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MUCCHI - MODENA

An early Late Pliocene right whale (Genus *Eubalaena*) from Tuscany (Central Italy)

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KEY WORDS – Mammalia, Cetacea, Mysticeti, Balaenidae, Pliocene, Tuscany, Central Italy.

ABSTRACT – A new partial skull from Ricavo (Tuscany, Central Italy) is described which belongs to a baleen whale. Morphological comparisons support its inclusion in the genus *Eubalaena* (Cetacea: Mysticeti: Balaenidae). The occurrence of the specimen is from the early Late Pliocene (around 3.5 Ma). To date, the Ricavo skull represents the oldest known whale of the genus *Eubalaena*.

RIASSUNTO – [Una balena franca (genere *Eubalaena*) proveniente dal Pliocene superiore basale della Toscana (Italia centrale)] – Viene descritto un nuovo cranio incompleto di misticete proveniente da Ricavo (Toscana, Italia centrale). La sua inclusione nel genere *Eubalaena* (Cetacea: Mysticeti: Balaenidae) è supportata da comparazioni morfologiche. L'esemplare, che proviene da sedimenti della parte basale del Pliocene Superiore (circa 3.5 Ma) di Ricavo, rappresenta la più antica segnalazione del genere *Eubalaena*.

INTRODUCTION

Extant Balaenidae (Mammalia: Cetacea: Mysticeti) are large, slow-swimming marine mammals that use baleen to filter-feed medium-sized zooplankton (copepods, euphausiids, amphipods, mysids, and pteropods). They have a long-arched rostrum which is transversely compressed. Their rostrum bears the longest baleen among the mysticetes (up to 3.5 m; Tomilin, 1967; Pivorunas, 1979; Sanderson & Wassersug, 1993). The feeding apparatus of bowhead and right whales is very similar (Tomilin, 1967; Gaskin, 1989).

The diversity of extant Balaenidae is lower than during the Pliocene. Van Beneden (1878), Capellini (1876), McLeod *et al.* (1993), Oishi & Hasegawa (1993a), Whitmore (1994), and Bisconti (2000) listed many different extinct Pliocene genera and species. Presently, only two genera are living: the Greenland bowhead whale, (genus *Balaena*, including the species *Balaena mysticetus*), and the right whale which is sometimes also called black right whale (genus *Eubalaena*). Based on morphology, just one species belonging to *Eubalaena* can be described whose name is *Eubalaena glacialis* (Cummings, 1985). Based on molecular biology, three different species should be considered as valid taxa: *Eubalaena glacialis*, *Eubalaena australis* and *Eubalaena japonica* (Rosenbaum *et al.*, 2000; Malik *et al.*, 2000; Perrin & Brownell, 2001). Morphological studies performed during the last century did not recognize the three species claimed on the basis of molecular phylogenetic studies. The present author had the chance to study several specimens belonging to *Eubalaena glacialis* from North Atlantic, one specimen from the Antarctic stock (representing the putative

species *Eubalaena australis*), and one specimen from the Japanese stock (representing the putative species *Eubalaena japonica*; see beyond the section dealing with Sources of Comparative Data); the differences among these specimens were so small to be easily explained by individual variation. However, it is possible that significant differences among the three stocks will be discovered through a morphological study including several specimens from each population. Presently it is not possible to distinguish these three putative species on the basis of morphology and for this reason we consider only one morphological species in the following text and maintain the name *Eubalaena glacialis* to term it.

Today, *Eubalaena glacialis* filter feeds in very cold Arctic and Antarctic oceans and completes its life cycle by reproducing in temperate waters. *Balaena mysticetus* is a northern hemisphere endemic which spends its total life cycle in Arctic seas (Tomilin, 1967; Gaskin, 1982; Cummings, 1985; Reeves & Leatherwood, 1985; Perry *et al.*, 1999).

