* sp. (CCNHM 1075) possesses 13 upper and 11 lower teeth (Figs. 1C, 2C). Therefore, 13 mandibular teeth in *Ankylorhiza tiedemani* is likely an overestimate by Boessenecker et al. (2020).

The right i2 is large, nearly straight, and procumbent (Figs. 1B, $2A_2$, A_3; Table 2), but slightly more curved than the i1 of other *Ankylorhiza* spp. The i2 crown is nearly conical but transversely compressed with sharp carinae. The basal 2/3 of the crown bears discontinuous low apicobasal ridges that dissipate apically. The root is conical and sheathed by a 3 mm thick layer of cementum.

Table 1. Mandibular measurements (in mm) of *Ankylorhiza serratidens* sp. nov. holotype (CCNHM 105). *, incomplete measurement; e, estimated measurement; ?, unknown measurement.

Measurement	Left	Right
Total length as preserved	?	847
Length of symphysis as preserved	150*	230
Depth/width at c1	?	46.6/29.5
Depth/width at symphyseal terminus	65.6/37.7	62e/35.8
Depth/width at pc7	62.6/?	65e/34
Mandibular depth at coronoid	232	200*
Length of toothrow as preserved	?	464

Table 2. Dental measurements (in mm) of *Ankylorhiza serratidens* sp. nov. holotype, CCNHM 105 (in mm). *, incomplete measurement; ?, unknown measurement; L, left; R, right.

Tooth	Crown height, L/R	Crown width, L/R	Crown length, L/R
i2	?/34.5	?/13.4	?/15.8
i3	?/?	?/12*	?/?
c1	24.2/25.7	11.3*/11.1	15.8*/16.2
pc1	24.5/24.4	11.4/11.4	19.3/17.0
pc2	?/29.3	13.7/14.1	24.7/25.5
pc3	28.9/?	14.2/?	24.7/?
pc4	29.1/?	13.8/?	25.3/?
pc5	23.6/?	13.5/?	24.0/?

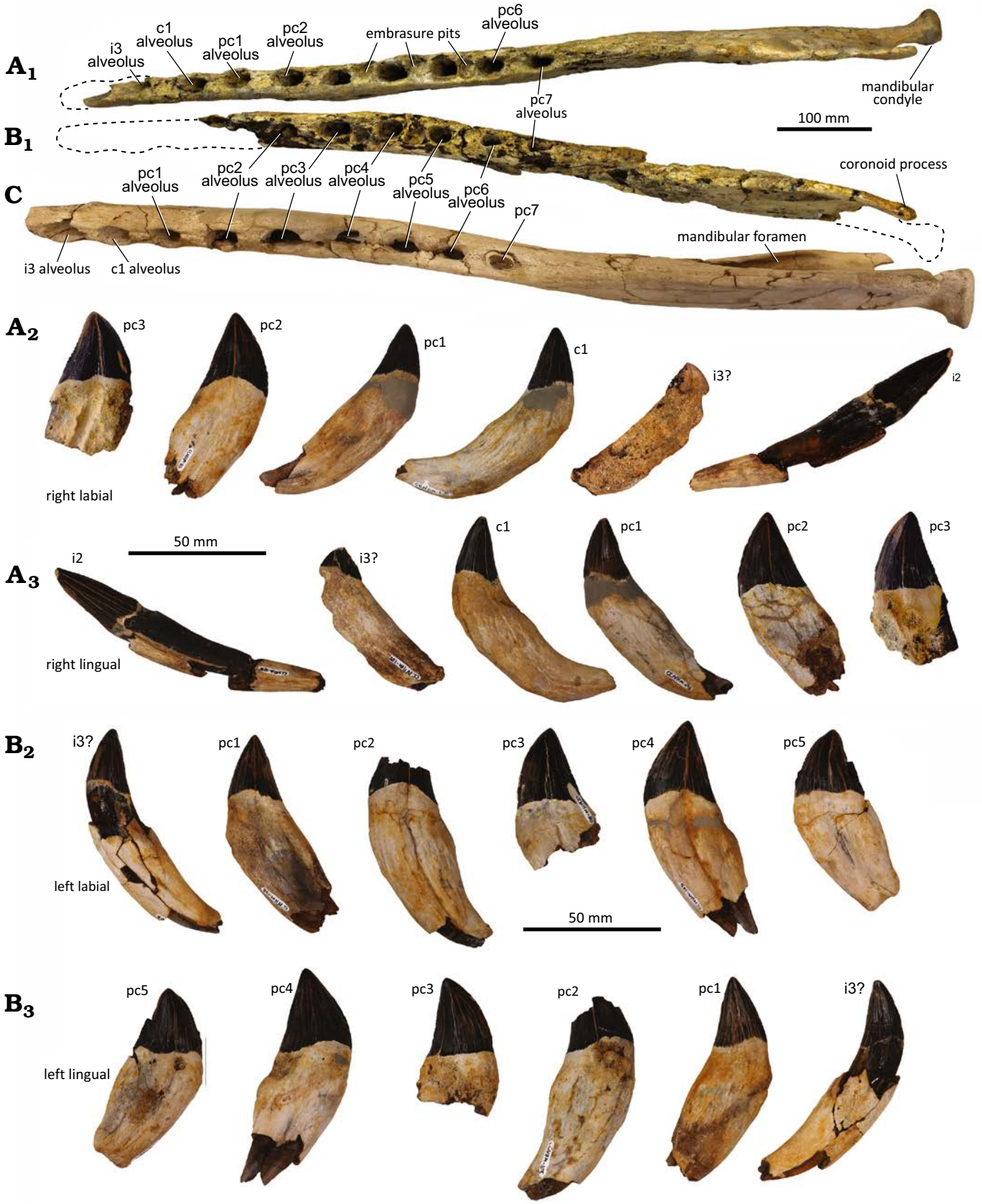

Fig. 2. Mandibles and teeth of the stem odontocete *Ankylorhiza* Boessenecker et al., 2020. **A**, **B**. *Ankylorhiza serratidens* sp. nov. (CCNHM 105) from lower Oligocene Ashley Formation of Charleston, South Carolina, USA. **A**. Right mandible in dorsal view (A_1), lower right anterior dentition in labial (A_2) and lingual (A_3) views. **B**. Left mandible in dorsal view (B_1), lower left anterior dentition in labial (B_2) and lingual (B_3) views. **C**. *Ankylorhiza* sp. (CCNHM 1075) from upper Oligocene Chandler Bridge Formation of Charleston, South Carolina, USA; left mandible in dorsal view.

