

Preliminary report on a late Tortonian/Messinian balaenopterid cetacean (Mammalia, Mysticeti) from Sistan and Baluchestan Province (Iran)

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Abstract

In this study we present the first description of a mysticete skeleton from the late Tortonian to Messinian greyish-green marl of the Coastal Makran, south of Negour in Chabahar County, Sistan and Baluchestan Province. This specimen is neither completely excavated, nor completely prepared, and therefore all our findings are preliminary. The identifiable components of this fossil thus far consist of an excellently preserved cranium, both dentaries which are partially obscured by the cranium and matrix, a partial vertebral column with a minimum of 15 vertebrae, and one flipper element. Preliminary evaluation of the cranium reveals some morphological similarities with that of the living blue whale, *Balaenoptera musculus* but also with “*Megaptera*” *miocaena* from the Tortonian of California (former E Pacific) of which the taxonomic status is still unclear. The new fossil specimen has both modern and ancient roqual characteristics, making the proper documentation of its anatomy of particular evolutionary importance.

Keywords: Upper Miocene, Coastal Makran, Cranium, Balaenopteridae, Iran.

Introduction

The partial skeleton of a baleen whale, discovered in 1989 by members of the Geological Survey of Iran consists of an exceptionally preserved cranium and two associated but slightly disarticulated dentaries. The postcranial remains, which include limb bones and elements of the vertebral column, are largely fragmentary. However, the vertebral elements are located in association *in situ*. Upon its discovery the skeleton was initially excavated, but only superficially, and subsequently protected with woollen blankets, layers of newspaper, plastic foil, and finally a layer of the surrounding sediment. Since its initial discovery and preliminary excavation, the whale skeleton has been awaiting complete recovery and scientific processing. In 2004, the Ministry of Industries and Mines and the Geological Survey of Iran facilitated the construction of a building to protect the fossil specimen (“Whale Fossil Museum”). The place of discovery is located in Sistan and Baluchestan Province, less than 4 km away from the Arabian Sea coast, south of the city of Negour, approximately 50 km west of the Iranian-Pakistanian border (Figure 1). This specimen will subsequently be referred to as the “Negour whale”,

or the Iranian whale to reflect the locality where it was discovered.

Based on preliminary morphological analysis, there is no doubt that the Negour whale belongs to the Balaenopteridae, a group that encompasses the modern roquals including the grey whales (Eschrichtiinae), and various extinct taxa (Marx & Fordyce, 2015; Marx & Kohno, 2016). However, it is important to note that the taxonomic position of the Eschrichtiinae is currently far from settled, as both molecular and morphology-based phylogenies are still hotly debated in literature and have yielded ambiguous results (e.g. Rychel *et al.*, 2004; McGowen *et al.*, 2009; Marx, 2011; Gol’din & Steeman, 2015, Árnason *et al.*, 2018). The Negour specimen does not display any morphological similarities with grey whales, so in that regard the comparisons are negligible; however, surprisingly closer morphological resemblance between the Negour cranium and the famous blue whale (*Balaenoptera musculus*) has persuaded us to publish this interim report.

Geological background

The site where the mysticete skeleton was found is located in a geologically active area (Figure 1). In

front of the south Iranian coast-line, the oceanic lithosphere of the Arabian plate is subducting northward under the Iranian Lut block and the Afghan Helmand block of the Eurasian plate (e.g. Stoneley, 1974; McCall & Kidd, 1982; Dercourt *et al.*, 1986; Byrne *et al.*, 1992). This subduction has caused one of the largest known accretion wedges in the world (Fruehn *et al.*, 1997). As a result of the aforementioned subduction, the Makran area has grown seawards by means of frontal accretion of the trench, which has been formed by the underplating of the oceanic crust of the Arabian plate since Miocene times (e.g. Schlüter *et al.*, 2002). The Makran prism, with the exception of the near-

coastal area, is covered discordantly by olistostromes containing large-scale igneous rocks and sedimentary blocks. The less deformed Coastal Makran is a wedge-top basin and has accumulated as a shallowing-upwards sequence from slope marls to coastal and continental deposits (Dolati, 2010).

The whale skeleton is embedded in a light greyish-green marl, which is correlated with the nannoplankton biozone NN11 (late Miocene: late Tortonian to Messinian, 9.0 – 7.0 Ma; Hadavi, 1992). This area belongs to the Coastal Makran, which contains late Miocene deposits of a former shallow shelf (Figure 2).



Figure 1. Simplified map of southeast Iran demonstrating the main geological/tectonic setting of the Makran deformation front with the subduction zone between Arabian (south) and Eurasian plates (north). The location of discovery of the whale skeleton is marked with a yellow underlaid cross south of the town of Negour.



Figure 2. Typical landscape of the Coastal Makran area showing a hill of the marl-dominated member of the Dar Pahn unit, NW of the locality where the mysticete skeleton was discovered. The age of the place here is correlated with the nannoplankton biozone NN11, but the member becomes younger than NN10 towards the coast line (Dolati, 2010). The photograph was shot from the site of discovery in northern direction. For scale: see power pylons on the right hand.

The sediments of the Dar Pahn Unit, which was introduced by McCall (1985), consist of a calcareous sandstone-dominated subunit and a marl-dominated subunit (see Dolati, 2010). The latter, in which the whale skeleton was found, consists of more than 70% marls with minor calcareous sandstones, and rare occurrences of gypsum (Dolati, 2010). The age was determined primarily on nannofossils of the haptophyte genera *Discoaster*, *Helicosphaera*, *Cyclococcolithus*, *Reticulofenestra*, and *Amaurolithus* (Hadavi, 1992; Dolati, 2010).

