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New species of *Ontocetus* (Pinnipedia: Odobenidae) from the Lower Pleistocene of the North Atlantic shows similar feeding adaptation independent to the extant walrus (*Odobenus rosmarus*)

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Ontocetus is one of the most notable extinct odobenine owing to its global distribution in the Northern Hemisphere. Originating in the Late Miocene of the western North Pacific, this lineage quickly spread out to the Atlantic Ocean during the Pliocene, with notable occurrences in England, Belgium, The Netherlands, Morocco and the eastern seaboard of the United States.

Reassessment of a pair of mandibles from the Lower Pleistocene of Norwich (Great Britain) and a mandible from the Upper Pliocene of Antwerp (Belgium) that were recognized as a species of the genus *Ontocetus* reveals existences of features of both *Ontocetus* and *Odobenus*. The presence of four post-canine teeth, a lower canine larger than the cheek-teeth and a lower incisor confirms the assignment to *Ontocetus*; simultaneously, characteristics such as a fused mandible, a shorter mandibular symphysis, a well-curved mandibular arch and ~~very~~ thin septa between teeth align with traits usually found in *Odobenus*. Based on a combination of these characters, we describe *Ontocetus posti*, sp. nov. Its mandibular anatomy suggests a better adaptation to suction-feeding than what was previously described in the genus suggesting that *Ontocetus posti* sp. nov. likely occupied a similar ecological niche to the extant walrus *Odobenus rosmarus*.

Originating from the North Pacific Ocean, *Ontocetus* dispersed via the Central American Seaway. Although initially discovered in the Early Pliocene deposits of thewestern North Atlantic, *Ontocetus* also left its imprint in the North Sea basin and Moroccan Plio-Pleistocene deposits. The closure of the Isthmus of Panama during the Mio-Pliocene boundary significantly impacted the contemporary climate, inducing global cooling. This event constrained *Ontocetus posti* in the North Sea basin leaving the taxa unable to endure the abrupt climate changes of the Early Pleistocene, ultimately going extinct before the arrival of the extant counterpart, *Odobenus rosmarus*.

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Abstract

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Keywords: *Ontocetus*, Pliocene, United Kingdom, Belgium, *Odobenus*, mandibles, Pleistocene, suction-feeding.

Introduction

The walrus (*Odobenus rosmarus*) stands as one of the most iconic mammals of the Arctic, distinguished from all other pinnipeds by its immense size and prominent tusks (Fay, 1982). The walruses is one of the largest extant Carnivora, males of this species weighing up to 2.5 tons with an average length of 3 meters. Walruses inhabit shallow, cold Arctic waters and males form small harems during the breeding season (Wiig et al. 2007).

Their primary diet consists of bivalve molluscs such as clams (*Ruditapes decussatus* or *Arctica islandica*) that they capture using a unique "suction-feeding" technique, utilizing lips, tongue, and arched palate as a piston to extract mollusk flesh (Fay, 1982; Kastelein and Gerrits, 1990; Kastelein et al., 1991). Emblematic anatomical characteristics of this feeding adaptation include the displacement of the upper incisors that have shifted laterally and adjacent to the upper canines, while the lower incisors have disappeared.

As the sole extant member of the family Odobenidae, walruses represent a lineage with notable diversity, particularly in the fossil record within the pinnipeds (Boessenecker and Churchill, 2021). While extant walruses predominantly inhabit the Arctic, their extinct relatives once occupied temperate and subtropical latitudes (Repenning and Tedford, 1977; Deméré, 1994a, b; Kohno, 1994; Miyazaki et al., 1995; Boessenecker, 2013a; Boessenecker, 2017; Magallanes et al., 2018).

Originating in the North Pacific, tusked walruses (Odobenini sensu Deméré 1994b) later dispersed to the North Atlantic, likely during Miocene-Pliocene transition (Barnes and Perry, 1989; Horikawa, 1995; Kohno et al., 1995, 1998; Boessenecker, 2017). The Odobenini comprises several fossil taxa, including poorly known ones like *Pliopedia pacifica* from the upper Miocene-Lower Pliocene deposits of California (Kellogg, 1921; Repenning and Tedford, 1977) and *Protodobenus japonicus* from Lower Pliocene formations in Japan (Horikawa, 1995; Magallanes et al., 2018), along with the highly specialized suction-feeder *Valenictus* Mitchell, 1961 with *V. chulavistensis* from the Upper Miocene-Lower Pleistocene of California (Deméré, 1994a; Boessenecler et al. 2013; Boessenecker, 2017).

Within the Odobenini, *Ontocetus* is the tusked walrus with the richest fossil record and geographically-wide distribution in the Northern Hemisphere (Boessenecker and Churchill, 2021). Over nearly a century and a half, *Ontocetus* has been a subject of controversy (Kohno and Ray, 2008). With its oldest fossil record tracked back to the Miocene/Pliocene boundary age of Japan (Okamoto and Kohno, 2019), indicating a North Pacific origin, *Ontocetus* dispersed around the Mio-Pliocene boundary, to the Atlantic Ocean through the Central American Seaway (Repenning et al., 1979; Kohno et al., 1995; Kohno et al., 1998; Okamoto and Kohno, 2019). A large amount of specimens have been discovered in younger deposits along the east coast of the United States (e.g. Leidy, 1859; Berry and Gregory, 1906; Ray, 1960; Morgan, 1994; Kohno and Ray, 2008; Boessenecker et al., 2018), in the North Sea basin such as England (e.g. Lankester, 1880, 1882; Newton, 1882, 1891), Belgium ((e.g. du Bus, 1867; van Beneden 1871, 1877; Hasse

1909, 1911; Rutten 1907; Misonne, 1958) or The Netherlands (e.g. van Deinse, 1944; van der Feen, 1968; Erdbrink and van Bree, 1990, 1999a, b, c) but also in Morocco (Geraads, 1997), mainly represented by isolated upper canines although a few dozen skulls, humeri, and mandibles have been discovered all over the Northern Hemisphere. In the past, a total of five genera and eight species of Plio-Pleistocene *Ontocetus*-like walruses from the North Atlantic and North Sea have been described: *Ontocetus emmonsi* Leidy 1859, *Trichecodon huxleyi* Lankester 1865, *Alachtherium cretsii* du Bus 1867, *Trichecodon koninckii* van Beneden 1871, *Prorosmarus alleni* Berry and Gregory 1906, *Trichechus antverpiensis* Rutten 1907, *A. antwerpiensis* Hasse 1909, *A. africanum* Geraads 1997. More recently, some specimens were discovered in Japan and described although no species name was attributed to those remains which includes tusks, skulls and appendicular elements (Yasuno, 1988; Kohno et al., 1995, 1998; Okamoto and Kohno, 2019). A key challenge has been the definition of these species based on disparate skeletal elements by the different authors (e.g. crania, humeri or tusks) (Hasse, 1911; Ray, 1960, 1975; Erdbrink and van Bree, 1986, 1990; Post, 2004; Boessenecker et al., 2018). A 2008 review by Kohno and Ray focused on North Atlantic fossil material from the Pliocene formations, concluded that all the specimens from the North Sea were thought to belong in the ontogenetic and sexual variation of *Ontocetus emmonsi* Leidy 1859 from the east coast of North America.

Ontocetus did not coexist with the genus *Odobenus* at least in the North Atlantic (Boessenecker et al., 2018), and did not share a direct common ancestor (Deméré, 1994b; Magallanes et al. 2018). *Odobenus* arrived in the North Atlantic not earlier than 244 Ka according to fossil occurrences (Sanders, 2002), while the last population of *Ontocetus* became extinct during Early Pleistocene (1.8 – 1.1 Ma) based on the record of the fossil from South Carolina, USA (Boessenecker et al., 2018). The factors behind the disappearance of *Ontocetus* from the North

Atlantic remain poorly understood, but given the temporal separation from *Odobenus,* competition between these two genera can be excluded.

The present study focuses on the re-evaluation of a pair of mandibles from the Lower Pliocene of Norwich, Great Britain and a mandible from the Upper Pliocene of Antwerp, Belgium at least the latter was historically reported under different taxonomic names (*Trichecodon koninckii* by van Beneden, 1877; *Odobenus koninckii* by Deméré, 1994b), but these names have been discarded as *nomen nodum* or *nomen dubium* (e.g., Rutten, 1907; van der Feen, 1968; Kohno and Ray, 2008). Using these materials, we aim (1) to re-evaluate two newly discovered mandibles from the Upper Pliocene of Belgium and the Lower Pleistocene of the United Kingdom and The Netherlands; (2) to discuss the paleoecology of *Ontocetus* concerning the vacant niche in the absence of *Odobenus*; and (3) to contextualize the extinction of *Ontocetus* in relation to climate changes during the Early Pleistocene.

Material and Methods

Institutional abbreviations

IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

NMNS, National Museum of Nature and Science, Tsukuba, Japan;

NMR, Natuurhistorisch Museum Rotterdam, Rotterdam, The Netherlands;

NWHCM, Norwich Castle Museum, Norfolk Museums and Archaeology Service, Norfolk, England, U.K;

USNM V, Paleobiology collections, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.

Methods

The original specimen (NWHCM 1996.1) was photographed by the last author on June 29, 2000 at the Norwich Castle Museum (NWHCM). The cast (NMR7472) was photographed by the senior author on March 3, 2020 at the Institut Royal des Sciences Naturelles de Belgique (IRSNB). Both mandibles (NMR7472, IRSNB M156) were taken via a Nikon D800E with AF-Nikkor 50mm F1.8 lens and a Panasonic Lumix G1 with Olympus 14-42mm lens. The figures were performed in Adobe Photoshop CS6 and Adobe Illustrator CS6. The anatomical terminology used in the present study follows Deméré (1994a, 1994b), Kryukova (2012), Boessenecker and Churchill (2013), Velez-Juarbe (2017) and Magallanes et al. (2018) for the walrus and Evans & deLahunta (2013) for the domestic dog, as a representative for the (caniform) Carnivora. Terminologies for the mandibular teeth have been abbreviated (incisors = i, canine = c, premolars = p, first premolar = p1, second premolar = p2, third premolar = p3, fourth premolar = p4, molars = m). Terminologies for the musculature and inference of muscle insertions (areas) are inspired by Valentin (1990), Kastelein et al. (1991), Lavergne et al. (1996), Naples et al. (2011), Tseng et al. (2011).

