


RAPID COMMUNICATION

THE OLDEST MARINE VERTEBRATE FOSSIL FROM THE VOLCANIC ISLAND OF ICELAND: A PARTIAL RIGHT WHALE SKULL FROM THE HIGH LATITUDE PLIOCENE TJÖRNES FORMATION

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Typescript received 5 August 2016; accepted in revised form 3 December 2016

Abstract: Extant baleen whales (Cetacea, Mysticeti) are a disparate and species-rich group, but little is known about their fossil record in the northernmost Atlantic Ocean, a region that supports considerable extant cetacean diversity. Iceland's geographical setting, dividing North Atlantic and Arctic waters, renders it ideally situated to shed light on cetacean evolution in this region. However, as a volcanic island, Iceland exhibits very little marine sedimentary exposure, and fossil whales from Iceland older than the late Pleistocene are virtually unknown. Here, we present the first fossil whale found *in situ* from the Pliocene Tjörnes Formation (*c.* 4.5 Ma), Iceland's only substantial

marine sedimentary outcrop. The specimen is diagnosed as a partial skull from a large right whale (Mysticeti, Balaenidae). This discovery highlights the Tjörnes Formation as a potentially productive fossil vertebrate locality. Additionally, this find indicates that right whales (*Eubalaena*) and bowhead whales (*Balaena*) were sympatric, with broadly overlapping latitudinal ranges in the Pliocene, in contrast to the modern latitudinal separation of their living counterparts.

Key words: Balaenidae, Iceland, Pliocene, biogeography, marine mammal, Tjörnes.

MUCH of the lower Tjörnes Formation of northern Iceland dates from the early Pliocene (Bucharadt & Símonarson 2003). This important period in cetacean evolutionary history documents the first appearance of many modern taxa that coexisted with archaic species that have since gone extinct (Fordyce & Barnes 1994). This geological period also has the potential to fill in gaps in the historical biogeographical record for extant cetacean subclades (Whitmore 1994; Fordyce 2002; Boessenecker 2013). Here, we report findings from the first vertebrate palaeontological expedition to the Tjörnes Formation, Iceland's only substantial marine sedimentary

exposure. Fieldwork in the Tjörnes Formation in the summer of 2011 revealed a partial skull of a mysticete whale. This study diagnoses the fossil and describes its stratigraphical setting to enable estimation of its temporal and environmental context.

We identify the fossil as a partial skull of a right whale (Balaenidae, cf. *Eubalaena*). Our find represents the twentieth balaenid fossil diagnosable to genus level from the North Atlantic and Mediterranean, and we provide a complete list reviewing the previously described material. The recovery of a right whale (*Eubalaena*) from this high-latitude Pliocene locality, combined with records of

bowhead whales (*Balaena*) in similarly-aged sediments at lower latitudes, suggests that these two balaenid taxa may have been sympatric during this temporal interval, in contrast to their allopatric modern distributions. The identification of the Tjörnes Formation as a marine mammal-bearing locality makes it one of only a small handful of high-latitude Pliocene localities worldwide that have produced marine mammals; future exploration of this locality may yield additional Pliocene marine mammals of biogeographical significance.

GEOLOGICAL SETTING

Overview of Tjörnes Geology

The fossil was discovered in a cliff on the west-facing edge of the Tjörnes Peninsula, in north-eastern Iceland (66°00'–66°12'N, 16°57'–17°24'W; Fig. 1). Four major lithological units are found on the Tjörnes Peninsula (Fig. 1): the Tertiary Kaldakvísl lavas, Tjörnes beds, Höskuldsvík lavas, and the Quaternary Bredavík Group (Eiríksson 1981; Buchardt & Símonarson 2003). The fossil derives from close to the middle of the Tjörnes beds. Although these deposits exhibit a rich fossil mollusc fauna (Bardarson 1925; Strauch 1972; Norton 1975; Gladenkov *et al.* 1980), the presence of vertebrate remains in these deposits is virtually unknown beyond a handful of isolated, undescribed elements ascribed to seals and whales. None of these previous finds have been excavated *in situ*, and are therefore unassociated with the well-circumscribed biozones within the Tjörnes Formation. The Tjörnes beds comprise the only significant pre-Quaternary marine deposits in Iceland (Einarsson 1958; Eiríksson 1981), and include intertidal, littoral and subtidal strata (Buchardt & Símonarson 2003). Age constraints on the Tjörnes beds date roughly to the middle Pliocene, although there is disagreement regarding the precise age of these strata (Verhoeven *et al.* 2011).