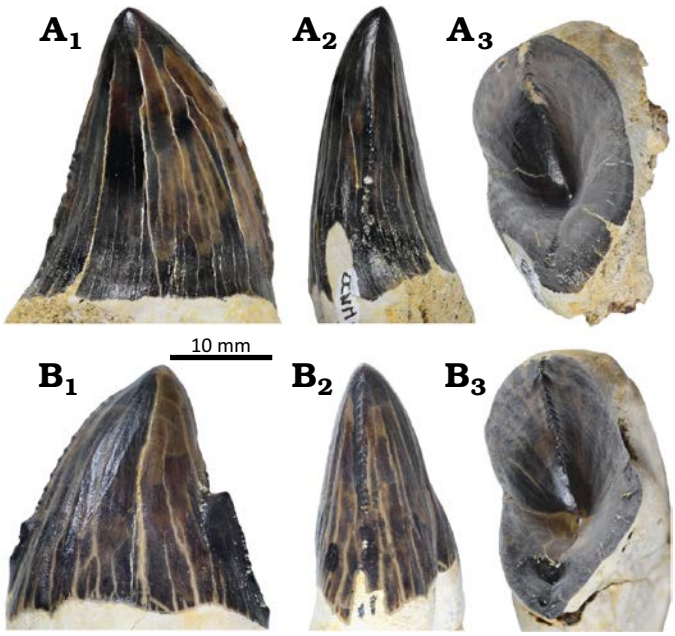

Fig. 3. Serrated postcanine teeth of of the stem odontocete *Ankylorhiza serratidens* sp. nov. (CCNHM 105) from lower Oligocene Ashley Formation of Charleston, South Carolina, USA. **A**. Left pc3 crown in lingual (A_1), distal (A_2), and apical (A_3) views. **B**. Left pc5 crown in labial (B_1), mesial (B_1), and apical (B_1) views.

The left i3 (Figs. 1A, $2B_2$, B_3; Table 2) has a conical crown that is more lingually recurved than the i2. The crown bears nearly continuous apicobasal ridges, the root is somewhat more laterally compressed, and curved than the i2. The right i3 is missing most of the crown and has a large labial wear facet.

The right c1 (Figs. 1B, $2A_2$, A_3; Table 2) is similar to the i3 but has a more inflated and posteriorly recurved root; the crown is triangular with a broader base than the incisors, and somewhat transversely narrower, and bears sharp mesial and distal carinae. The root bears a pronounced anteroposterior swelling at the alveolar margin. Left and right pc1 are similar to the c1 but possess a lower triangular crown with an anteroposteriorly longer base. The root is more moderately recurved. It bears prominent apicobasal ridges, smooth distal carina, but a weakly serrated mesial carina. The root is anteroposteriorly thickened, transversely narrow, and bears a faint labial sulcus. The root is also anteroposteriorly swollen at the alveolar margin, about 15 mm below the crown.

Left and right pc2 (Figs. 1A, B, $2A_2$, A_3, B_2, B_3; Table 2) are well preserved and exhibit a transversely narrow crown that is only slightly higher than anteroposteriorly long. The crown bears somewhat more widely spaced apicobasal ridges labially. The mesial carina is worn but bears clear denticles on the basal 2/3 of the carina; weaker denticles are present on the basal half of the distal carina. The root is slightly more massive than in pc1, but bears a deeper labial sulcus and a faint lingual sulcus.

Left and right pc3 were initially preserved (Figs. 1A, B, $2A_2$, A_3, B_2, B_3, 3A; Table 2), though right pc3 is now missing and presumed lost. The left pc3 is similar to pc2 but has a slightly transversely wider and anteroposteriorly shorter crown, and a more inflated root at the alveolar margin. The labial sulcus is much deeper; pc3 bears stronger mesial and distal serrations, with coarse serrations on the basal 3/4 of the distal carina. Serrations are even more coarsely developed in right pc3. In left pc3, there are 19 denticles which measure 0.9–1.1 mm in apicobasal diameter (measured between notches) and become larger basally. Tooth wear on larger denticles exposes dentin within, indicating that these are true denticles (sensu Bennion et al. 2023). Many teeth preserve a line of dental calculus, preserved best as a small, dark, raised ridge on the labial side of left pc3 about 1 cm below the crown base along the thickest part of the cementum.

The left pc4 (Figs. 1A, $2B_2$, B_3; Table 2) is similar to pc3 but distal serrations are not developed on the preserved carina. A deep labial sulcus and a shallow labial sulcus are developed on the root. The shallow labial sulcus extends onto the basal third of the crown. Mesial serrations are damaged but clearly present along the basal 2/3 of the carina.

The left pc5 (Figs. 1A, $2B_2$, B_3, 3B; Table 2) is complete and bears a triangular crown (similar in anteroposterior length to pc4, but lower crowned) with a well-developed coarsely serrated mesial carina. The basal 2/3 of the distal carina is serrated (serrations measuring 1.1–1.3 mm between notches), but more finely than the mesial carina. A single large posterior accessory cusp is located midway along the distal carina; two cuspules (= enlarged denticles) are present mesially about 6–9 mm above the base of the crown. Apicobasal ridges are present basally and become fainter apically. The basal 1/4 of the crown is somewhat more rugosely ornamented posterolingually. The lingual surface is more convex than the labial surface, which has a vertical labial furrow extending onto the crown. The labial sulcus on the root is very deep relative to other teeth, and two shallow lingual sulci are developed, the anterior one being somewhat deeper. The tips of the roots exhibit small knobs.

The gumline appears to have been at the apical margin of the thickest part of the roots in CCNHM 105, as in CCNHM 103 (*Ankylorhiza tiedemani*). This interpretation is also supported by a faint line of dental calculus, best preserved labially in left pc3, paralleling and about 10 mm below the basal margin of the enamel; it is developed as a small, raised ridge, and dissipates lingually. Wear in left PC3 has exposed dentine in the core of individual serrations, indicating development of shallow interdental folds (e.g., Brink et al. 2015). All serrations are best characterized as being macroziphodont sensu Young et al. (2013).