Material and Methods

In April 2012, a preliminary evaluation of the mysticete skeleton was undertaken in preparation for a future research project. The fossil, which was left *in situ*, was partially uncovered from the enclosing sediment, plastic foil and wool. Then, initial measurements (Figure 3) were taken using mechanical calipers and measuring tapes. Photographs were taken using a digital SLR camera (Nikon D300). The unfinished preparation of the specimen allowed initial description and preliminary systematic classification based on features of the cranium. The morphological comparisons of the cranium concentrate on other well-documented extinct balaenopterids of Miocene to Pliocene age, but this assessment also includes living species. Many balaenopterids have recently been studied with the help of morphometric methods (Hampe & Baszio, 2010; Tsai & Fordyce, 2014; Fahlke & Hampe, 2015).

Systematic Palaeontology

Class Mammalia Linné, 1758

Order Cetacea Brisson, 1762

Suborder Mysticeti Flower, 1864

Infraorder Chaemysticeti Mitchell, 1989

Parvorder Balaenomorphia Geisler & Sanders, 2003

Clade Plicogulae Geisler *et al.*, 2011

Superfamily Balaenopteroidea Gray, 1868

Family Balaenopteridae Gray, 1864

Genus et species indet.

Locality: N 25°13'38.53", E 61°6'38.88", South of Negour, Dashtyari District, Chabahar County, Sistan and Baluchestan Province, Iran.

Horizon and age: Dar Pahn Unit, Coastal Makran, NN11, late Tortonian to Messinian, late Miocene.

Referred material: complete cranium, both dentaries, 15 vertebrae, one metacarpal (or proximal phalanx).

General remarks and skull measurements

The cranium of the Negour whale is long and slender, with antero-posteriorly elongate supraorbital processes and remarkably short nasals. The rostral bones (premaxilla, maxilla) interdigitate with the frontals. The frontals are characterised by an abrupt depression from the median portion to a level distinctly lower than the vertex, which displays a typically balaenopterid condition (e.g. Marx *et al.* 2016). Overall, the cranium is well preserved with minimal distortion or damage.

The complete length of the cranium (condylo-basal length) was measured to be 2770 mm. The minimum width of the rostrum, obtained from the posterior third of the specimen, is 650 mm. The rostral length from the anterior margin of the nasals to the anterior tip of the premaxillae is 2100 mm, which covers 77% of the total length of the cranium. The bizygomatic width can be extrapolated to be about 1100 mm (Figure 3).

The overall length of the skeleton is roughly estimated to be about 8.3 m, based on the preserved skeletal parts as exposed in the field.

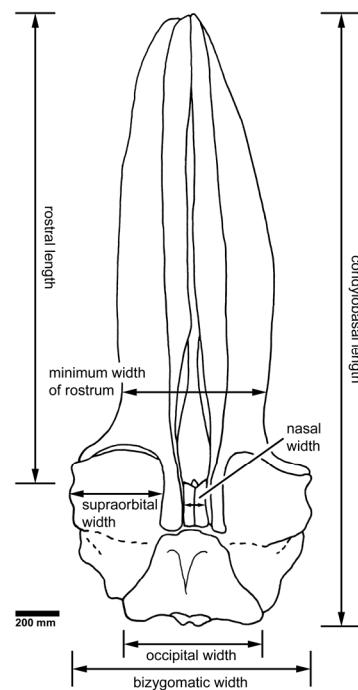


Figure 3. First approximate reconstruction of the uncovered dorsal aspect of the cranium based on a series of photographs, with measured sections indicated.

Premaxilla

In dorsal view, the premaxillae are slender, increasing in width for the anterior quarter of the

length, and terminating in a distinct tip (Figure 4A). The premaxillae are straight with no significant dorso-ventral distortion or curvature. The ascending processes of the premaxillae are thin and contact the nasals medially. However, the ascending processes of the premaxillae are wedged between the nasals and the ascending processes of the maxillae and are

not externally apparent about halfway across the nasal length. The premaxillae border the mesorostral fossa medially, which increases in width posteriorly, starting at the posterior fifth of the premaxilla, and reaches a depth of about 100 mm in front of the nasals.

