A balaenopterid from the Lower Pleistocene of southern Italy and the Quaternary baleen whales (Cetacea, Mysticeti) of the Mediterranean

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Abstract

An almost complete and partially articulated skeleton of an Early Pleistocene baleen whale is here described. The fossil, measuring 11 m in length, was discovered in the Calcarenite di Gravina Formation at Lama Lamasinata site (Bari, southern Italy) in 1968. The bifurcated first rib combined with other characters supports the identification of the fossil whale as a possible undescribed species of *Balaenoptera* (Mysticeti, Balaenopteridae), close to or nested in the *B. borealis* - *B. edeni*- *B. ricei* clade. However, the limited number of preserved diagnostic characters suggests a prudent assignation of the Bari whale to *Balaenoptera* sp. The associated molluscs suggest a mid-shelf setting deposition near to the boundary between infralittoral and circalittoral environments, probably 40-60 m deep. An associated *Carcharodon carcharias* tooth and shark bite marks on a rib support the hypothesis that an early scavenger action prevented the rising of the whale carcass because of the removal of abdominal tissues and the consequent reduction of the decomposition gas

accumulation. The occurrence of chemosymbiotic bivalves near the skeleton could testify the development of the sulphophilic stage during decay. The Bari specimen sheds new light on the diversity and disparity of the mysticete fauna in the Mediterranean Pleistocene also related to the geodynamic, palaeoclimatic and palaeoceanographic conditions that favoured upwelling events and nutrients supply into the southern Adriatic basin.

Key-words: Mysticeti, *Balaenoptera*; Pleistocene, Mediterranean, Taphonomy, Palaeoceanography

1. Introduction

For some centuries, several naturalists and palaeontologists reported significant fossil remains of baleen whales (Cetacea, Mysticeti) from Neogene deposits of Italy (Bianucci, 2014; Collareta et al. 2020). These discoveries provided a significant dataset potentially useful to reconstruct the changes in the composition and structure of the Mediterranean mysticete fauna, partially related to the complex geodynamic and climatic history of this basin.

Italian baleen whale remains have been found beginning since the middle Miocene (e.g., Bisconti, 2006, 2010), to become extraordinarily frequent in the Pliocene clays and sands exposed in the hills of Tuscany, Piedmont and Emilia Romagna (e.g., Bisconti, 2009; Bisconti et al. 2020). On the whole, this well-known Pliocene fossil assemblage indicates that in the Mediterranean during this epoch lived an highly diversified mysticete fauna represented by balaenids, basal balaenopteroids, balaenopterids, cetotheriids and eschrichtiids.

By contrast, the Pleistocene baleen whale fauna is poorly known and only on a fragmentary fossil record mostly based on rare and recent discoveries. Preliminary studies on these fossil remains (Tsai et al. 2017; Bianucci et. al. 2019), together with indirect observations based on the analysis of fossil whale barnacles (Collareta et al. 2016, 2018a,b), evidenced the presence of balaenids, balaenopterids, and neobalaenids in the Pleistocene Mediterranean Sea. However, this scenario is still poorly defined

and, for example, it does not yet allow to understand the causes which led to the present dramatical low diversity of baleen whales in the Mediterranean. In fact, today only one mysticete species, the fin whale *Balaenoptera physalus*, regularly frequents the Mediterranean (Notarbartolo-Di-Sciara et al., 2003). In particular, the few data on the Mediterranean Quaternary mysticete assemblage are not sufficient to clarify if the decline in diversity started in the Pleistocene, possibly related to the Plio-Pleistocene turnover observed on a global scale (Marx et al., 2016), or if it is an even more recent phenomenon only affecting the Mediterranean.

Notwithstanding the necessity to better investigate the mysticete Pleistocene paleocommunity of the Mediterranean, the scarcity of cetacean fossil record of this period is a global phenomenon that has been related to the Holocene sea level rising making these fossils inaccessible beneath the ocean floor (Marx et al., 2016; Bianucci et al., 2019). Recently, a taphonomic explication has also been proposed: the progressive increase of the efficiency of bone-eating bioeroders reduced the preservation of whale skeletons (Dominici et al., 2020).

Therefore, the diversity and numerical consistency of fossil mysticetes in the Pleistocene Mediterranean deposits appear to be the result of a combination of factors on global and regional scale, as well as of selective taphonomic processes.

In the present work, an almost complete skeleton of a baleen whale is described. It was discovered in 1968 from the Lower Pleistocene calcarenites exposed at Lama Lamasinata site (Bari, southern Italy) (Fig. 1A). A new view of the Mediterranean mysticete fauna in the Quaternary is herein proposed, based on systematic and taphonomic observations, and on palaeoceanographic considerations.

2. Material and methods

2.1. Institutional abbreviations

BM, British Museum, London, England; **GNHM**, Gamagori Natural History Museum, Japan; **MB**, Museumfür Naturkunde, Berlin, Germany; **MSNUP**, Museo di Storia Naturale, Università di

Pisa;Calci (Pisa), Italy; **MST**, Museo Scienze della Terra, Dipartimento di Scienze della Terra e Geoambientali, Università degli Studi di Bari Aldo Moro, Italy; **SAM**, South Australia Museum, Adelaide, Australia; **WMA**, Whale Museum, Ayukawa, Japan; **WRI**, Whales Research Institute, Tokyo, Japan.

2.2. Anatomical terminology

The anatomical terminology follows Mead and Fordyce (2009) for the skull, Ekdale et al. (2011) for the tympanic bulla, and Evans and de Lahunta (2012) for the postcranial skeleton.

3. Systematic palaeontology

Cetacea Brisson, 1762

Mysticeti Gray, 1864

Chaeomysticeti Mitchell, 1989

Balaenopteridae Gray, 1864

Balaenoptera Lacepede, 1804

Balaenoptera sp.

Figures 2-5, Table 1

Referred specimen. Partially articulated almost complete11 m long skeleton, still partially embedded in hard matrix and exposed dorsal side-up, kept at the Museo di Scienze della Terra, Università degli Studi di Bari Aldo Moro with access number MSTQ1 (Fig. 2). It consists of: fragmentary cranium; both mandibles; right and left tympanic bullae (the left removed by the matrix); vertebral column lacking of the atlas, some thoracics and the posterior caudals; nine right and nine left ribs, more or less complete; right scapula, radius, ulna, carpal?, and phalanx; left radius and ulna.

Preservation state. A significant part of the dorsal portion of almost all the bones was destroyed during the canal excavation. Moreover most of the bones are still partially covered by sediment and for several bones only their cutting section is visible and consequently only the bidimensional shape can be observed. Unfortunately, the cranium, the most diagnostic skeletal element of neocetes, was seriously damaged, before burial and fossilization, and during the canal excavation.

Locality, horizon and age. This skeleton was discovered in 1968 by Enzo Indraccolo, Vittorio Stagnani, Oreste Triggiani, and Nicola Cervini in an artificial drainage channel at Lama Lamasinata site in the northern part of Bari town (Puglia, southern Italy) (Montenegro, 2016). The sediment embedding the fossil belongs to the Gelasian?-Calabrian (Lower Pleistocene) Calcarenite di Gravina Formation, a carbonate unit exposed extensively in Apulia region and usually showing shoreface to offshore transition facies associations (Pieri et al., 2011) (Fig. 1A). Unfortunately, a more precise age was not possible, due to the poorly preserved calcareous nannofossil assemblages observed in examined sediments collected for biostratigraphy near the skeleton. However, the occurrence of gephyrocapsids> 3-4 μm allows an early Calabrian age to be inferred, at least tentatively, according to Rio et al.(1990).

Ontogeny. The vertebral epiphyses are free and disarticulated from the centra in all preserved thoracics posterior to T2 one and in the first and fifth lumbars posterior to the last preserved rib. In the other vertebrae (all the cervicals, the first two thoracics and most of the lumbars and caudals) the epiphyses are joined to their respective corpora, although sutures are always clearly visible except for the last preserved caudals. This ossification pattern is compatible with that observed in 9-year-old male and 13-year-old female *Balaenoptera acutorostrata* (Kato, 1988). The body size of a such sexually mature, but not physically mature, whale is already close to that of an adult (Kato, 1988). A similar ossification pattern, with the epiphyses of the thoracic vertebrae, the last to join the respective centra, is common in both mysticetes (Kato, 1988; Kemper and Leppard, 1999) and odontocetes (Galatius and Kinze 2003).

Total body length estimate. The total body length (hereafter TBL) of MST Q1was estimated 12.28

m using a mandible length value of 271 cm by means the Pyenson et al. (2013) equation.

Remarks on the systematic assignation. MSTQ1 belongs to a baleen-bearing mysticete (Chaeomysticeti) by having edentulous laterally bowed mandibles with short unfused symphysis; it belongs to a Balaenopteridae by having the mandible with a sinusoidal dorsal outline and the tympanic bulla with an anterolateral shelf and with involucral and main ridges not coincident. It is referred to the genus *Balaenoptera* by having double-headed first rib, a peculiar character only shares with *Balaenoptera borealis* and *B. edeni*, two species well nested within the *Balaenoptera* clade.