Tooth wear and enamel erosion: Incisors and canines all have small apical wear facets. Right i2 also has an obliquely oriented apicomesial facet. The presumed left i3 is partial and only bears a small labial remnant of the crown, and a massive anteromesial wear facet is present; the large facet is best interpreted as catastrophic breakage followed by attritional wear. Some chipping is present on the mesial carinae of many teeth (right i2, left pc3, left and right pc4), but is

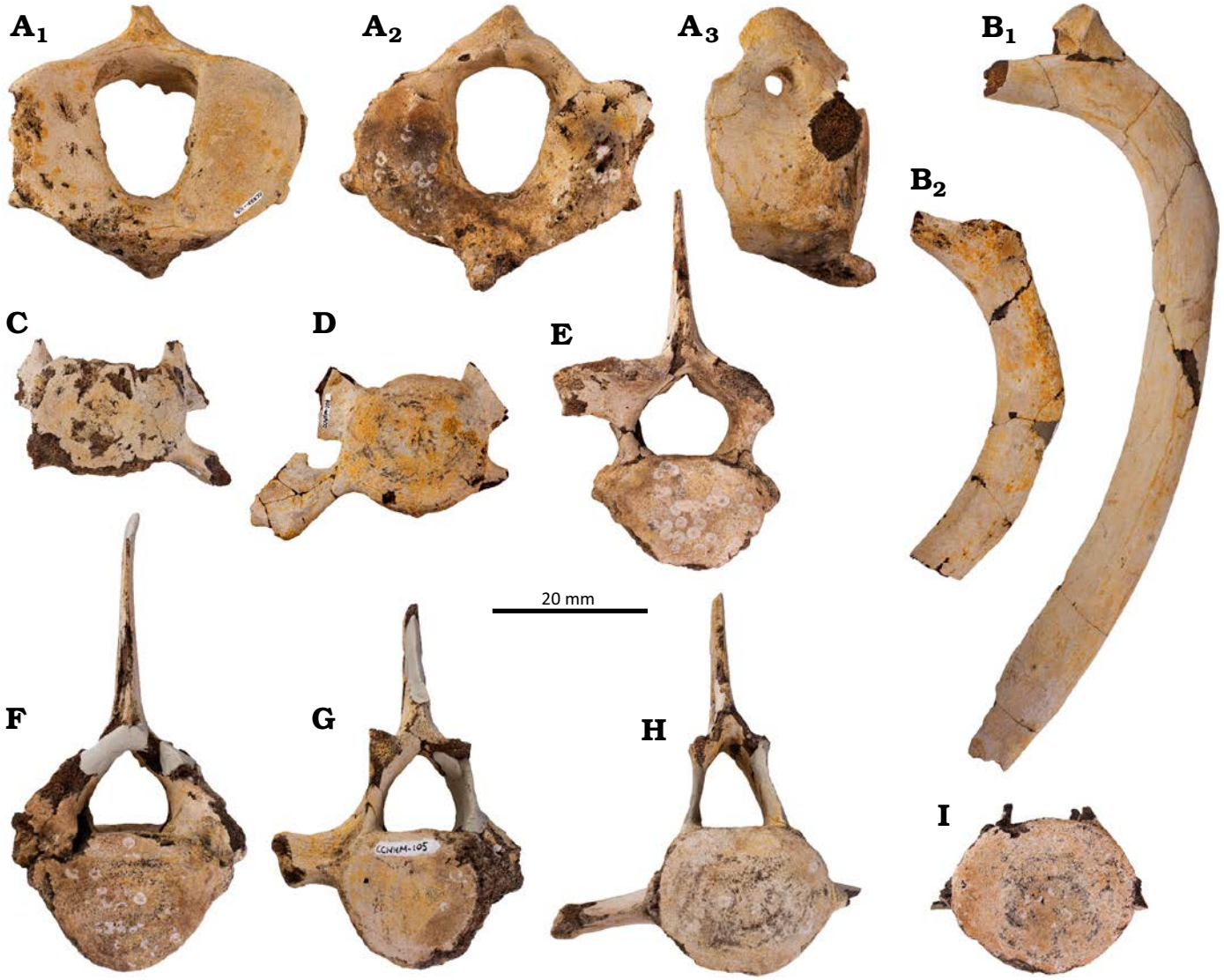

Fig. 4. Postcranial elements of of the stem odontocete *Ankylorhiza serratidens* sp. nov. (CCNHM 105) from lower Oligocene Ashley Formation of Charleston, South Carolina, USA. **A**. Atlas in anterior (A_1), posterior (A_2), and left lateral (A_3) views. **B**. Anterior left ribs in anterior view (B_1, B_2). Third cervical vertebra (**C**), fourth or fifth cervical vertebra (**D**), sixth or seventh thoracic vertebra (**E**), eight thoracic vertebra (**F**), ninth thoracic vertebra (**G**), eleventh thoracic vertebra (**H**), and lumbar vertebra (**I**) in anterior view.

rare on the distal carinae, and completely absent on left pc5. A single large concave facet (10 mm radius) is present distally at the base of right i2, and is 2–3 mm deep. Right pc2 bears a narrow, apicobasally oriented facet along the distal third of the distal carina, but is not present in left pc2. Left pc3 has an oval facet basally on the labial side of the distal carina (Figs. $2B_2$, $3A_2$, A_3); this facet does not damage or cross the carina, and is likely caused by wear from the opposing upper tooth. Left pc4 bears an apicobasal facet on the basal third of the distal carina, like the right pc2.

Some teeth preserve a spongy basal margin of the enamel, with circular holes measuring 40–160 µm exposing dentine and coalescing into larger cavities near the crown base. This may potentially be a result of enamel erosion in vivo. This is most clear in left pc1 (labial and lingual), right and left pc2 (labial and lingual, respectively), right c1 (labial and lingual), and to a lesser degree in left pc3–4.

Cervical vertebrae: The atlas (Fig. 4A; Table 3) and two mid cervicals are preserved, likely C3 and C4 or C5 (Fig. 4C, D; Table 4). The atlas is similar to that of CCNHM 220, a referred specimen of *Ankylorhiza tiedemani*. It possesses well-separated dorsal and ventral transverse processes (parapophyses/diapophyses?), a well-developed and posteriorly directed hypapophysis, a low neural spine, and relatively anteroposteriorly thick proportions. C3 (Fig. 4C) is small and possesses an oval-shaped centrum, a large oval-shaped transverse foramen, and ventrolaterally projecting, rod-like transverse process. C4/5 (Fig. 4D) has a larger transverse process, a proportionally smaller transverse foramen, and a nearly circular centrum.

Thoracic and lumbar vertebrae: Four thoracic vertebrae are preserved in CCNHM 105 (Fig. 4E–H; Table 4), and are relatively similar to those of the most complete specimen of *Ankylorhiza tiedemani*, CCNHM 103, but are rel-

Table 3. Atlas measurements (in mm) of *Ankylorhiza serratidens* sp. nov. holotype, CCNHM 105. *, incomplete measurement.

Transverse width of occipital facets	117.2
Greatest transverse width	128*
Anteroposterior length	56.5
Dorsoventral depth of occipital facet	65.9
Greatest dorsoventral depth	114.1
Neural foramen, dorsoventral depth	51.4
Neural foramen, transverse width	40.9
Transverse width, posterior articular facets	103.3

Table 4. Vertebral measurements (in mm) of *Ankylorhiza serratidens* sp. nov. holotype, CCNHM 105. *, incomplete measurement.