The Italian fossil record of Balaenidae was described and figured during the second half of 19th century and early in the 20th principally by Capellini (1873, 1876, 1902, 1904, 1905) and Del Prato (1900); further discoveries were discussed by Trevisan (1941) and Cusani-Politi (1966). A tentative revision of the whole record was published by Pilleri (1987) but his work on baleen whales was criticized by McLeod *et al.* (1993) and Bisconti (2000). For this reason, there is a critical need for taxonomic and systematic revisions of the Italian fossil Balaenidae taxa. To solve this problem, a research program, started some years ago at the University of

Pisa (Italy), was carried on fossil Balaenidae. The first results of that program were new systematic and phylogenetic assessments of *Balaena montalionis* and *Balaenula astensis* (Bisconti, 2000).

In 1974, a new large cetacean was found in Pliocene sediments of the San Miniato Basin (Florence Province, Central Italy). Members of the Gruppo Archeologico Castelfranchese (Archaeological Group from Castelfranco, a little town about 30 km SW of Florence) led by Gianluca Pasqualetti, found a disassociated skull at Ricavo, near the town of Montopoli (Florence). The skull was studied briefly by Pilleri (1987, pp. 30-31) who identified it as *Physeter* cf. *macrocephalus*. Recently, this specimen was shown in two exhibitions on the fossil vertebrates from Montopoli and it was made available for a systematic revision. The skull bears apomorphies of the family Balaenidae and it is here referred to the extant genus *Eubalaena*.

According to a recent stratigraphic assessment of the San Miniato Basin (Dominici *et al.*, 1995), the specimen comes from early Late Pliocene sediments being about 3.5 Ma old. A search of the early occurrence of *Eubalaena* performed in literature (Savage & Russell, 1983; Carroll, 1988; McLeod *et al.*, 1993; Oishi & Hasegawa, 1993b; Fordyce & Barnes, 1994; Whitmore, 1994) and on the Internet (Damuth, 1997; Alroy, 1999) resulted in few citations. Due to some confusion in ancient literature dealing with living and fossil Balaenidae, we performed also searches with key-words as "*Balaena*", "*Balaenula*", "*Balaenidae*", "right whale", "bowhead whale", "balaenid" and assessed how much the found descriptions matched the characteristics of the genus *Eubalaena*; this second strategy was not more successful than the first one. The more relevant results of this search are discussed below.

Pilleri (1987) described two fossil specimens tentatively identified as *Eubalaena glacialis* from Tuscany and Emilia (northern Italy). Unfortunately, as discussed later, they are based on non-diagnostic fragments and their chronological assessment is unclear. In all of the other papers, only very Late Pliocene to Recent *Eubalaena* specimens are described (among others: Anonymous, 1888; Nybelin, 1846; Nishiwaki & Hasegawa, 1969; Freden, 1975; Fidalgo *et al.*, 1981; Cunha, 1985; Howchin, 1919; Fordyce, 1982, 1987). In light of the results of this search, the skull from the early Late Pliocene of Tuscany here discussed is the oldest known fossil record of the genus *Eubalaena*.

The goal of this work is the detailed description of the specimen and the discussion of its implications in our understanding of the evolution of Balaenidae.

Institutional abbreviations – MSNT: Museo di Storia Naturale e del Territorio (Natural History and Territory Museum), University of Pisa, Italy; MSNM: Museo di Storia Naturale del Mediterraneo (Natural History Museum of Mediterranean Sea), Livorno, Italy; USNM: United States National Museum, Smithsonian Institution, Washington DC, USA; ZML: Zoologisch Museum (Zoological Museum), Leiden, The Netherlands; IRSN: Institut Royal des Sciences Naturelles (Royal Institute of Natural Sciences), Bruxelles, Belgium.

Anatomical abbreviations – anf: anterior nuchal fossa; asc: anterior sagittal crest; asp: anterior supraoccipital process; bdp: basioccipital descending process; fm: foramen magnum; lc: lambdoidal crest; oc: occipital condyle; p: parietal; pnf: posterior nuchal fossa; psc: posterior sagittal crest; s: squamosal/parietal suture; sd: supraoccipital dome; sq: squamosal.