The Tjörnes beds comprise approximately 500 m of fossiliferous siliciclastic sediments, which are primarily made up of marine sandstones, with intermittent terrestrial/estuarine lignite beds and muddy sandstones (Buchardt & Símonarson 2003). Bardarson (1925) grouped this sequence into three biozones on the basis of their most abundant mollusc fossils; from oldest to youngest, these are the *Tapes* Zone, the *Mactra* Zone, and the *Serripes* Zone. The whale fossil described here derives from the middle of the *Mactra* Zone (Fig. 1).

Dating the Tjörnes beds and palaeoenvironment

Aronson & Saemundsson (1975) dated samples from the Kaldakvísl lava flows, which underlie the Tjörnes beds, to

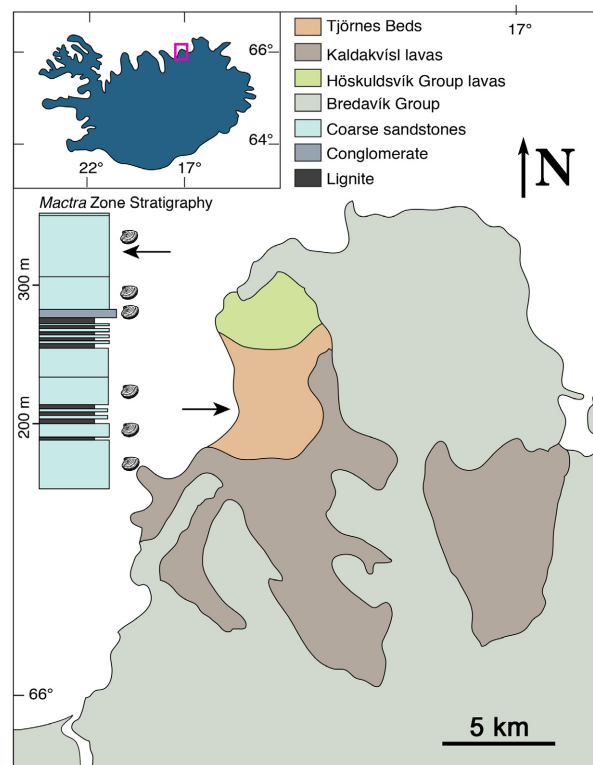


FIG. 1. Geology of the Tjörnes Peninsula (66°00'–66°12'N, 16°57'–17°24'W). Geological map and stratigraphic column modified from Buchardt & Símonarson (2003). Arrows denote the stratigraphical and geographical provenance of the whale fossil. The major lithological units exposed on the peninsula are the Tjörnes beds, the Kaldakvísl lavas, the Höskuldsvík Group lavas, and the Bredavík Group. The *Mactra* Zone is comprised of coarse sandstones, conglomerate and lignite layers, representing alternating marine tidal flat and nonmarine swamp palaeoenvironments. Shells denote layers with high densities of fossil molluscs. Colour online.

9.9 ± 1.8 and 8.6 ± 0.4 Ma, and Albertsson (1976) dated a lava flow in the lowermost part of the Tjörnes beds to 4.3 ± 0.17 Ma. The Höskuldsvík Group, directly overlying the Tjörnes beds, has been dated to 2.55 ± 0.27 Ma (Albertsson 1978).