Vertebra	Centrum, anteroposterior length	Centrum, dorsoventral depth	Centrum, transverse width
C3?	32.3	50.2	58*
C4 or C5	28.3	59.4	61.8
T6 or T7	64.5	52.0	85.7
T8	69.5	58.4	84.3
T9	72.9	56.3	66.5
T11	80.4	59.5	75.4
L?	74.2	67.6	79.0

atively smaller and preserve more complete neural arches and spines. Based on comparison with CCNHM 103, these are identified as T6/7, T8, T9, and T11. The anteriormost vertebra, T6/7, has widely separated capitular and tubercular facets for the ribs; the latter are positioned on the pedicle and prezygapophysis and elevated near the top of the neural foramen. T8 has a surprisingly tall spine and a triangular neural foramen; the capitular facets are unclear owing to bioerosion, and the transverse processes appear to have been short. T9 is similar to T8 and T10 of CCNHM 103 but bears a narrower neural foramen and a short transverse process with a flat ventrolaterally facing capitular facet. T11 is nearly identical to the T11 of CCNHM 103, but possesses a slightly shorter transverse process that is angled slightly more ventrally. A single incomplete lumbar of uncertain position is preserved (Fig. 4I), and compares well with most lumbars preserved in CCNHM 103.

Ribs: Several (n = 7) ribs are preserved, including a complete left first or second rib (Fig. $4B_1$), a partial anterior left rib (Fig. $4B_2$), and several additional fragments. They are similar in morphology to *Ankylorhiza tiedemani*, but slightly smaller.

Bone and dental modifications.—Certain skeletal elements of CCNHM 105 are extensively bioeroded. Both mandibles have isolated pockmarks (5–10 mm diameter) and regions where these have laterally coalesced into regions of irregular, bioeroded bone (e.g., Boessenecker and Fordyce 2015b); the former is more typical of the posterior end of each mandible whereas the horizontal ramus in both left and right mandibles is more strongly bioeroded. Well-preserved traces on the atlas vertebra consist of small 5–13 mm diameter crater-like pockmarks (Fig. 5B). The pockmarks are 150–330 μm diameter fine, vermiform tunnels around the periphery surrounding a large and deep (2–5 mm) cavity with one or more radial fissures. These central cavities are at least 600 μm in diameter and typically at least 1–3 mm, with radial fissures extending up to 2 mm; these cavities are floored by crumbly, porous bone penetrated by extensive bioeroded tunnels. The extremities of vertebrae in CCNHM 105 are bioeroded with irregular fractured surfaces (e.g., Fig. 4C). These, and the crater-like traces on the atlas, are best identifiable as *Osedax* borings (e.g., Boessenecker and Fordyce 2015b). *Osedax* borings also occur in the roots of many teeth of CCNHM 105, typically as pockmarks, single boreholes (Boessenecker and Fordyce 2015b), or as a network of minute radiating tunnels, mostly in the cementum. The lingual side of the left pc3 is lightly bioeroded, and approximately two thirds of the root is bioeroded away on the lingual side of right i3. In right i3, dentine and even enamel appears to be bioeroded through with several similar crater-like pockmarks and fine bioeroded tunnels in the enamel and dentine. Left pc5 bears many fine scratches on the tip of the root; these are subparallel, 2–3 mm long scratch marks. Some similar traces are present just below the crown of right pc2.

The more complete rib of CCNHM 105 exhibits abundant traces preserved as incised grooves (Fig. 5A). The majority of these are straight to subparallel linear gouges, chiefly on the posterior side of the middle part of the rib. Some of these further distally are wider. Many of the smaller gouges positioned proximally are also arcuate. These traces are best identified as the ichnospecies *Linichnus bromleyi* Muñiz et al., 2020 (e.g., Muñiz et al. 2020). On the medial edge of the rib is a series of parallel, shallow, wavy grooves (Fig. $5A_2$), and identifiable as *Knethichnus parallelum* Jacobsen & Bromley, 2009 (e.g., Jacobsen and Bromley 2009).

Stratigraphic and geographic range.—Lower Oligocene (Rupelian) Ashley Formation of Charleston, South Carolina, USA.

Discussion

Comparisons and assignment to *Ankylorhiza*.—Mandibular, dental, and atlas vertebra morphology supports identification of CCNHM 105 as *Ankylorhiza*. Published specimens of *Ankylorhiza tiedemani* preserve mandibular teeth but no mandibles. However, specimens of the unpublished species of *Ankylorhiza* (assignment to *Ankylorhiza* confirmed by phylogenetic analysis; Boessenecker et al. 2020: fig. S4), like CCNHM 1075, include well-preserved mandibles (Figs. 1C, 2C). The mandible of CCNHM 1075 shares with CCNHM 105 large size, a long symphysis (albeit 40% of mandibular length in *Ankylorhiza serratidens* sp. nov. vs. 20% in CCNHM 1075), large embrasure pits, and large teeth with thickened cementum, and subtle heterodonty with procumbent incisors and conical, bicarinate anterior teeth bearing apicobasal ridges transition-