This study includes the following morphological measurements.: the minimum mandible thickness (MT) and the least mandible depth (MD), following Wiig et al. (2007). The MT is the minimum transverse thickness of the mandible posterior to the last postcanine, The MD is the minimal vertical height of the mandible posterior to the last post-canine. MT and MD have been measured using a digital caliper with an accuracy of 0.01 mm. Five angular measurements have also been taken, following Mohr (1942), Deméré (1994a) and showing in Boisville et al. (2022): angle between (a) the anterior and dorsal margin; (b) the anterior and ventral margins; (c) the ventral and dorsal margins; (d) the medial edge of the condyle and the mandibular symphysis; e) the lateral edge of the mandibular terminus and the symphysis; f) the horizontal and vertical rami; and g) the coronoid process and the mandibular condyle. Other mandibular and tooth measurements follow Erdbrink and van Bree (1986, 1990), Deméré (1994b), Kohno and Ray (2008) and Magallanes et al. (2018). All measurements are provided as supplemental information (Supplemental Table S1).

Results

Systematic Paleontology

Mammalia Linnaeus, 1758
Carnivora Bowdich, 1821
Pinnipedia Illiger, 1811
Odobenidae Allen, 1880

Odobeninae Mitchell, 1968

Odobenini Deméré, 1994b

Genus *Ontocetus* Leidy, 1859

Type species: *Ontocetus emmonsi* Leidy, 1859; Yorktown Formation, North Carolina, Pliocene

Ontocetus posti sp. nov.

Trichecodon huxleyi (in part) Lankester, 1865

Trichecodon koninckii (in part) van Beneden, 1877

Trichecodon huxleyi (in part) Kellogg, 1922

Odobenus huxleyi (in part) Hooijer, 1957

Odobenus koninckii (in part) Déméré, 1994b

Ontocetus emmonsi (in part) Kohno and Ray, 2008

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Diagnosis

A species of *Ontocetus* that exhibits mosaic characters including some shared traits with the genus *Odobenus*. These diagnostic features of *Ontocetus* comprise a lower canine markedly larger and distinctly separated from the cheek toothrow, presence of the first premolar (p1), specifically four postcanine cheek teeth (p1-p4), a broad and short edentulous mandibular terminus exhibiting incisors, an elevated and slanted anterior margin, its relative size, a high, thin, and posterolaterally projected coronoid process, as well as a short distance between the dorsal margin and coronoid process.

This species also shares certain characteristics with *Odobenus,* such as the fusion of the mandible, a mandibular symphysis less elongated and oval in shape, a mandibular symphysis shorter in proportion to the total length of the mandible, a horizontal ramus with laterally a well-curved occlusal outline, accounting for shortening of the rostrum. Additionally, a space between the canine and the cheek teeth can be observed, as well as between the ~~very~~ thin cheek tooth alveoli themselves. Other shared traits encompass an underdeveloped angular process, and a flat, less developed mandibular condyle.

Etymology

The species is named in honor of Mr. Klaas Post, curator of Vertebrate Paleontology at Natuurhistorisch Museum Rotterdam, in recognition of his extensive contributions to geology and paleontology in the North Sea district, and as a token of appreciation for his continuous support, encouragement, and invaluable assistance provided to all of us throughout this study.

Holotype

NWHCM 1996.1, complete pair of mandibles of an adult male individual, collected by Ian James Cruickshanks and Allister Cruickshanks on February 15th 1993, from the sandstone layer cropped out on the South Cliff at Easton Bavents, Suffolk County, East Anglia, England (Figure 1). The plastoholotype is deposited as NMR 7472 and NMNS-PV 23873.

Formation and age

The Easton Bavents cliff comprises marine sands containing fossil shells and mammal bones, discovered at beach level or just beneath it (Holt-Wilson, 2015). The sandstone layer of the South Cliff site that produced the holotype corresponds to the base of the Norwich Crag Formation (Holt-Wilson, 2015) (Figure 1). An age of 2.2-1.7 Ma is assigned to the Norwich Crag Formation, corresponding to the Early Pleistocene (Funnell and West, 1962; Daley and Balson, 1999; Westerhoff, 2008; Wood et al., 2009; Holt-Wilson, 2015; Boessenecker et al., 2018). This age is concurrent with the Dutch Tiglian Stage within the Norwich Crag Formation (Wersterhoff, 2009; Holt-Wilson, 2015; King, 2016), representing a temperate climatic period known as the Antian-Bramertonian, approximately two million years ago. The sandstone layer where NWHCM 1996.1 was discovered has also yielded remains of fossil mammals washed out to sea, including falconer's deer *Eucladoceros falconeri*, giant beaver *Trogontherium* sp., robust horse *Equus robustus* and proboscideans (*Mammuthus meridionalis* and *Anancus arvernensis)*. Some other marine mammals like cetaceans (killer whale *Orca* and dolphins) have also been discovered (Holt-Wilson, 2015).

Referred specimen

IRSNB M156, partial left mandible from an adult male individual, featuring a fused anteromedial wall of the mandibular symphysis (Supplemental Figure S1), collected from Antwerp, Belgium (van Beneden, 1876, 1877; Deméré 1994b; Kohno and Ray, 2008; Boessenecker et al., 2018). Benthic foramina indicate correlation with zone NS44 and diatoms indicate correlation with zone DP2, providing an age of 3.71 – 2.5 Ma (late Pliocene) (De Schepper et al., 2009; King, 2016). The exact locality of the specimen remains unclear, as van Beneden (1876) only mentioned various locations (Deurne district, Seefhoek district but also Fort I from Wyneghem district) all belonging to Antwerp Basin, Belgium. IRSNB M156 was initially described as a referred specimen of *Trichecodon koninckii* by van Beneden (1877), it was subsequently assigned to *Odobenus koninckii* (Déméré, 1994b) and eventually included in the hypodigm of *Ontocetus emmonsi* (Kohno and Ray, 2008).

RGM.St.119589, an incomplete fused mandible representing only the symphysis portion, is assigned to an adult female individual (Supplemental Figure S1). RGM.St.119589 was collected at the bridgehead near Domburg, Walcheren, Zeeland (The Netherlands). Marine mammals collected from the seafloor, rivers, and estuaries in the vicinity of the mouth of the river Scheldt are likely derived from the Westkapelle/Brielle Ground Formation (Post and Boesselaers, 2005; Boessenecker et al., 2018). The Westkapelle/Brielle Ground Formation is Reuverian, corresponding to an age of 3.4 - 2.1 Ma (King, 2016; Boessenecker et al., 2018). The specimen was assigned to *Odobenus huxleyi* (Hooijer, 1957) with Lankester's mention, corresponding to *Trichecodon huxleyi* (1865).

Remarks

The taxonomic history of *Trichecodon koninckii* is characterized by differing interpretations. Initially proposed by van Beneden (1871) based on a fragment of the left upper canine (original lost, but plastoholotype IRSNB 2892 survives) collected from the "Scaldisian sands" of Antwerp, Belgium, van Beneden (1877) later added a fragmentary mandible IRSNB M156 to this species as mentioned above. However, the original holotype, being a fragmentary tusk, lacks diagnostic character(s) for species-level identification. Rutten (1907) and van der Feen (1968) therefore dismissed *T. koninckii* as a nomen nudum due to this limitation. In contrast, Déméré (1994b) retained this species under the genus *Odobenus* based on the morphological characters of IRSNB M156. Kohno and Ray (2008) took a different approach, not following Deméré (1994a); instead, they included this referred mandible in the hypodigm of *Ontocetus emmonsi,* designating "*koninckii*" as a nomen dubium solely for the holotype tusk. In this study, we refrain from adopting either taxonomic stance for *Trichecodon koninckii* and IRSNB M156. This decision is motivated by the need to avoid confusion in species-level taxonomy and acknowledge the morphological disparities and diversification evident in the Pliocene of North Sea. *Trichecodon huxleyi*, originally proposed by Lankester (1865) based on several fragmentary tusks from the Upper Pliocene deposits (Red Crag) in Suffolk, England. Deméré (1994b) retained this species under the genus *Odobenus* with *Odobenus huxleyi* based on cementum and outer orthodentine layer thinner than those of *Odobenus rosmarus*. Kohno and Ray (2008) considered it as synonymy of *Ontocetus emmonsi* only for the tusks.

Description

Mandible – NWHCM 1996.1 is an almost complete pair of mandibles (296.8 mm anteroposterior length, 67.2 mm transverse width at c1; see Table S1) (Figure 2 - Figure 5). The mandibular symphysis is fused, vascularized, particularly thicker anterodorsally and slightly thinner posteroventrally (49 mm symphysis length, 86.1 mm symphysis height) with a ratio reaching 1.75. In medial view, the mandibular symphysis is oval in shape and occupies approximately 29% of the maximum length of the mandible. In occlusal view, the lateral edge of the mandibular terminus and the symphysis form an angle of about 30° (see Angle (e) in Supplemental Table S1). The posteroventral margin of the symphysis reaches p2 in lateral view (Fig. 2). The anterior tip of the symphyseal region is broken away but the shape of the anterior margin of the mandible suggests a slight convexity. The anterior margin must have been high, if we refer to the remnants at the base of the clinical crown of the lower canine. In lateral view, the genial tuberosity is less developed anteroposteriorly, as a small and smooth tubercle (Fig. 2). The anterior portion of the genial tuberosity reaches the anterior margin of the canine. A clear concavity is present between the posteriormost tip of the genial tuberosity and the anteriormost tip of the broken mandibular terminus, with an angle between the anterior and ventral margin (see Angle (b) in Supplemental Table S1) reaching 117°, corresponding to an extremely vertical condition of the anterior margin of the symphysis (Fig. 2). The ventral margin of the horizontal ramus is straight and starts at the level of p2. The dorsal margin of the horizontal ramus is concave and the angle between the anterior and dorsal margin (see Angle (a) in Supplemental Table S1) reaches 131°. Mental foramina are present with a large oval medial mental foramen located behind canine, oriented antero-laterally and deeply hollowed out (Fig. 2). A second, smaller one, considered as an accessory mental foramen, is located posterior to the larger one and placed more ventrally. Its shape is circular, well hollowed and located beneath p2. Another circular-shaped accessory mental foramen is located anterior to p3, close to the occlusal outline, slightly hollowed out and opened posterolaterally. Anterior mental foramen is not visible in NWHCM 1996.1 due to the incomplete preservation of the anterior part of the mandible. In the occlusal view, the horizontal ramus is posteriorly divergent and laterally inflated, not presenting a sigmoidal occlusal outline (Fig. 3). In anterior view, the anterior extensions of both left and right genial tuberosities project anteriorly to the anteroventral surface of the symphyseal region, and therefore, its sagittal portion is slightly indented and makes a lateral furrow (Fig. 4). In the medial region of the horizontal ramus, a slightly swollen space can be observed, corresponding to the insertion of the *mylohyoideus* muscle (Fig. 5). Mylohyoideus insertion is delimited ventrally in NWHCM 1996.1. The mylohyoid line corresponds to the ventral limit of the *mylohyoideus* muscle, following an anteroposterior axis along the horizontal ramus and reaches p4. The mylohyoid groove corresponds to the posterior continuity of the mylohyoid line and is located next to the mandibular foramen. The superior mental spines are present, notably due to the fusion of the mandible (Fig. 5). These spines delimit the insertion area for the *genioglossus* muscle, one of the muscles of the tongue (Fig. 5). The inferior mental spines are also present and delimit the insertion area for the *geniohyoideus* muscle, one of suprahyoid muscles, which also includes the *mylohyoideus* muscle (Fig. 5). The ventral margin of the mandible corresponds to the insertion of another suprahyoid muscle, the *digastricus* muscle (Figs. 2 and 5). In lateral view, the digastric prominence is distinct, even if underdeveloped (Fig. 2). Ventral ridges seem to be present and represent the ventral part of the *digastricus* insertion zone (Fig. 2).