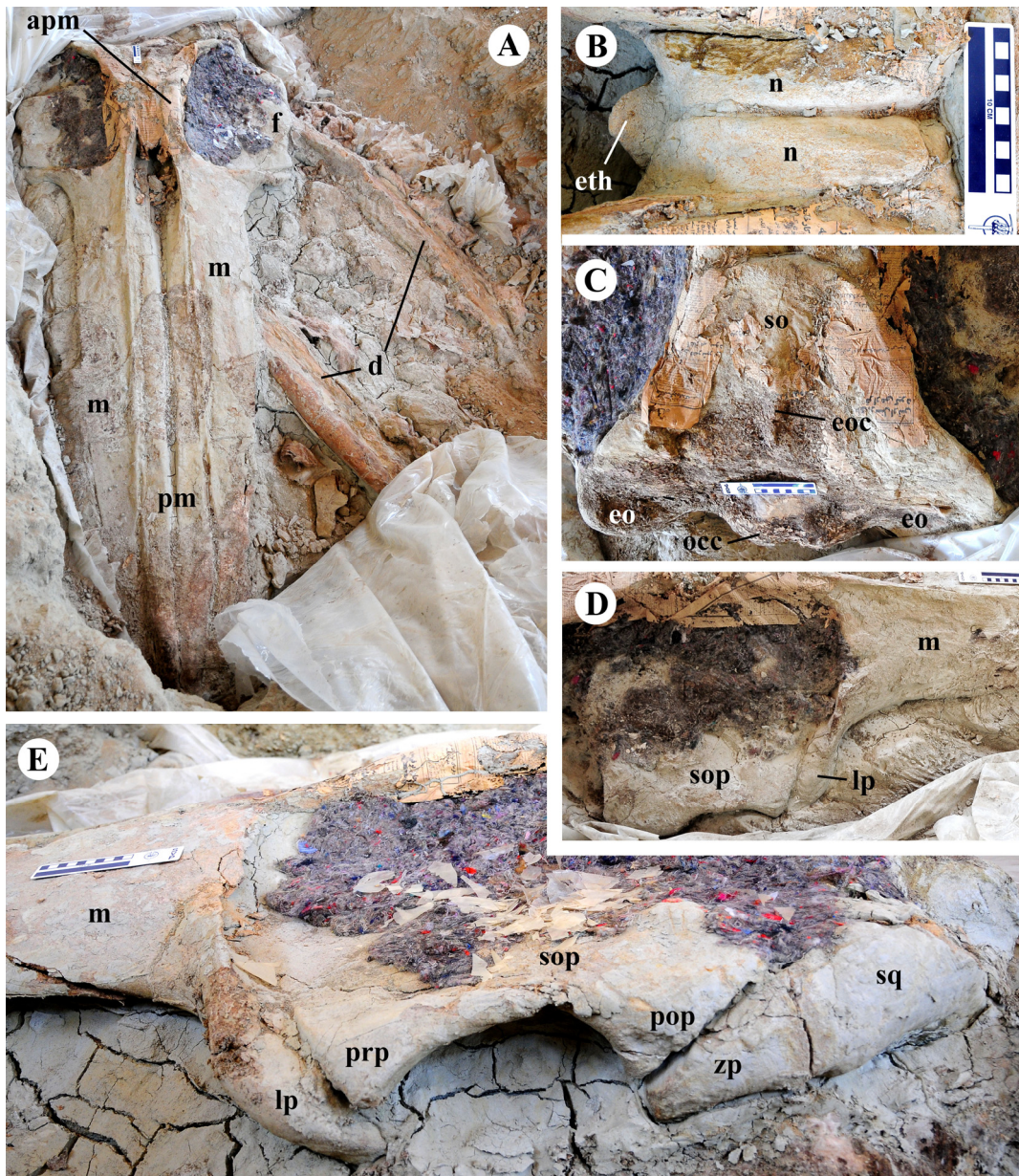


Figure 4. The mysticete fossil from the late Tortonian/Messinian of Negour; A- complete cranium with sheared off dentaries in anterodorsal view, B- detail of the nasals and protruding ethmoid bone in dorsal view, C- supraoccipital shield in dorsal view, D- right supraorbital process in dorsal view, E- cranial portion from the left side. Abbreviations: apm, ascending process (maxilla); d, dentary; eo, exoccipital portion; eoc, external occipital crest (supraoccipital); eth, ethmoid; f, frontal; lp, lateral process (maxilla); m, maxilla; n, nasal; occ, occipital condyles; pm, premaxilla; pop, postorbital process (frontal); prp, preorbital process (frontal); so, supraoccipital; sop, supraorbital process (frontal); sq, squamosal; zp, zygomatic process (squamosal).

Maxilla

The maxillae are straight, slender, and elongate anteriorly; these elements are barely distorted or damaged (Figure 4A). The lateral edges of the maxillae are slightly convex, converging and terminating in contact with the premaxillae at the anterior end of the rostrum (Figures 3, 5). The lateral edges of the maxillae are notably abraded for their anterior half. Each maxilla is characterised by a thick lateral process, which laterally rotates in a downward (ventral) direction to maintain contact with the preorbital process of the frontal bone. The posterior margin of the lateral process overlaps the proximal portion of the supraorbital process of the frontal, while the spoon-like broadened distal end of the lateral process curves ventrally under the preorbital process of the frontal (Figure 4E). A distinct antorbital notch is not developed – an even laterally concave course to the lateral process is documented on the left maxilla. Proximally, the

lateral process of the maxilla displays a blunt, transverse crest directed towards the anterior edge of the supraorbital process of the frontal (Figure 4E). A narrow cleft may be present between the lateral and supraorbital processes. However, this cannot be determined with certainty because of the incomplete preparation of the specimen.

The ascending processes of the maxillae are parallel to the midline of the cranium alongside the nasals, partly overlapping the ascending processes of the premaxillae. The ascending processes of the maxillae increase in thickness posteriorly prior to contacting the supraoccipital bone (Figure 4A).

A lacrimal was not identified in the exposed portion of this specimen.

Nasal

The Negour specimen preserves paired, short symmetrical nasals with a longer lateral (maxillary) margin and shorter medial (internasal) margin.