SOURCES OF COMPARATIVE DATA

Eubalaena glacialis – MSNT 264, USNM 267612, 333999, 23077, 301637, a specimen from ZML without inventory number identified by means of the '*Eubalaena australis*' label. Putative *Eubalaena japonica*: a nearly complete skeleton without inventory number held by ZML (the specimen is labelled as "*Balaena japonica*").

Balaena mysticetus – USNM 257513, IRSN 1532.

Balaena montalionis – MSNT 12357, holotype skull.

Caperea marginata – IRSN 1536.

Physeter macrocephalus – Two uncatalogued specimens held by MSNT and MSNM.

Balaenoptera physalus – Specimens held by MSNT: 251, 253, 255, 257, three MSNM specimens without inventory numbers.

Balaenoptera musculus – Specimens held by MSNT: 250, one MSNT specimen lacking inventory number.

Balaenoptera acutorostrata – Specimens held by MSNT: 260, 261.

Megaptera novaeangliae – MSNT 263.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order CETACEA Brisson, 1762

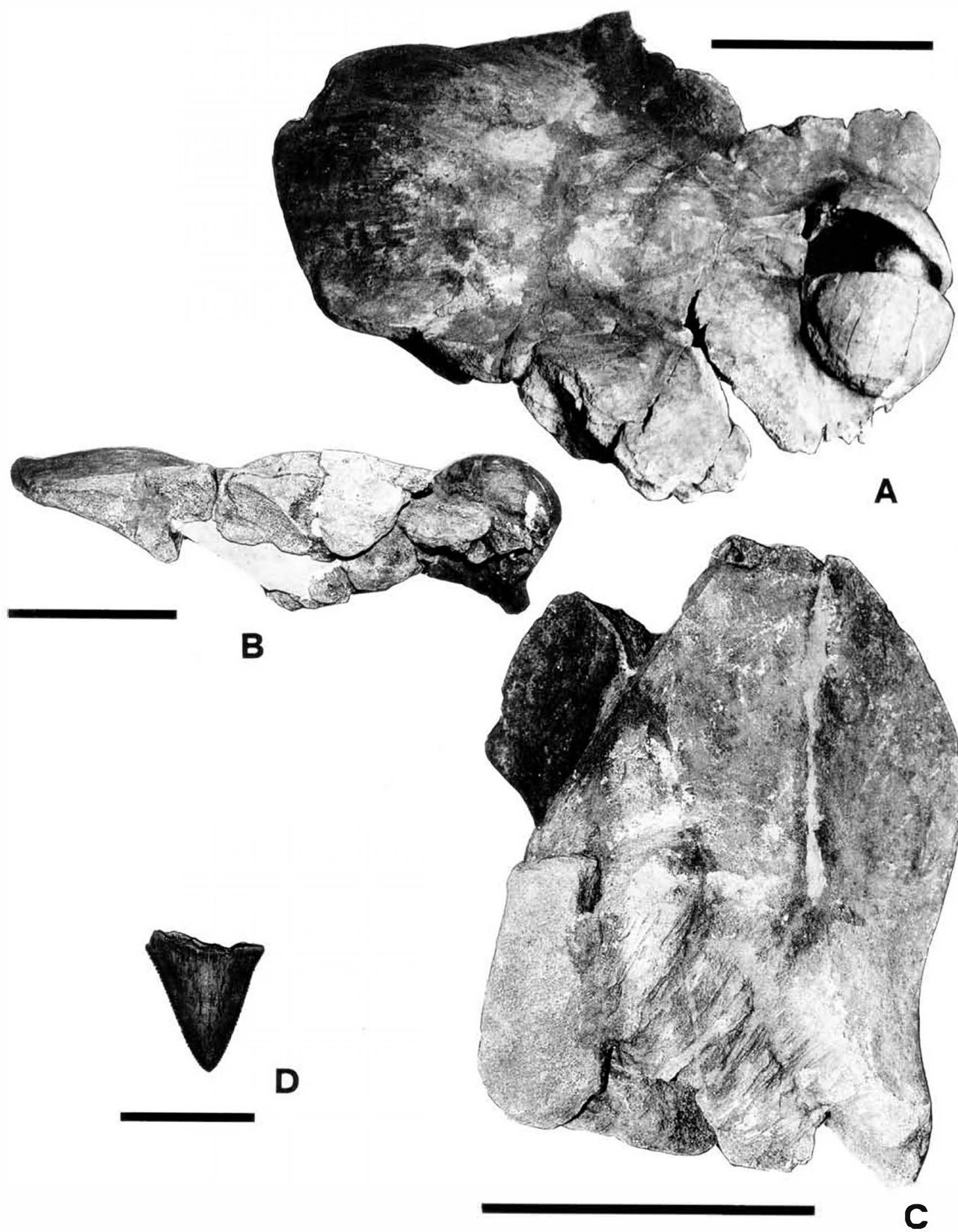
Suborder MYSTICETI Flower, 1864

Superfamily BALAENOIDEA Gray, 1868

Family BALAENIDAE Gray, 1825

Genus EUBALAENA Müller, 1776

Text-fig. 1 - The *Eubalaena* sp. skull and associated white shark tooth from Ricavo (Tuscany, Central Italy). A) dorsolateral view of the skull; B) lateral view; C) lateral view of the right squamosal; D) *Carcharodon carcharias* tooth. A, B, C scale bar is approximately 30 cm; D scale bar corresponds approximately to 4 cm.



EUBALAENA sp.
Text-figs. 1-3

1987 *Physeter* cf. *macrocephalus* - PILLERI, pp.30-31.

Referred specimen – A supraoccipital shield with the occipital condyles; both parietals and squamosals. The specimen is held by the Museo Archeologico di Santa Chiara in Castelfranco (Florence) and lacks an inventory number.