The distance between the most posterior point of the dorsal margin and the base of the coronoid process in proportion to the entire mandibular length is short (Fig. 2). A large part of the ascending ramus is missing and does not allow to establish the exact shape of the coronoid process. The masseteric fossa is well marked, large and located on the lateral side of the coronoid process. The fossa corresponds to the insertion area for the *masseter pars profundus* muscle (Fig. 2). The dorsal limit of the fossa is a ridge following the anteroposterior axis. This longitudinal surface above the ridge is tight. The superior posterior-most tip corresponds to the insertion area for the *temporalis pars lateralis* muscle, located at the apex of the coronoid process (Fig. 2). On the medial surface of the coronoid process the pterygoid fossa is also large and well deepened. The pterygoid fossa corresponds to the insertion area for the *temporalis pars medialis* muscle (Fig. 5). A marked line in the anterior part of the fossa delimits the anterior border of the muscle. Despite the incompleteness of the ascending ramus, a vertical line is present, corresponding to the posterior limit of the *temporal pars medialis* muscle (Fig. 5). The ventral border of the pterygoid fossa is delimited by the mandibular foramen, an opening of the masseteric canal, connecting the mental foramina and the mandibular foramen. The mandibular foramen is circular in shape and opens posteriorly toward the mandibular condyle, with a small surface area (Figs. 3 and 5). Ventrally to the mandibular foramen, a crest ~~corresponding to a lamina~~ delimits the dorsal part of the *pterygoideus medialis* muscle (Fig. 5). The pre-angular space separates the ventral margin from the angular process through the digastric prominence. In NWHCM 1996.1, this space is short and straight. The angular process is located posterior to this space and is weakly developed. The articular facet of the angular process is projected posteroventrally and located ventrally to the mandibular condyle, close to the mandibular foramen. In medial view, the *pterygoideus medialis* muscle is inserted on the major part of the angular process. In lateral view, the condyloid crest is slightly prominent and corresponds to the insertion area for the *masseter pars superficialis* muscle ventrally, delimiting dorsally the *masseter pars profundus* muscle (Fig. 2). The mandibular condyle lies posteriorly to the condyloid crest and its most lateral portion is broken; however; what remains from its articular surface appear flat and not ~~very~~ well developed (Figs. 2, 3 and 5). The angle between the medial edge of the mandibular condyle and the mandibular symphysis in occlusal view (Fig. 3) (see Angle (d) in Supplemental Table S1) is nearly perpendicular (95°). The mandibular notch, separating the coronoid process from the mandibular condyle, is long, giving an angle between the coronoid process and the mandibular condyle virtually vertical (see Angle (g) in Supplemental Table S1). In occlusal view, the coronoid process is aligned with the cheek tooth row.

Dentition – The functional dental formula proposed for NWHCM 1996.1 is i2-3, c, p1-4. The specimen presents two incisors (i2 and i3). The root of the right i2 is preserved and located close to the medial walls of canines. A cavity just anterior to the canine is the alveolus for i3 (Figs. 3 and 4). It is sub-triangular and twice the size of the alveolus for i2. The canine is premolariform, followed by four cheek teeth. The cheek toothrow is almost straight in occlusal view (Fig. 3), however the canine is not exactly aligned with the cheek teeth, located more medially especially in p3-4. The alveolar septum between c and p1 is reduced proportionally and septa between the cheek tooth alveoli are ~~very~~ thin. The canine is much larger in size than premolars, p1-p4 having equal-sized alveoli. The alveolus for i2 has a circular shape, while c is more oval in shape and p1-p4 nearly circular. All teeth are single-rooted, acuspid, and show no sign of enamel. The i2 is posteriorly projected and has anteromedial wearing. On the canine, the wear facet is anteromedial and inclined laterally while the wear on cheek teeth is anterolaterally at p1-2 and posteriorly at p3-p4. The right p1 is preserved with a lateral wear on its crown.

Comparisons

The sequence of changes in mandibular and dental morphology in odobenids is fairly well documented (Boessenecker and Churchill, 2013), the family being characterized by dental reduction and mandibular fusion associated with suction-feeding specializations (Fig. 6, Supplemental Figure S2). Amongst the Odobenidae, species of the Odobeninae are characterized by having permanent postcanine tooth crowns showing no sign of enamel, a vascularized mandibular terminus, and a divergent mandibular arch (Deméré, 1994b). Within odobenines, *Aivukus cedrosensis* can be distinguished by an elongated rostrum without an arched palate, C^1 not enlarged as a tusk, presence of M_1 and the lack of a central column of globular dentine. A monophyletic clade, the Odobenini, within the Odobeninae encompasses *Protodobenus*, *Ontocetus*, *Odobenus* and *Valenictus* and is characterized by a palate that is arched transversely and longitudinally; tusk-like upper canines with globular osteodentine core and premolariform C_1 reduced in size. *Protodobenus japonicus* differs from other Odobenini by having two lower incisors transversely positioned, lower canine still caniniform and slightly reduced, a smaller upper canine and a shorter skull. *Ontocetus* is characterized by a combination of both primitive and derived characters such as an enlarged mastoid process, an elongated and upturned horizontal ramus, an unfused mandible, postcanine teeth widely spaced, and curved tusk-like C_1, and it is separated from the monophyletic *Odobenus* + *Valenictus* clade. *Odobenus* and *Valenictus* are characterized by the fusion of the mandible, loss of lower incisors, genial tuberosity developed as a small tubercle, and an elongated and vaulted palate. Between them, *Valenictus* can be distinguished from *Odobenus* by its loss of dentition except C^1 with an edentulous mandibular terminus considered as “a pad”, and a pachyosteosclerosis of postcranial bones. Based on these comparisons, NWHCM 1996.1, IRSNB M156 and RGM.St.119589 are safely recognized as belonging in the genus *Ontocetus* or *Odobenus*.

The relative size of NWHCM 1996.1 and IRSNB M156 is similar to IRSNB M168, an *On. emmonsi* adult male mandible. NWHCM 1996.1 and IRSNB M156 also exhibit other characteristics of the genus *Ontocetus* such as a lower canine much larger and separated from the cheek toothrow, the presence of the first premolar (p1); i.e., four postcanine cheek teeth (p1-p4). Moreover, NWHCM 1996.1 exhibits other traits similar to *On. emmonsi* such as a broad and short edentulous mandibular terminus with incisors, elevated and slanted anterior margin, a high, thin, and posterolaterally projected coronoid process, and short distance between the dorsal margin and coronoid process. However, NWHCM 1996.1 and referred specimens differ from *Ontocetus emmonsi* in some aspects, and share common features with *Odobenus* (*Od. rosmarus*), such as a fusion of mandible with symphyseal furrow. Deméré (1994b) recognized the fusion of the mandibular symphysis as a synapomorphy of *Odobenus* and *Valenictus* differentiating them from other odobenins (i.e., tribe Odobenini). However, dusignathine odobenids such as *Dusignathus seftoni* also have a fused symphysis, and this character is thought to have evolved several times and might be linked to the feeding strategy within the Odobenoidea (i.e., Dusignathinae and Odobeninae). Nevertheless, even in the extant walrus *Od. rosmarus*, the fusion of the symphyseal region seems to show some degree of ontogenetic and intraspecific variation. IRSNB M156, the referred mandible, has also had a broad and fused symphysis (van Beneden, 1877, fig. 5,6,7; Supplementary Figure S1), sharing strong similarities with NWHCM 1996.1 and another referred mandible RGM. St.119589. The mandibular symphysis ratio for NWHCM 1996.1 (1.75) is closer to male individuals of extant *Od. rosmarus* and differs from high ratio measured in individuals of *On. emmonsi* (Supplementary Table S1). In cross-section, the mandibular symphysis is oval in shape, similar to *Odobenus*, while more rectangular and elongated anterodorsally and posteroventrally in *Ontocetus.* The ratio between the size of the symphysis in NWHCM 1996.1 and the maximum length of the mandible is close to the values observed in extant *Odobenus*. In other words, the length of the symphysis of NWCHM 1996.1 but also in IRSNB M156 in occlusal view is relatively short like that of *Od. rosmarus* and much shorter than that of *On. emmonsi* represented by IRSNB M168 (Fig. 3, Supplementary Figure S2). NWCHM 1996.1 and IRSNB M156 also share with *Od. rosmarus*, a horizontal ramus with a well-curved occlusal outline. The space between the canine and the cheek teeth, but also between the cheek teeth alveoli themselves, are also thinner in proportion, than in *On. emmonsi*, close to *Od. rosmarus* measurements. Lastly, NWHCM 1996.1 presents an underdeveloped angular process, and a flat and less developed mandibular condyle, different to the morphology presented in *On. emmonsi*. Based on those comparisons, identification of NWHCM 1996.1, IRSNB M156, and RGM.St.119589 as a distinct species within the genus *Ontocetus* is warranted. Thus, we recognize those mandibles as representatives of an unknown species and accordingly propose *Ontocetus posti* as a new species.