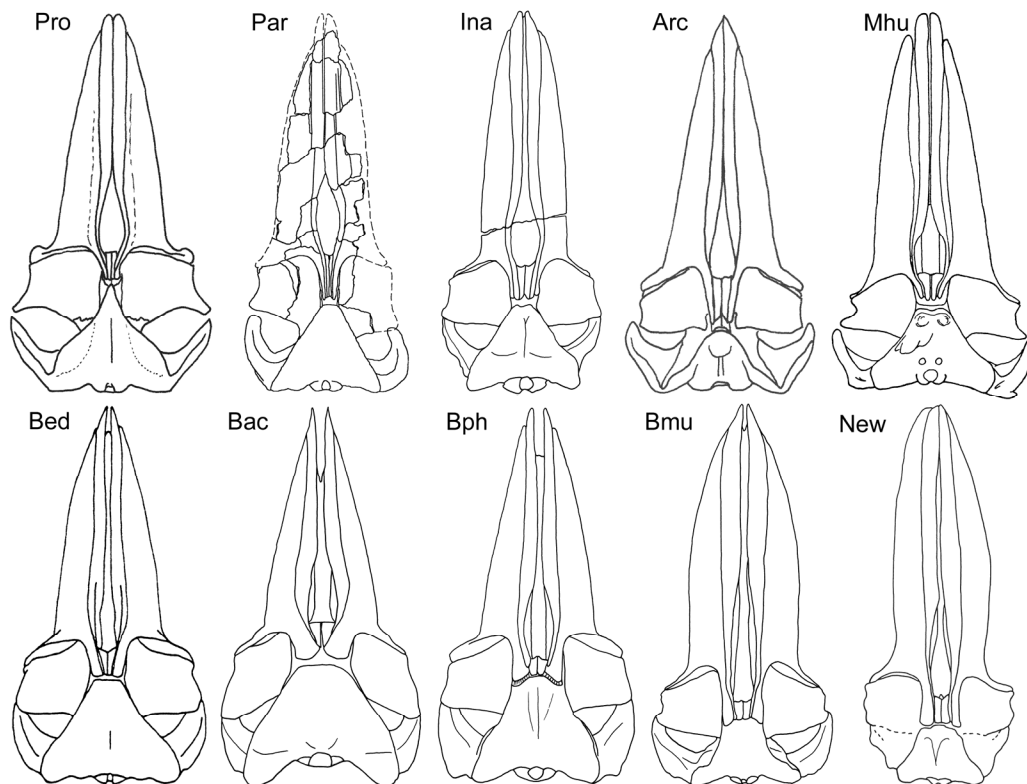


Figure 5. Balaenopterid crania in dorsal view. Note the position and shape of the ascending processes of the premaxillae and maxillae, the nasals, the supraorbital processes, and the supraoccipital shield. *Protororqualus cuvieri* (Pro) after Bisconti (2009), *Parabalaenoptera baulinensis* (Par) after Zeigler *et al.* (1997), *Incakujira anillodefuego* (Ina) after Marx & Kohno (2016), *Archaeobalaenoptera castriarquati* (Arc) after Bisconti (2009), “*Megaptera*” *hubachi* (Mhu) after Dathe (1983), *Balaenoptera edeni* (Bed) after Omura (1959), *Balaenoptera acutorostrata* (Bac) after Nakamura & Kato (2014), *Balaenoptera physalus* (Bph) after True (1904), *Balaenoptera musculus* (Bmu) after Brown (1995), and the Negour whale (New). The drawings are all scaled to the same condylobasal length.

Together, the anterior margins of the nasals form an angle of 240°. The total width of both nasals is 100 mm. Dorsally, the nasals are roughly trapezoidal in shape with posterior rounded edges, and a concave anterior border (Figure 4B). The posterior ends face the supraoccipital shield. There are no signs of a separate interparietal at this stage of preparation. The nasals and the ascending processes of the maxillae together form a slight elevation, which then makes up the highest point of the cranium (vertex). A portion of a bony element projects anterior to the nasals and is likely to be a portion of the ethmoid. Dorsally, this projection forms a slightly pointed, semilunar shape. This is an uncommon feature for mysticetes (Figure 4B).

Frontal

The frontals are large with their most characteristic feature being the supraorbital processes, which consist of broad and flat portions that project laterally from the median line of the cranium (Figure 4D). In lateral view, the supraorbital process forms a crescent shape, which borders the dorsal portion of the orbit. The crescent formed by the supraorbital process is anteriorly and posteriorly confined by the preorbital and postorbital processes respectively (Figure 4E). The preorbital process is short, only slightly bending ventrally, whereas the postorbital process is somewhat longer and ends in a point that is oriented anteroventrally. The ends of both pre- and postorbital processes are composed of thicker bone, in comparison to the rest of the supraorbital region. The frontals, which are excluded from the vertex, show an abrupt depression from the median portion to a level distinctly lower than the vertex (Figure 4A, E). The dorsal outline of the frontals reveals a posterior margin perpendicular to the sagittal plane and a backward oriented anterior margin (Figure 4D). The transverse width of the left supraorbital process was measured at 520 mm.

Squamosal

The massive squamosal bones are not completely uncovered from sediment. The visible portion of the squamosals reveals a thick zygomatic process, which gradually tapers anteriorly and forms a portion of the posterior edge of the orbit (Figure 4E). The zygomatic processes terminate more or less at the same level as the anterior margin of the supraoccipital.

The postglenoid process has a consistent

semicircular rounded inferior angle and is not very extended ventrally. Nothing can be said about the parietal at this stage of preparation and the probably delicate jugals could not be viewed.

The dimensions of the temporal fossa are not yet determined due to obstruction by sediment that is yet to be removed from the back portion of the cranium.

Supraoccipital

The dorsal outline of the supraoccipital shield is trapezoidal with the anterior margin being narrower than the posterior. The relatively broad anterior margin of the supraoccipital has a somewhat wavy course (Figure 4C) and terminates at about at the same level as the point where the zygomatic processes terminate. The lateral margins (nuchal crests) show a slightly concave edge. The nuchal plane is moderately depressed with an external occipital crest on the upper part beginning about halfway through the element (Figure 4C). The lower portion of the supraoccipital overhangs the parietal and squamosal regions and is fused with the exoccipitals. The maximum width of the occipital complex is 800 mm.

Exoccipital

The occipital condyles are thick and reniform bony elements at the most posterior end of the cranium and surround the foramen magnum. Laterally, the posteriorly swollen paroccipital processes protrude distinctly.

Dentary

Both the dentaries are preserved, but are slightly disarticulated. Left and right dentaries are parallel to each other and make an angle of about 35°–40° with the cranium (Figure 4A). The posterior portions of the dentaries are hidden below the cranium. Without further preparation nothing can be said about the development of the coronoid portion. An appreciation of the full morphology of the lower jaw element is important for the interpretation of the possible feeding strategies (for example, the shape of the jaws can be informative to the development of muscles, as well as the range of gape, see Lambertsen *et al.*, 1995; Bouetel 2005). The anterior rami are found with their dorsal side up and exhibit elliptical gingival foramina that open anteriorly. The maximum width of the right dentary is 170 mm.

Postcranium

The incomplete excavation of this specimen limits our knowledge of the postcranial material. Preliminarily, we can see that the vertebral column seems to be incomplete with a minimum of 15 vertebrae. Here, the vertebral bodies are preserved. Some of the transverse processes and neural spines are intact, whereas others are incomplete or damaged. One metacarpal or proximal phalanx of the flipper skeleton could be identified. No further details can be described here due to the unprepared nature of the specimen.

