

Youngest record of the extinct walrus *Ontocetus emmonsii* from the Early Pleistocene of South Carolina and a review of North Atlantic walrus biochronology

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The extinct North Atlantic walrus *Ontocetus emmonsii* is widely reported from Pliocene marine deposits in the eastern USA (New Jersey, Florida), Belgium, Netherlands, Great Britain, and Morocco. *Ontocetus* was slightly larger than the modern walrus *Odobenus rosmarus*, may have had wider climatic tolerances (subtropical), and likely originated in the western North Pacific before dispersing through the Arctic. Owing to geochronologic uncertainties in the North Atlantic Plio-Pleistocene walrus record, it is unclear whether *Ontocetus* and *Odobenus* overlapped in time and thus may have competed, or whether the two were temporally separate invasions of the North Atlantic. A new specimen of *Ontocetus emmonsii* (CCNHM-1144) from the Austin Sand Pit (Ridgeville, South Carolina, USA) is a complete, well-preserved left tusk that is proximally inflated and oval in cross-section, relatively short (maximum length: 369 mm) and markedly curved (radius of arc of curvature 197 mm). Globular dentine is present, confirming assignment to Odobenini; proportions and curvature identify the specimen as *Ontocetus emmonsii* rather than *Odobenus*. Hitherto unstudied deposits in the Austin Sand Pit lack calcareous macro and microinvertebrates, but vertebrate biochronology provides some temporal resolution. The co-occurrence of a giant beaver (*Castoroides* sp.) and a snaggletooth shark (*Hemipristis serra*) indicate an age of 1.1–1.8 Ma (Early Pleistocene) and correlation with the Lower Pleistocene Waccamaw Formation. The vertebrate assemblage is named the Ridgeville Local Fauna. The composition of the marine mammal assemblage from the Austin Sand Pit is intermediate between that of the lower Pliocene Yorktown Formation (North Carolina, USA) and the modern North Atlantic fauna. This record reported here is the youngest of *Ontocetus emmonsii* from the Atlantic Coastal Plain. A review of North Atlantic Plio-Pleistocene walrus records reveals no overlap between extinct *Ontocetus* and extant *Odobenus*—suggesting independent dispersal to the North Atlantic and a lack of competition.

Key words: Mammalia, Carnivora, Odobenidae, *Ontocetus*, *Odobenus*, Pliocene, Pleistocene, North Atlantic.

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Introduction

The extinct Pliocene walrus *Ontocetus emmonsii* is a tusked walrus (family Odobenidae, tribe Odobenini) closely related to the extant walrus *Odobenus rosmarus* and the extinct eastern North Pacific toothless walrus *Valenictus* (Deméré 1994a; Kohno and Ray 2008). Unlike extant *Odobenus rosmarus*, fossils of *Ontocetus* are known from temperate

and subtropical latitudes (Kohno and Ray 2008), similar to its close relative *Valenictus* (Deméré 1994b; Boessenecker 2017). *Ontocetus* was roughly 15% larger than modern walrus (*Odobenus rosmarus*, Deméré 1994a). Relative to *Odobenus*, the tusks of *Ontocetus* are generally more curved, proportionally shorter and proximally inflated with deeper lingual furrows. *Ontocetus emmonsii* is reported from the Eastern North Atlantic Coastal Plain (New Jersey through Florida), the North Sea (Belgium, Netherlands, Great Britain) and