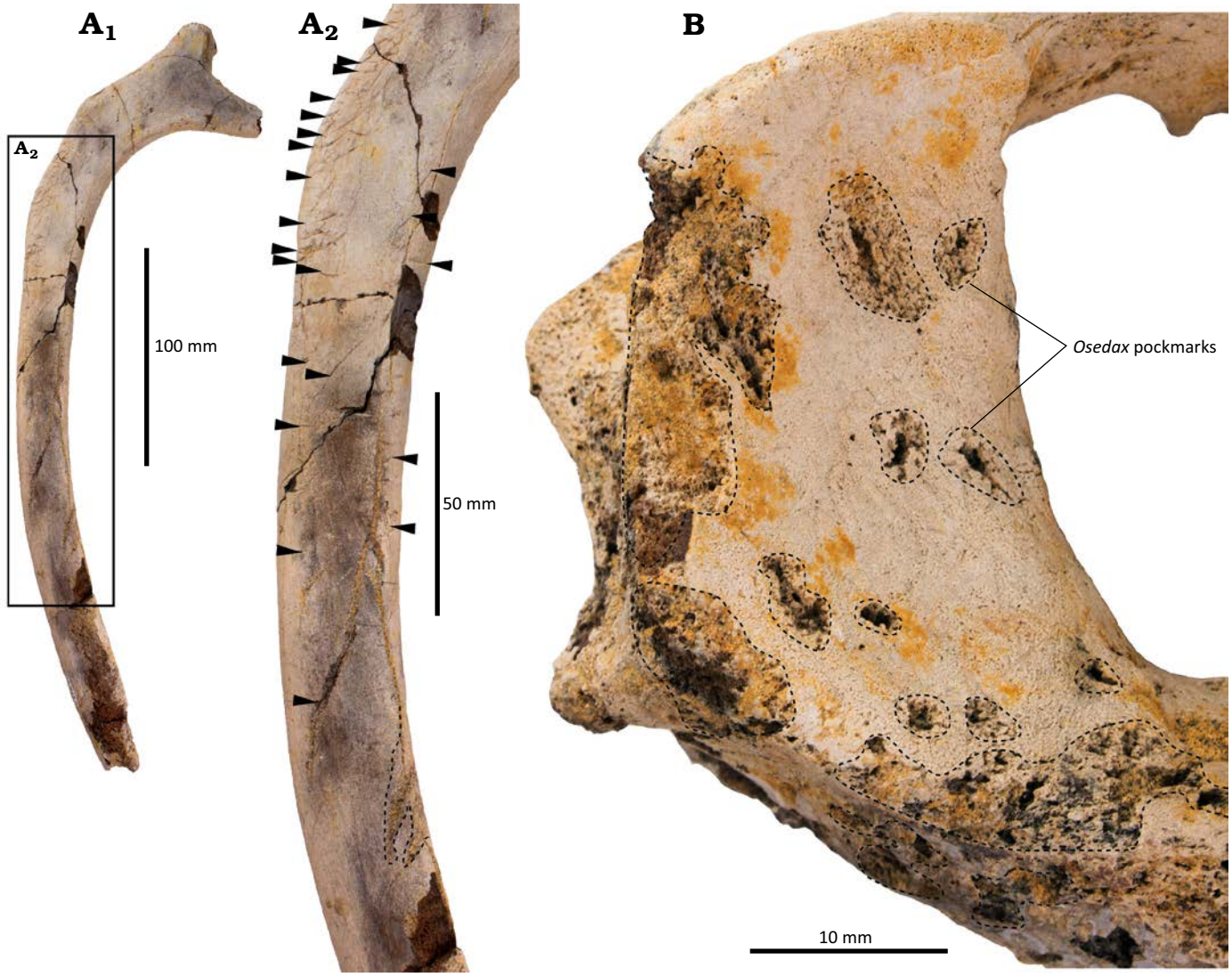

Fig. 5. Bone modifications in the stem odontocete *Ankylorhiza serratidens* sp. nov. (CCNHM 105) from lower Oligocene Ashley Formation of Charleston, South Carolina, USA. **A**. Left first rib in posterior view (A_1), posterior face of rib (A_2), showing location of traces attributed to shark feeding including linear bite marks (triangles) and shallow parallel grooves (dashed line). **B**. Right side of atlas in anterior view showing traces attributable to *Osedax*.

ing to triangular, transversely narrow crowns on posterior postcanine teeth. However, CCNHM 1075 is slightly larger (8–12% larger than *Ankylorhiza serratidens* sp. nov., with a mandible length of 98–100 cm). Mandibular teeth of *Ankylorhiza* sp. (CCNHM 1075) and *Ankylorhiza tiedemani* (CCNHM 103) lack serrations (two possible maxillary teeth of CCNHM 220 are serrated, but their provenience is dubious), though these specimens (CCNHM 103, 1075) possess the remaining shared features listed above with CCNHM 105 to the exclusion of all other Oligocene odontocetes. Owing to much smaller size than CCNHM 1075 and the possession of serrations, CCNHM 105 represents neither *Ankylorhiza tiedemani* nor the large as-yet unnamed species of *Ankylorhiza* represented by CCNHM 1075 and ChM PV 2764 (*Ankylorhiza* sp. nov. 1), and is best considered a new species, *Ankylorhiza serratidens* sp. nov.

Comparisons with other odontocetes from the Oligocene of South Carolina, the Squalodontidae, and species of *Phoberodon* and *Patriocetus* are warranted. *Ankylorhiza serratidens* sp. nov. differs from *Agorophius pygmaeus* in its larger size, larger teeth lacking accessory cusps (except for a single distal cusp on posteriormost postcanines, such as pc5), and possessing serrated carinae. *Ankylorhiza serratidens* sp. nov. differs from Squalodontidae in lower tooth count (14 mandibular teeth in *Squalodon bellunensis*; Nelson et al. 2025b; likely 15–17 mandibular teeth in *Squalodon calvertensis*, *Squalodon murdochi*, and *Squalodon whitmorei*; Kellogg 1923; Dooley 2004; Godfrey and Lambert 2023), postcanines with greater development of single rootedness, fewer accessory cusps (1 distal cusp vs. 3+), and generally smoother, striated to fluted (rather than rugose) enamel on postcanine teeth. *Eosqualodon langewieschei* has an uncertain mandibular tooth count since the posteriormost teeth are obscured (Nelson et al. 2025b), but likely 15 (given that the mandibular tooth count of *S. bellunensis* is just one less than the upper tooth count); *E. langewieschei* further dif-

fers, like *Squalodon* spp., in possessing three or more distal accessory cusps and rugose enamel. One undescribed specimen of *Eosqualodon* sp. (CCNHM 170) from the Chandler Bridge Formation of South Carolina has 13 mandibular teeth, versus 11 in *Ankylorhiza serratidens* sp. nov. and CCNHM 1075, and further differs from *Ankylorhiza* spp. in having rugose rather than fluted enamel and cheek teeth with more numerous accessory cusps (three to four cusps in the cheek teeth of *Eosqualodon* sp., versus no mesial cusps and one distal cusp in *Ankylorhiza* spp.). *Eosqualodon* sp. also differs from *Ankylorhiza* spp. in having a much greater degree of double-rooted teeth, with seven out of nine postcanine teeth possessing double roots (78% double rooted) in CCNHM 170, versus few double rooted teeth in *Ankylorhiza* (0% double rooted in *Ankylorhiza serratidens* sp. nov., 14% in *Ankylorhiza* sp. (CCNHM 1075), and likely 0 or 14% in *Ankylorhiza tiedemani*).

Ankylorhiza serratidens sp. nov. has a mandible similar in morphology to the putative squalodontid *Phoberodon arctirostris*, though it is somewhat smaller (approximately 90 cm, vs. estimated mandible length of 96 cm in *P. arctirostris*); it differs from *P. arctirostris* in possessing a lower tooth count (11 vs. 13–15 in *P. arctirostris*), lacking numerous accessory cusps (1–3 mesial and 3–5 distal cusps in *P. arctirostris*), and a greater proportion of single rooted teeth in the mandibular dentition (14% double rooted vs. 36–40% double rooted in *P. arctirostris*).

Ankylorhiza serratidens sp. nov. differs from Waipatiidae and other waipatiid-grade odontocete species in its larger size, greater degree of root fusion (2 of 7 postcanines with bilobate or double roots, vs. 10 of 15 postcanines in *Waipatia*), simpler tooth morphology (e.g., only a single accessory cusp, absence of lingual cingulum, and more subtle apicobasal ridges) and possessing a lower tooth count (11 mandibular teeth vs. ~19 in *Waipatia maerewhenua*; Fordyce 1994).

