Field, D. J., Robert, B., Racicot, R. A., Ásbjörnsdottir, L., Jónasson, K., Hsiang, A., ... Vinther, J. (2017). The oldest marine vertebrate fossil from the volcanic island of Iceland: a partial right whale skull from the high latitude Pliocene Tjörnes Formation. *Palaeontology*, *60*(2), 141-148. https://doi.org/10.1111/pala.12275

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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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 geographic 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 (~4.5Ma), 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 (Buchardt and Simonarson 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 and Barnes 1994). This geological period also has potential to fill in gaps in the historical biogeographic record for extant cetacean subclades (Whitmore 1994; Fordyce 2002; Boessenecker 2013). Here, we report findings from the first vertebrate paleontology 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 stratigraphic 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 Mediterannean, and we provide a complete list reviewing this 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 biogeographic significance.

GEOLOGICAL SETTING

Overview of Tjörnes Geology

The fossil was discovered in a cliff on the west-facing edge of the Tjörnes Peninsula, in northeastern 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, and Höskuldsvík lavas, and the Quaternary Bredavík Group (Eiríksson 1981; Buchardt and Simonarson 2003). The fossil derives from close to the middle of the Tjörnes beds. Although these deposits exhibit a rich fossil mollusk 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 and Simonarson 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 500m of fossiliferous siliciclastic sediments, which are primarily made up of marine sandstones, with intermittent terrestrial/estuarine lignite beds and muddy sandstones (Buchardt and Simonarson 2003). Bardarson (1925) grouped this sequence into three biozones on the basis of their most abundant mollusk fossils; from oldest to youngest, these are the *Tapes* Zone, the *Mactra* Zone, and the *Serripes* Zone (Fig. 1). The whale fossil described here derives from the middle of the *Mactra* Zone (Fig. 1).

Dating the Tjörnes Beds and palaeoenvironment

Aronson and Saemundsson (1975) dated samples from the Kaldakvísl lava flows, which underlie the Tjörnes beds, to 9.9Ma ± 1.8Ma and 8.6Ma ± 0.4Ma, and Albertsson (1976) dated a lava flow in the lowermost part of the Tjörnes beds to 4.3Ma ± 0.17Ma. The Höskuldsvík Group, directly overlying the Tjörnes beds, was dated to 2.55Ma ± 0.27Ma (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 (Buchardt and Simonarson 2003; Verhoeven*, et al.* 2011; Einarsson *et al.* 1967; Albertsson 1978; Eiríksson *et al.* 1990), 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 and Simonarson 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 *Mactra* Zone. The minimum estimate (Einarsson*, et al.* 1967; Albertsson 1978) for the age of these beds is 3.4Ma, and the maximum is 4.63Ma (Verhoeven*, et al.* 2011). As such, we can conclude that the fossil whale IMNH 9598 (cf. *Eubalaena*) dates to the early Pliocene (4.63Ma-3.4Ma, Zanclean-Piacenzian).

Tjörnes facies description

The upper *Mactra* Zone and the *Serripes* Zone represent a shallow-water sublittoral setting. The mollusk fauna in the lower *Serripes* Zone is highly diverse relative to the *Tapes* and *Mactra* Zones, due to the immigration of Pacific and Arctic taxa in addition to the existing Atlantic fauna (Durham and MacNeil 1967; Norton 1975; Buchardt and Simonarson 2003). The bivalve shells in the upper *Mactra* 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 and Simonarson 2003). The whale described here came to rest and was buried in this nearshore environment.

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

MATERIALS AND METHODS

The specimen (IMNH 9598) was collected by a YPM crew in July 2011. The skull was discovered weathering out of a cliff, approximately 7 meters above sea level. In order to safely excavate the specimen, the crew rappelled down the cliff from a fixed point ~30m 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 Company), 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 and Fordyce (2009).

SYSTEMATIC PALAEONTOLOGY

Order CETACEA Brisson 1762
Suborder MYSTICETI Cope, 1891
Parvorder BALAENOMORPHA Geisler and 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 and lateral in all other Mysticeti, versus 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 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 paleoclimatic studies have focused on the middle Pliocene since the 1970's, and researchers generally agree that this period was the warmest of the last 5 million years (Shackleton and Opdyke 1977; Cronin 1991a, 1991b; Chandler *et al.* 1994; Dowsett *et al.* ; Shackleton *et al.* 1995; Buchardt and Simonarson 2003). The isotopic analysis of Buchardt and Símonarson (2003) described the *Mactra* Zone as warm, with several temperature fluctuations. This agrees with earlier palynological conclusions (Schwarzbach and 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 *Mactra* 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^{o} 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 (Fedorov *et al.* 2013; Lawrence *et al.* 2010; Williams *et al.* 2009). Temperatures in Atlantic-North Atlantic latitudes from the early Pliocene through the 'mid-Pliocene warm period' are modeled to have ranged between 0 and 7^{o} 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 paleotemperatures 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 (Bannister 2008; Nowak 2003).