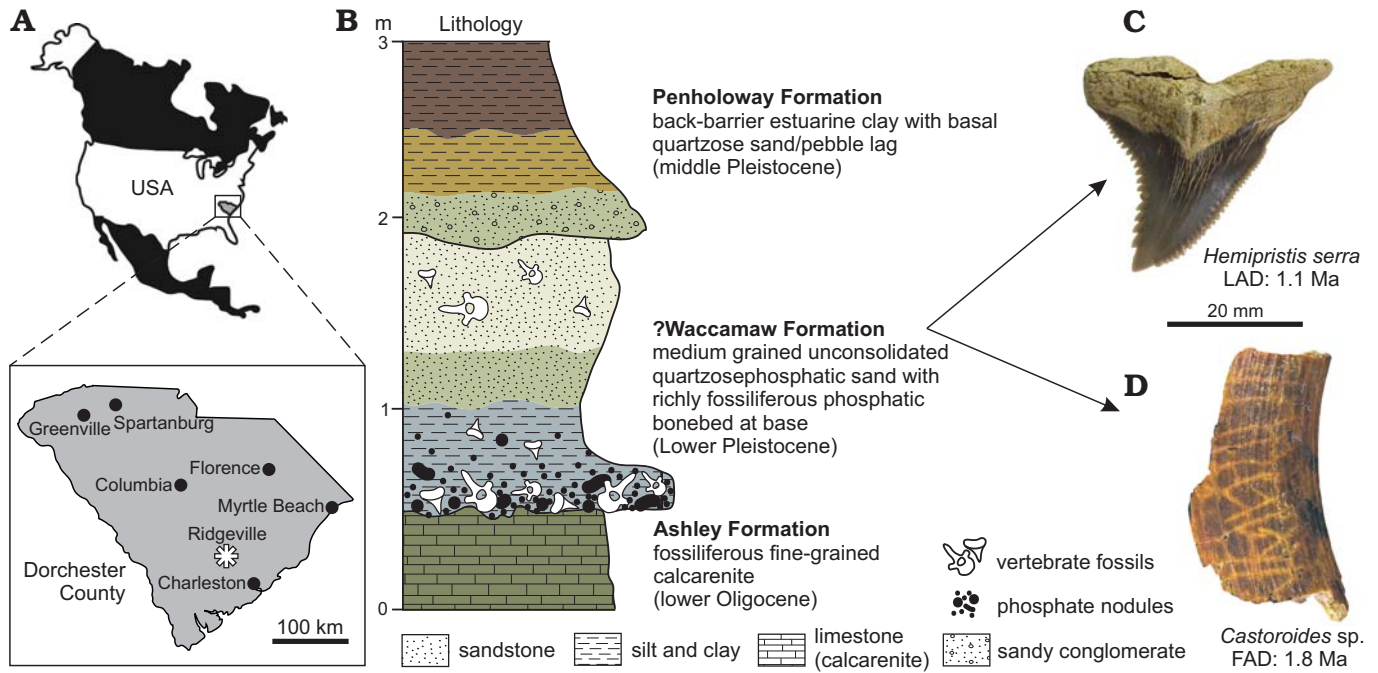


Fig. 1. **A.** Map showing the location of South Carolina and Austin Sand Pit near Ridgeville in Dorchester County (asterisked). **B.** Generalized stratigraphic column of the Austin Sand Pit with biostratigraphically significant vertebrate fossils from the ?Waccamaw Formation (**C**, **D**). Colors approximate sediments exposed in the Austin Sand Pit.

Morocco (Kohno and Ray 2008), indicating a circum North Atlantic distribution. Early studies assumed some form of ancestor-descendant relationship between *Ontocetus* and *Odobenus*, and an Atlantic origin for modern walrus, followed by a Pleistocene reinvasion of the north Pacific by the Pacific walrus subspecies *Odobenus rosmarus divergens* (Repenning and Tedford 1977; Repenning et al. 1979; Tomida 1989; Miyazaki et al. 1995). However, a new wealth of walrus fossils indicate a North Pacific center of origin for the Odobenidae (Deméré 1994a; Kohno et al. 1995a, b; Miyazaki et al. 1995), and a central American Seaway dispersal of walrus was revised by Kohno et al. (1995b) and Kohno and Ray (2008). Early Pliocene fossils from of Japan suggest a western North Pacific origin for *Ontocetus*, followed by a dispersal through the Arctic (Kohno et al. 1995b: 125, 1998). Similarly, fossils of *Odobenus* in Japan appear to predate those from the North Atlantic, suggesting a North Pacific center of origin for *Odobenus* as well (Kohno et al. 1995b). Several questions regarding Recent walrus evolution remain, including (i) when exactly did *Ontocetus* become extinct?; (ii) when did *Ontocetus* and *Odobenus* first arrive in the Atlantic?; and (iii) did *Ontocetus* and *Odobenus* overlap and compete with one another? We report a new specimen from the Austin Sand Pit in Ridgeville, South Carolina, USA and review the biochronology of the North Atlantic walrus fossil record as it pertains to these questions. Updated geochronology of walrus-bearing deposits on the Atlantic Coastal Plain invites a new hypothesis for walrus biogeography in the North Atlantic.

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

PV, Charleston Museum (vertebrate paleontology collection), USA; SC, South Carolina State Museum, Columbia, USA.

Other abbreviations.—FAD, first appearance datum; LAD, last appearance datum; NALMA, North American Land Mammal Age.