Discussion

The Negour whale doubtlessly belongs to the Balaenopteridae, a family that includes the extant rorquals (blue whale, fin whale, sei whale, etc.), and therefore is one of the oldest known fossil representatives of the group (Table 1). Characters which qualify the Negour whale as a balaenopterid are: the interdigitating of the rostral bones with the frontals, an abrupt depression of the frontals from the median portion to a level distinctly lower than the vertex, and remarkably short nasals, which are clearly observable in spite of the incomplete preparation of the specimen (e.g. True, 1912; Steeman 2007; Marx *et al.*, 2016). There are several extinct balaenopterid species known to date from the eastern Pacific area (Repenning & Tedford, 1977; Dathe, 1983; Pilleri, 1989; Whitmore, 1994; Zeigler *et al.*, 1997; Deméré *et al.*, 2005; Boessenecker, 2013; Marx & Kohno, 2016), two

from the North Sea Basin (Behrmann, 1995; Bosselaers & Post, 2010; Hampe & Baszio, 2010), and two notable, well preserved and comparable forms from the Mediterranean (Bisconti, 2005, 2007). Despite the current preparation stage, the Negour whale can indeed be compared with other well-known balaenopterid species.

We start the comparisons to the Negour whale with fossils known from the Pacific realm. Here we find, according to the current state of knowledge, the so far second oldest known balaenopterid, *Balaenoptera ryani* from the early late Miocene of California (after Deméré *et al.*, 2005), which is only documented by its occipital region. The supraoccipital of *B. ryani* seems to have a convex course of nuchal crests overhanging the parietals and a more rounded and pointed anterior margin (Hanna & McLellan, 1924: pl. 5), a characteristic that is different from that found in the Negour whale.

The recently described balaenopterid *Incakujira anillodefuego* from the Peruvian Pisco Formation (after radiometric methods 8 – 7.3 Ma old) is extremely well preserved and known from two specimens (Marx & Kohno, 2016). *I. anillodefuego* has a slender cranium with several similarities to the Negour whale specimen. The outline of the supraorbital processes along with the presence of an external occipital crest on the supraoccipital are features that are similar to those found in the Negour whale (Figure 5).

Table 1. Distribution and stratigraphic age of balaenopterid fossils discussed in the present study. References for the ages are indicated in the text.

Species	Habitat	Locality	Age (in Ma)
<i>Balaenoptera physalus</i>	all oceans of the world	California (fossil)	since 1.3
<i>Balaenoptera bertae</i>	Pacific Ocean	California	3.35-2.5
<i>Protororqualus cuvieri</i>	West Mediterranean Sea	N Italy	middle-late Pliocene
<i>Archaebalaenoptera castriarquati</i>	West Mediterranean Sea	N Italy	3.6-3.1
<i>Diunatans luctoretmergo</i>	North Sea Basin (Atlantic)	Netherlands	5.0-4.4
" <i>Megaptera</i> " <i>hubachi</i>	Pacific Ocean	Chile	5.3-3.6
<i>Parabalaenoptera baulinensis</i>	Pacific Ocean	California	7.6-6.7
<i>Megaptera miocaena</i>	Pacific Ocean	California	7.6-7.3
<i>Incakujira anillodefuego</i>	Pacific Ocean	Peru	8.0-7.3
<i>Balaenoptera siberi</i>	Pacific Ocean	Peru	8.0-7.0
Negour whale	Arabian Sea (Indian Ocean)	Iran	9.0-7.0
<i>Balaenoptera ryani</i>	Pacific Ocean	California	11.6-9.5
<i>Praemegaptera pampauensis</i>	North Sea Basin (Atlantic)	N Germany	11.8-10.6

I. anillodefuego differs greatly from the Negour whale in having thicker ascending processes of the premaxillae, a broader mesorostral fossa, nasals with longer internasal margins plus concave emarginated anterior margins, a narrower anterior margin of the supraoccipital, more ventrally extended postglenoid process, and distinctly open layered interparietal between the frontal and the supraoccipital on the vertex (Marx & Kohno, 2016: figs. 5-8).

Pilleri (1989) described *Balaenoptera siberi* from the late Miocene (8.0 – 7.0 Ma) of Aguada de Lomas, Peru. This species has a longer cranial portion than the Negour specimen and the anterior margin of the supraoccipital is rounded. The nasals of the Peruvian species are also short but are characterised by longer internasal margins. Another notable difference between *B. siberi* and the Negour whale is the presence of a broader mesorostral fossa in the former. The structure of the vertex and the general shape of the supraorbital process of the frontal are quite similar in the aforementioned specimens.

“*Megaptera*” *miocaena*, discovered in Lompoc, Santa Barbara Co., California, is only known from cranial material as the rostrum is not preserved. Marx & Fordyce (2015) interpret this species as a basal relative to both living rorquals and grey whales due to various character combinations. The age of the “*Megaptera*” *miocaena* fossil was a matter of some debate in the past: while some authorities (Whitmore, 1994), consider the sediments to be at 12 – 10 Ma old, Repenning & Tedford (1977:24) conclude that the age is even younger with 10 – 9 Ma. Boessenecker (2013:939) recently found additional material (ear bones) of “*Megaptera*” *miocaena* in younger formations (6.9 – 1.8 Ma). Finally, Marx & Fordyce (2015: supplementary material) present a convincing summary of the geological data available and suggest a time interval between 7.6 and 7.3 Ma for this fossil. The anterior margin of the supraoccipital of the Negour whale is reminiscent of that of “*Megaptera*” *miocaena*, whereas in the Californian taxon the anterior margin differs by clearly exceeding the level of the anterior end of the zygomatic processes. The nasals of “*Megaptera*” *miocaena* are similar to the Negour whale in also showing a shorter internasal margin. The squamosal of “*Megaptera*” *miocaena* has a more ventrally extended postglenoid process (Kellogg, 1922: pl. 4) in comparison to the Negour specimen.