A pillow lava with reverse remanent magnetism, lying just above the *Mactra/Serripes* Zone boundary within the Tjörnes beds (and thus important for dating the whale fossil), has presented problems for radiometric dating (Einarsson *et al.* 1967; Albertsson 1978; Eiríksson *et al.* 1990; Buchardt & Símonarson 2003; Verhoeven, *et al.* 2011), leading to widely varying age estimates. Regardless, most researchers have accepted that the *Tapes* Zone dates from the early Pliocene, and that the *Serripes* Zone dates from the late Pliocene (Buchardt & Símonarson 2003), but see Verhoeven *et al.* (2011). As precise K–Ar

dates for the interbedded lavas in the Tjörnes Formation have remained elusive, we can only constrain the fossil between the oldest and youngest available estimates for the age of the middle of the *Maetra* Zone. The minimum estimate (Einarsson *et al.* 1967; Albertsson 1978) for the age of these beds is 3.4 Ma, and the maximum is 4.63 Ma (Verhoeven *et al.* 2011). As such, we can conclude that the fossil whale IMNH 9598 (*cf.* *Eubalaena*) dates to the early Pliocene (4.63–3.4 Ma, Zanclean–Piacenzian).

Tjörnes facies description

The upper *Maetra* Zone and the *Serripes* Zone represent a shallow-water sublittoral setting. The mollusc fauna in the lower *Serripes* Zone is highly diverse relative to the *Tapes* and *Maetra* Zones, due to the immigration of Pacific and Arctic taxa in addition to the existing Atlantic fauna (Durham & MacNeil 1967; Norton 1975; Buchardt & Simonarson 2003). The bivalve shells in the upper *Maetra* Zone and the *Serripes* Zone are broken and disarticulated, indicating post-mortem transport and crushing of the shells in a high-energy coastal environment (Buchardt & Simonarson 2003). The whale described here came to rest and was buried in this near-shore environment.

Institutional abbreviations. IMNH, Icelandic Museum of Natural History; YPM, Yale Peabody Museum of Natural History.

MATERIAL AND METHOD

The specimen (IMNH 9598) was collected by a YPM crew in July 2011. The skull was discovered weathering out of a cliff, approximately 7 m above sea level. In order to excavate the specimen safely, the crew rappelled down the cliff from a fixed point c. 30 m above the specimen using technical climbing gear. Following a roughly two-week excavation, a pulley system was devised to safely lower the specimen to sea level from the site of the excavation. IMNH 9598 was prepared by Mr Brian T. Roach at the Yale Peabody Museum. Matrix was initially removed by using pneumatic air scribes and hand tools. Glue joins were made with Paraloid® B-72 (Rohm and Haas Co., Philadelphia, USA), an ethyl methacrylate and methyl acrylate copolymer, and this same material was also used in a more dilute form as a consolidant. Large cracks in the specimen were infilled with a mortar-like mixture of sifted matrix and 50% Paraloid® B-72 in acetone. Anatomical terminology follows Mead & Fordyce (2009).

SYSTEMATIC PALAEOLOGY

Order CETACEA Brisson, 1762

Suborder MYSTICETI Cope, 1891

Parvorder BALAENOMORPHA Geisler & Sanders, 2003

Family BALAENIDAE Gray, 1821

Genus EUBALAENA Gray, 1864

cf. EUBALAENA Gray, 1864

Description

IMNH 9598 (Fig. 2) consists of an isolated right squamosal preserving the zygomatic process, postglenoid process and supramastoid crest. The incomplete nature of this squamosal complicates the determination of its original orientation; as a result, it has been described in isolation using cardinal orientations that are universal among Mysticeti (e.g. medial/lateral in all other Mysticeti, vs anterior/posterior in Balaenidae) in order for the description to be readily comparable with other mysticetes.

The zygomatic process is relatively short, triangular in lateral outline, and transversely narrow. Posterior to the zygomatic the squamosal rapidly increases in dorsoventral depth owing to the large postglenoid process (ventrally) and the prominent supramastoid crest (dorsally); although the squamosal transversely tapers gently towards the zygomatic apex, it is generally transversely narrow along the proximodistal axis. A prominent supramastoid crest is developed dorsally with an arcuate dorsal margin; the supramastoid is medially inclined such that it obscures part of the posterior temporal wall in dorsal view, giving the medial surface a concave profile. The dorsal apex of the supramastoid crest is positioned at the level of the anterior margin of the postglenoid process and glenoid fossa; distally and proximally the supramastoid crest decreases in height. The postglenoid process is ventrally prominent and robust, and is situated posteroventrally to the concave glenoid fossa encircled by a distinct ridge. The postglenoid process is transversely thickened; the lateral margin of the postglenoid process is damaged but clearly forms the ventral apex of the squamosal and descends far ventral to the zygomatic process. The anterior margin of the glenoid fossa is formed as a robust ridge that is retracted somewhat dorsally from the broken lateral margin so that the glenoid fossa would have been obliquely oriented, facing ventromedially. The ventral margin of the squamosal between the zygomatic and postglenoid processes is slightly concave and forms a sharp ventral crest. The postglenoid process descends abruptly from the proximal squamosal; the posterior