Discussion

Functional Interpretations Toward Suction-Feeding Specialization

While the first odobenids were piscivorous, they rapidly evolved toward molluscivory (Adam and Berta, 2002), with some taxa, like *Valenictus chulavistensis*, exhibiting an extreme reduction of dentition except for the upper canines just as the extant walrus. *Ontocetus,* previously considered a molluscivore (Deméré 1994a, b; Adam and Berta, 2002; Boessenecker et al., 2018), however, exhibits features suggesting less specialization, making its diet a bit more complex to assess. *Odobenus rosmarus* exhibits a unique combination of characters that optimize its ability to engage in suction feeding (Kastelein and Gerrits, 1990; Kastelein et al., 1991). NWHCM 1996.1 and IRSNB M156 exhibit characteristics specific to *Ontocetus,* such as a significantly larger lower canine compared to the cheek teeth, four post-canine teeth, and incisors (i2). However, some features of those specimens are also found in *Odobenus* including mandibular fusion and shortening, oval mandibular arch, less developed and flatter mandibular condyle, and ~~very~~ fine septa between the various teeth. The robustness of the mandibular symphysis is directly associated with its condition, subjected to torsional forces experienced during feeding. Mandibular fusion, concomitant with symphysis size reduction, serves as a preventive measure against substantial mandibular deformation, particularly during tongue retraction in suction-feeding scenarios (Gordon, 1984; Kastelein and Gerrits, 1990; Deméré, 1994a; Adam and Berta, 2002). The fusion of the mandible and the pachyosteosclerotic reinforcement of the anterior part of the mandible further contributes to enhanced resistance, by supporting the large tusks. Suction-feeding specialization is further evidenced by the dorsally concave vaulting of the hard palate in the Odobenini, evident in both transverse and longitudinal planes. This palatal configuration, as proposed by Kastelein and Gerrits (1990), results in an enlarged intraoral space, facilitating a more extensive tongue protraction before retraction during suction-feeding. The curvature and oval shape of the mandible in occlusal view correspond to the arched structure of the hard palate vaulting. Additionally, the shortening of the skull, and consequently of the mandible, enhances the containment of negative intraoral pressure, facilitating the suction of mollusks when water reaches the palate (Werth, 2006a, b). Concurrently, the reduction in dental series among the Odobenini, as documented by Boessenecker and Churchill (2013), manifests in

Odobenus with narrower spacing between teeth compared to *Ontocetus*. This dental morphology is likely a consequence of *Odobenus* specialization in suction-feeding, accompanied by diminished reliance on teeth and a relatively free of obstruction feature into the oral cavity that would enhance the efficiency of suction feeding (Adam and Berta, 2002). Additionally, the reduced and flattened mandibular condyle in *Odobenus* is indicative of an adaptation to suction-feeding, paralleling the morphological similarity observed in *Valenictus*, identified as the most specialized suction-feeder among the Odobenini (Deméré, 1994a). This suggests that *Ontocetus posti* was able to use suction to catch its prey and may have once occupied an ecological niche similar to the extant *Odobenus rosmarus* in the Pliocene of the eastern North Atlantic before the latter species came into the North Atlantic.

Suction-feeding is observed independently in various groups of marine mammals, starting with pinnipeds, as in the bearded seal *Erignathus barbatus*. Nevertheless, its adaptations differ somewhat. The rostrum of the bearded seal is flatter, highly mobile, and capable of diverse shape changes (Marschall et al., 2008; Marschall, 2016). The bearded seal retains incisors and possesses a relatively flat palate, although the maxillary alveolar processes are expanded, resulting in a concave ventral rostral surface in transverse section. Adam and Berta (2002) propose that *Erignathus barbatus* may employ suction-feeding, although possibly to a lesser extent than *Odobenus rosmarus*. Other pinnipeds, such as the leopard seal *Hydrurga leptonyx* and the harbor seal *Phoca vitulina*, employ suction for prey capture (Hocking et al., 2013; Marshall et al, 2014; Churchill and Clementz, 2015; Kienle and Berta, 2016; Hocking et al., 2017), albeit without undergoing modifications as significant as those observed in the mandible and skull of *Odobenus rosmarus*. Suction-feeding is also present independently in contemporary toothed whales and dolphins (beaked whales, monodontids and sperm whales), involving the loss of elongated mandibles and skulls, accompanied by a reduction in teeth, and an arched and vaulted palate (Heyning and Mead, 1996; Werth, 2000; Kane and Marschall, 2006). This specific feeding technique is also surprisingly present in baleen whales, in the sole gray whale *Eschrichtius robustus*, predominantly employing this capability for aspirating prey-laden sediment residing on the seabed. This behavior aligns more closely with suction-filter feeding than a complete suction-feeding specialization (Ray and Schevill, 1974). In the fossil record, suction feeding has been observed with the cetacean *Odobenocetops* (de Muizon and Domning, 2002), possessing an arched and vaulted palate, distinctive of this feeding specialization.

NWHCM 1996.1 demonstrates distinctive muscular insertions, particularly evident on both the horizontal and vertical ramus. Observable variations are discernible among *Odobenus rosmarus*, *Ontocetus posti*, and *Ontocetus emmonsi* (Fig. 7). On the horizontal ramus, the hyoid muscle insertion zones can be identified, bounded ventrally by the mylohyoid line (anteriorly) and the mylohyoid groove (posteriorly), proximate to the mandibular foramen. To some extent, the insertion zone for the *mylohyoideus* muscle appears broader in *Ontocetus* compared to *Odobenus rosmarus*. Specimen preservation enables the observation of inferior mental spines, corresponding to the *geniohyoideus* muscle insertion, and, to some extent, superior mental spines, corresponding to the *genioglossus* muscle insertion. *Ontocetus* appears to possess proportionally more developed *genioglossus* and *geniohyoideus* muscles. The *digastricus* muscle can be estimated, characterized by the presence of a digastric prominence. However, *Ontocetus posti* exhibits a less pronounced digastric prominence, resembling that of *Odobenus rosmarus*. On the vertical ramus, the masseteric fossa is notably more pronounced in *Ontocetus* compared to *Odobenus rosmarus*. This fossa corresponds to the muscular insertion area of the *masseter profundus* muscle. Ventral to the condyloid crest, the muscular insertion area of the *masseter* *superficialis* appears distinguishable, with *Ontocetus emmonsi* having a proportionally larger muscular insertion area. Consequently, it is plausible that *Ontocetus emmonsi* possesses a more developed masseteric muscle compared to *Ontocetus posti* and *Odobenus rosmarus*. The pterygoid fossa on the medial face of the coronoid process also appears more pronounced in *Ontocetus* compared to *Odobenus rosmarus*. This fossa corresponds to the insertion zone of the temporalis muscle, differentiating into the *temporalis pars medialis* in the medial zone of the coronoid process and the *temporalis pars lateralis* located at the apex of the process. *Ontocetus* also exhibits a proportionally larger zone and, consequently, a more developed temporal muscle than *Odobenus rosmarus*. Lastly, the insertion zone of the *pterygoideus* muscle, specifically its medial part (*pterygoideus medialis*), can be observed. This zone appears smaller in *Ontocetus emmonsi* compared to *Odobenus rosmarus* and *Ontocetus posti*. In general, the comparison and interpretation of muscle functions between the fossil record and the present pose challenges. Considering the proportions of muscular insertion zones found on the mandibles of *Ontocetus* and *Odobenus rosmarus*, it appears that fossil taxa have larger muscular insertion areas, potentially indicative of more developed muscles. This suggests a possible moderately lesser specialization toward suction-feeding, given the different proportional changes in muscular insertion zones related to this mechanism. Although we have attempted to describe these insertion zones, Kienle et al. (2021) conducted a comparative examination of craniofacial musculature in pinnipeds and its role in aquatic feeding. Contrary to their initial hypothesis, approximately half of the biting species in this study (i.e., harbor seals and ringed seals) do not exhibit specific musculoskeletal adaptations for biting or suction feeding. Moreover, several pinniped species without morphological adaptations for suction have been shown to be extremely capable suction feeders (e.g., Hocking et al., 2013; Marshall et al., 2014; Kienle et al., 2018).

Thus, it seems that most pinnipeds are opportunistic predators, and their non-specialized craniofacial musculature allows flexible feeding behavior. In light of this information, it is more likely that osteological changes (mandible fusion, reduction of teeth, skull shortening, or vaulted and arched palate) are specific to the walrus lineage in the specialization for suction-feeding, rather than representing a change in craniofacial musculature.

In this regard, *Ontocetus emmonsi* is inferred to be moderately less specialized in suction feeding based on observations of a lower canine wider than the cheek teeth, the presence of incisors and the absence of mandibular fusion. On the other hand, some features observed in both *Ontocetus posti* and the extant walrus such as the presence of a fused and reduced mandibular symphysis and a well-curved mandibular arch attesting of a shorter skull this taxon might have been more specialized in suction feeding than previously thought for the genus *Ontocetus*. Indeed, the absence of the *Odobenus rosmarus* left this specialized molluscivore/suction feeder niche open for *Ontocetus* in the Early Pleistocene of the North Sea. We hereby suggest that *Ontocetus posti* might have occupied a similar niche to *Odobenus rosmarus*.