Locality and age – The specimen was found near Ricavo, a village approximately 1.75 Km SW from Montopoli (Florence province, central Italy). The discovery area is in the Pliocene marine member of the San Miniato Basin (Dominici *et al.*, 1995) in which a large assemblage of cetaceans and other marine organisms (sharks and mollusks) was collected. This member was described by Dominici *et al.* (1995) as an alternate between “Argille sabbiose, sabbie argillose, limi talora con livelli torbosi” (sandy clays, clayey sands, silts, sometimes with turfaceous levels) and “sabbie a *Flabellipecten* di facies marina, talora con livelli a *Cerastoderma* di facies salmastra; calcari detritici di facies marina” (sands with *Flabellipecten*, marine facies, sometimes with levels with *Cerastoderma*, brackish facies; debris limestone, marine facies). By the discovery of microfossils belonging to the *Globorotalia aemiliana* Zone (Nencini, 1984), all of this member is stratigraphically assessed as middle Pliocene (Piacenzian *sensu* Rio *et al.*, 1994) by Dominici *et al.* (1995, p.16). This chronological assessment corresponds to the early Late Pliocene *sensu* Sprovieri (1992; around 3.5-3.3 Ma).

Associated fauna – A single white shark (*Carcharodon carcharias*) tooth was found among the disassociated cranial bones (Text-fig. 1D).

Description – The Ricavo skull consists of the supraoccipital shield with attached parietal bones, and both the squamosals (Text-fig. 1A-C, Text-fig. 2A-B, Text-fig. 3). Linear measurements are furnished in table 1.