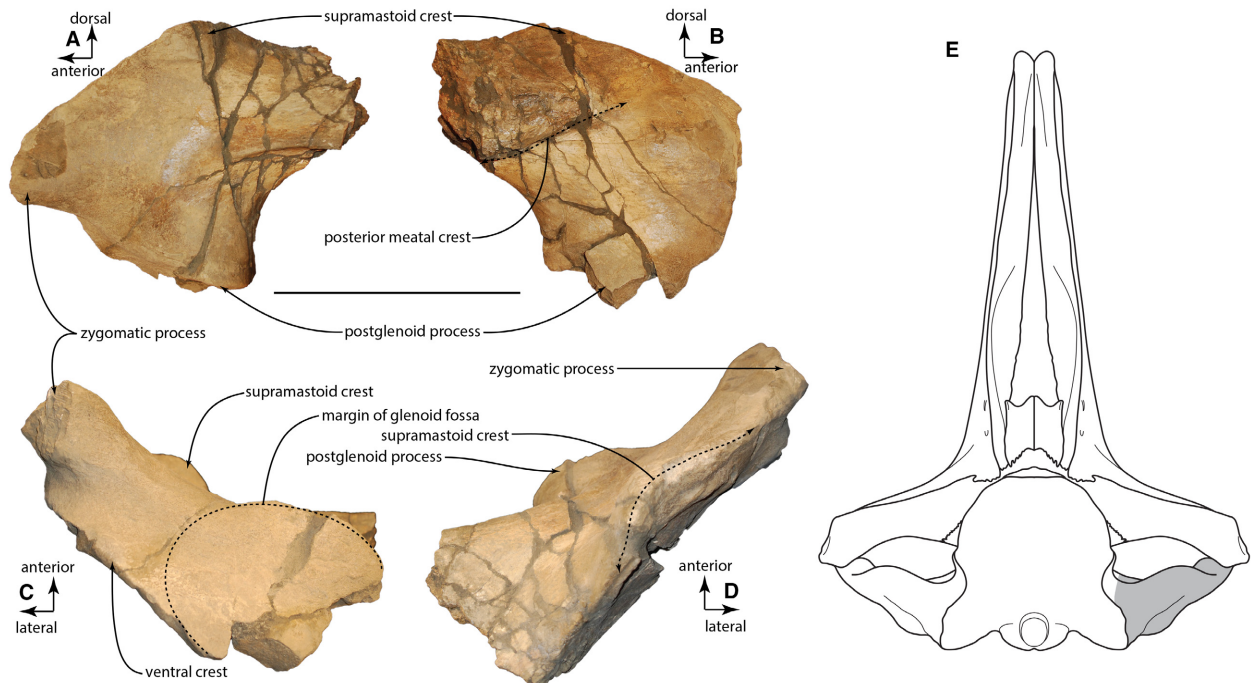


FIG. 2. Partial skull of *Eubalaena* sp., IMNH 9598. A, medial view. B, lateral view. C, ventral view. D, dorsal view. E, reconstruction. Scale bar represents 50 cm. Colour online.

margin of the postglenoid process is straight and vertical. Proximally, the squamosal is dorsoventrally shallow and abruptly increases in dorsoventral height owing to the postglenoid process and supramastoid crest. A horizontal, trough-like external acoustic meatus is present dorsal to the postglenoid process and is diffuse distally; the posterior meatal crest is positioned dorsally adjacent to the meatus and forms the ventral portion of a large robust lateral prominence.