Geological setting

The Austin Sand Pit is a now-inundated sandpit in Ridgeville, Dorchester County, South Carolina, USA prospected by amateur fossil collectors in the 1990s but never seriously studied by stratigraphers or paleontologists. The Austin deposit consists of a basal bluish-gray sandy, unconsolidated silt (~60 cm thick) with a basal bone and phosphate nodule lag overlying the lower unconformable contact with the Ashley Formation (early Oligocene; Weems et al. 2014); the silty unit is overlain by an unconsolidated tan-gray medium-coarse quartzose sand (Fig. 1). A stratigraphic section was never formally recorded for the original pit while open in the 1990s. A new sand pit located 100 m to the southeast, freshly dug in 2017 has a similar stratigraphic succession for the Austin deposit, permitting re-analysis of the unit. In the new pit, it consists of a basal bluish-white clay (50-cm thick; base not exposed) overlain by a richly fossiliferous granule-pebble conglomeratic sand (20–50 cm thick) with abundant phosphate nodules and with a sharp, irregular lower contact, overlain in turn by a fine-grained white sand (~1 m thick). The Austin deposit is overlain by 2–3 m of brown-purple clay and sandy interbeds of the Penholoway Formation (Middle Pleistocene; Weems et al. 2014).

Table 1. List of fossil vertebrates from the Ridgeville Local Fauna, ?Waccamaw Formation, Austin Sand Pit, Ridgeville, South Carolina, USA.

Pisces	<i>Macrochelys</i> sp.
Chondrichthyes	Trionychidae indet.
<i>Alopias vulpinus</i>	Aves
<i>Carcharias taurus</i>	Aves indet.
<i>Carcharhinus leucas</i>	Mammalia
<i>Carcharhinus obscurus</i>	Artiodactyla
<i>Carcharodon carcharias</i>	Camelidae indet.
<i>Carcharodon hastalis</i>	Cetacea
<i>Dasyatis centroura</i>	cf. <i>Astadelphis</i>
<i>Galeocerdo cuvier</i>	<i>Balaena</i> sp., cf. <i>B. mysticetus</i>
<i>Ginglymostoma</i> sp.	<i>Balaenoptera</i> sp.
<i>Hemipristis serra</i>	<i>Balaenoptera</i> “borealina”
<i>Myliobatis</i> sp.	<i>Balaenula</i> sp.
<i>Negaprion eurybathrodon</i>	Delphinidae indet.
<i>Notorhynchus</i> sp.	<i>Eschrichtius</i> sp., cf. <i>E. robustus</i>
<i>Parotodus benedeni</i>	<i>Herpetocetus</i> sp.
<i>Rhincodon typus</i>	Kogiidae indet.
<i>Rhizoprionodon</i> sp.	cf. <i>Physeterula</i>
cf. <i>Rhynchobatos</i>	<i>Megaptera</i> sp.
<i>Squatina</i> sp.	Perissodactyla
Osteichthyes	<i>Equus</i> sp.
<i>Acipenser oxyrinchus</i>	<i>Tapirus</i> sp.
<i>Aluterus</i> sp.	Pinnipedia
<i>Chilomycterus schoepfi</i>	<i>Ontocetus emmonsi</i>
<i>Istiophorus albicans</i>	Proboscidea
cf. <i>Sciaenops</i>	cf. <i>Cuvieronius</i>
<i>Sphoeroides hyperostosus</i>	Rodentia
<i>Sphyaena</i> sp.	<i>Castoroides</i> sp.
<i>Pogonias</i> sp.	<i>Nechoerus pinkneyi</i>
<i>Prionotus</i> sp.	Xenarthra
Reptilia	<i>Eremotherium</i> sp.
Diapsida	cf. <i>Holmesina</i>
<i>Alligator</i> sp.	
Emydidae indet.	

The identity of this unit is unknown, though it overlies the Givhan's Ferry Member of the Ashley Formation (fossiliferous fine-grained calcarenite) and is overlain by the Middle Pleistocene Penholoway Formation (back-barrier estuarine clay with basal quartzose sand and pebble lag; Fig. 1). The Ashley Formation is late early Oligocene in age and dated to 26.57–29.0 Ma based on Sr isotope ratios (Weems et al. 2016); locally the Penholoway Formation is approximately 700–900 Ka in age based on calcareous nannofossils and U-Th ratios (Middle Pleistocene; Weems et al. 1994, 2014). The Austin deposit lacks calcareous micro- and macrofossils, precluding precise dating. However, some biochronological control is afforded by vertebrate fossils. A diverse assemblage of 52 taxa is recorded (Table 1) including sharks, rays, bony fish, alligators, turtles, whales, birds, dolphins, land mammals, and the walrus *Ontocetus*; we propose the name Ridgeville Local Fauna for the assemblage. A maximum age is provided by two partial incisors of giant beavers (CCNHM 1924, CCNHM 1925) identifiable as *Castoroides* sp. owing to well-developed longitudinal grooves and ridges in the incisor enamel. *Castoroides* has a first appearance datum (FAD) of 1.8 Ma in the Bermont Formation at Leisey Shell Pits 1 and 3 in Florida (Morgan and Hulbert 1995; Bell et al. 2004; Morgan 2005), indicating