Sexual Dimorphism in *Ontocetus Posti*

Sexual dimorphism is a key morphological characteristic in pinnipeds, usually associated with their polygynous behavior (Bartholomew, 1970; Kovacs and Lavigne, 1992; Garlich-Miller and Stewart, 1998; Weckerly, 1998; Lindenfors et al., 2002; Ralls and Mesnick, 2009; Jones and Goswami, 2010; Velez-Juarbe, 2017; Mesnick and Ralls, 2018). In *Odobenus rosmarus*, adult males exhibit conspicuous differences in size and weight compared to adult females, and several studies highlight sex-dependent morphological variations in their crania and mandibles (Mohr, 1942; Fay, 1982; Kovacs and Lavigne, 1992; Garlich-Miller and Stewart, 1998; Boisville et al., 2022). Among the odobenins, *Ontocetus emmonsi* has been confirmed to display extreme sexual dimorphism, even more marked than in *Od. rosmarus* (Kohno and Ray, 2008). Larger individuals (males) are approximately 20-40 percent larger than smaller individuals (females) according to cranial, mandibular and postcranial sizes, based on Lee Creek mine sample (Kohno and Ray, 2008). Similarly, a clear difference in upper canines indicates distinctions between males (larger and stocky tusks) and females (smaller and slender tusks). Consequently, it is justified to investigate the sexual dimorphism~~s~~ in *Ontocetus posti*. The size of mandible as well as the circumference of the lower canines in NWHCM 1996.1 corresponds to the dimensions of male specimens of *On. emmonsi* (IRSNB M168). Although incomplete, IRSNB M156 also exhibits proportions consistent with the male morphotype of *On. emmonsi*, whereas RGM.St.119589 displays proportions much similar to the female morphotype (USNM V 9343). It is noteworthy that IRSNB M156 presents measurements larger than any documented *Ontocetus*. Males and females can be easily distinguished using the symphysis height/symphysis length ratio, with females exhibiting a lower ratio indicative of a slender mandible (Kohno and Ray, 2008). IRSNB M156 exhibits values similar to the male *On. emmonsi*, while RGM.St.119589 exhibit values closer to females. Mandibular height (see MD in Supplementary Table S1) and mandibular width (see MT in Supplementary Table S1) after the last cheek tooth, indicate that NWHCM1996.1 aligns with male *On. emmonsi* values, and IRSNB M156 surpasses these values, suggesting an increased mandibular thickness. The length of the cheek toothrow and the length between the last cheek tooth and ascending ramus (see Supplementary Table S1) is also sexually dimorphic, NWHCM 1996.1 appears closer to female *On. emmonsi* values (USNM V 9343), whereas IRSNB M156 exhibits broader proportions, particularly with a longer cheek toothrow than the largest males. Based on these comparisons, we identify NWHCM 1996.1 as a mature male, RGM.St.119589 as a mature female, and due to its extreme proportions, IRSNB M156 is recognized as a ~~very~~ old male, likely considered the largest *Ontocetus* individual ever found. *Ontocetus posti* may have had an extreme sexual dimorphism, similar to *Ontocetus emmonsi*.

Biochronological Dispersal and Evolution of *Ontocetus* in the North Atlantic

The youngest record of *Ontocetus* in the North Atlantic is dated to the Early Pleistocene (1.8 - 1.1 Ma) ~~in the Austin San Pit deposits (North Carolina, USA)~~ (Boessenecker et al., 2018). Although the Easton Bavents specimen is slightly older (2.2 - 1.7 Ma), it represents the final occurrence of this genus in the North Sea. The biochronology and dispersal of *Ontocetus* is well-established, with its initial appearance traced back to the Upper Miocene/Lower Pliocene boundary age Tatsunokuchi Formation (Okamoto and Kohno, 2019) and Lower Pliocene Joshita Formation in Nagano Prefecture, Japan (Kohno et al., 1998). Additional specimens have been uncovered in analogous deposits in Japan (Yasuno, 1988; Kohno et al., 1995). This suggests that *Ontocetus* originated in the North Pacific; those more primitive forms also seem distinct from those discovered in Lower Pliocene deposits on the United States east coast or in the North Sea (Kohno et al., in prep.). The dispersal of *Ontocetus* from the North Pacific to the North Atlantic has traditionally been proposed to have occurred via the Central American Seaway around the Mio-Pliocene boundary (Repenning et al., 1979; Kohno et al., 1995; Boessenecker et al., 2018; Boessenecker and Churchill, 2021). This perspective suggests that *Ontocetus* evolved during the Late Miocene in the North Pacific before migrating to the North Atlantic. Considering the corresponding latitudinal occurrences in Early Pliocene deposits (Florida, North Carolina, South

Carolina), *Ontocetus* may appear to be adapted to warmer temperate water than the extant species, especially given the absence of *Ontocetus* occurrences at high latitudes. Consequently, traversing the Arctic might have been challenging for this taxon. Additionally, the presence of *Valenictus* (Late Miocene up to Late Pliocene) on the west coast of the USA (California) supports a more southerly migration of Pliocene tusked walruses via the Central American Seaway rather than through the Arctic (Repenning and Tedford, 1977; Deméré, 1994a, b). It is suggested that *Ontocetus* may have migrated from the North Pacific to the North Atlantic via the still-open Central American Seaway at the time (Naafs et al., 2010; O'Dea et al., 2016) (Fig. 8a). *Ontocetus* then dispersed in the western North Atlantic during the Early Pliocene, populating fossil-rich formations such as the Palmetto Formation, Raysor Formation, and Yorktown Formation (Berry and Gregory, 1906; Kohno and Ray, 2008). However, around 4.6 - 4.2 Ma, the closure of the Panama Isthmus disrupted equatorial currents between the Pacific and Atlantic Oceans, leading to the cooling of the Atlantic Ocean and eventual ice cap formation (O'Dea et al., 2016).

Between these glaciations, during the warm periods around the late Early Pliocene (3.8 Ma), a population from the western North Atlantic may have migrated towards the North Sea. This migration was facilitated by the intense North Atlantic current transporting warm waters northward and maintaining the higher latitudes' warmth (Naafs et al., 2010) (Fig. 8b). However, during the late Pliocene (3.1 Ma), sea-level oscillations, likely acting in conjunction with other oceanographic alterations such as changes in productivity, ocean circulation, and biotic drivers such as prey availability, impacted neritic areas and led to the extinction of the Pliocene marine megafauna (Pimiento et al., 2017). The loss of abundant shallow embayments and seaways, coupled with faunal turnover in the Late Pliocene, likely contributed to the disappearance of mid-latitude walruses, which were highly specialized in feeding adaptations (Boessenecker, 2013a, b; Pimiento et al., 2017).

No occurrences of otariids or phocids were found in the North Atlantic during the Pliocene, except a monachinae indet. (Dewaele et al., 2018), and two undescribed occurrences (cf. *Pagophilus* sp., cf. *Pusa* sp.; Post and Boesselaers, 2005). Given the robust morphology of its forelimb as well as its craniomandibular anatomy (relative elongation of the skull, characterized by a more slanted cranial roof, non-fused and longer mandible, more complete dentition, particularly with functional incisors, and a more developed mandibular condyle) *Ontocetus emmonsi* likely captured its prey in the same way as extant sea lions, which could explain the absence of sea lions from the North Pacific until the end of the Pliocene (Okamoto and Kohno, 2019).

The global cooling during the Plio-Pleistocene transition had a profound impact on the warm North Atlantic Current, causing the ice cap to extend to lower latitudes (Naafs et al., 2010; Batchelor et al., 2019). During the late Pliocene, a North Sea population of *Ontocetus* may have evolved and specialized in suction-feeding techniques, particularly in response to changes in mollusk fauna dominated by immigrants from the Pacific Ocean (*Macoma balthica*) and other bivalves (Riches, 2010). In the cold periods of the Early Pleistocene, the warm North Atlantic Current did not flow northwards but rather west-eastwards, directly towards Morocco, where the Arctic ice cap likely reached Spain (Naafs et al., 2010). *Ontocetus* has also been identified in the Ahl al Oughlam deposits of Morocco through the Plio-Pleistocene boundary (3.0 - 2.2 Ma) (*Alachtherium africanum* Geraads, 1997) (Fig. 8c). This raises the possibility that the Moroccan population of *Ontocetus* became endemic due to the altered direction of the North Atlantic Current and ice cap expansion. A population of *Ontocetus* from the western North Atlantic may have migrated towards Morocco, or that part of the eastern North Atlantic population may have migrated southwards through the paleo-Bay of Biscay toward Morocco (Fig. 8c). Later, as the Early Pleistocene unfolded, warm periods became increasingly rare, contributing to an overall colder climate with drastic falls in sea levels due to ice cap expansion.

Extinction of *Ontocetus* In Relation To Global Cooling Through Early Pleistocene

Despite its suction-feeding adaptation to the exclusive molluscivorous diet in the North Sea, *Ontocetus posti* became extinct around 1.7 Ma. This extinction may also be explained by the confinement of the taxa in the North Sea and unable to escape northwards to the Atlantic Ocean due to ice sheet expansion (Van Vliet-Lanoe et al. 2002; Gibbard and Cohen, 2015; Gibbard and Lewin, 2016; Rea et al., 2018; Lein et al., 2022) (Fig. 9). Moreover, the Dover Strait was closed and would not have reopened until the middle of the Chibanian or Holsteinian of about 400 Ka (Meijer and Preece, 1995; Westerhoff et al., 2020). *Ontocetus posti* may have been overly specialized in suction-feeding for molluscivorous diet, rendering it more vulnerable to rapid changes in sea level oscillation and the general global cooling during this period. Additionally, during the Late Tiglian (1.8 Ma), there was a significant drop in mollusk species, with ~~very~~ few "warm" mollusks (Meijer and Preece, 1995). The Late Pliocene marine mammal assemblage in the southern North Sea also includes other species coexisting with *Ontocetus*, some of which using a similar suction feeding technique, such as *Mesoplodon* sp. (Ziphiidae), *Delphinapterus* sp. (Monodontidae), and *Globicephala* sp. (Delphinidae) (de Vos et al., 1998; Post and Boesselaers, 2005). However, it is highly likely that these cetaceans did not enter into competition with *Ontocetus posti*, considering their more pelagic distribution, whereas *Ontocetus* was in nearshore areas, in shallow waters. The only other pinnipeds found are two Phocidae (cf. *Pagophilus* sp. and cf. *Pusa* sp.) and a monachinae indet., which, based on their contemporary representatives, did not occupy the same niche as *Ontocetus* (Post and Boesselaers, 2005; Dewaele et al., 2018).

Interestingly, one final population of *Ontocetus emmonsi* managed to survive at much lower and warmer latitudes in the Upper Waccamaw Formation, South Carolina, USA, until 1.1 Ma (Boessenecker et al., 2018). Although this is at present evidenced only by the fossil record of a relatively short and strongly curved tusk, it suggests that the oral cavity or the rostrum of this animal had still retained a relatively generalized one. As a result, it might have been facilitated much broader dietary preferences by a less specialized feeding apparatus and suffered less quickly or significantly suffered the environmental changes during the Pliocene and Early Pleistocene. More stable and favorable climatic conditions, at more southerly latitudes compared to the North Sea, also enabled *Ontocetus* to survive until 1.1 Ma. The temporal separation of *Odobenus* and *Ontocetus* in the North Atlantic for approximately 1 million years suggests that they did not compete for resources and reflects separate Early Pliocene (*Ontocetus*) and Middle–Late Pleistocene (*Odobenus*) dispersals into the North Atlantic from the North Pacific. These dispersals occurred through the Central American Seaway for the warmer-tolerant *Ontocetus* and the Arctic for the colder-tolerant *Odobenus* (Kohno et al., 1995; Boessenecker et al., 2018).