IMNH 9598 exhibits a robust postglenoid process with distinct glenoid fossa, a short zygomatic process and a large arcuate supramastoid crest. These features are present only in modern and fossil Balaenidae (right whales) and clearly diagnose this specimen as a fossil balaenid. IMNH 9598 is similar in morphology and size to extant bowhead whales (*Balaena mysticetus*) and right whales (*Eubalaena* spp.), and can be readily distinguished from other Pliocene balaenids like *Balaenella* and *Balaenula* based upon its much greater size. IMNH 9598 differs from extant *Balaena mysticetus* in lacking a transversely expanded postglenoid process and ventrally facing glenoid fossa (= anteroposteriorly expanded when in articulation with the skull); instead, the glenoid fossa in IMNH 9598 faces anteromedially with a dorsally retracted medial margin of the glenoid fossa, and the squamosal is transversely narrow as in *Eubalaena* spp. The supramastoid crest is variable in *Balaena mysticetus*, but the apex of the crest is typically positioned medial to the postglenoid process whereas it is more prominent in *Eubalaena* with a

laterally shifted apex. Complete crania of *Eubalaena* and *Balaena* can be differentiated on the basis that in the former the supramastoid crest extends somewhat anteriorly and obscures the posterior wall of the temporal fossa and squamosal-parietal suture in dorsal view (Churchill *et al.* 2012); indeed, in IMNH 9598 the supramastoid crest is perhaps less prominent than in extant *Eubalaena*, and appears to have been anteriorly inclined. Owing to its large size, its distally positioned and anteriorly inclined supramastoid crest, and its obliquely oriented glenoid fossa and transversely narrow postglenoid process, IMNH 9598 is best identified as cf. *Eubalaena*.

DISCUSSION

Climatic conditions during Mactra Zone deposition

Many palaeoclimatic studies have focused on the middle Pliocene since the 1970s, and researchers generally agree that this period was the warmest of the last five million years (Shackleton & Opdyke 1977; Cronin 1991a, b; Chandler *et al.* 1994; Dowsett *et al.* 1994; Shackleton *et al.* 1995; Bucharth & Simonarson 2003). The isotopic analysis of Bucharth & Simonarson (2003) described the *Mactra* Zone as warm, with several temperature fluctuations. This agrees with earlier palynological conclusions (Schwarzbach & Pflug 1957), which suggested that the *Mactra* Zone represents the warmest interval in the

Tjörnes section. Bardarson (1925) suggested that temperatures in northern Iceland during *Maetra* Zone deposition were comparable to those surrounding the present-day British Isles.

Pliocene sea surface temperatures, and balaenid historical biogeography

Pliocene climate models indicate that North Atlantic temperatures at latitudes in which extinct *Balaena* and *Eubalaena* ranged (37.1–66.1°N; see Table 1) were warmer than the present day. These temperature differences are highest in latitudes south of present-day Iceland, where increased meridional heat transfer and changes in albedo due to reduced polar ice sheets (among other factors) may have influenced temperature fluctuations (Williams *et al.* 2009; Lawrence *et al.* 2010; Fedorov *et al.* 2013). Temperatures in Atlantic and North Atlantic latitudes from the early Pliocene to the ‘mid-Pliocene warm period’ are modeled to have ranged between 0 and 7°C, with the highest end of the range closest to an area extending from south of Iceland to the east coast of North America (Fedorov *et al.* 2013). These estimated palaeotemperatures are within the range of the preferred temperatures of modern balaenids based on their present distributions. Indeed, these temperatures are relatively cool compared to those of the modern winter calving grounds of some extant balaenids; for example,

Eubalaena glacialis off the coast of Florida (Nowak 2003; Bannister 2008).