correlation with the early Irvingtonian North American Land Mammal Age (NALMA). A minimum age is provided by teeth of the snaggletooth shark *Hemipristis serra* (CCNHM 1926, ChM PV 5132, ChM PV 5135, ChM PV 5136, ChM PV 5178), which is known from upper Oligocene through Pleistocene deposits of the Atlantic Coastal Plain (Cicimurri and Knight 2009; Scudder et al. 1995). The last appearance datum (LAD) of *Hemipristis serra* is 1.1 Ma, based on the minimum age of strata within the Leisey Shell Pit (pits 1A and 3B) of Florida, the youngest known occurrence for this species (Morgan and Hulbert 1995: 30; Scudder et al. 1995: 266–267). The FAD of *Castoroides* in concert with the LAD of *Hemipristis serra* constrains the age of the fossiliferous deposit in the Austin Sand Pit to 1.1–1.8 Ma (Early Pleistocene, Irvingtonian NALMA correlative). The deposit is too young to be mapped as either the Pliocene Raysor Formation (3.1–3.6 Ma; Tseng and Geisler 2016, and references therein) or the Goose Creek Limestone (3.1–3.6 Ma; Tseng and Geisler 2016, and references therein). Further, both the Raysor Formation and Goose Creek Limestone are highly calcareous and fossiliferous; this deposit entirely lacks calcareous microfossils and macroinvertebrates. The Austin deposit is best tentatively identified as the Pliocene Pleistocene Waccamaw Formation, which is mapped nearby

(Weems et al. 2014) and reported from auger holes 4.5 km to the northeast (= auger hole RI-6 of Weems et al. 1987, 1994). Further northeast, the Waccamaw Formation is preliminarily dated to earliest Pleistocene (1.55–2.8 Ma) based on $^{86}\text{Sr}/^{87}\text{Sr}$ ratios from exposures in southeastern North Carolina (MacGregor et al. 2011).

Another locality that may be related to the Austin Sand Pit is the Walrus Ditch Local Fauna (Fields et al. 2012), a locality 20 km southwest in Summerville, South Carolina, USA which has yielded a large vertebrate assemblage including *Otocetus emmonsi* (Kohn and Ray 2008) and terrestrial mammals (Fields et al. 2012). Biochronologically significant land mammals include the horse *Nannipus* and the porcupine *Erethizon*, constraining the age to 2.6–2.2 Ma (Fields et al. 2012: 8); this led Fields et al. (2012) to identify the Walrus Ditch Local Fauna as occurring within the Waccamaw Formation. The deposit in the Austin Sand Pit is entirely younger than the Walrus Ditch deposit, and it is possible that the Walrus Ditch deposit may represent the lower Waccamaw and the Austin deposit may represent the upper Waccamaw. Further geologic and paleontologic studies of the newly excavated pit will permit further observations on the stratigraphy, taphonomy, and paleontology of the ?Waccamaw Formation.

Chronostratigraphic framework, subdivision of the Pleistocene, and the definition of the Pliocene–Pleistocene boundary follows Gradstein et al. (2012).

Systematic palaeontology

Mammalia Linnaeus, 1758

Carnivora Bowditch, 1821

Pinnipedia Illiger, 1811

Odobenidae Allen, 1880

Odobeninae Mitchell, 1968

Odobenini Deméré, 1994

Genus *Otocetus* Leidy, 1858

Type species: Otocetus emmonsi Leidy, 1859; Yorktown Formation, North Carolina, Pliocene.

Otocetus emmonsi Leidy, 1858

Fig. 2.

Material.—CCNHM 1144, a complete left canine, collected by Matthew Swilp (Shamokin, Pennsylvania, USA) in the 1990s from the ?Waccamaw Formation exposed in the now-inundated Austin sand pit, Ridgeville, South Carolina, USA. A second tusk of *Otocetus emmonsi* (SC 98.51.1) was referred by Kohn and Ray (2008) but not figured or described and is not considered further in this study.

Description.—CCNHM-1144 is a complete, well-preserved left canine (linear length 369 mm; anterior curvilinear length 345 mm; posterior curvilinear length 477 mm), which is markedly curved posteriorly (radius of arc of curvature

197 mm; Fig. 3). The tusk evenly tapers distally and bears a blunt tip with a posterolingual oval-shaped wear facet (35 mm long and 19 mm wide). Though expected, there is no obvious dentine exposed in the wear facet. The tusk is oval in cross-section and compressed transversely (transverse basal diameter 67 mm; anteroposterior basal diameter 90 mm). Two deep longitudinal furrows are present labially, the posterior furrow being slightly deeper and extending further distally; these furrows become diffuse distally, and terminate 54 mm from the apex. Though mostly curved in the parasagittal plane, the tusk is slightly twisted about its longitudinal axis from proximal to distal so that the tip is rotated and slightly reverted lingually. Longitudinal furrows are also present lingually, though they are diffuse and less deeply incised, terminating only 239 mm from the apex. The position of the gum line is unclear. However, subparallel anteroposterior scratches are present lingually but are absent from the proximal 150 mm of the tusk. If these were produced in vivo (e.g., sediment abrasion during benthic feeding) it would suggest the gum line was positioned at about 150 mm from the proximal end of the tusk. External annular growth rings are not visible under low angle light.