Ankylorhiza serratidens sp. nov. differs from Xenorophidae in its much larger size, procumbent incisor alveoli, anterior incisors enlarged relative to c1 and anterior premolars, postcanines with mostly single-rooted teeth, and cheek teeth with highly reduced accessory cusps, teeth lacking lingual cingula, absence of embrasure pits on posterior mandible, and atlas with short and widely separated apices of the transverse process. *Ankylorhiza serratidens* sp. nov. differs from most other stem odontocetes in its larger size (e.g., *Simocetus rayi*, *Olympicetus* spp.). The teeth of *Ankylorhiza* spp. generally resemble *Patriocetus kazakhstanicus* in their large size, possession of fluted enamel, and inflated cementum on the roots; *Ankylorhiza serratidens* sp. nov. differs from *P. kazakhstanicus* in possessing teeth with fewer distal accessory cusps (one vs. 3–4 in *P. kazakhstanicus*; Dubrovo and Sanders 2000), lacking lingual cingulum (a strong ridge is present in the b12 of *P. kazahlstanicus*, in the dental numbering terminology of Dubrovo and Sanders 2000), and a greater degree of root fusion (most of the postcanine teeth, b6–12 of *P. kazakhstanicus*, are double-rooted).

Feeding morphology.—*Ankylorhiza serratidens* sp. nov. is distinctive amongst cetaceans, and odontocetes in particular, for possessing serrated postcanine teeth (Fig. 3). Aside from weakly developed and sporadically occurring "pseudoserrations" on the carinae of some teeth of the coeval Oligocene toothed mysticete *Coronodon* (Boessenecker et al. 2023: figs. 42, 46K, L), more comparably serrated teeth occur, albeit sporadically, in some archaeocetes including pakicetid (Gingerich and Russell 1990; Cooper et al. 2009), protocetid (McLeod and Barnes 2008; Uhen 2014; Gingerich et al. 2019), basilosaurid whales (Andrews 1906; Kellogg 1936; Uhen 2004), and early odontocetes such as the Oligocene simocetid *Olympicetus avitus* (Velez-Juarbe 2017: fig. 7O) and the Miocene macrophagous odontocete *Squalodon* (e.g., *Squalodon calvertensis* holotype, USNM 10484, personal observation 2016; *Squalodon bellunensis*, Pilleri 1985: pl. 18E). Few contemporary descriptions of *Squalodon* exist and few historical (or contemporary) studies include detailed dental descriptions; in many early studies it is unclear if serrations, or accessory cusps are being referenced. However, at least some individuals of *Squalodon* possess true serrations (Nelson et al. 2025a, b).

Otherwise, Basilosauridae and many early diverging Neoceti (e.g., *Xenorophus*, *Coronodon*) possess up to five to six mesial and/or distal accessory cusps (or alternatively, accessory denticles) that may function in a similar fashion but are classified as cusps as they are much larger than serrations. Many stem odontocete and toothed mysticete lineages possess multicuspate teeth inherited from these basilosaurid ancestors. The performance of this tooth morphology during feeding is uncertain, though may have functioned similar to serrations. Accessory cusps in archaeocetes and early Neoceti are proportionally quite large, measuring (notch to notch) 10–22% of mesiodistal crown length in *Cynthiacetus* (Basilosauridae), 10–21% in *Coronodon havensteini* (Mysticeti), 14–25% in *Xenorophus* spp. and *Patriocetus kazakhstanicus* (Odontoceti). Though challenging to measure since only one notch is present, the single posterior cusp in the right pc5 of *Ankylorhiza serratidens* sp. nov. is at least 15% of the crown length, whereas the largest serrations of this tooth measure 5% of crown length. The presence of cuspules on the carinae of some of these teeth hint at a possible continuum in relative size between accessory cusps and serrations (or denticles, sensu Bennion et al. 2023). It is here proposed that relatively large (>10–15% of crown length) and numerically few structures (typically 1–6) separated by deep notches be classified as accessory cusps within archaeocetes and early Neoceti. More numerous, regular, and repeating structures measuring much less than 10% of crown length not separated by deep notches should be identified as serrations or denticles. A similar distinction between serrations and accessory cusps was made by Andrews (1906: 240–241). Further study is required beyond this preliminary proposal.

Other synapsids with true serrated teeth include machairodontine cats and some macrophagous gorgonopsians (Whitney et al. 2020); serrated teeth are however more wide-

spread amongst non-mammalian terrestrial predators, including numerous theropod dinosaurs, terrestrial crocodilians, rauisuchians, and varanid lizards (Brink et al. 2015), and several aquatic reptiles including phytosaurs, marine crocodiles, certain ichthyosaurs, some mosasaurs, and short-necked plesiosaurs (Massare 1987; Andrade et al. 2010; Bennion et al. 2023); in all such cases serrations have been interpreted as evidence of hypercarnivory or macrophagy (Massare 1987; Andrade et al. 2010; Bennion et al. 2023). Convergent evolution of serrated teeth in lamniform and carcharhiniform sharks is associated with feeding on marine tetrapods with thick skin and blubber (Cooper et al. 2023).

Coarsely serrated vertebrate teeth function like a saw blade, where movement of the flesh parallel to the serrated edge results in a "grip and rip" action, concentrating tissues, including tough connective tissue and skin, into the notches and ripping the tissue with relative motion between the tooth and prey item (Abler 1992; Corn et al. 2016).

Ankylorhiza tiedemani possesses a number of adaptations towards macrophagy; some of these, including sharp carinae, thickened cementum, and large body size, are also evident in *Ankylorhiza serratidens* sp. nov. Serrated teeth imply a refined ability to cut flesh (Frazzetta 1988; Alber 1992; Corn et al. 2016) and indicate that *Ankylorhiza serratidens* sp. nov. was likely even more macrophagous than the similarly sized contemporary *Ankylorhiza tiedemani*, inasmuch as it possessed more derived dental adaptations for macrophagy. The undescribed species of *Ankylorhiza* represented by ChM PV 2764 and CCNHM 1075 (*Ankylorhiza* sp. nov. 1) is larger (mandibular length approx. 100 cm) than both *A. tiedemani* and *A. serratidens* sp. nov., suggesting that this taxon simply evolved larger body size to overcome prey. *Ankylorhiza serratidens* sp. nov. also possesses more numerous and sharper apicobasal ridges than *A. tiedemani*, perhaps suggesting greater efficiency at puncturing the flesh of marine tetrapods (McCurry et al. 2019). Lastly, despite similar overall size, the teeth of *Ankylorhiza tiedemani* are approximately 80% the absolute size of *A. serratidens* sp. nov., perhaps suggesting a relatively more generalized diet in *A. tiedemani*. Curiously, the teeth of *A. serratidens* sp. nov. are similar in absolute size to those of the larger undescribed species of *Ankylorhiza* (*Ankylorhiza* sp. nov. 1, e.g., ChM PV 2764, CCNHM 1075).