Description. Cranium. Unfortunately, the cranium is almost totally lost, being a portion of the basicranium ad some isolated pieces of flat rostral bones the only preserved remains (Fig. 3). The well preserved flat dorsal surface of the basioccipital is exposed between the disarticulated squamosals. The squamosals lacks the zygomatic processes and their dorsal surface is badly preserved. On the left anterior side of the preserved portion of the neurocranium, between the squamosal and the basioccipital, is visible a fragmentary bone that could be a piece of the left pterygoid. Another larger and anteroposteriorly elongated bone, possibly a portion of the right palatine, lies anteriorly to the basioccipital. Anteriorly to the basicranium, between the two mandibles, some displaced fragments of bones are exposed. The two largest fragments consists of two flat sheets referable to rostral portions of the maxilla.

Tympanic bulla. In dorsal view the tympanic bulla exhibits a reniform shape with its medial margin, corresponding to the main ridge, regularly arcuated (Fig. 4). On the dorsal surface the involucral ridge is weak but clearly distinct along the anteoposterior length of the bone. This ridge is laterally retracted from the medial margin of the tympanic bulla for most of its extension but reaches the main ridge at the anterior corner of the tympanic bulla. The dorsolateral surface of the involucrum is sculptured by weak transverse creases and the Eustachian opening is transversally narrow. The well-developed sigmoid process is positioned posterior to the transverse middle line, it is perpendicular to the main axis of the bone, and its posterior margin is straight. In medial view, an

almost straight dorsal margin (corresponding to the involucral surface) and a convex and half circle-shaped ventral margin are well visible. The main ridge extend anteroposteriorly along the main axis of the bone. The lateral surface is well exposed in the right bulla, although its posterior portion, including the conical process, is partially covered by the transverse process of the second cervical. The lateral furrow is deep and transversely oriented and the involucral surface is planar. The anterolateral shelf was present, although only partially preserved in the right tympanic bulla and completely lost due to brakeage in the left bulla. The ventral surface is covered by the sediment in the right tympanic bulla and it is seriously damaged in the left bulla. The latter presents most of the ventral wall missing and consequently only the mold of the internal cavity is visible in ventral view.

Mandible. Both mandibles are preserved in anatomical position (Fig. 3A). Although their general outline is roughly traceable, they are strongly abraded and therefore some anatomical parts, significant for the systematic determination are missing (e.g. coronoid process) or badly preserved (e.g. mandibular condyle). In dorsal view, the mandibles are moderately bowed laterally with the mandibular condyle projecting posterolaterally, with a distinct mandibular neck. Consequently the entire lateral outline of the mandible is sigmoid in shape. The two mandibles converge anteromedially without any contact between them, being the very short symphysis unsutured. Trace of the vestigial alveolar groove is discernible near and parallel to the dorsomedial margin of the mandible.

Cervical vertebrae. The atlas is missing whereas the C2-C7 are preserved, articulated and unfused (Fig. 3B,C). Only the half ventral part of the centra and the ventral transverse processes of C2-C7 of MST Q1 are preserved, even if all more or less covered by sediment. The length of the centra is almost constant, ranging from 4.1 to 6.1 cm, with C3 and C4 slightly shorter than the other cervical centra (Tab. 1). The broken surfaces of the vertebrae clearly show the epiphyses well sutured to the centra, although the sutural surfaces are well discernible. When exposed, the dorsal surface of the ventral transverse processes show some breakages, suggesting a missing proximal dorsal widening of the ventral transverse processes that could have been originally joined with the dorsal transverse

179 processes forming wide vertebroarterial foramina.

180 Thoracic vertebrae. The first two thoracic vertebrae are in anatomical connection (T1 articulated with
181 the C7 and with T2), whereas the other preserved thoracics show a progressive degree of
182 disarticulation toward the posterior portion of the skeleton (Fig. 3B,C). The preserved right transverse
183 processes of T1-T3 are anterolaterally directed. The length of the centra increases progressively
184 posteriorly passing from 7.8 cm in T1 to slightly more than 10 cm in T4 and T5. The epiphyses are
185 fused to the vertebrae in T1 and T2 and more or less unfused and disarticulated in the other preserved
186 thoracics. The original number of thoracics is unknown since the posteriormost thoracics are missing
187 or badly preserved. However, the minimal possible number of thoracics is nine, as indicated by the
188 number of ribs preserved in both the right and the left side.

189 Lumbar and caudal vertebrae. About 22 articulated lumbar and caudal vertebrae, for a total length of
190 9.5 m, are exposed posteriorly to the disarticulated rib cage (Fig. 2). Nevertheless, only the
191 longitudinal sections of the centrum of these vertebrae are visible on the surface of the stone slab.
192 The sections do not necessary cross the maximum diameter of the centra and therefore they provide
193 just information about the maximum length of the centra but not about the maximum width. In
194 particular, it can be observed that the length of the centrum progressively increases towards the back,
195 and then decreases in the last six preserved centra, probably belonging to caudals. Since the ventral
196 surface of the vertebrae is not exposed, it is not possible to observe if the vertebral tubercles for
197 chevrons are present and consequently it is not possible to recognize the limit between lumbars and
198 cervicals.

199 Ribs. Nine right ribs and nine left ribs, more or less complete, are exposed on the large slab of
200 calcarenite stone (Figs 2, 3B,C). Although disarticulated, the ribs are close to their life position. The
201 first left rib, partially covered by other ribs and sediment, is double-headed, shorter than the other
202 ribs, and distally widened (Fig. 5A,B). The bifurcation affects the proximal ca 20 cm of the first rib
203 and the two headed portions have approximately the same size. The first right rib is still partially
204 articulated with the dorsal transverse process of C7 and lacks one of the heads for breakage. Only a

205 small proximal portion of the second left rib is visible, whereas the third and fourth left ribs are well
206 exposed above the first left rib. The second and the third ribs are similar in length and show the same
207 L-shape, due to an almost-right-angle formed by their proximal portion (tuberculum and capitulum)
208 with the roughly straight main body of the rib. The next preserved ribs are slender and more regularly
209 curved.
210 Forelimbs. The right scapula, exposed in medial view, is incomplete lacking its half posterior
211 portion (Fig. 5D,E). Moreover its margins are partially eroded and consequently its outline cannot
212 be reconstructed in detail. A fragment of bone placed near the head of the right humerus could be a
213 part of the missing ventral portion of the scapula. The acromion is elongated, apparently slender
214 (but it is rather eroded) and its main axis roughly forms a straight angle with the vertical axis of the
215 scapula. Only an eroded longitudinal section of the right humerus is preserved, providing the
216 silhouette of this bone. It is moderately short (length humerus/length radius: ca 0.55), moderately
217 robust (width at middle length/length: ca 0.39, but the width could be sub-estimated due to the bad
218 preservation), straight, and slightly distally widened. Its half circled head represents the 31% of the
219 total humerus length, but also for this feature it needs some caution due to the fragmentary state of
220 the bone. The radial and ulnar facets form an angle of ca 135 degrees. The radius is slender (width
221 at middle length/length: ca 0.13) and slightly curved (Fig. 5F,G). Its distal epiphysis is not well
222 preserved in both right and left radius. The left ulna bears a large olecranon process extending
223 significantly more proximal than the proximal anterior corner of the ulna (i.e. coronoid process).
224 However, it is not possible to reconstruct the exact shape of the olecranon since its distal margin is
225 broken. The ulna is even slender than the radius (width at middle length/length: ca 0.12) and more
226 arcuated (posterior margin distinctly convex). It slightly widens distally. A small globose bone in
227 contact with the distal epiphysis of the right radius could be a carpal and more specifically,
228 considering its position in respect to the radius, the scaphoid. However, its irregular shape due to
229 bad preservation and/or original partial ossification prevents a sure identification of this small bone.
230 About 20 cm from the distal epiphysis of the right radius and ulna is a phalange partially covered by

231 the fourth left rib. Its well exposed proximal articulation is concave.

232 **Comparison.** Body size. The body size estimations reported above indicate a TBL for MST Q1 of
233 about 12 m and some considerations made on the ontogenetic stage suggest that this whale died
234 when sexually mature and very close to be fully adult. Among balaenopterids, such size falls within
235 the average male-female TBLs of adults of extant *Balaenoptera omurai* (ca 10-12 m), *B. ricei* (ca
236 11-12 m), and *Megaptera novaeangliae* (ca 12-14 m). Balaenopterids with TBL larger than that
237 estimated for MST Q1 are the extant *Balaenoptera edeni* (ca 13-14 m), *B. borealis* (ca 14-15), and
238 *B. physalus* and *B. musculus,* both exceeding 20 m in length. By contrast, the extant *Balaenoptera*
239 *bonaerensis* and *B. acutorostrata,* both roughly 8-9 m in length, are smaller than MST Q1.
240 Compared with the fossil balaenopterids, the estimated TBL of MST Q1 is larger than in *Incakujira*
241 *anillodefuego* (8.2 m; Marx and Kohno, 2016) and '*Megaptera*' *hubachi* (8.5 mm; Lambert et al.
242 2010).