The pulp cavity is open and forms the widest part of the tusk, indicating continuous growth. The shape of the pulp cavity is oval, and the depth is 82 mm; the globular orthodentine core is developed within as a proximally tapering cone. Individual bead-like dentine globules are visible proximally within the pulp cavity, confirming assignment of CCNHM 1144 to *Odobenini* (Deméré 1994a).

The tusk lacks evidence of post-mortem abrasion; irregular, circular-oval crater-like pits (2–16 mm diameter, 0.7–1 mm deep) are evenly distributed proximo-distally along the tusk and several occur inside the pulp cavity. Pitting is more common on the labial side and often coalesced so that large areas are missing cementum. The margins of the pits are smooth and lack evidence of fracturing, resembling enamel cupping reported in dolphin teeth by Loch et al. (2013).

Remarks.—CCNHM 1144 is identifiable as *Otocetus emmonsi* owing to its strong curvature, marked distal tapering, transverse compression, and deeply incised longitudinal furrows (Kohn and Ray 2008: 45). This specimen has a transverse width:anteroposterior diameter ratio of 0.74, which is relatively wide for *Otocetus emmonsi* (Fig. 3). However, the deeply incised labial grooves and small radius of the arc of curvature (Fig. 3) clearly differentiate this specimen from *Valenictus* (Deméré 1994b) and *Odobenus* (Kohn and Ray 2008), and are characteristic features identifying this specimen as *Otocetus emmonsi*.

North Atlantic walrus biochronology

A review of fossil occurrences and available stratigraphic literature was implemented to evaluate the exact chronol-