Conclusions

We described a novel taxon of *Ontocetus*, identified through a re-evaluation of a nearly complete pair of mandibles from the Lower Pleistocene of Easton Bavents (United Kingdom) and a fragmentary mandible from the Upper Pliocene of Belgium. Key diagnostic features, such as the presence of four post-canine teeth including p1, a lower canine larger than the cheek-teeth, and an i2 clearly characterize the extinct genus *Ontocetus*. However*, Ontocetus posti* shares features with the extant *Odobenus*, such as a fused and shorter symphysis, a well-curved horizontal ramus and ~~very~~ thin septa between the canine and cheek-tooth alveoli. Some of those characters being associated with suction feeding adaptation in the extant walrus we hereby suggest that *Ontocetus posti* occupied an ecological niche similar to the extant *Odobenus rosmarus* in the Late Pliocene of the eastern North Atlantic.

Odobenus and *Ontocetus* did not coexist in the North Atlantic, *Odobenus* appearing almost a million years later subsequent to the extinction of *Ontocetus*. Described as a temperate to warm-tolerant tusked walrus, *Ontocetus* colonized the western North Atlantic during the Early Pliocene before migrating to the North Sea during the warm periods of the Late Pliocene. Its prevalence in warmer waters contrasts with the genus *Odobenus*. Global climatic cooling during the Early Pleistocene invariably impacted North Sea mollusc faunas and contributed to the isolation of the North Sea from the North Atlantic. Those extrinsic factors associated with the specialization in suction feeding of *Ontocetus posti* likely contributed to its extinction around 1.7 Ma. A more in-depth investigation holds promise in unveiling the past diversity of *Ontocetus* and *Odobenus* on a global scale, elucidating the eventual dominance of the cold-tolerant *Odobenus rosmarus* as the sole survivor.

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Figure 1

The geologic context of *Ontocetus posti* sp. nov.

A. Map of the locality of holotype mandible NWHCM 1996.1, Easton Bavents, East Anglia in southeast of the United Kingdom (based on data from Wood et al., 2009). B. Stratigraphic column of the East Anglian Crags containing fossil horizon with relevant chronology (based on data from Daley and Balson, 1999; Wood et al., 2009).

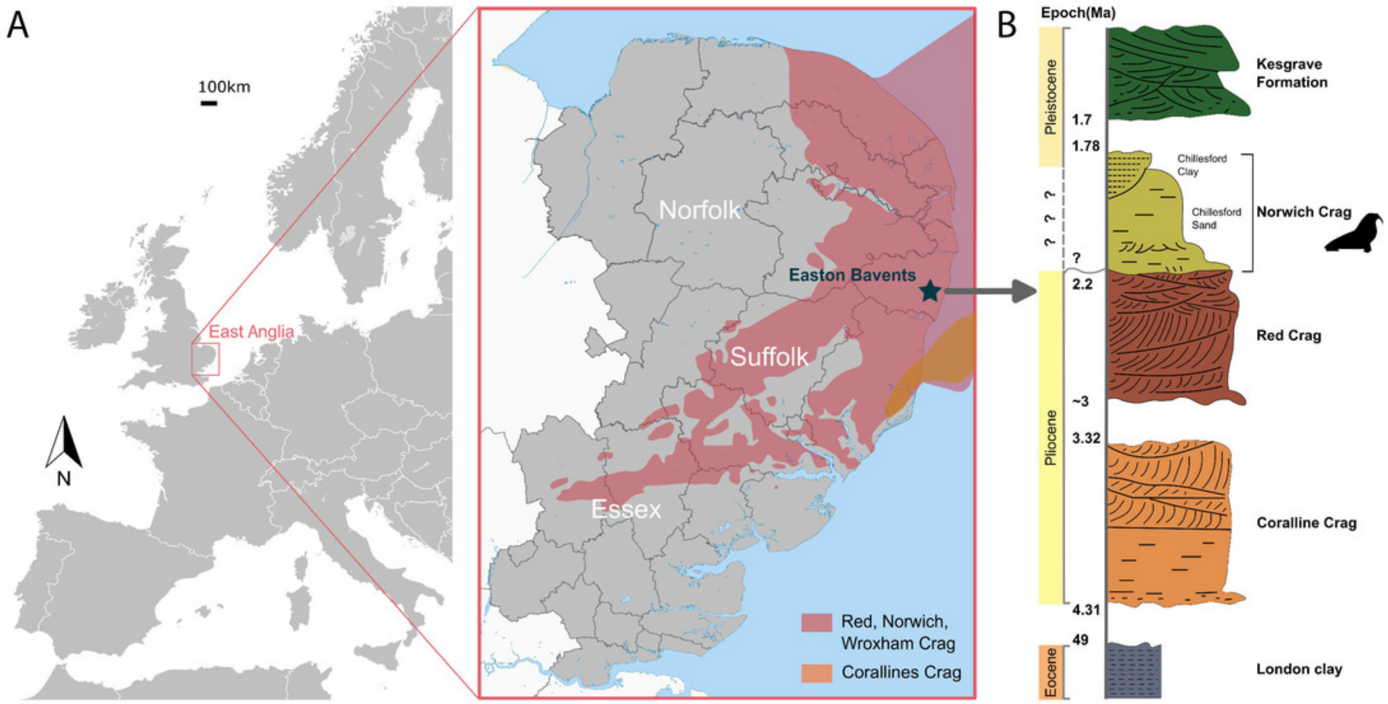

Figure 2

Holotype mandibles of *Ontocetus posti* in lateral view.

NWHCM 1996.1, adult male. Scale bar equals 5 cm. The hatched parts correspond to broken surfaces.

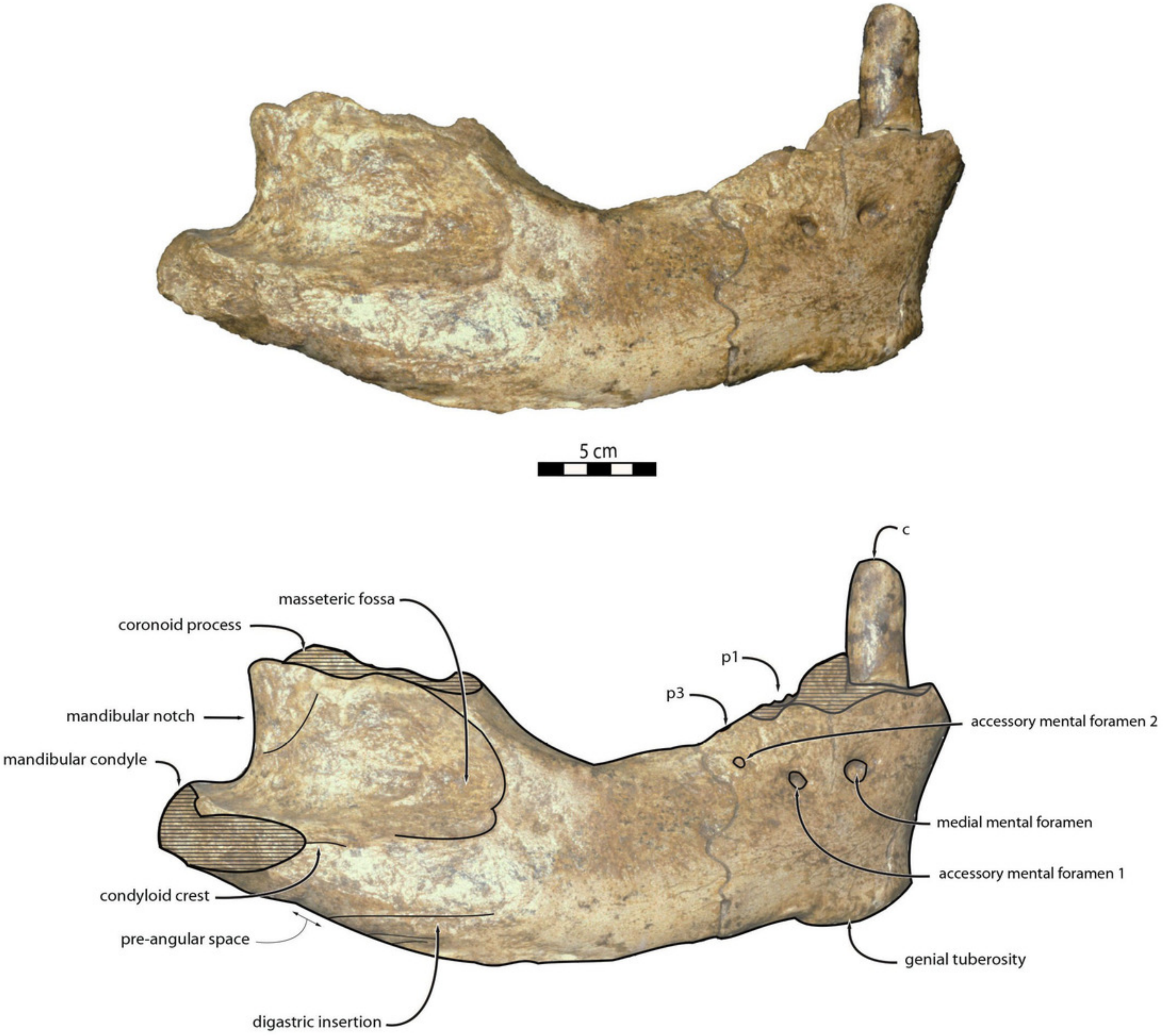

Figure 3

Holotype mandibles of *Ontocetus posti* in occlusal view.

NMR 7472, cast of NWHCM 1996.1, adult male. Scale bar equals 5 cm. The hatched parts correspond to broken surfaces.