243 Cranium. Due to its fragmentary state, no diagnostic characters were detected in the MST Q1
244 cranium. However, if we assume that the mandibles have not significantly dislocated from their
245 original anatomical position, the bizygomatic width of the cranium may havenot been very large in
246 relation to the length of the cranium. Therefore, we could exclude the appurtenance of MST Q1 to
247 the genus *Megaptera* whose zygomatic processes of the squamosal significantly extend laterally
248 generating a wide cranium.

249 Tympanic bulla. The MST Q1 tympanic bulla exhibits a synapomorphy of the balaenopterids: the
250 presence of an anterolateral shelf (state 1 of char. 7 in Ekdale et al. 2011). This shelf is partially
251 preserved in the right bulla and missing for breakage in the left bulla.

252 The size of the MST Q1 tympanic bulla (total length: 100 mm) is close to *Balaenoptera*
253 *bonaerensis* (90-100 mm), slightly larger than *B. acutorostrata* (78-94 mm) and larger than all other
254 extant balaenopterids. In this regard it is important to underline that the tympanic bulla does not
255 grow significantly after birth in a mysticete (Cozzi et al., 2012;G.B. pers. obs.) and therefore the
256 size of the tympanic bulla of the estimated sexually mature MST Q1 whale was probably very close

to the size of an adult animal. Compared with the fossil balaenopterids, the length of MST Q1 tympanic bulla is slightly larger than in *Incakujira anillodefuego* (89.5 mm; Marx and Kohno, 2016) and close to *Plesiobalaenoptera quarantellii* (97-98 mm; Bisconti, 2010).

The MST Q1 tympanic bulla differs from *Balaenoptera musculus* by not having a dorsal posterior prominence (state 1 of char. 5 in Ekdale et al., 2011), a posteriorly extended involucrum (state 1 of char. 10 in Ekdale et al., 2011), a dorsal involucral surface in medial view markedly sinuous and strong concave (state 1 of char. 11 in Ekdale et al., 2011), and a sigmoid process located approximately at the transverse midline. The MST Q1 tympanic bulla differs from *Balaenoptera musculus* and *B. physalus* by not having an elevated and flattened posterior portion of medial margin of main ridge (state 1 of char. 13 in Ekdale et al. 2011) and a sigmoid process with a linear posterior margin. The MST Q1 tympanic bulla differs from *Balaenoptera acutorostrata* and *B. bonaerensis* by having a more robust sigmoid process and by not having a planar dorsal surface of the involucrum adjacent to the Eustachian opening (state 1 of char. 12 in Ekdale et al., 2011), and an involucral ridge extends further anterior than main ridge(state 1 of char. 17 in Ekdale et al., 2011). The MST Q1 tympanic bulla differs from *Megaptera novaeangliae* by having an involucral ridge retracted from the posterior end of the bulla (state 0 of char. 16 in Ekdale et al., 2011) and a narrower eustachian opening; moreover the tympanic bulla of *M. novaeangliae* exhibits a unusual inflated shape well evidenced in ventral view by the broadly rounded ventral margin. The MST Q1 tympanic bulla mainly differs from *Incakujira anillodefuego* for the shape of the sigmoid process, straight and with a linear posterior margin in MST Q1 and slightly anteriorly deflected in *I. anillodefuego* (Marx and Kohno, 206). The tympanic bulla of *Plesiobalaenoptera quarantellii* seems to have a more globose shape in dorsal and ventral view and the sigmoid process nearer to the transverse midline (Bisconti, 2010a).The remaining balaenopterids whose tympanic bulla is well known, namely the extant *Balaenoptera borealis*, *B. edeni* and *B. omurai*, have the tympanic bulla compatible in shape with the one of MST Q1. Unfortunately, due to the incompleteness and the partially covering by sediment, a more detailed comparison of the MST Q1 tympanic bulla with

these three balaenopterid species is not possible.

Mandible. Unfused symphysis and absence of functional alveoli observed in the MST Q1 mandible are characters shared with all the baleen-bearing mysticetes (Chaeomysticeti). The sigmoid shape of the MST Q1 mandible, due to the combination of a moderate curvature with a mandibular neck slightly posterolaterally recurved, is a derived character of the balaenopterids.

Ribs. A peculiar double-headed first rib such as in MST Q1 was only observed in *Balaenoptera borealis* (Fig. 5C) and *B. edeni* among the other cetaceans (Van Beneden and Gervais, 1869-1879, pl. 15, fig. 34; Andrews, 1916, fig. 30; Omura, 1959pl. 6, fig. 1; Nishiwaki and Kasuya, 1971pl. 2, fig. 6;Omura et al. 1981, fig. 7; Kinze, 2005, fig. 2; pers. obs.). This rib bifurcation clearly differs from that described by Buchholtz (2011) in *Caperea marginata* and also from the anomalies observed in some individuals of *Eschrichtius robustus* and *Balaenoptera musculus* (Fig. 6).

In *C. marginata* the first rib is two-headed in the juvenile stage but subsequently expands distally changing its shape from a single medial head to a triangular bifurcated plate of variable width in the adults (Buchholtz et al.2011, fig. 2). The anomalous first ribs of *E. robustus* and *B. musculus* have thin heads lacking distinct tuberculum and capitulum and their general shape clearly differs from that of the firs rib of MST Q1.

Balaenoptera borealis and *B. edeni*, the two extant balaenopterids having bifurcated first rib as MST Q1, form a distinct clade in several phylogenies, both morphological (e.g. Bisconti et al.,2019) and molecular (e.g. McGowen et al., 2020). Whiting *B. edeni* two subspecies, *B. edeni edeni* and *B. edeni brydei*, are recognized, the latter sometimes considered a separate species (*B. brydei*) (Kato and Perrin, 2018). Recently the new extant species *B. ricei*, belonging to the same *B. borealis*-*B.edeni* clade, has been described (Rosel et al., 2021). *B. ricei* shares with *B. borealis* and *B. edeni* the double-headed first rib (P. Rosel, pers. com. 2021).

Vertebrae. The unfused cervical vertebrae is a plesiomorphic condition shared by MST Q1 with most mysticetes with the exception of the Balaenidae and *Caperea* (Neobalaenidae), having C1-C7 fusion (*Balaena*, *Eubalena, Caperea*) or C2-C7 fusion (*Antwerpibalaena*; Duboys de Lavigerie et

al., 2020). Actually, also in balaenopterids a fusion of the cervicals, although partial, can be present, such as in *Balaenoptera physalus* with the first two-three cervicals sometimes fused, and in *B. borealis* with a few cases with the first two cervicals fused (Tomlin, 1967). By contrast, completely unfused C1-C7 have been reported for other balaenopterids (e.g. *Balaenoptera edeni*; Kato and Perrin, 2018). Unfused C1-C7 has also been observed in the holotype and in the referred skeleton of *Incakujira anillodefuego* (Marx and Kohno, 2016). It seems, therefore, that although in balaenopterids unfused C1-C7 is the prevalent condition, two-three fused cervicals can be sometimes observed in some species. Therefore a total non-fusion, as observed in MST Q1, cannot be used as a diagnostic character, excepted to exclude its appurtenance to the Balaenidae or Neobalaenidae.

The few information available from the poorly preserved vertebral column prevents an exhaustive comparison of this part of the skeleton with that of other mysticetes. Nevertheless, measurements of the centrum length (CL) taken on the broken vertebrae exposed on the calcarenite slab allowed the pattern of CL from the second cervical to the last preserved caudal to be reconstructed, at least in part. This CL pattern was graphed and compared with the CL patterns of some extant balaenopterids (Fig. 7). Interesting, although incomplete, the CL pattern of MST Q1exhibits a greater overlap with the CL pattern of *Megaptera novaeangliae,* with an acute peak followed by an abrupt decrease in the CL values. This peak represents the maximum length of the vertebrae and roughly corresponds, in the extant balaenopterids, to the transition between the last lumbars to the first cervicals. The similar CL patterns of *Balaenoptera musculus* and *B. physalus* clearly differ from MST Q1 for a wider upper convexity and a less prominent and more centrally displaced peak. An intermediate condition between *B. musculus* + *B. physalus* and the MST Q1 + *M. novaeangliae* is observed for the similar patterns of *Balaenoptera borealis* and *B. edeni.* Finally, the pattern of *Balaenoptera acutorostrata* differs from the one of MST Q1 mainly for the small number of vertebrae a for the peak forming a more open angle. Despite these affinities between the CL pattern of MST Q1 with *M. novaeangliae*, a general view of the curves plotted in the graph of figure 7 suggests that the CL

pattern could be linked to body size, being, for example, the patterns of *B. musculus* and *B. physalus* very similar although the two largest whales are not closer to each other than to other congeners (Marx and Kohno, 2016; McGowen et al., 2020). Therefore, considering the CL pattern as a diagnostic character for mysticetes requires some caution.