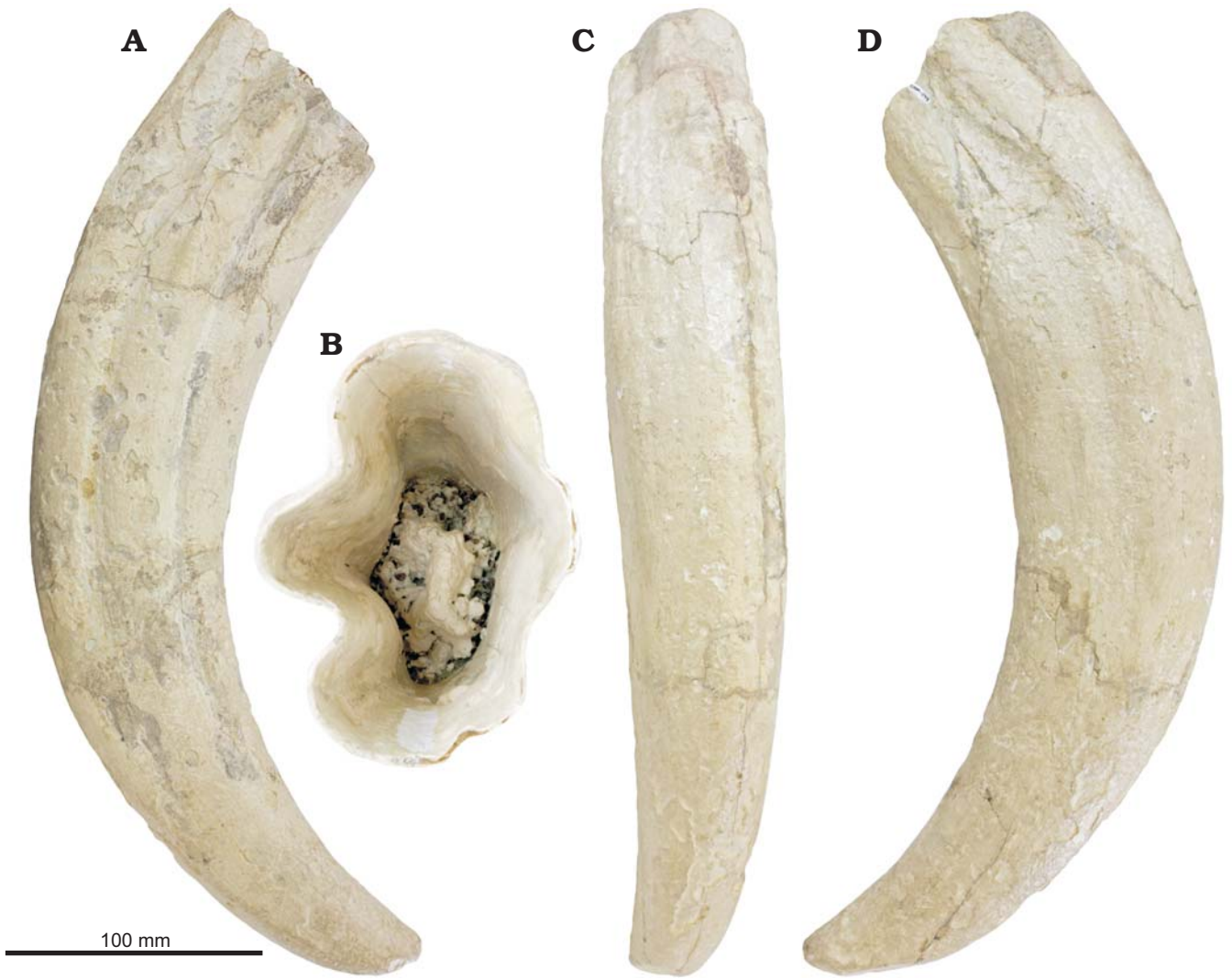


Fig. 2. Right canine tusk of odobenid walrus *Ontocetus emmonsi* (CCNHM 1144) from the Lower Pleistocene ?Waccamaw Formation, Austin Sand Pit, South Carolina, in lingual (A), proximal (B), anterior (C), and labial (D) views.

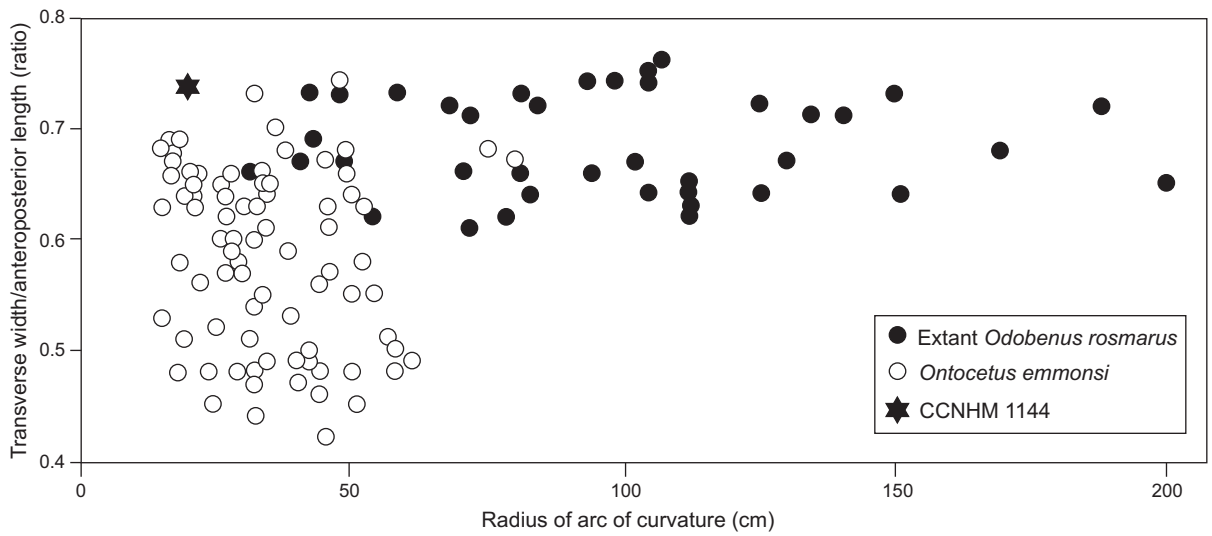


Fig. 3. Scatterplot of ratio of proximal transverse width/anteroposterior length versus radius of the arc of curvature for tusks of *Odobenus* and *Ontocetus*, including CCNHM 1144. Original plot modified from Kohno and Ray (2008: fig. 27).

ogy of walruses in the North Atlantic. This review emphasized specimens identifiable to *Ontocetus* or *Odobenus* and ignored specimens identifiable only to the subfamily Odobeninae or tribe Odobenini. In many cases, fossil occurrences were reported long before formal stratigraphic study commenced, were reported without provenance, or were specimens discovered ex situ and thus isolated from geological context (see discussions in Ray 1960, 1975; Kohno and Ray 2008). Rather than rely on outdated age data published in the original articles reporting walrus specimens, in all cases where specimens were reported with stratigraphic provenance, the most current literature on the stratigraphy and geochronology of these strata was used to compile geochronologic ranges for each occurrence (e.g., Parham et al. 2012: 350–352).