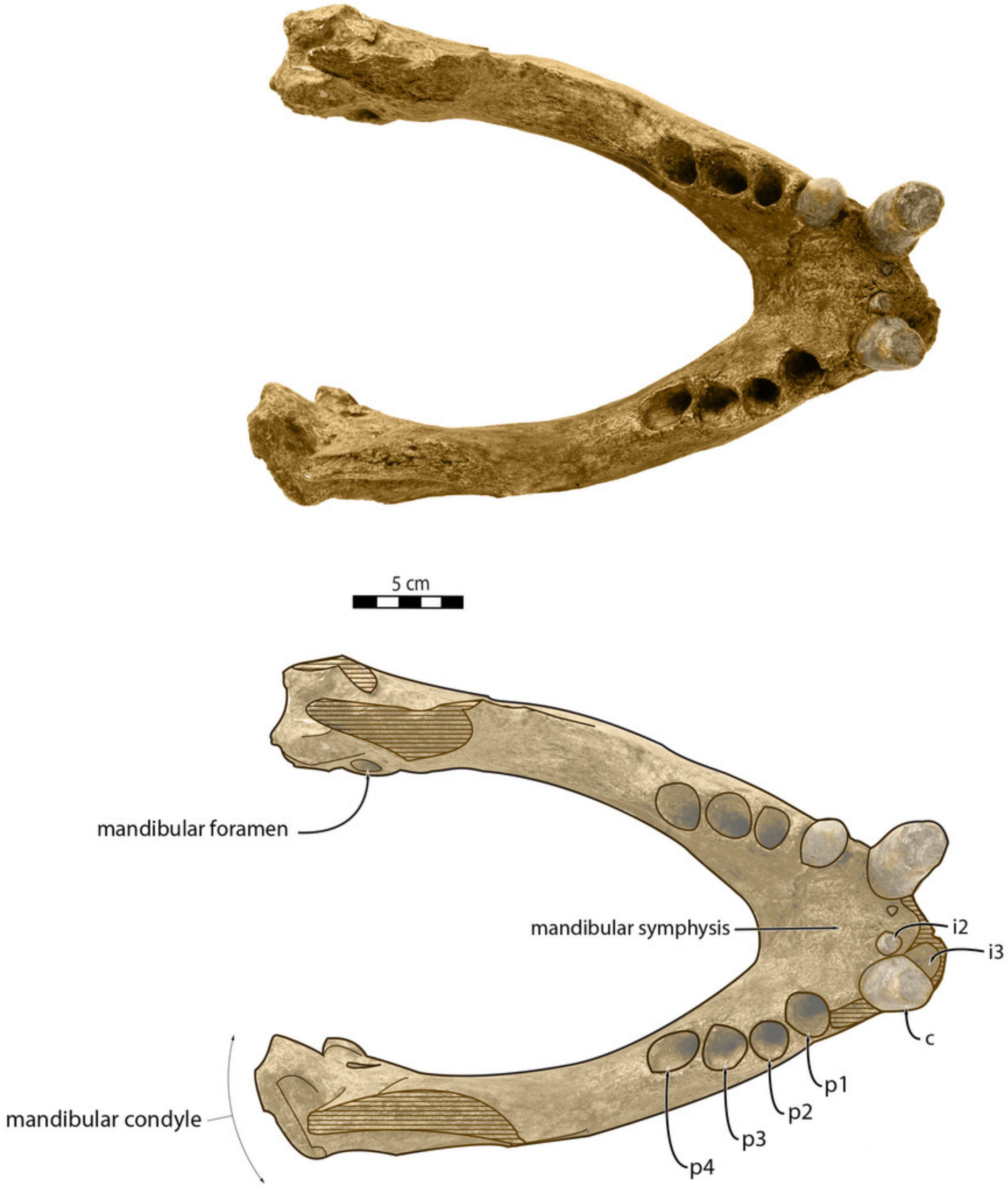
5 cm
mandibular foramen
mandibular symphysis
i2
i3
c
p1
p2
p3
p4
mandibular condyle

Figure 4

Holotype mandibles of *Ontocetus posti* in anterior view.

NWHCM 1996.1, adult male. Scale bar equals 5 cm. The hatched parts correspond to broken surfaces.

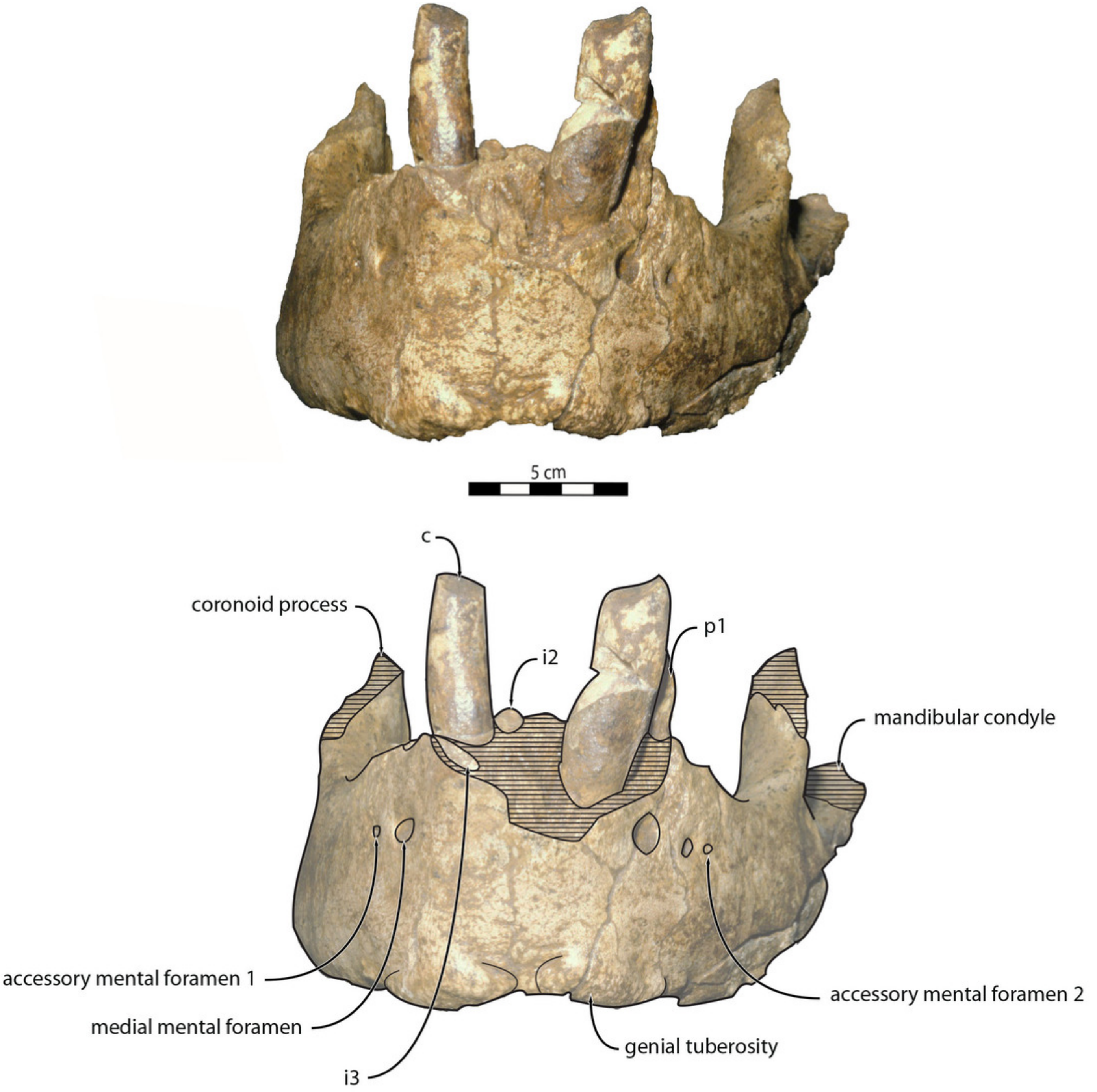
5 cm
c
coronoid process
p1
i2
mandibular condyle
accessory mental foramen 1
medial mental foramen
i3
genial tuberosity
accessory mental foramen 2

Figure 5

Holotype mandibles of *Ontocetus posti* in posterior view.

NMR 7472, cast of NWHCM 1996.1, adalt male. Scale bar equals 5 cm. The hatched parts correspond to broken surfaces.

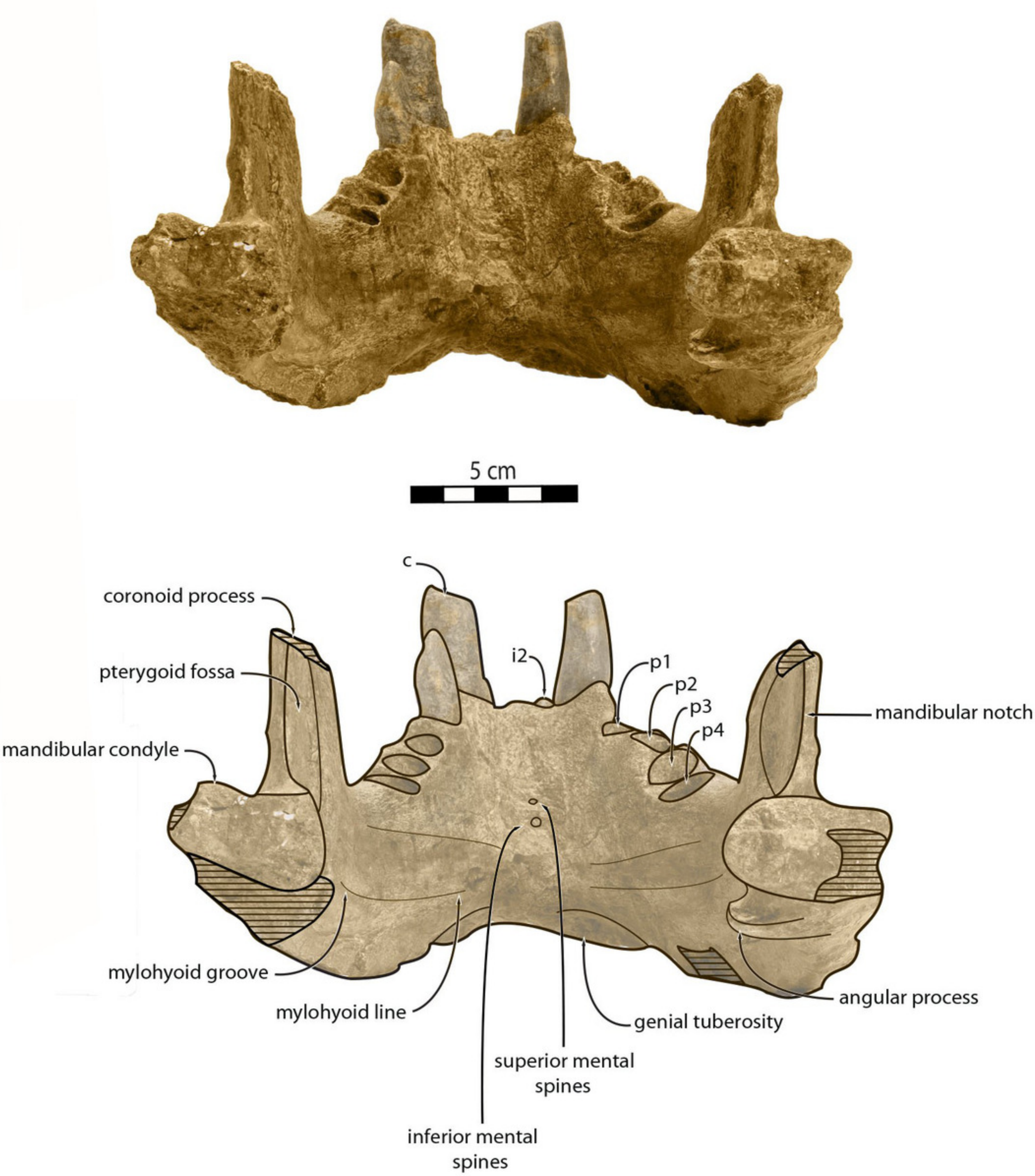
5 cm
c
coronoid process
i2
p1
p2
p3
p4
pterygoid fossa
mandibular notch
mandibular condyle
mylohyoid groove
mylohyoid line
genial tuberosity
angular process
superior mental spines
inferior mental spines

Figure 6

Hypothesized sequence of cranial, mandibular, and dental character transformations during odobenine evolution toward the suction-feeding specialisation.