Forelimb. The fragmentary right scapula of MST Q1 is poorly informative from a diagnostic point of view, although the well preserved acromion represents a remarkable difference with *Megaptera novaeangliae*, the only mysticete lacking of this process.

A comparison of the MSTQ1 humerus with that of other balaenopterids (Fig. 8), evidences a value of its relative length (b/a = 0.36) near to the other species of *Balaenoptera* (b/a = 0.37-0.33) with *B. acutorostrata* showing the lower value. The same value of MSTQ1 for this ratio is also observed in "*Megaptera*" *hubachi*, whereas *Incakujira anillodefuego* and *Megaptera novaeanglae* exhibit more elongated humeri (b/a = 0.43 and 0.43 respectively).

The MSTQ1 humerus is apparently slender than those of all other balaenopterid but this character could be an artefact of the breakage and poor preservation of this bone. The head of the MSTQ1 humerus is relatively small (c/b = 0.31; Fig. 8), particularly if compared with *B. musculus* (c/b = 0.44) and *M. novaeangliae*(c/b = 0.51). The outlines of ulna and radius of MSTQ1 seem to be better preserved than those of humerus, evidencing in this case a genuine slender and gracile shape of both bones, similarly to *B. borealis* and *B, edeni* among the other balaenopterids. In this aspect the radius and ulna of MST Q1 clearly differ from those significantly more robust of *B. acutorostrata*, *B. musculus* and *I. anillodefuego.* The ulna and radius of *M. novaeangliae*, instead, differs from MSTQ1 and from the other balaenopterid in their pronounced distal widening. The MSTQ1 olecranon process of the ulna is well developed both posteriorly and proximally as in all other balaenopterids excepted *M. novaeangliae,* which have this process very reduced. In conclusion, the whole shape of the MST Q1 forelimb is roughly similar to that of the extant rorqual species, showing the better affinities with *B. borealis* and *B. edeni*.

Conclusive comparison remarks. Unfortunately, the incompleteness of the some diagnostic parts of

361 the MSTQ1 skeleton (e.g., the skull) dramatically limits the comparison with other mysticetes. The
362 most significant character observed in the MST Q1 skeleton is the bifurcated first rib, only known
363 in *Balaenoptera borealis*, *B. edeni*, and *B. ricei*. Such a shared character leads to the hypothesis that
364 MST Q1 belongs in the same clade of the three extant rorquals. Indeed, the morphology of the
365 tympanic bulla and forelimb bones of MST Q1 are compatible with both *B. borealis* and *B. edeni,*
366 but unfortunately it is not possible to confirm a closer affinity with one of these two species, due to
367 the limited diagnostic value and incompleteness of these bones. On the other hand, based of body
368 size estimation, MST Q1 was smaller than *B. edeni* and *B. borealis*, as confirmed by the relative
369 small size of the MST Q1 tympanic bulla. Rather, in body size MST Q1 is more similar to *B. ricei*
370 of which, however, the tympanic bulla is not sufficiently known for a detailed comparison (Rosel et
371 al., 2021, fig. S9d).
372 Regarding the small size, however, it should be remarked that the extant rorqual species include
373 several subspecies of reduced size, due to partial geographic segregation (e.g. the pygmy blue whale
374 *Balaenoptera musculus brevicauda*). Finally, MST Q1 differs from *B. edeni* and *B. borealis*, also for
375 the CL vertebral pattern, a character that in turn could be related to the smaller body size.
376 All the observations suggest that MST Q1 likely belong to an undescribed fossil species of
377 *Balaenoptera,* close to or nested in the *B. borealis-B. edeni-B. ricei* clade. So, pending the discovery
378 of a more complete specimen, MST Q1 is assigned to *Balaenoptera* sp.
379

380 ## 4. Taphonomy

381 ### 4.1. *Descriptive taphonomy*

382 A significant part of the preserved bones is articulated whereas the disarticulated bones are closely
383 associated near their anatomical position as, for example, most of the thoracic vertebrae, the ribs and
384 the forelimb bones (Fig. 2). The completeness degree of skeleton is moderately high, with the missing
385 bones being the hyoids, the atlas, some thoracics, about one meter of the posterior portion of the

386 column (i.e. the last about 10 caudals), the sternal bones, and some forelimb bones (left scapula and
387 most of hand bones), and the destroyed portion of the cranium. However, some of these missing bones
388 could be still fully embedded in the matrix and not visible on the upper surface of the calcarenite slab,
389 or to have been destroyed during the canal excavation.
390 The analysis of the bones preservation has been partially compromised by the recent damage due to
391 the excavation that, for example, destroyed about the half dorsal portion of most of the vertebrae.
392 However, even some bones that do not appear to have suffered evident recent damage (e.g. the
393 forelimb bones), show some fractures, breakages and deformations.
394
395 4.2. *Shark bite marks*
396 The exposed surface of the seventh? right rib is affected by at least five subparallel 5-10 mm long
397 marks identified as shark bites (Fig. 9A), in particular as type 1 marks, produced by a tooth impacting
398 the surface of the bone from the above downward (Cigala Fulgosi, 1990; Bianucci et al., 2010).
399 However, due to the bad preservation of the cortical bone surface, it was not possible to establish
400 whether marks were produced by unserrated or serrated teeth and therefore is not possibile to
401 speculate on shark species .
402
403 4.3. *Associated fauna*
404 A *Carcharodon carcharias* tooth was found near the end of the fourth left rib and in close proximity
405 of the isolated right phalanx (Fig. 9B).
406 The embedding calcarenite contains scarce benthic invertebrate macrofauna, consisting only of
407 bivalves and gastropod shells, preserved as external and internal moulds. Some of these molluscan
408 remains were found in the same horizon and strictly associated to the whale skeleton. Among the
409 bivalves, articulated *Acanthocardia echinata* and molds of articulated *Anodontia* cf. *fragilis* were
410 found between mandibles and between the second? and third? right ribs. Molds of *A.* cf.*fragilis* are
411 also seen near the fifth left rib and between the left radius and the left ulna. An articulated specimen

412 of *Venus nux* (as external mold) apparently is in life position (about 45° with respect to vertical),
413 between the epiphysis and the respective centrum of one of the first lumbars (Fig. 9C). Among the
414 gastropods, a mold of *Gibbula magus* was found ca 40 cm posterior to the last preserved left ribs.
415
416 4.4. *Reconstruction of the taphonomic history*
417 The high degree of skeletal articulation and completeness of MST Q1 suggests a limited or absence
418 of refloating of the carcass after falling. In fact, during a long refloating phase a whale carcass
419 gradually dismembers due to decay and scavenging, with mandibles, cranium, tail, and forelimbs fall
420 to the bottom (Schäfer, 1972). According to Allison et al. (1991), the permanence of a whale carcass
421 on the seafloor depends on the hydrostatic pressure, temperature and on the interplay between two
422 main biological factors: production of decomposition gas and rate of scavenging. Decomposition can
423 produce a volume of gas sufficient to bloat and refloat the carcass if not previously partially
424 dismembered and if the hydrostatic pressure (and consequently the depth) is not too strong (Smith et
425 al., 2015; Moore et al., 2020). The depth preventing the refloating was estimated 1000 m by Allison
426 et al. (1991) and successively reduced by Reisdorf et al. (2012) who reported that whale carcasses
427 "may rise from water depths up to 50 m, but never from below 100 m". A proxy for palaeodepth
428 inference is provided by the associated molluscan assemblage, which suggests a mid-shelf setting
429 near to the boundary between infralittoral and circalittoral environment, probably 40-60 m. In
430 particular, the bivalves *Acanthocardia echinata* and *Venus nux* are shallow burrowers in sandy-muddy
431 bottoms (Poutiers, 2016; Tirado et al., 2011), and are common components of Plio-Pleistocene shelf
432 assemblages (Spano, 1989; Moshkovitz, 2012; Crippa and Raineri, 2015). The rising of the whale
433 carcass from such a shallow depth may have been prevented by early scavenger action suggested by
434 the occurrence of a *Carcharodon carcharias* tooth near a phalanx and by shark bite marks on a rib.
435 Scavenging during initial flotation, or soon after sinking, would have favoured a fast removal of
436 abdominal tissues, thus reducing the accumulation of decomposition gasses. The partial
437 disarticulation of the thoracic region could be related to shark scavenging, together with collapse of