Today, Iceland is positioned close to the northernmost extent of the range of *Eubalaena glacialis* (Fig. 3). Although the bowhead whale (*Balaena mysticetus*) only inhabits waters of the high arctic today, the southernmost records of *Balaena* extend far south of the location of our Icelandic specimen (e.g. *Balaena ricei*, from the Yorktown Formation of the eastern US). In addition to records of *Balaena* from the Pliocene of Italy, Belgium and elsewhere (and various temperate latitude occurrences of Pliocene *Eubalaena*), this indicates that these two clades with mostly non-overlapping modern distributions were perhaps broadly sympatric during the Pliocene, potentially highlighting greater climatic flexibility of Pliocene balaenids than is exhibited today. Indeed, these taxa appear to have been latitudinally separated in the Holocene and latest Pleistocene (Foote *et al.* 2013). Marine mammal assemblages from the Pliocene are noteworthy for including a mix of taxa closely allied with modern species (often in extant genera), bizarre taxa with novel adaptations, archaic taxa with smaller body sizes than extant relatives, and taxa with geographical ranges widely differing from extant relatives Boessenecker (2013). These observations are broadly applicable to Pliocene balaenids, which include strange or archaic dwarf taxa such as *Balaenella* and *Balaenula* (Bisconti 2005; Kimura 2009), extinct species in extant genera like *Balaena ricei* and *Eubalaena shinshuensis* (Westgate & Whitmore 2002; Kimura 2009)

TABLE 1. List of published Pliocene balaenid records from the north Atlantic and Mediterranean.

Taxon	Locality	References	Palaeolatitude
<i>Balaena ricei</i>	Rice’s Pit, Yorktown Fm., Virginia, USA	Westgate & Whitmore (2002)	37.1°N
<i>Balaenula</i> sp.	Lee Creek, Yorktown Fm., North Carolina, USA	Whitmore & Kaltenbach (2008)	35.4°N
<i>Balaena</i> sp.	Lee Creek, Yorktown Fm., North Carolina, USA	Whitmore & Kaltenbach (2008)	35.4°N
<i>Eubalaena</i> sp.	F and W Mine, Nashua Fm., Florida, USA	Morgan (1994)	28.4°N
<i>Balaenella brachyrhynchus</i>	Kallo, Kattendijk Fm., Belgium	Bisconti (2005)	51.4°N
<i>Eubalaena belgica</i>	Anvers, Lillo Fm., Belgium	Abel (1941)	51.3°N
<i>Balaenula balaenopsis</i>	Stuyvenberg, ‘Sables gris’, Belgium	van Beneden (1872)	51.3°N
<i>Balaenula balaenopsis</i>	Wommelgem, unnamed unit, Belgium	Misonne (1958)	51.3°N
<i>Balaenotus insignis</i>	Louvain and Stuyvenberg, unnamed units, Belgium	van Beneden (1872)	51.0–51.3°N
<i>Eubalaena</i> sp.	Rio Ricavo, Villamagna Fm., Italy	Bisconti (2002)	43.6°N
<i>Balaena</i> sp.	Capannoli, Villamagna Fm., Italy	Lawley (1876)	43.5°N
<i>Balaena</i> sp.	Volterra, unnamed unit, Italy	Bianucci & Landini (2005)	43.3°N
<i>Eubalaena</i> sp.	Montopoli, unnamed unit, Italy	Bianucci & Landini (2005)	43.6°N
<i>Balaenula astensis</i>	Portacomaro, unnamed unit, Italy	Trevisan (1942)	44.9°N
<i>Balaena montalionis</i>	Casina, unnamed unit, Italy	Capellini (1904)	44.4°N
‘ <i>Balaenula</i> ’ <i>praediolensis</i>	San Casciano dei Bagni, unnamed unit, Italy	Cuscani Politi (1961)	42.3°N
<i>Idiocetus guicciardinii</i>	Montopoli, unnamed unit, Italy	Capellini (1876)	43.6°N
<i>Balaena</i> sp.	Castellarano, unnamed unit, Italy	Danise & Dominici (2014)	44.5°N
<i>Balaena</i> sp.	Poggia Tagliato, unnamed unit, Italy	Borselli & Cozzini (1992)	43.6°N
cf. <i>Eubalaena</i> sp.	Tjörnes, Tjörnes Fm., Iceland	This study	66.1°N

The list has been restricted to diagnosable specimens and records identifiable to at least the genus level. Palaeolatitudes were retrieved from the Paleobiology Database (www.paleodb.org).