The supraoccipital shield bears a large anterior process with slightly damaged rostral borders. Anteriorly, the borders of the shield are rounded (anteriorly convex). At about 70 cm anterior to the foramen magnum, the lateral borders of the shield become linear and parallel to the sagittal plane. At about 33 cm from the foramen magnum, they diverge outward again. At the divergence point, the borders rise and, from a lateral viewpoint, obliterate the view of the posterior part of the supraoccipital shield (Text-fig. 1A; Text-fig. 2B). The lateral borders rise where the lambdoidal crests begin to appear as posterior continuations of the temporal crests.

The anterior surface of the supraoccipital is raised in respect to the posterior one; it is dorsally convex

maximum width of supraoccipital	900
width of the supraoccipital anterior process	660
lateral diameter of foramen magnum	130
longitudinal diameter of foramen magnum	108
lateral diameter of right condyle	149
lateral diameter of left condyle	150
longitudinal diameter of right condyle	243
longitudinal diameter of left condyle	249
distance between the anterior border of foramen magnum and the anterior limit of the posterior nuchal fossa	429
right squamosal height (1)	620
right squamosal length (2)	460
left squamosal height (1)	430
left squamosal length (2)	400

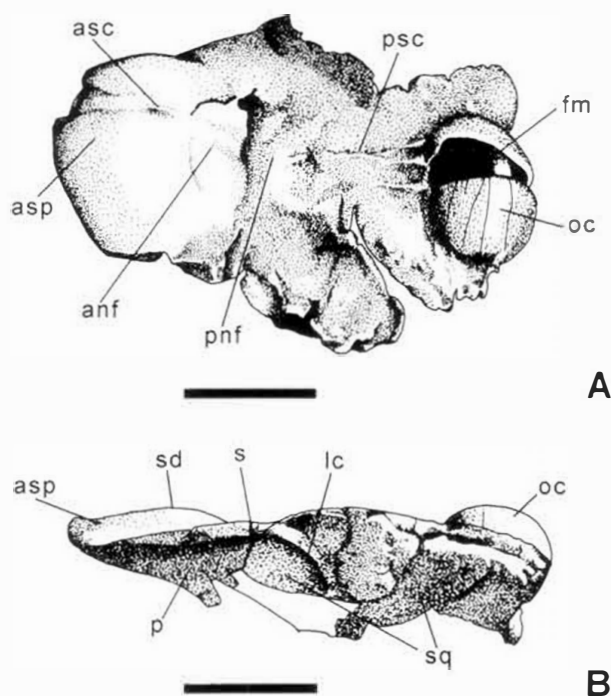
(1) As preserved on the specimen.

(2) It corresponds grossly to the anteroposterior diameter of the glenoid cavity.

Tab. 1 - Measurements of the Ricavo specimen, *Eubalaena* sp., Museo Archeologico di Santa Chiara, Castelfranco (Florence). Data in mm.

assuming a dome-shaped morphology; in the following text it will be termed the *supraoccipital dome*. The posterior half of the shield is flat and the only elevations are a sagittal crest and the lateral borders.

Anterior to the condyles, a low posterior sagittal crest develops to the half of the supraoccipital length. Caudally, it forms 5 low crests that go to the foramen magnum (Text-fig. 2A, Text-fig. 3). The more lateral



Text-fig. 2 - The *Eubalaena* sp. skull from Ricavo (Tuscany, Central Italy). A) lateral view; B) dorsolateral view. See Anatomical abbreviations for the lettering. Scale bar is approximately 30 cm.