Parabalaenoptera baulinensis, which is known from the late Miocene (7.6 – 6.7 Ma) of California (Zeigler et al., 1997), does not seem to have a close relationship with the Negour whale. The rostrum of *Parabalaenoptera* has large sections missing and lateral margins of the maxillae are mostly abraded, and therefore not comparable to that of the Negour specimen, due to its poor preservation (Figure 5). The preserved ascending processes of the maxillae of *Parabalaenoptera* are more slender and the nasals are distinctly long and narrow, an unusual feature for a balaenopterid, regarded as being a primitive character state in the literature (Zeigler et al., 1997: figs. 3, 6). Another notable difference to the Negour whale is at the level of cranial proportions; *Parabalaenoptera* has a longer cranial portion in comparison to the rostral portion (for cranial/rostral lengths, see Bouetel & Muizon, 2006). The anterior margin of the supraoccipital in *Parabalaenoptera* is narrower than that of the Negour specimen. Similarities between the specimens are mostly found in the squamosal bone, where the robust zygomatic process and the short postglenoid process are comparable.

The early Pliocene “*Megaptera*” *hubachi* from Chile (Dathe, 1983; Bisconti, 2010; Hampe et al., 2014) has a rather similar shape of the supraoccipital to that of the Negour whale, but with a median concave indentation of the anterior margin (Figure 5). The surface structure of the “*Megaptera*” *hubachi* supraoccipital is different as it lacks an external occipital crest, but it has a pair of round parasagittal condyloid fossae anterior to the occipital condyles (Dathe, 1983: pls. I, II). The mesorostral fossa of “*Megaptera*” *hubachi* is quite short, making up slightly less than ¼ of the length of the entire rostrum, but broader than in the Negour specimen because the medial margins of premaxillae and maxillae diverge outward in front of the nasals. The nasals of “*Megaptera*” *hubachi* differ morphologically from those of the Negour specimen in morphology as they become distinctly broader anteriorly. The general shape of the supraorbital process of “*Megaptera*” *hubachi* is typically balaenopterid. It is notable that the postorbital process projects more laterally (Bisconti, 2010: figs. 5, 8) than that of the Negour whale. The generic affiliation of the “*Megaptera*” *hubachi* specimen is still unresolved as Deméré et al. (2005) were unable to document any apomorphic characters of the living *Megaptera novaeangliae* in the Chilean species. Furthermore, *Megaptera* has

ben recently identified as a paraphyletic taxon (Marx & Kohno, 2016).

Represented by a partial cranium, *Balaenoptera bertae* from the early to late Pliocene (3.35 – 2.5 Ma; Piacenzian-Gelasian) of California is another balaenopterid from the west coast of North America (Boessenecker, 2013). This specimen includes a cranial portion made up of the occiput, a forwardly-directed vomer, and incomplete zygomatic and supraorbital processes on the right side. Only the supraoccipital shield of *B. bertae* is comparable with the Negour whale at this stage. The *B. bertae* specimen does not display an external occipital crest, but rather a pair of parasagittal tubercles (Boessenecker, 2013: fig. 11), which are reminiscent to the eschrichtiid condition. The parietals in *B. bertae* are visible in front of the anterior margin of the supraoccipital, whereas this is not the case in the Negour specimen. The anterior margin of the supraoccipital is also somewhat broader in the Negour whale.

An unnamed balaenopterid from the late Miocene of Miyako Island, Okinawa, Japan (Kimura *et al.*, 2015: pl. 1) reveals the abruptly depressed supraorbital process, but is hardly comparable with the Negour whale because of its poor preservation condition. Oishi *et al.* (1985: fig. 5, pl. 3) presented evidence for further Pliocene balaenopterid whale remains from Iwate Prefecture, Japan, but this material from the western Pacific awaits further investigation.

Basal but younger members of the Balaenopteridae are known from the Mediterranean (e.g., Marx, 2011; Bisconti & Bosselaers, 2016). The North Italian *Archaeobalaenoptera castriarquati* is younger than 3.5 Ma (Piacenzian) and has a few similarities with the Negour whale. The Negour specimen and *Archaeobalaenoptera* are similar in having a short open mesorostral fossa in front of the nasals, the typical shape of supraorbital processes with abrupt vertical depression from the vertex, and the presence of an external occipital crest on the supraoccipital (Figure 5). *Archaeobalaenoptera* differs from the Negour whale by its extremely elongated nasals and the presence of a pair of prominent tubercles usually observed in some cetotheres and in eschrichtiids (Bisconti, 2007: figs. 4, 5). However, it must be mentioned that the elongate nasals of *Archaeobalaenoptera* display a shorter internasal margin opposite to the lateral margin. This character is unique and apart from that genus, only documented in the living blue whale (*B. musculus*),

the Negour whale, and, partially, in Bryde's whale (*B. edeni*).

The species *Protororqualus cuvieri* was revised by Bisconti (2005). This was done solely from previous descriptions and figures, as the only known specimen of the species was destroyed during WWII. *P. cuvieri* bears no resemblance to the Negour whale, and therefore is unlikely to be closely related. This North Italian specimen is a young representative (middle-late Pliocene) of the Balaenopteridae, bearing some primitive characters, and differs from the Negour whale by having the following features: a more tapered rostrum, a triangular supraoccipital with a pointed anterior margin, and strong attachment sites on the supraoccipital for the neck musculature (Figure 5). Unlike the Negour whale, *Protororqualus* has no crest on the supraoccipital but rather a longitudinal furrow. In *Protororqualus* the postorbital process of the frontal is prominently developed and directs outwards and backward (Figure 5). The nasals of *Protororqualus* have concave anterior margins, as documented in the figures by Van Beneden (1875, as *Plesiocetus cortesii*) and Strobel (1881, as *Cetotherium cuvieri*). The end of the infraorbital process of the maxilla is thicker in *Protororqualus* than the one found in the Negour whale. The stronger outward divergence of the zygomatic process is another important difference between *Protororqualus* and the Iranian specimen (Figure 5). Other extinct balaenopterids are documented from the North Sea embayment. *Praemegaptera pampauensis* seems to be the oldest known so far and comes from the Serravallian/Tortonian boundary of the Groß Pampau locality of North Germany. *P. pampauensis* was originally erected by Behrmann (1995), on what later proved to be insufficient evidence for a diagnosis (Hampe, 1999). *Praemegaptera* differs from the Negour whale in the following characters: the mesorostral fossa is relatively longer, the ascending process of the maxilla is very short, the supraorbital processes are also significantly shorter – however, they do exhibit the typical abrupt depression from the vertex (balaenopterid condition) – and the postorbital process projects backwards. Furthermore, unlike the Negour whale, the supraoccipital in *Praemegaptera* is depressed on its dorsal surface with a triangular shape and an anteriorly pointed apex, like that documented in *Protororqualus* (Hampe & Baszio, 2010). Ultimately, *Praemegaptera* combines both modern

balaenopterid and primitive, “stem-balaenopterid” characters and is not comparable to the Negour whale.