The majority of *Ontocetus* specimens from the Atlantic Coastal Plain were collected from the Yorktown Formation (lower Pliocene) of North Carolina and Virginia (Berry and Gregory 1906; Kohno and Ray 2008). The geochronologically earliest *Ontocetus* are reported from the Bone Valley Formation (Palmetto Fauna, Mio-Pliocene) in Florida Morgan (1994). The geochronologically latest appearance of *Ontocetus* is reported from the ?Waccamaw Formation at the Austin Sand Pit (Ridgeville Local Fauna), dating to 1.8–1.1 Ma (this study).

This new specimen and the biochronologic dating of the ?Waccamaw Formation, in concert with updated dates for the Palmetto Fauna, provides an updated maximum geochronologic range for *Ontocetus emmonsi* of 5.8–1.1 Ma. Our survey of published record of *Odobenus* failed to identify any reliable fossil records of the extant genus before the late Middle Pleistocene in the North Atlantic. An *Odobenus*-like mandible from the “Scaldisian sands” (= Lillo Formation) was referred to *Odobenus koninckii* by Van Beneden (1877), possibly representing a Pliocene occurrence of *Odobenus* in the Atlantic (Deméré, 1994a). However, recognition of a singular Pliocene Atlantic occurrence awaits redescription and stratigraphic reassessment of this specimen. All specimens with reliable stratigraphic provenance are a maximum of 0.24 Ma (Marine isotope stage 7), supporting the conclusion of Kohno and Ray (2008: 63) that no walruses are known from the Middle Pleistocene of the Atlantic basin. Despite the range extension for *Ontocetus*, there is a nearly 1 Ma gap between the *Ontocetus* LAD (1.1 Ma) and the *Odobenus* FAD (0.24 Ma) in the North Atlantic (Fig. 4).

Discussion

The marine mammal assemblage of the ?Waccamaw Formation at the Austin Sand Pit (Table 1) is notable in that the taxonomic composition is intermediate between the lower Pliocene Yorktown Formation (e.g., *Ontocetus emmonsi*, Kogiidae gen. nov., cf. *Kogiopsis*, *Balaenula* sp., *Balaenoptera* sp., “*Balaenoptera*” *borealina*, *Herpetocetus*

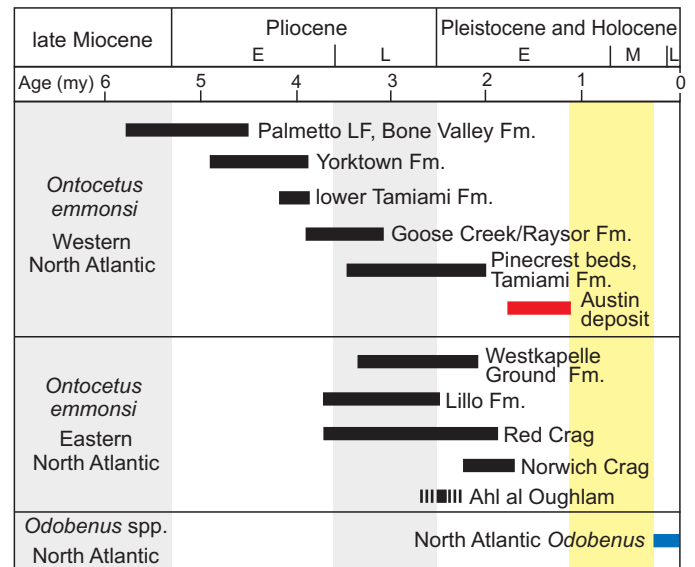


Fig. 4. Biochronology of the walruses *Ontocetus* and *Odobenus* in the North Atlantic basin. Yellow vertical bar denotes temporal gap between the last occurrence of *Ontocetus* and the first occurrence of *Odobenus* in the North Atlantic. See SOM 1, 2 (Supplementary Online Material available at http://app.pan.pl/SOM/app63-Boessenecker_etal_SOM.pdf) for discussion of the geochronologic age of each occurrence. Abbreviations: E, early; L, late; M, middle.

sp.; Kohno and Ray 2008; Whitmore and Barnes 2008; Whitmore and Kaltenbach 2008) and the modern fauna (*Eschrichtius* sp., *Megaptera* sp.). Cf. *Astadelphis* sp. is preliminarily recorded from the Plio-Pleistocene ?Waccamaw Formation, a first for North America; *Astadelphis* has been previously reported only from the late Pliocene (Piacenzian) of Italy (Bianucci 1996). Additional petrosals of cf. *Astadelphis* (CCNHM 1908) have also been collected ex situ from Folly Beach, South Carolina, USA likely originating from the Pliocene Goose Creek Limestone. Further study of this chronologically unique marine mammal assemblage may shed light on the emergence of the modern marine mammal fauna (e.g., Whitmore 1994; Boessenecker 2013).