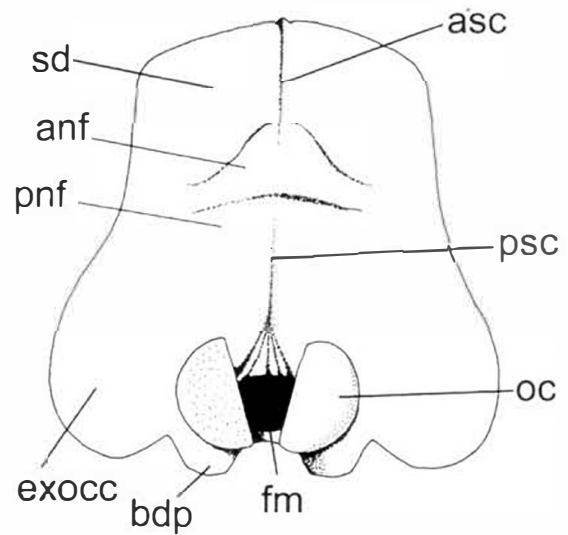
of these crests continue with the anteromedial margins of the occipital condyles. The posterior sagittal crest disappears anteriorly where the dome starts to develop. Anterior to the posterior sagittal crest is the anterior border of an extended fossa that is at the starting level of the anterior supraoccipital dome. That is the anterior nuchal fossa. The supraoccipital dome is laterally defined by two stocky protrusions between which an anterior nuchal fossa exists. A low anterior sagittal crest develops along the longitudinal axis of the supraoccipital dome to the anterior border of the shield. The described nuchal fossae are insertion areas of *Eubalaena* epaxial neck musculature.

The foramen magnum is dorsoventrally compressed and it is defined by two exquisitely preserved occipital condyles. The condyles have slightly convex articular surfaces and their medial walls are concave. Posteroventrally, the condyles are divided by a deep sulcus that tapers posteriorly. The foramen magnum occupies the anterior one third of the cavity defined by the medial borders of the condyles. Ventrolaterally to the occipital condyles, a damaged paroccipital process protrudes defining a lateral jugular notch. Its medial edge is lacking.

The large and flat exoccipital shows a rounded posterior border that projects downward. This morphology, in a complete skull, allows the exoccipital to be posterodorsal to the squamosal. On the right side, the lateral edge of the exoccipital is 44 cm from the medial side of the right condyle.

In ventral view, the anterior half of the supraoccipital shield is superimposed on both parietals. These elements are flat and large and their morphology is approximately quadrangular in ventral view. The sagittal suture between the parietals is not fused and their anterior borders are slightly posterior to the anterior process of the supraoccipital. It suggests that in this specimen the supraoccipital extended over the posterior portion of the frontal excluding the parietals from the cranial vertex. This sutural pattern is typical of extant and fossil Balaenidae. Just a very dorsal part of the lambdoidal suture is preserved. It starts at the posterior limit of the anterior nuchal fossa and extends to anterior limit of the anterior one.

The posterior half of the supraoccipital covers the braincase. The dorsal wall of the braincase is preserved and shows three bilateral cavities that are divided by a sagittal crest 13 cm long. The crest extends posteriorly to the foramen magnum. From the anterior border of the rostral ellipsoidal endocranial cavity, a channel projects anteriorly and outward. Its width is 2.5 cm at the exit from the braincase. This channel continues in a deep and narrow sulcus more laterally. Caudally, a small flat ridge divides the anterior part of the endocranial cavity from the posterior. The latter is transversely elongated and its surface is concave. It is possible to observe crests and valleys on the surface of both endocranial cavities; these could reveal the pattern of vascularization of the brain but, presently, an endocranial cast is unavailable.



Text-fig. 3 - *Eubalaena* sp. from Ricavo (Tuscany, Central Italy), skull in posterior view. See Anatomical Abbreviations for the lettering. Distance between the dorsal border of the foramen magnum and the anterior apex of the supraoccipital = 92.9 cm.