Diunatans luctoretemergo from the early Pliocene (Zanclean stage) of the Netherlands is only known from an incomplete cranium comprising the occipital portion of the skull. The anterior margin of the supraoccipital in *Diunatans* is similar to that in the Negour specimen, but the ventrally deep postglenoid process is distinctly different (Bosselaers & Post, 2010: fig. 5). Overall, the *Diunatans* specimen is difficult to compare to the Negour whale due to its incompleteness.

The Negour whale shows a number of characters in common with the living blue whale *Balaenoptera musculus*, famous for being the largest animal in the history of the Earth in terms of both size (the largest recorded individual was 33.58 m long; Risting, 1922) and weight (heaviest individual is a 190 t female; Tomilin, 1957). The Negour specimen shares the following similarities with the blue whale: convex lateral margins of the rostrum (maxillae), a laterally prominent postorbital process, zygomatic processes that end approximately at the same level as the anterior margin of the supraoccipital, and nasals that are positioned far behind the anterior margin of the supraorbital process of the frontal (Figure 5). Further similarities include the supraoccipital shield which is isosceles trapezoidal in shape with a broad and wavy rounded anterior margin. In both the aforementioned whales the supraoccipital is dorsomedially moderately depressed. The lateral margins of the supraoccipital are slightly concave, a feature also seen in “*Megaptera*” *hubachi* and *Balaenoptera omurai*. The proportionally long rostrum is another similarity between the blue whale (78% of the condylobasal length) and Negour whale (77% of the condylobasal length; see Table 2). However, unlike the Negour specimen, the blue whale develops no recognizable external occipital crest (Yochem & Leatherwood, 1985: fig. 7; Brown, 1995: fig. 150). Lastly, some features cannot be directly compared due to the incomplete preparation of the Negour whale. For example, the supraoccipital contacts the nasals in the blue whale but this feature is not yet clear in the Negour whale. *Balaenoptera physalus*, also known as the fin whale, is distributed predominantly in polar and temperate zones, and most recently known from Pleistocene deposits of northern California; Tsai & Boessenecker (2017) discovered a fossil tympanic

bullula with an attached malleus and attributed it to the species.

Table 2. Rostral length of Balaenopteridae in relation to the condylobasal length of the cranium (in percentage), demonstrating a close resemblance of the Negour whale with the living blue whale. Calculations are based on depictions and reconstructions after True (1904), Andrews (1916), Omura (1959), Dathe (1983), Pilleri (1989), Brown (1995), Zeigler et al. (1997), Bisconti (2009), Nakamura & Kato (2014), and Marx & Kohno (2016).

Species	Ratio L rostrum : L condylobasal
<i>Balaenoptera musculus</i>	78%
Negour whale	77%
<i>Archaeobalaenoptera castriarquati</i>	71%
" <i>Megaptera</i> " <i>hubachi</i>	70%
<i>Balaenoptera physalus</i>	67%
<i>Incakujira anillodefuego</i>	67%
<i>Balaenoptera siberi</i>	66%
<i>Protororqualus cuvieri</i>	66%
<i>Megaptera novaeangliae</i>	65%
<i>Balaenoptera edeni</i>	64%
<i>Parabalaenoptera baulinensis</i>	64%
<i>Balaenoptera borealis</i>	61%
<i>Balaenoptera acutorostrata</i>	60%

The fin whale differs from the Negour specimen in having extremely short and pointed nasals, which possess longer internasal margins, and rostral bones that form a triangular pattern with straight lateral maxillary margins (Figure 5). In the fin whale, the cranial portion of the skull is proportionally larger than in the Negour whale or the blue whale. The Negour whale and the fin whale both share the following characters: nasals that are located more posteriorly, the general shape of the supraoccipital which has a broad, wavy anterior margin, and an external occipital crest (True, 1904: pl. 1, fig. 3). It is also important to note that the blue and fin whales are capable of hybridizing (Árnason et al., 1991; Spilliaert et al., 1991; Árnason & Gullberg, 1993), which complicates morphological characterization as the hybrids may exhibit a gradient of morphological characteristics.

The minke whale *Balaenoptera acutorostrata* has been well documented by Nakamura & Kato (2014), who investigated 144 crania from the North Pacific population. There were no significant differences in the morphology of the crania between sexes or individual ages, except for the width of the supraoccipital and exoccipital bones. However, it is

important to mention that different subgroups of minke whales exist worldwide, possibly representing different subspecies or even species (Rice, 1998; Sokolov & Arsen'ev, 2006; Pastene et al., 2007; Perrin & Brownell, 2009). Therefore, it may be that the sample mentioned here does not encompass the full morphological diversity shown by minke whales. In contrast to the Negour whale, the minke whales of the well documented North Pacific population have a posteriorly-shifted supraorbital process (parallelogram in dorsal view; see also True, 1904: pl. 22, fig. 1). Further differences include the rostrum, which is sharply pointed in the minke whale, the nasals, which have longer internasal margins, and the exoccipital portions, which are more prominent than those in the Negour whale. In *Balaenoptera acutorostrata* the nasals are strongly triangular with broad anterior margins and a pointed posterior end, and the ascending processes of the maxillae diverge medially and are transversely wide (Figure 5).