438 the rib cage due to decay. The occurrences of shark bite marks on the bones and shark teeth in
439 association with fossil whales are well documented, testifying both predation and scavenging
440 activities (Deméré and Cerutti, 1982; Cigala Fulgosi, 1990; Bianucci et al., 2000, 2010, 2018;
441 Collareta et al., 2017; Bosio et al., 2021). Interestingly, the extant great white sharks do not actively
442 prey on baleen whales but rather feed on their floating carcasses, showing initial preference for the
443 tail and the blubber-rich regions (Long and Jones, 1996; Curtis et al., 2006; Fallws et al., 2013). The
444 lack of tail on the MST Q1 skeleton, the shark bite marks and the *C. carcharias* tooth, both found in
445 the fat abdominal region, supports a scavenging action.
446 The occurrence of the bivalve *Anodontia fragilis* in the molluscan assemblage could testify the
447 development of a sulphophilic stage, usually following mobile-scavenger and enrichment-opportunist
448 stages during the development of a whale fall community (Smith et al., 2002, 2014; Danise et al.,
449 2010; Danise and Dominici, 2014). *A. fragilis* is a representative of the Lucinidae, one of the bivalve
450 families known to host chemosynthetic bacteria (Taylor and Glover, 2005; 2006; Duperron et al.,
451 2013). Chemosymbiotic bivalves are components of recent (Smith and Baco, 2003) and fossil
452 (Amano and Little, 2005; Dominici et al., 2009; Danise et al., 2010) whale fall communities during
453 the sulphophilic stage (Smith et al., 2002, 2014). Finally, the presence of non-chemosymbiotic
454 molluscs close to the skeleton , such as *Venus nux,* suggests its colonization during the following reef
455 stage (Smith et al., 2002, 2014).
456

457 ## 5. Paleobiogeography

458 *5.1. The Mediterranean Pleistocene baleen whale fauna*
459 The attribution of the MST Q1 skeleton to *Balaenoptera* sp. within the *B. borealis-B. edeni-B. ricei*
460 clade provides new data on the still poorly known Pleistocene cetacean fauna of the Mediterranean
461 Sea. In particular, the Mediterranean Pleistocene fossil record of mysticetes until now was mainly
462 represented by two finds: a large skeleton referred to *Balaenoptera* cf. *musculus* from the Lower

463 Pleistocene (1.5–1.25 Ma) of Matera, southern Italy (Bianucci et al., 2019), and an isolated tympanic
464 bulla referred to cf. *Caperea* sp. (Neobalaenidae) from the Lower Pleistocene (1.9–1.7 Ma) of Sicily
465 (Tsai et al., 2017). Furthermore, indirect evidences provided by the study of fossil whale barnacles
466 from Salento Peninsula and Sicily (South Italy) suggested a breading/calving area in the
467 Mediterranean during the Early Pleistocene for at least a balaenopterid belonging or closely related
468 to *Megaptera* and a balaenid belonging or closely related to *Eubalaena* (Collareta et al. 2016,
469 2018a,b). In summary, by adding the new balaenopterid here described, during the Early Pleistocene
470 two rorquals (*Balaenoptera* cf. *musculus* and *Balaenoptera* sp.), one humpback whale (*Megaptera*?),
471 one right whale (*Eubalaena*?), and one pygmy right whale (cf. *Caperea* sp.) swam in the
472 Mediterranean. This baleen whale assemblage shows a high disparity evidenced by the significant
473 differences in morphology and size (from the ca 26 m in length of *B*. cf. *musculus* to the 5-6 m of cf.
474 *Caperea* sp.).
475
476 *5.2. The modern Mediterranean baleen whale fauna*
477 The present-day mysticete community of the Mediterranean contrasts dramatically with the Early
478 Pleistocene scenario. Indeed, today the fin whale *Balaenoptera physalus* is the only mysticete that
479 regularly frequents the Mediterranean (Notarbartolo-Di-Sciara et al., 2003). However, the *B. physalus*
480 distribution in the Mediterranean is not uniform, e.g. it is regularly present in the relatively cool and
481 productive northwestern Mediterranean while it is rarer and not regularly present in the Adriatic Sea
482 (Notarbartolo-Di-Sciara et al., 2003). Concerning other baleen whales reported in the Mediterranean
483 occasionally, *Balaenoptera acutorostrata*, and *Megaptera novaeangliae* are considered visitor
484 species, being their record represented by a few individuals from North Atlantic populations
485 occasionally entered in the Mediterranean (Reeves and Notarbartolo di Sciara, 2006; Notarbartolo di
486 Sciara and Birkun, 2010; Russo et al., 2016). Two other baleen whales, *Balaenoptera borealis* and
487 *Eubalaena glacialis* are considered vagrant species, being only recorded with five and two specimens
488 respectively in the Mediterranean (Reeves and Notarbartolo di Sciara, 2006; Notarbartolo di Sciara

and Birkun, 2010). In particular, *B. borealis* is a cosmopolitan species preferring temperate and subpolar waters (Gambell, 1985; Horwood 1987) and it does not seem to usually enter the semi-enclosed basins (Reeves et al., 1998). Its Mediterranean records are limited to the northwestern coasts (two reports in Spain and three in France) (Notarbartolo di Sciara and Birkun, 2010).

5.3. Palaeoceanographic changes as keys to understand the Mediterranean Pleistocene baleen whale diversity and disparity

Recent studies indicate that the intensification of glacial-interglacial phases and an high interchanges between the two hemispheres were the main drivers to shape the biological distribution of whales, during the Quaternary (Tsai et al., 2017; Tsai and Chang, 2019). In the Mediterranean, beginning since the late Piacenzian, the teleostean fauna records an increasing number of Atlantic taxa, including several subpolar and temperate taxa that spread into the central and eastern Mediterranean sectors as a consequence of climatic deterioration and oceanographic changes (Girone et al., 2006; Agiadi et al., 2011; 2018). The importance of the Atlantic faunistic flow increased during the Gelasian and went on throughout Middle and Late Pleistocene. In analogy, we can hypothesize that climate variability and related oceanographic changes in terms of temperatures and nutrients have driven the dispersal of oceanic baleen whales from the North Atlantic to the Mediterranean. The Pleistocene southern Italy paleogeography could have also played a role in the baleen whale frequentation of the Adriatic, which today is not regularly inhabited by *Balaenoptera physalus*. At least since the beginning of Pleistocene (about 2.5 Ma ago), this Mediterranean sector was affected by subsidence that caused the drowning of most of the Apulian peninsula, giving origin to a vast archipelago (Tropeano and Sabato, 2000; Tropeano et al., 2002a; 2002b; 2018). The widest and deepest seaway was the Bradanic Trough, connecting Adriatic Sea with Ionian Sea (Tropeano et al., 2018) (Fig. 1B). High productivity could have favoured the arrival of *Balaenoptera* sp. in the Adriatic through the Sicily Channel. This route probably followed the path of the Modified Atlantic Waters (MAW) entering through the Strait of Gibraltar and flowing eastward (Fig. 1A). The influx of MAW into the Ionian basin originated

upwelling events and nutrients supply at the periphery of an anticyclonic gyre along the south Italian coasts before reaching the south Adriatic Sea (Civitarese et al., 2010). The strengthening of the Atlantic Ionian Stream jet, during more arid and colder conditions, shifts towards the north the influence of Atlantic waters (Poulain et al., 2012) that enter in the northern area of the Ionian Sea. It cannot be excluded that the influence of productive waters at the studied site was reinforced through the Bradanic Trough seaway during Pleistocene (Fig. 1B). This condition is in line with the modern distribution of the fin whale in the Mediterranean, mainly occurring in deep water, as well as in slope and shelf waters with coastal upwelling and high concentration of zooplankton (Notarbartolo di Sciara et al., 2003; Notarbartolo di Sciara and Birkun, 2010).

Conclusions

Although MST Q1 represents one of most complete cetacean skeletons from Pleistocene ever found, its skull, the most diagnostic anatomical part for neocetes, is strongly damaged leading its systematic assignment rather complicated. However, after a detailed comparison MST Q1 is here referred to a possible undescribed fossil species of *Balaenoptera* close to or nested in the clade formed by *B. borealis*, *B. edeni* and *B. ricei*, three extant species sharing with MST Q1 the bifurcated first rib. Nevertheless, the scarcity of significative diagnostic characters suggests a prudent assignation of MST Q1 to *Balaenoptera* sp.

The high degree of skeletal articulation and completeness supports a limited or absent refloating of the carcass after falling, whereas the associated molluscs suggest that it settled at a deep of 40-60 m. Rising of the whale carcass from such a shallow depth may have been prevented by early scavenger action suggested by the associated *Carcharodon carcharias* tooth and by the shark bite marks. The associated bivalve *Anodontia fragilis* could testify the development of a sulphophilic stage, whereas non-chemosymbiotic molluscs, such as *Venus nux,* indicate the colonization of the skeleton in the subsequent reef stage.

The Bari skeleton here described provides new data for the knowledge of the Pleistocene mysticete fauna of the Mediterranean, so far known on very few remains and indirect evidences from baleen whale barnacles. In particular, this whale fauna included at least two rorquals (*Balaenoptera* cf. *musculus* and *Balaenoptera* sp.) and one pygmy right whale (cf. *Caperea* sp.) based on skeletal remains, plus one humpback whale (*Megaptera*?) and one right whale (*Eubalaena*?) based baleen whale barnacles. This scenario contrasts with the current mysticete community of the Mediterranean, only represented, considering the regular species, by the fin whale *Balaenoptera physalus*.