Among the disassociated temporal regions, the right one is better preserved (Text-fig. 1C). The temporal regions are formed by the squamosal bones. In lateral view, the right squamosal is approximately triangular. Its anterior border coincides with the convex and rounded lateral squamosal crest that is vertically oriented. Just the dorsal portion of the lateral squamosal crest is anteriorly convex but its rounded profile becomes concave ventrally. Here, it forms the stocky anteroventral zygomatic process of the squamosal that does not protrude anteriorly, in contrast to all of the mysticetes other than Balaenidae. The lateral surface of the squamosal is planar. The posterior border of the squamosal is posteriorly convex. The ventral portion of the squamosal (including the glenoid cavity for articulation with the dentary) is missing. Ventrally, there is a deep excavation that exposes delicate bone trabeculae and large lacunae (diameter 4 mm). The posterior part of this excavation is a large, heavy pillar (anteroposterior diameter = 280 mm; lateral diameter = 230 mm) that represents a portion of the postglenoid process. The posteroventral portion of the dorsal surface of the right squamosal is crushed and its restoration shows a sulcus that divides the most ventral part of the bone from the dorsal one. The sulcus is anteroposteriorly oriented and is also present on the left squamosal. It seems the sulcus is due to some compression due to post-mortem processes and it has not anatomical meaning.

COMPARISONS

Pilleri (1987) identified the Ricavo specimen as *Physeter* cf. *macrocephalus* based on the morphology

of the occipital condyles. To test this assessment, a comparative analysis was performed between the Ricavo specimen and two Recent specimens belonging to *P. macrocephalus* housed at MSNT and MSNM, and all the other mysticetes listed in the section dealing with Sources of Comparative Data. Information from the literature on *E. glacialis*, *Balaena mysticetus* (Cuvier, 1823; Van Beneden & Gervais, 1868-1879; True, 1904; Cummings, 1985; Reeves & Leatherwood, 1985), on the neobalaenid *Caperea marginata* (Baker, 1985; Beddard, 1901), on the balaenopterids *Balaenoptera physalus*, *B. acutorostrata*, *B. musculus*, *B. edeni*, *B. borealis*, *Megaptera novaeangliae*, and on the eschrichtiid *Eschrichtius robustus* (Van Beneden & Gervais, 1868-1879; True, 1904; Ridgway & Harrison, 1985) were also used to supplement the personal observations.

In *Physeter macrocephalus* the posterodorsal surface of the supraoccipital shield is completely convex. It is vertical and its anterior border projects slightly posteriorly. In lateral view, the anterior edge of the supraoccipital is posterior to the condyles (pers. obs.). This pattern cannot be found among the Balaenidae. The Ricavo skull exhibits a supraoccipital shield in which the anterior process is entirely anterior to the condyles. In *P. macrocephalus*, dorsal to the exoccipitals, the lateral borders of the supraoccipital diverge in a very marked way. On the Ricavo skull and other Balaenidae, in the anterior portion of the supraoccipital shield, the lateral borders do not diverge laterally but they converge to the sagittal axis. No nuchal fossae or sagittal crests are present on the uniformly convex supraoccipital of *P. macrocephalus*.

The rostral supraoccipital bears two nuchal fossae (anterior and posterior) that are divided along the midline by a continuous sagittal crest. The anterior nuchal fossa is nearly triangular. It is very small and its posterior border is obliquely oriented. In all the specimens belonging to *Eubalaena* we studied and in the Ricavo specimen the posterior border of the anterior nuchal fossa is transversely oriented. In roquals, the posterior nuchal fossa is wide and very concave but in *E. glacialis* and the Ricavo specimen it is flat-to-slightly concave. No supraoccipital dome is present in balaenopterids nor in balaenids other than *E. glacialis*.

The vertex structure of the Ricavo skull can be inferred based on the preserved parietals and anterior process of the supraoccipital shield. In the Ricavo skull, the supraoccipital is superimposed on both parietals; these bones do not extend more anteriorly than the anterior border of the supraoccipital and, for this reason, it can be inferred that the supraoccipital was superimposed also on the posterior portion of the frontal. Unfortunately, the frontal is not preserved on the specimen. No clues of articulation between the parietals and an hypothesized interparietal bone are found by the observation of the anterior borders of the parietals. It seems the parietals were in contact

with the frontal without the interposition of an interparietal. The parietals are not divided anteriorly by the interposition of the anterior process of the supraoccipital. This pattern excludes the skull from belonging to balaenopterids and eschrichtiids. Moreover, the superimposition of the supraoccipital on the posterior portion of the frontal, excluding the parietal from the cranial vertex, rules out the Ricavo skull from belonging to any nominal cetothere taxa.