Unlike most examples of serrations in the dentition of archaeocete whales where they occur sporadically, serrations are present on most posterior cheek teeth in *Ankylorhiza serratidens* sp. nov. Serrations appear on pc3–5, and may have been present on pc6–7, which are not preserved; serrations are therefore restricted to but generally consistently distributed amongst posterior cheek teeth. Anterior cheek teeth possess smooth carinae. The posterior tooth row is the region of highest bite force among mammals (Snively et al. 2015). Despite a near-homodont (or subtly heterodont) dentition in *Ankylorhiza* (Boessenecker et al. 2020), the presence of serrations limited to the posterior dentition suggests some retention of functional segregation of the tooth row into prey capture and prey processing, unlike modern pierce-feeding odontocetes with homodont teeth that only use teeth for prey capture (Werth 2000, 2006). Anterior teeth with smooth carinae, and exhibiting a greater degree of tooth wear, were likely used for prey capture as in many other odontocetes (Boessenecker and Geisler 2023), certain toothed mysticetes (Geisler et al. 2024), archaeocetes, and piscivorous marine tetrapods (e.g., Massare 1987; McCurry et al. 2019); anterior tusk-like incisors in *Ankylorhiza* may have been used for prey ramming, or alternatively intraspecific combat (Boessenecker et al. 2020). Finite element modeling of the killer sperm whale *Zygophyseter*, which lacks serrations and possesses a homodont dentition, suggests that posterior teeth were used for "grip and tear" feeding (Peri et al. 2021). Indeed, "grip and tear" feeding (Berta and Lanzetti 2020), perhaps using powerful bite force or even lateral shaking, would have been enhanced by serrations in this sector of the dentition in *Ankylorhiza serratidens* sp. nov. In sharks, serrated teeth function as part of a "cutting" dentition and are an adaptation to cut through flesh of large fish and marine tetrapods into smaller bites that can be swallowed (Frazzetta 1994; Corn et al. 2016).

In contrast to *Ankylorhiza serratidens* sp. nov., the extant macrophagous killer whale (*Orcinus orca*) and false killer whale (*Pseudorca crassidens*) lack serrations. Instead, these macrophagous delphinids have conical anteroposteriorly flattened teeth that interlock, forming mesiodistal wear facets that keep the teeth sharp for feeding (Young et al. 2012), accomplished by piercing and shaking large prey items into smaller pieces (Berta and Lanzetti 2020). Similar feeding morphology is documented in many extinct macrophagous sperm whales (Lambert et al. 2016) and these physeteroids likely engaged in similar feeding behavior to *Orcinus*. The absence of serrations in these or any other extant odontocetes is possibly a developmental constraint imposed by the absence of carinae in modern odontocetes. Conical teeth with a circular cross-section seem to characterize the dentition of all crown Odontoceti as well as perhaps some later-diverging stem taxa including squaloziphiids, eurhinodelphinids, and the "*Chilcacetus*-clade"; or, defined another way, all odontocetes crownward of *Prosqualodon* (e.g., Boessenecker et al. 2020: fig. S4). The loss of carinae may be correlated with rampant dental simplification already documented in crown Odontoceti (Loch et al. 2015).

Curiously, *Ankylorhiza serratidens* sp. nov. is geochronologically older (29–28.4 Ma) than undescribed specimens of a new, larger species of *Ankylorhiza* (*Ankylorhiza* sp. nov. 1, represented by ChM PV 2764 and CCNHM 1075) as well as some specimens of *Ankylorhiza tiedemani* (CCNHM 103), which originate from the geochronologically younger Chandler Bridge Formation (24.7–23.5 Ma). Other specimens of *A. tiedemani* (CCNHM 220) also originate from the Ashley Formation, like *A. serratidens* sp. nov. Specimens from the Chandler Bridge Formation do not exhibit extensive serrations, though sporadic serrations are present on some loose cheek teeth of one specimen from the Ashley

Formation (CCNHM 220). However, provenience was poor for the dentition of this specimen and they may be mis-allocated teeth of *A. serratidens* sp. nov. For example, in 2015, several teeth stored with this specimen strongly differed in preservation and were separated as they seemed to represent other specimens. In comparison, teeth of *Ankylorhiza tiedemani* specimen CCNHM 103 mostly possess smooth carinae. It therefore seems as though *A. serratidens* sp. nov. was an earlier short-lived experiment in macrophagous feeding ecology, and is from the older cetacean-bearing Oligocene rocks from the Charleston Embayment despite being more dentally derived than other *Ankylorhiza* spp. The diversity of coronodonid whales with likely macrophagous capabilities or adaptations (Geisler et al. 2024) is higher in the Chandler Bridge Formation (n = 3) than it is in the Ashley Formation (n = 1), and it is possible that coronodonid whales occupied some of the niche space utilized by *A. serratidens* sp. nov. earlier in the Oligocene.

Tooth count in *Ankylorhiza*.—Description of *Ankylorhiza serratidens* sp. nov. and the mandibular morphology of CCNHM 1075, an undescribed specimen *Ankylorhiza* sp., reveals the mandibular tooth count of *Ankylorhiza*. Boessenecker et al. (2020) reported 13 upper teeth in *Ankylorhiza tiedemani* and inferred 13 lowers based on the incompletely preserved lower dentition. However, CCNHM 1075 has an identical upper tooth count (n = 13) as *Ankylorhiza tiedemani*, and two fewer teeth in the mandibular dentition (n = 11). Eleven teeth also appear to be present in *Ankylorhiza serratidens* sp. nov., and 13 uppers and 11 lowers is interpreted as typical for *Ankylorhiza tiedemani*, *Ankylorhiza serratidens* sp, nov., and *Ankylorhiza* sp. (CCNHM 1075). In contrast, other stem odontocetes possess one fewer mandibular tooth, including typical specimens of the xenorophid *Xenorophus* (13 uppers and 12 lowers; Boessenecker and Geisler 2023), the waipatiid-grade *Nihohae* (17 and 16; Coste et al. 2023), and the squalodontids *Squalodon grateloupii* (15 and 14; Nelson et al. 2025a), and *Eosqualodon langewischei* (16 and 15; Nelson et al. 2025b).