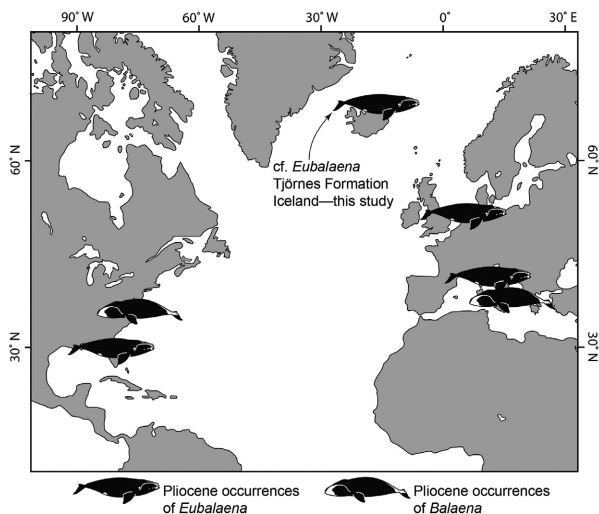


FIG. 3. Map illustrating all confirmed Pliocene fossil occurrences of balaenids in the north Atlantic. IMNH 9598 is the northernmost Pliocene balaenid recovered to date.

and multispecies assemblages from several regions, contrasting with non-sympatric extant populations (Fig. 3; Bisconti 2003; Whitmore & Kaltenbach 2008; Kimura 2009; Boessenecker 2013). Although it should be noted that modern balaenid distributions may have been altered by nineteenth century whaling, initial analysis of the North Atlantic Pleistocene–Holocene record of balaenids suggests that the latitudinal separation of *Balaena* and *Eubalaena* is not a recent phenomenon (Foote *et al.* 2013).

CONCLUSIONS

Although the Tjörnes beds have been studied extensively by geochronologists, invertebrate palaeontologists and palaeoclimatologists, they represent *terra incognita* for vertebrate palaeontologists. Preliminary vertebrate fossil prospecting of the Tjörnes beds has revealed a skull fragment of a large mysticete whale in the middle of the *Macra* Zone. This whale died in a high-energy nearshore environment, and dates from between 3.4 and 4.63 Ma. Ocean temperatures in northern Iceland at this time were considerably warmer than today. Our discovery of a partial *Eubalaena* skull in the Pliocene of Iceland highlights potential sympatry between *Eubalaena* and *Balaena* early in their evolutionary history; suggestive of greater climatic flexibility of Pliocene balaenids than is exhibited by the extant representatives of this clade.

This discovery identifies the Tjörnes Formation of northern Iceland as a potentially productive marine vertebrate fossil locality, and one that warrants further exploration by vertebrate palaeontologists. This locality may provide

previously elusive insights into Pliocene marine vertebrate communities and evolution at high latitudes of the north Atlantic. Given that pre-Quaternary marine mammal faunas are exceedingly rare from high latitude localities, comprising only a handful of localities worldwide (e.g. Vestfold Plains, Antarctica (Pliocene); Seymour Island, Antarctica (Eo-Oligocene); Dutch Harbor, Alaska (Miocene); and Gubik Formation, Alaska (Pliocene)), the addition of Iceland's Tjörnes Formation to this list has exciting potential to shed new light on marine vertebrate evolution during an understudied interval in Earth history.

Acknowledgements. Funding for this project was provided by National Geographic Society Young Explorer's Grant #EC0488-11, a Yale Field Ecology Pilot Grant, and the Lougheed Award of Distinction to DJF. DJF was supported by an NSERC Graduate Fellowship. RAR is presently supported by NSF (grants DEB 1331980 and PLR 134175). We thank M. D. Uhen for productive discussions, M. Fox and J. A. Gauthier for prioritizing the fossil's mechanical preparation, A. Fornal for assistance in the field, and B. T. Roach for expert preparation of this challenging specimen. M. D. Uhen and H. Ichishima provided helpful comments that substantially improved the manuscript.

Author contributions. Conceived and designed study: DJF, RB, RAR, JV. Contributed to fieldwork: DJF, LA, KJ, ADB, RAR, JV. Prepared manuscript: DJF, RB, RAR, AYH.

Editor. Hannah O'Regan

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