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 United States). This – as well as records of *Balaena* from the Pliocene of Italy, Belgium, and elsewhere (in addition to various temperate latitude occurrences of Pliocene *Eubalaena*) – indicate 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 geographic 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 and Whitmore 2002; Kimura 2009), and multispecies assemblages from several regions, contrasting with non-sympatric extant populations (Fig. 3; Bisconti 2003; Whitmore Jr and Kaltenbach 2008; Kimura 2009; Boessenecker 2013). Although it should be noted that modern balaenid distributions may have been altered by 19th century whaling, initial analysis of the North Atlantic Pleistocene-Holocene record of balaenids suggests that the latitudinal separation of *Balaena* and *Eubalaena* is a not a recent phenomenon (Foote *et al.* 2013).

CONCLUSIONS

Although the Tjörnes beds have been studied extensively by geochronologists, invertebrate paleontologists, and paleoclimatologists, they represent *terra incognita* for vertebrate paleontologists. Preliminary vertebrate fossil prospecting of the Tjörnes beds has revealed a skull fragment of a large mysticete whale in the middle of the *Mactra* Zone. This whale died in a high-energy nearshore environment, and dates from between 3.4Ma and 4.63Ma. 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 paleontologists. 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.

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EXPLANATIONS OF FIGURES AND TABLES

TABLE 1. List of published Pliocene balaenid records from the north Atlantic and Mediterranean. The list has been restricted to 1) diagnosable specimens, and 2) records identifiable to at least the genus level. Paleolatitudes were retrieved from the Paleobiology Database (www.paleodb.org).

Taxon	Locality	Reference	Paleolatitude
Balaena ricei	Rice's Pit, Yorktown Fm., Virginia, USA	(Westgate and Whitmore, 2002)	37.1° N
Balaenula sp.	Lee Creek, Yorktown Fm., North Carolina, USA	(Whitmore and Kaltenbach, 2008)	35.4° N
Balaena sp.	Lee Creek, Yorktown Fm., North Carolina, USA	(Whitmore and Kaltenbach, 2008)	35.4° N
Eubalaena sp.	F and W Mine, Nashua Fm., Florida, USA	(Morgan 1994)	28.4° N
Balaenella brachyrhynus	Kallo, Kattendijk Fm., Belgium	(Bisconti, 2005)	51.4° N

Eubalaena belgica	Anvers, Lillo Fm., Belgium	(Abel 1941)	51.3° N
Balaenula balaenopsis	Stuyvenberg, "Sables gris", Belgium	(Van Beneden 1872)	51.3° N
Balaenula balaenopsis	Wommelgem, unnamed unit, Belgium	(Misonne 1958)	51.3° N
Balaenotus insignis	Louvain and Stuyvenberg, unnamed units, Belgium	(Van Beneden, 1872)	51.0-51.3° N
Eubalaena sp.	Rio Ricavo, Villamagna Fm., Italy	(Bisconti 2002)	43.6° N
Balaena sp.	Capannoli, Villamagna Fm., Italy	(Lawley 1876)	43.5° N
Balaena sp.	Volterra, unnamed unit, Italy	(Bianucci and Landini 2005)	43.3° N
Eubalaena sp.	Montopoli, unnamed unit, Italy	(Bianucci and Landini, 2005)	43.6° N
Balaenula astensis	Portacomaro, unnamed unit, Italy	(Trevisan 1942)	44.9° N
Balaena montalionis	Casina, unnamed unit, Italy	(Capellini 1904)	44.4° N
"Balaenula" praediolensis	San Casciano dei Bagni, unnamed unit, Italy	(Cuscani Politi 1961)	42.3° N
Idiocetus guicciardinii	Montopoli, unnamed unit, Italy	(Capellini 1876)	43.6° N

Balaena sp.	Castellarano, unnamed unit, Italy	(Danise and Dominici 2014)	44.5° N
Balaena sp.	Poggia Tagliato, unnamed unit, Italy	(Borselli and Cozzini 1992)	43.6° N
cf. *Eubalaena* sp.	Tjörnes, Tjörnes Fm., Iceland	(This study)	66.1° N

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 and Simonarson (2003). Arrows denote the stratigraphic and geographic 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 paleoenvironments. Shells denote layers with high densities of fossil mollusks.

FIG. 2. Partial skull of *Eubalaena* sp., IMNH 9598. A, medial view; B, lateral view; C, ventral view; D, dorsal view. Scale bar equals 50 cm.

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.