Tooth wear.—Tooth wear provides further clues to interpret the feeding behavior of *Ankylorhiza serratidens* sp. nov. Wear is present in three varieties: apical wear present on anterior teeth and anterior postcanines; distolabial wear facets from dental occlusion in postcanine teeth; and chipping of the mesial carina in anterior postcanines. Apical wear is absent in the posterior postcanines, and these teeth instead possess wear facets from occlusion, perhaps suggesting interlocking teeth (e.g., Young et al. 2012). Though specimens of *Ankylorhiza* are not yet known with rostrum, mandible, and teeth articulated in life position, many Miocene specimens of *Squalodon* spp., which have a similar dentition, are preserved in articulation and possess an interlocking dentition (Pilleri 1985). Extensive chipping of the mesial carinae suggests that prey items were impacting the anterior side of the teeth. Though lacking carinae, similar enamel chipping is documented in extinct macrophagous sperm whales (Lambert and Bianucci 2019). This may corroborate the interpretation that *Ankylorhiza tiedemani* rammed prey with its enlarged, thickened, and procumbent incisor tusks (Boessenecker et al. 2020). Similar damage to the mesial cusps (but not distal cusps) was reported in the toothed mysticete *Coronodon havensteini* (Geisler et al. 2017), also from the Ashley Formation.

Tooth wear is generally light in the holotype of *Ankylorhiza serratidens* sp. nov. in comparison to *Xenorophus sloanii*, another large odontocete from the Ashley Formation (Boessenecker and Geisler 2023). Apical wear is limited, and a few teeth have wear on the carina or wear labial wear facets near the base of the crown, suggesting interlocking of upper and lower teeth similar to both species of *Xenorophus*. More limited tooth wear in *A. serratidens* sp. nov. could be a result of a less abrasive diet or poor occlusion, or perhaps even avoiding risky predation behaviors that might compromise the serrations (e.g., Hocking et al. 2013). Nevertheless, the most extreme tooth wear is concentrated anteriorly, with apical wear facets on i2 and catastrophic crown breakage on i3, followed by continued apical wear of the broken surface. This wear is consistent with the ram feeding hypothesis of Boessenecker et al. (2020).

Taphonomy.—Several of the teeth of CCNHM 105 exhibit borings attributable to the bone-eating worm *Osedax*. *Osedax* traces were preliminarily identified by Boessenecker and Fordyce (2015b) in fossil marine mammals of the Oligocene Ashley and Chandler Bridge formations of South Carolina from published images. CCNHM 105 marks one of only a few occurrences of *Osedax* bioerosion in vertebrate teeth (Kiel et al. 2013; Collareta et al. 2025; Jamison-Todd et al. 2025). The atlas vertebra of CCNHM 105 also exhibits unusual *Osedax* traces consisting of large craters with a rim of highly tunneled bone and a central window with radial fissures. This morphology does not readily match modern *Osedax* borings described by Higgs et al. (2014), and may represent a new ichnotaxon. The most complete rib of CCNHM 105 additionally preserves numerous linear scrape marks identifiable as the ichnospecies *Linichnus bromleyi*, and best interpreted as tooth marks from some kind of small shark. Fine scratches on the teeth may originate from a small fish or crab. Traces identifiable as of *Knethichnus parallelum* represent the carinae of serrated teeth scraping lengthwise along the bone surface, and in this case, likely represents feeding traces of the megatoothed shark *Carcharocles angustidens* (e.g., Boessenecker and Geisler 2023). These feeding traces may represent post-mortem scavenging, or possibly active predation. CCNHM 105 therefore represents two taphonomic phases: initial predation and/or post-mortem scavenging, followed by *Osedax* bioerosion after skeletonization of the carcass. Subparallel scratch marks on the bones differ from the pentaradial geometry of regular echinoid scratch traces (e.g., *Gnathichnus*), and instead are likely to be traces from scavenging action by fish teeth or crab claws. These could have been inflicted during either taphonomic phase.

Concluding remarks

The discovery of new fossil odontocetes from the lower Oligocene Ashley Formation of South Carolina has resulted in the description of the new species *Ankylorhiza serratidens* sp. nov., a large stem odontocete. The only known specimen of this species was collected from the Ashley Formation, which previously has produced specimens referred to *Ankylorhiza tiedemani*, suggesting that the two species were coeval. *Ankylorhiza serratidens* sp. nov. has a similar tooth count and body size as *Ankylorhiza tiedemani*, proportionally and absolutely larger postcanine teeth, and serrated teeth. While *Ankylorhiza tiedemani* is not yet known from a mandible, a larger undescribed species of *Ankylorhiza* represented by ChM 2764 and CCNHM 1075, is known from a mandible. The mandible of *Ankylorhiza serratidens* sp. nov. differs from this larger form in possessing a much longer mandibular symphysis and a narrower coronoid process. Like *Ankylorhiza tiedemani*, and unlike *Ankylorhiza serratidens*, this larger form possesses nonserrated teeth. Two or more species of *Ankylorhiza* are represented by complete to partial skulls and skeletons (e.g. CCNHM 204, CCNHM 1075, CCNHM 6857, CCNHM 6923, ChM PV 3, ChM PV 501, ChM PV 2764) that await formal study.

The holotype specimen of *Ankylorhiza serratidens* sp. nov. additionally has a number of traces indicating a long postmortem history of the specimen. Linear gouges assignable to the ichnospecies *Linichnhus bromleyi* and parallel sets of wavy gouges assignable to *Knethichnus parallelum* reflect predation and/or scavenging by sharks. Most of the bones are extensively bioeroded, and where these traces are isolated and well-preserved (rather than coalesced together), they resemble traces produced by the bone eating worm *Osedax*. Oligocene marine vertebrate remains from the Ashley and Chandler Bridge formations exhibit a high degree of *Osedax* bioerosion, unlike later Neogene fossils from the Atlantic Coastal Plain.

At least two species of *Ankylorhiza* are known from the Ashley Formation (*Ankylorhiza serratidens* sp. nov., *Ankylorhiza tiedemani*) and the overlying upper Oligocene (*Ankylorhiza tiedemani*, unnamed *Ankylorhiza* sp. nov. 1, unnamed *Ankylorhiza* sp. nov. 2). The fossil record of large odontocetes suggests considerable niche partitioning, likely mediated by differences in feeding morphology in the lower Oligocene (large, serrated teeth in *Ankylorhiza serratidens* sp. nov. vs. smaller, nonserrated teeth in *Ankylorhiza tiedemani*) and body size in the upper Oligocene (smaller body size in *Ankylorhiza tiedemani*, vs. larger body size in the unnamed *Ankylorhiza* sp. nov. 1 represented by CCNHM 1075 and ChM PV 2764). Formal description of these specimens, and other fossil odontocetes from the Oligocene sediments of Charleston, will no doubt bring further clarity to the formerly mysterious state of stem odontocete evolution and ecology in the Oligocene.

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