CCNHM 1144 is now the youngest record of *Ontocetus* worldwide. Despite the range extension of *Ontocetus* to the Early Pleistocene, the available fossil record indicates *Ontocetus* and *Odobenus* are separated by 0.9 Ma (Fig. 4). Similarly, in the western North Pacific *Ontocetus* and *Odobenus* are not contemporaneous; *Ontocetus* has a LAD of 3.6 Ma (Kohno et al. 1998; Kimura et al. 2007) and *Odobenus* has a FAD of 2.7 Ma (Kohno et al. 1995b) and are separated by approximately 1 my (Kohno et al. 1995b, 1998). We hypothesize that *Odobenus* and *Ontocetus* represent independent (early Pliocene, Late Pleistocene, respectively) dispersals of tusked walruses (Odobenini) into the North Atlantic from the North Pacific, and did not directly compete in either ocean basin according to present biochronologic evidence.

The FAD of *Ontocetus* in the Atlantic basin is from the Palmetto Fauna of the Bone Valley Formation (Morgan 1994; Kohno and Ray 2008). Land mammals from the

Palmetto Fauna correspond with the latest Hemphillian (Hh4) NALMA (Wallace and Hulbert 2013), indicating an age of 5.8–4.6 Ma (Tedford et al. 2004). Because this does not significantly predate the opening of the Bering Strait (5.4–5.5 Ma; Gladenkov et al. 2002), *Ontocetus* most likely dispersed through the Arctic (Kohno et al. 1995b; Kohno and Ray 2008).

We hypothesize that *Ontocetus* and *Odobenus* were completely temporally disjunct within the Atlantic basin, but note that the Middle Pleistocene record is likely incomplete, and similarly note an equivalent 1 my gap between the two lineages in the western North Pacific record (e.g., Kohno et al. 1995b, 1998; Miyazaki et al. 1995). Few fossils of *Odobenus* exist from high latitudes, suggesting either collection bias or perhaps suggesting that *Odobenus* was not cold-adapted until geologically recent times. The earliest high-latitude fossil occurrences of *Odobenus* date to the latest Middle Pleistocene (~127 Ka) of Amchitka Island, Alaska, USA associated with a cold temperate foraminiferal assemblage (Whitmore and Gard 1977). This occurrence notably post-dates specimens from Virginia, indicating an earlier trans-Arctic dispersal (Fig. 4). Furthermore, dispersal may have taken place entirely during interglacial periods. We note that at present, the majority of the fossil record of *Odobenus* is associated with ice-free regions. This fact, in concert with evidence of temperate latitude haulout and breeding sites as recent as the 18th century (McLeod et al. 2014) may have implications for of modern walrus conservation as several populations are being affected by rapid loss of sea ice driven by warming climate (Laidre et al. 2008). More field exploration of Pliocene–Middle Pleistocene fossil localities within the Arctic Circle (e.g., Gubik Formation, Alaska) with special attention towards walrus fossils and associated paleoclimatic indicators is necessary to further evaluate the timing of dispersal and timing of cold climate adaptation within the *Odobenus* lineage.

Conclusions

We report a new specimen of *Ontocetus emmonsii* from a previously unstudied vertebrate fossil assemblage from the Austin Sand Pit in Ridgeville, South Carolina, consisting of a complete, well-preserved tusk. The large size, curvature, labial grooves, and narrow cross-section indicate it is the extinct walrus *Ontocetus* rather than extant *Odobenus*. A brief stratigraphic description of the unstudied deposit is provided, and the rich vertebrate assemblage (52 taxa) is herein named the Ridgeville Local Fauna. Biochronologically significant vertebrate fossils from the locality, namely the giant beaver *Castoroides* sp. and the snaggletooth shark *Hemipristis serra*, constrain the age of the deposit to 1.8–1.1 Ma (latest Pliocene to Early Pleistocene), permitting correlation of the deposit at the Austin Sand Pit with the Waccamaw Formation. This is the youngest record of *Ontocetus emmonsii*. A comprehensive survey of up to date stratigraphic

literature for walrus-bearing deposits in the North Atlantic found a range of 5.8–1.1 Ma for *Ontocetus emmonsii* and also indicates that no Atlantic fossil occurrences of *Odobenus* are older than 244 Ka. Given available evidence, *Odobenus* and *Ontocetus* were temporally separated in the North Atlantic for approximately 1 my and thus did not compete for resources and reflect separate early Pliocene (*Ontocetus*) and Middle–Late Pleistocene (*Odobenus*) arctic dispersals into the North Atlantic from the North Pacific rather than in-situ evolution. Further study of Plio-Pleistocene walrus biogeography may shed light on contemporary environmental pressures faced by walruses owing to the rapidly warming Arctic climate.

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