The Bryde's whale *Balaenoptera edeni*, living in the subtropics and tropics, has nasals which seem to be intraspecifically inconsistent in their shape. Wada et al. (2003: fig. 1g-i) documented a range of variation which limits discussion here. Differences include the straight anterior margin of the supraoccipital and the more pointed rostrum of Bryde's whale in comparison to the Negour whale. The pointed rostrum of Bryde's whale is attributed to premaxillae as they extend the length of the adjacent maxillae (Kellogg, 1928: fig. 2; Omura, 1959: pl. 1, fig. 1), a character found in many other mysticetes, including the blue whale (Figure 5).

The sei whale, *Balaenoptera borealis* is different from the Negour whale in having a pointed rostrum, straight lateral margins of the maxillae, large cranial portion relative to the total skull length, a supraoccipital with a completely rounded anterior end, and pointed nasals with longer or equal internasal margins (Andrews, 1916: pl. XLI).

Omura's whale *Balaenoptera omurai* can be distinguished from the Negour whale by its possession of very broad, medially-expanded ascending processes of the maxillae (Wada et al., 2003: fig. 1a, f).

The humpback whale *Megaptera novaeangliae* differs from the Negour specimen in having distinctly laterally-projecting supraorbital processes (Martin, 1995). The orbit in humpback whales appears to be short, a feature caused by the straight posterior margin and the distinctly concave anterior

margin of the frontal (True, 1904: pl. 29, fig. 2). The nasals in *M. novaeangliae* also differ from those in the Negour whale as they have a longer internasal margin which forms a pointed, arrow-like anterior tip. Humpback whales develop an external occipital crest on the supraoccipital surface starting at the vertex and reaching the foramen magnum.

In summary, the Negour whale cranium shares a number of morphological features with that of the blue whale. The most important of these include: the convex lateral margins of the maxillae, a laterally prominent postorbital process in dorsal view, the position of the nasals distinctly behind the anterior margin of the supraorbital process, and the zygomatic process which ends approximately at the same level as the anterior margin of the supraoccipital. However, it has to be kept in mind, that the blue whale is divided into three subspecies with different geographical habitats (Yochem & Leatherwood, 1985), and that there may be differences in cranial morphology between them.

It is worth repeating that the Negour whale also shares several features with the fin whale. These include the more posteriorly located nasals distinctly behind the level of the proximal part of the anterior margin of the supraorbital processes, the broad, wavy anterior margin of the supraoccipital, and the presence of an external occipital crest.

The similarities between the Negour whale and the Tortonian "*Megaptera*" *miocaena*, are quite peculiar. Unfortunately, "*Megaptera*" *miocaena* is only known by an incomplete cranial portion of the skull, and well-preserved right ear bones (periotic and tympanic bulla). The Negour whale and "*Megaptera*" *miocaena* have a similarly shaped anterior margin of the supraoccipital, but the anterior margin exceeds the level of the anterior end of the zygomatic processes in "*Megaptera*" *miocaena*. The nasals in "*Megaptera*" *miocaena* are similar with those in the Negour specimen as they have a short internasal margin. With other balaenopterids there are only minor similarities to the Negour whale, such as a broader anterior margin of the supraoccipital, a character which occurs in a number of other taxa as well: the living representatives of *Balaenoptera* and *Megaptera* in addition to "*Megaptera*" *miocaena*, "*Megaptera*" *hubachi*, *Incakujira anillodefuego*, and *Diunatans lucoretmergo*.

The complete recovery and preparation of the Negour whale specimen will allow a more detailed

description of both the cranial, and postcranial material. This additional information is critical for analysing the morphological characters of this taxon, and for generating a proper diagnosis.

Conclusions and prospects

Our initial appraisal of the find demonstrates similarities with the extant blue whale, of which to date no fossil record is documented. When later completely removed and prepared, the Negour whale may show additional morphological characters of importance, the ventral aspect of the cranium for example, which could contribute further to the discussion concerning the early evolution of the Balaenopteridae and *Balaenoptera*-related forms. The specimen described above was discovered in an area which is not otherwise known for finds of fossil cetaceans. It belongs, with a stratigraphic age of about 9 – 7 Ma, to the oldest known balaenopterids in the fossil record. The phylogenetic split of the crown balaenopterids is estimated to have occurred already by about 19.5 Ma (Marx & Fordyce, 2015; 19.3 ± 2.9 Ma after Sasaki *et al.*, 2005). In addition, the suggested appearance of *Balaenoptera* at the Miocene-Pliocene boundary implies that *B. ryani* (11.6 – 9.5 Ma) may not belong to the genus as already proposed by Deméré *et al.* (2005) and Tsai & Boessenecker (2017). Even *B. siberi*, with an age of 8 – 7 Ma, falls out of the genus on the basis of available molecular data from extant relatives and the phylogenetic analysis of Bisconti *et al.* (2013). The Negour whale, therefore, may also help to clarify the position and taxonomic status of “*Megaptera*” *miocaena*, which is interpreted by

Marx & Fordyce (2015) as a basal relative to both living balaenopterids and eschrichtiids.

Future careful restoration and conservation of the Negour specimen is proposed, with particular focus on the cranium, which is strikingly well preserved. The surface of the fossil has to be cleaned first from its provisional coat, and then it has to be impregnated and hardened with paraloid, a soluble agent in acetone, to close the fissures and capillary cracks in the fossilised bone. Cyanacrylate glue and two-component glue will help to fix loose or broken parts of the fossil to ensure the strength and integrity of its internal structures. The cranium has to be excavated from the rock, then subsequently prepared to enable a broader scientific investigation and description. Post-preparation, the specimen should be photographed carefully from various angles in order to facilitate a proper anatomical description and a morphometric study with the aid of various computer programs. This specimen from Sistan and Baluchestan Province is of high scientific importance, especially pertaining to resolving the evolutionary path of modern rorquals.

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