A possible key to understand the greater diversity and disparity of the Mediterranean baleen whale assemblage in the Pleistocene in respect to the present could be the paleoclimatic, oceanographic and geodynamic changes, and related reassessment of the distribution of nutrients, causing dispersal processes of these cetaceans from the North Atlantic to the Mediterranean and, within the Mediterranean, from west to the southern Adriatic Sea.

Future discoveries in southern Italy, where Pleistocene marine deposits are widely exposed, could allow a better definition of this still fragmentary picture of the Quaternary whale fauna of the Mediterranean.

Author contributions

Andrea Zazzera, Angela Girone and Giovanni Bianucci: Data curation, Formal analysis, Investigation, Methodology, Conceptualization, Writing - original draft; Reviewing and Editing.

Rafael La Perna: Conceptualization, Investigation, Formal analysis, Original draft preparation

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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839

840 **FIGURE CAPTIONS**

841

842 **Figure 1.A**, Mediterranean map with the location of the main Pleistocene records of baleen whales
843 including the here described skeleton of *Balaenoptera* sp. (MST Q1) collected near Bari from the
844 Calcarenite di Gravina Formation. The main surface water circulation in also reported.
845 Abbreviations: AW = Atlantic Water; MAW = Modified Atlantic Water; AIS = Atlantic Ionian
846 Stream. **B**, schematic map of Early Pleistocene paleogeography of southern Italy (from Tropeano et
847 al., 2002, modified).

848

849 **Figure 2.** Skeleton of *Balaenoptera* sp. (MST Q1) from the Lower Pleistocene Calcarenite di
850 Gravina Formation. The fossil is partially embedded in hard matrix and exposed dorsal side-up. The
851 small circles indicate the position of the associated fossil fauna and fossil traces on the bones.
852 Abbrevations: b1 = *Anodontia* cf.*fragilis*; b2 = *Acanthocardia echinata*; b3 = *Gibbula magus*; b4 =
853 *Venus nux*; st = shark tooth; stb = shark tooth bite marks.

854

855 **Figure 3**. Skeleton of *Balaenoptera* sp. (MST Q1) from the Lower Pleistocene Calcarenite di
856 Gravina Formation. **A**, fragmentary cranium and mandibles; **B,C**, posterior portion of the skull,
857 cervicals, thoracics, ribs, and portion of the right forelimb regions. Note the shark tooth near the
858 distal end of the left fourth rib. Linear hatching indicates major breaks. For the colours associated
859 with the different bones, see figure 2.

860

861 **Figure 4**. Tympanic bullae associated to the skeleton of *Balaenoptera* sp. (MST Q1) from the
862 Lower Pleistocene Calcarenite di Gravina Formation. **A-D**, right tympanic bulla still partially
863 embedded in hard matrix in anterodorsal (A,B), dorsal (C), and lateral (D) views; **E,F**, left tympanic
864 bulla removed by the matrix in dorsal (E) and medial (F) views. Linear hatching indicates major
865 breaks.

Figure 5. **A,B,D-G**, skeleton of *Balaenoptera* sp. (MST Q1) from the Lower Pleistocene Calcarenite di Gravina Formation: proximal portion of the double-headed first left rib (A,B); incomplete right scapula and right humerus (D,E); and left radius and ulna (F,G). **C**, proximal portion of the double-headed first left rib of *Balaenoptera borealis* (MSNUP M262). Linear hatching indicates major breaks. For the colours associated with the different bones, see figure 2.

Figure 6. Comparison of the first double-headed rib of *Balaenoptera borealis* and *B. edeni* (redrawn from Omura, 1959, pl. 6, fig. 1) with the first rib of a juvenile of *Caperea marginata* (redrawn from Buchholtz, 2011, fig. 2D), and with the anomalous first ribs of *Balaenoptera musculus* (redrawn from Dubar, 1828, pl. 8) and *Eschrichtius robustus* (redrawn from Slijiper, 1936, fig. 131). Scale bars equal 10 cm.

Figure 7. Vertebral count and centrum length (CL) in *Balaenoptera* sp. (MST Q1) and the following other balaenopterids: *Balaenoptera edeni* (WRI 77M62, measurements from Omura et al. 1981); *B. borealis* (MSNUP M262), *B. physalus* (MSNUP M251), *B. musculus* (MSNUP M250), *B. acutorostrata* (MSNUP M260), and *Megaptera novaeangliae* (MSNUP M263).

Figure 8. Comparison of the shape in lateral view and ratios of main measurements of the humerus, radius, and ulna of MSTQ1 with the balaenopterids *Incakujira anillodefuego* (redrawn from Marx and Kohno, 2016, fig. 14), *Megaptera novaengliae, Balaenoptera edeni* (redrawn from Omura, 1959, pl. 5, fig. 3), *B. musculus*, *Balaenoptera borealis*, *B. physalus*, *B. acutorostrata*, and '*Megaptera*' *hubachi* (redrawn from Bisconti, 2010, fig. 15). Scale bars equal 10 cm.

889 **Figure 9**. Skeleton of *Balaenoptera* sp. (MST Q1) from the Lower Pleistocene Calcarenite di
890 Gravina Formation: close ups of the associated fossil fauna and fossil traces. A, articulated
891 specimen of *Venus nux* located between the epiphysis and the respective centrum of one of the first
892 lumbars (b4 in fig. 2); B, *Carcharodon carcharias* tooth located near the distal end of the fourth left
893 rib (st in fig. 2); C, shark bite marks on the seventh? right rib (stb in fig. 2).
894
895
896 **TABLE CAPTION**
897
898 **Table 1.** Measurements (in millimetres) of the skeleton of *Balaenoptera* sp. (MST Q1).
899

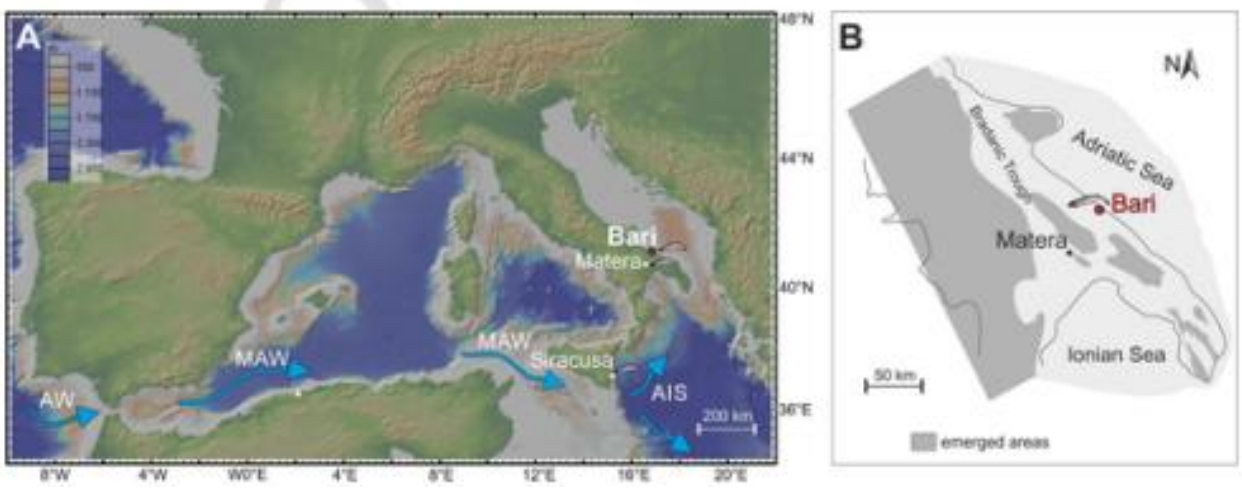
A
B
Bari
Matera
MAW
MAW
Siracusa
AW
AIS
200 km
48°N
44°N
40°N
36°E
8°W
4°W
0°E
4°E
8°E
12°E
16°E
20°E
N
Adriatic Sea
Bari
Matera
Ionian Sea
50 km
emerged areas