Cranial, mandibular and dental characters from Deméré (1994b) and Boessenecker and Churchill (2013). Scale bar equals 10cm. The restored mandible of *Ontocetus posti* sp. nov. based on NWHCM 1996.1.

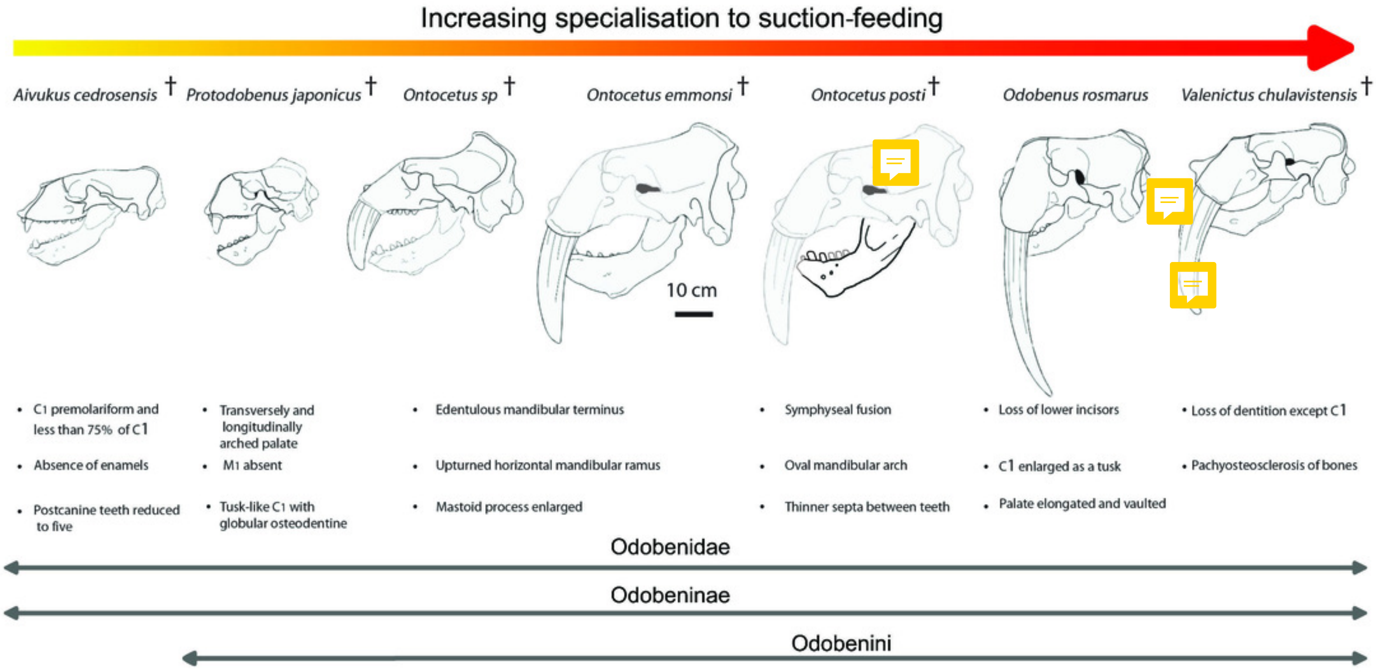

Figure 7

Anatomical interpretations for muscle insertions in *Odobenus rosmarus* (A, D), *Ontocetus posti* (B, E), and *Ontocetus emmonsi* (C, F).

Lateral view on the upper part, posterior view on the lower part. Scale bar equals to 5cm. IRSNB 1150B (male morphotype) represents *Odobenus rosmarus*, NWHCM 1996.1 (male morphotype) represents *Ontocetus posti*, IRSNB M168 (male morphotype) represents *Ontocetus emmonsi*.

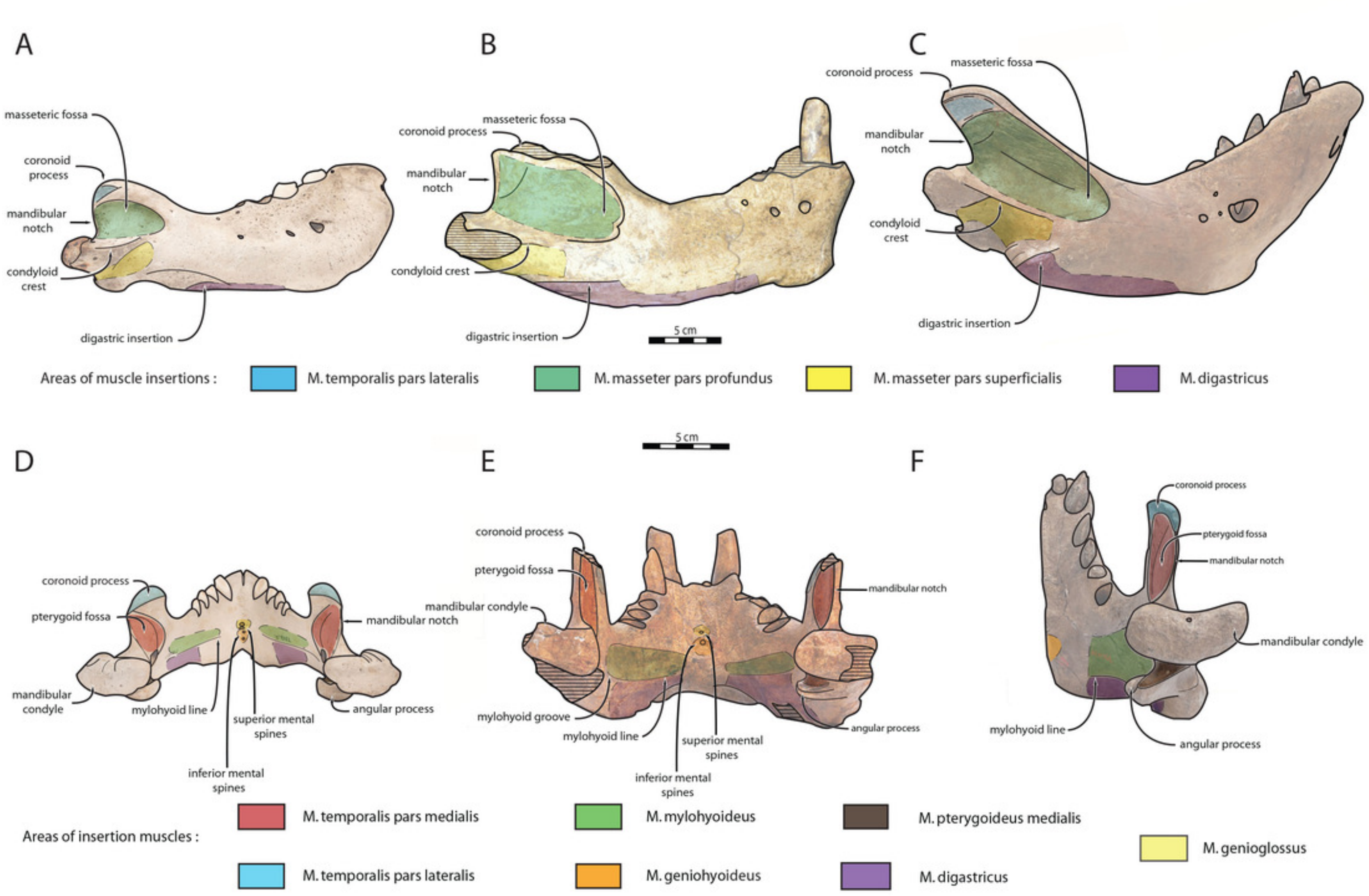

Figure 8

Ontocetus biogeographic hypothesis, as proposed by Repenning and Tedford (1977), Kohno et al. (1995), Geraads (1997) and Kohno and Ray (2008).

(a) the Late Miocene-Early Pliocene map: (1) evolution of *Ontocetus emmon*si from western North Pacific followed by dispersal through the Central American Seaway to the western North Atlantic during the Early Pliocene; (b) the late Early Pliocene map: (2) dispersal of *Ontocetus emmonsi* to the eastern North Atlantic during interglacial periods; (c) the Late Pliocene-Early Pleistocene map: (3) the dispersal to Morocco during glacial periods, and isolation of an *Ontocetus* population in the North Sea, or (4) alternatively southerly expansion or emigration from the supposed area of the paleo-Bay of Biscay to Morocco. Ice sheets reconstructed from Naafs et al. (2010) and Batchelor et al. (2019). Pliocene occurrences are represented by orange color.


a
b
c

Figure 9

Reconstruction of *Ontocetus posti* occurrences during the Early Pleistocene in the North Sea (2.2 – 1.7 Ma).

Ice-sheets and sea shores reconstructed from Meijer and Preece (1995), Van Vliet-Lanoe et al. (2002), Gibbard and Cohen (2015), Gibbard and Lewin, (2016), Rea et al. (2018), Batchelor et al. (2019), Westerhoff et al. (2020) and Lein et al. (2022). Pleistocene occurrences are represented by blue color.