Fig 1

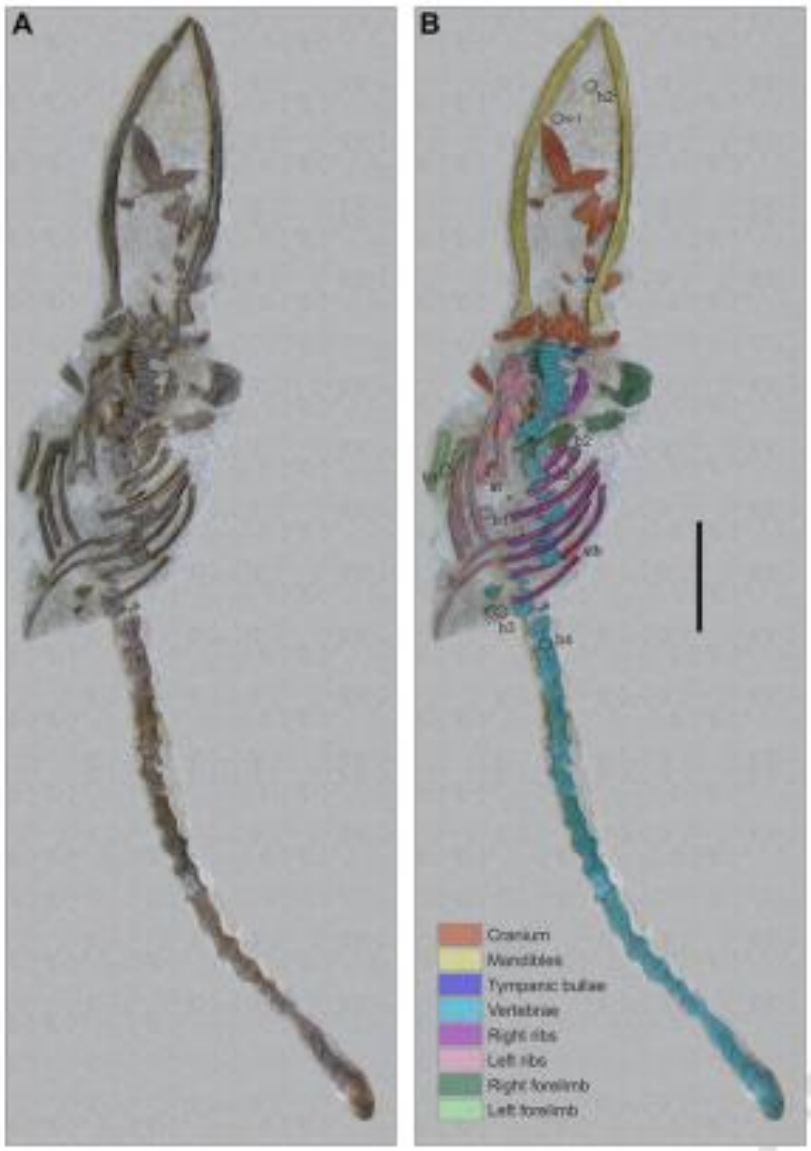
A
B
Cranium
Mandibles
Tympanic bullae
Vertebrae
Right ribs
Left ribs
Right forelimb
Left forelimb

Fig. 2

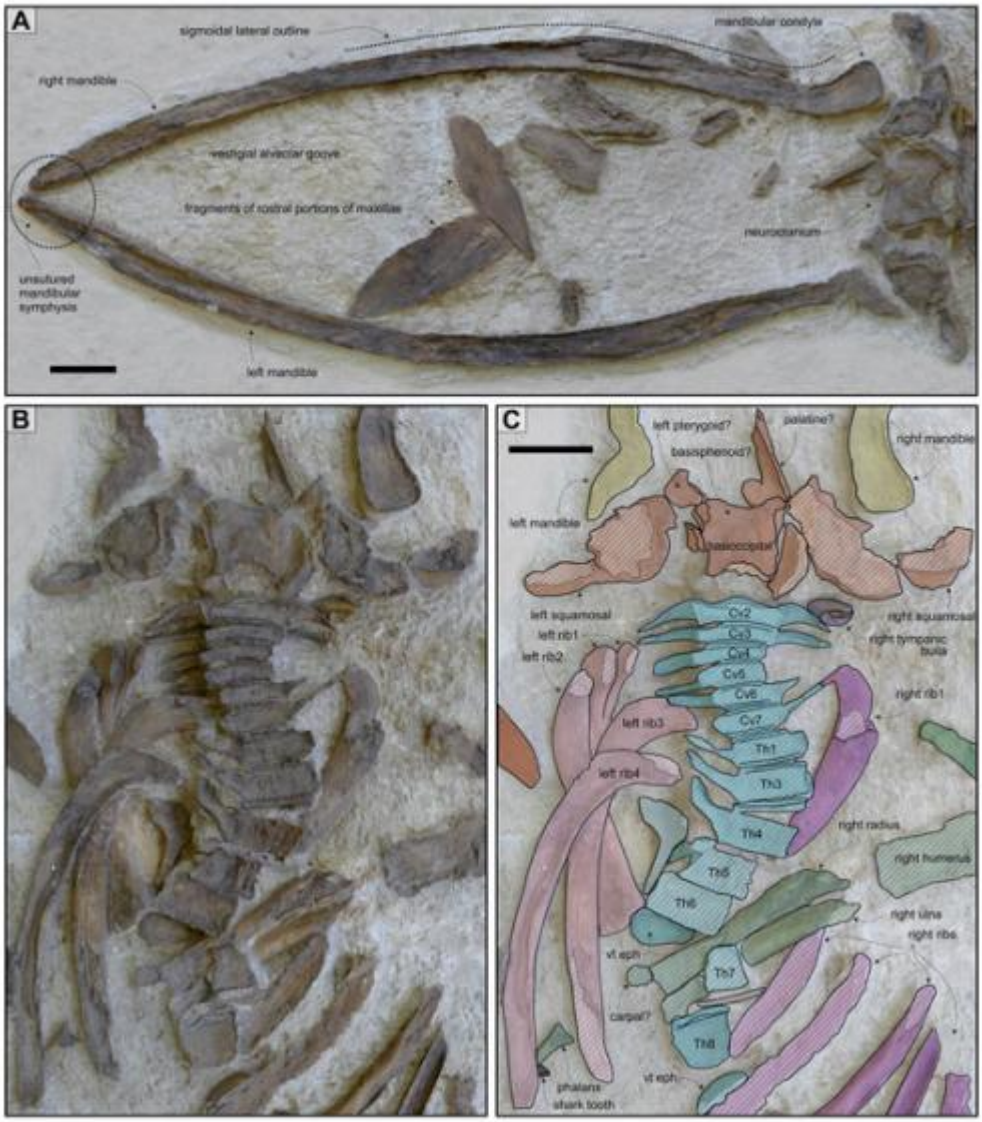
A
sigmoidal lateral outline
mandibular condyle
right mandible
vestigial alveolar groove
fragments of rostral portions of maxillae
neurocranium
unsutured mandibular symphysis
left mandible
B
C
left pterygoid?
palatine?
right mandible
basisphenoid?
left mandible
basioccipital
left squamosal
right squamosal
left rib1
right tympanic bulla
left rib2
Cv2
Cv3
Cv4
Cv5
Cv6
Cv7
right rib1
left rib3
Th1
left rib4
Th3
Th4
right radius
right humerus
Th5
Th6
right ulna
right ribs
vt eph
Th7
carpal?
Th8
phalanx
shark tooth
vt eph

Fig 3

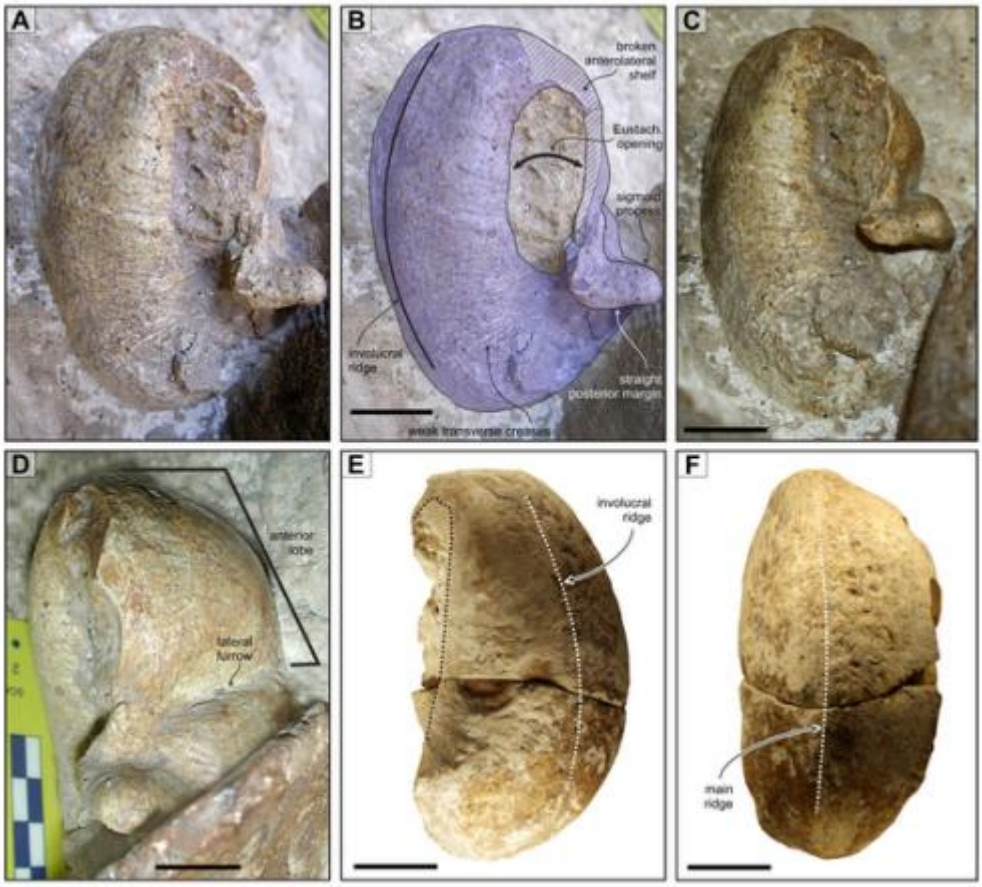
A
B
broken anterolateral shelf
Eustach. opening
sigmoid process
involucral ridge
straight posterior margin
weak transverse creases
C
D
anterior lobe
lateral furrow
E
involucral ridge
F
main ridge

Fig 4

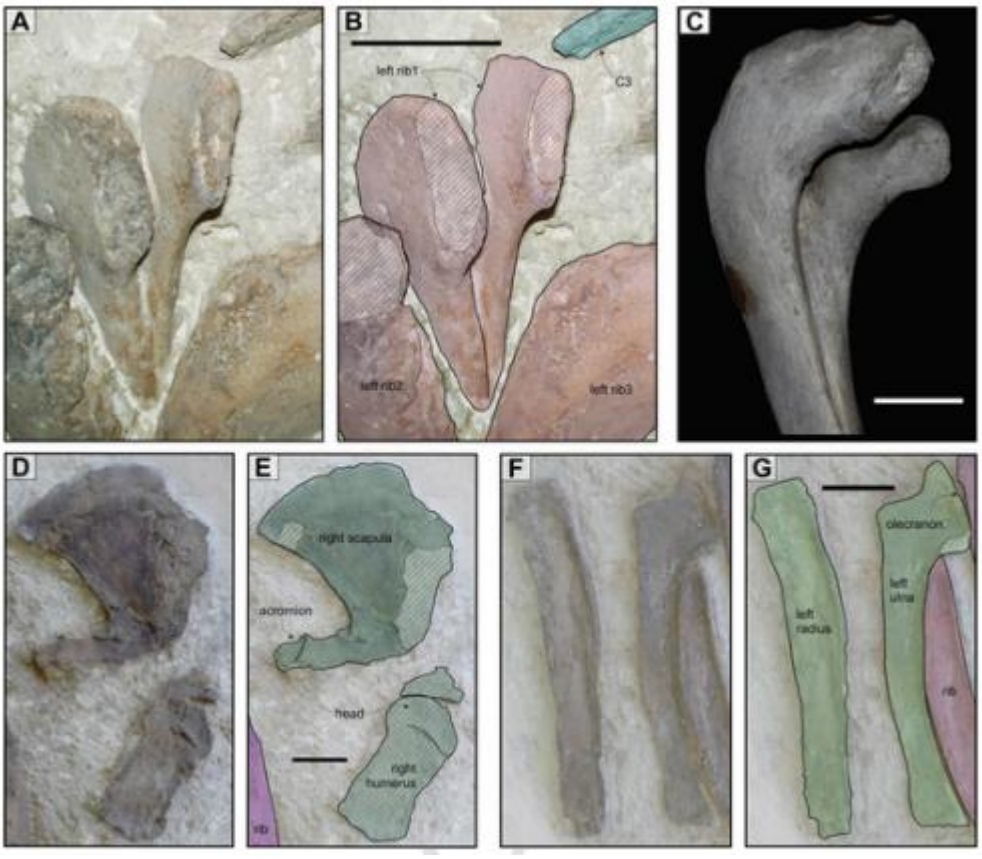
A
B
left rib1
C3
left rib2
left rib3
C
D
E
right scapula
acromion
head
right humerus
rib
F
G
olecranon
left ulna
left radius
rib

Fig 5

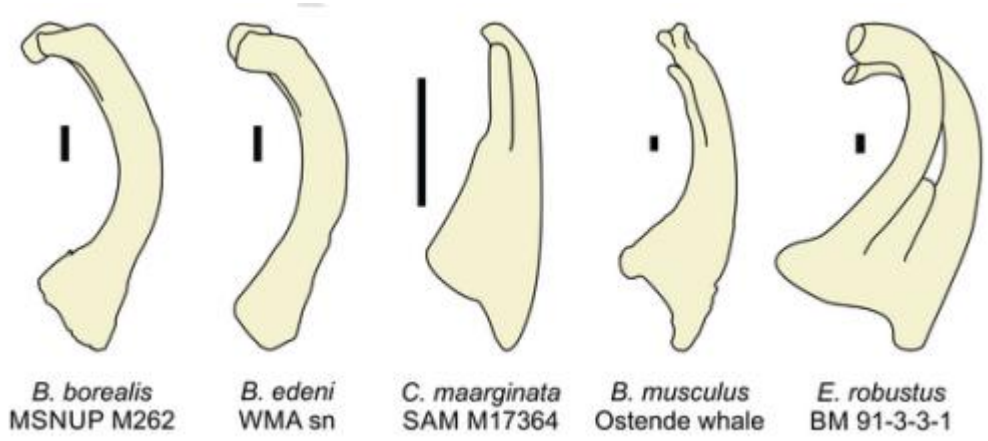

Fig 6

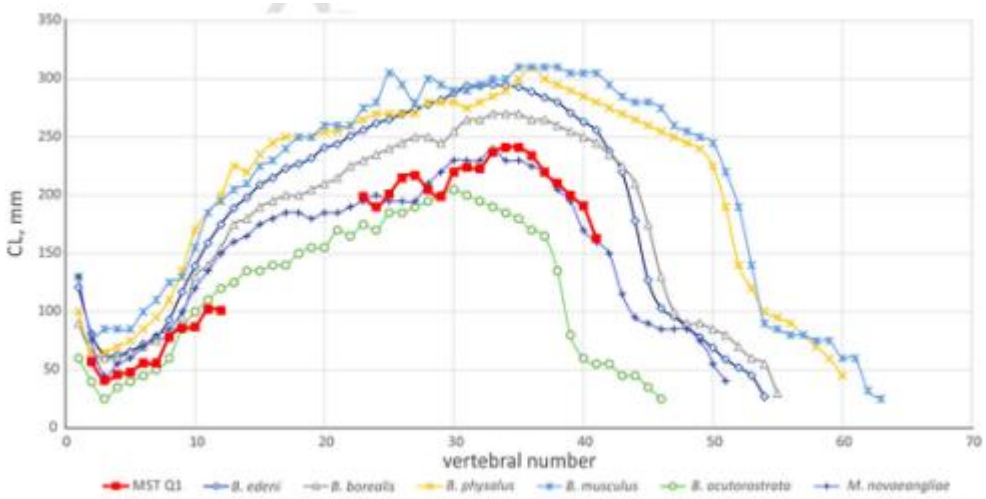

Fig 7

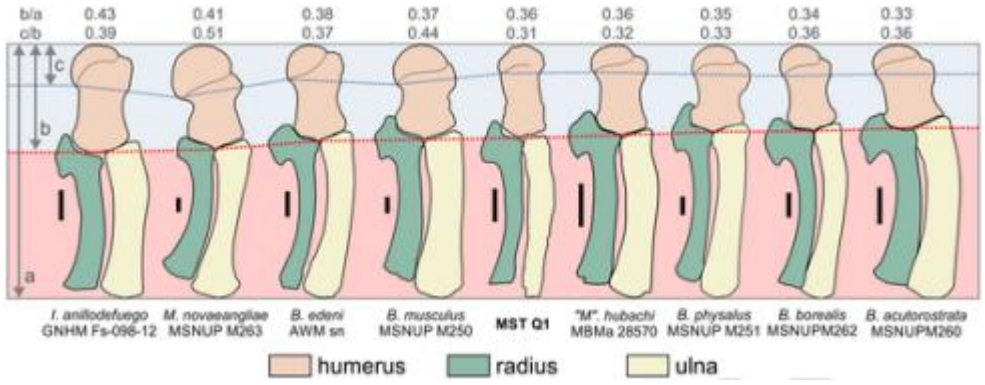

Fig 8

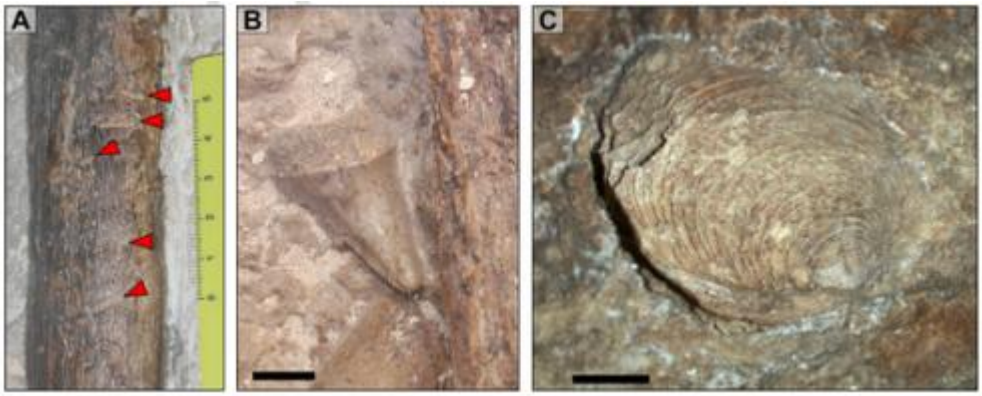

Fig 9