In Neobalaenidae (represented only by the living *Caperea marginata*) the supraoccipital shield does not show well defined nuchal fossae and it is furrowed by one continuous sagittal crest along the midline (Beddard, 1901, pl. 8, p. 113). This pattern is different from that observed on the Ricavo specimen.

In extant and fossil mysticetes other than Balaenidae and Neobalaenidae, the glenoid cavity of the squamosal bone is nearly horizontal or slightly oblique with anteroventral concavity, and the squamosal bone is not significantly developed along the dorsoventral axis of the skull. The squamosals of the Ricavo skull are massive and dorsoventrally oriented; the orientation is inferred by observing the position of the glenoid cavity and the morphology of squamosal crest and zygomatic process. The squamosal crest is rounded and the general morphology of the squamosals is more similar to the corresponding bone of *E. glacialis* than *Balaena mysticetus*. In fact, in lateral view, in *B. mysticetus* the squamosal is oblique (i.e., the apex of the zygomatic process of the squamosal is posterior relative to the anterior convexity of the squamosal crest and the posterior wall of the temporal fossa can be seen when the skull is in lateral view) while in *E. glacialis* it is vertical (i.e., the apex of the zygomatic process of the squamosal and the anterior convexity of the squamosal crest are on the same vertical line and the posterior wall of the temporal fossa cannot be seen when the skull is observed in lateral view; see Bisconti, 2000).

One of the apomorphies listed by McLeod *et al.* (1993) to support the monophyly of the superfamily Balaenoidea (including Balaenidae and Neobalaenidae) is the glenoid fossa and zygomatic portion of squamosals moved far ventrally on the skull. Bisconti (2000) noted that only balaenids exhibit rounded squamosal crests whose external convexity is anterior (and not dorsal or anterodorsal as in roquals, eschrichtiids and many cetotheres). Both of these characters are observed on the Ricavo skull and they exclude it from belonging to Mysticeti families other than Balaenidae.

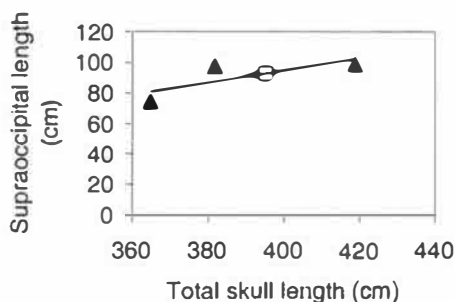
The supraoccipital organization of nuchal fossae, the presence of a supraoccipital dome and the rostrally enlarged anterior process exclude the Ricavo skull from belonging to the genus *Balaena*. In fact, supraoccipital shields of *Balaena montalioni* MSNT #12357 holotype (Capellini, 1904; Bisconti, 2000) and *Balaena mysticetus* (Reeves & Leatherwood, 1985) do not show both nuchal fossae and sagittal

crests. Linear dimension and supraoccipital and squamosal morphologies exclude the Ricavo skull from belonging to the genus *Balaenula* (Van Beneden, 1878, pl. 1, 1880, pp. 52-65; Bisconti, 2000). Among the *Balaenula* specimens, the nuchal fossae are less marked (Bisconti, 2000) and a sagittal crest is lacking. Further, the squamosal of *Balaenula* shows a less marked squamosal crest and a flat posterior wall of the temporal fossa. In the Ricavo specimen, and in the other large balaenids the squamosal crest is very high and the posterior wall of the temporal fossa is very concave.

Tomilin's (1967) linear measures of *E. glacialis* provide a basis to infer total skull length and total body length of the Ricavo skull. In Text-fig. 4 the relationship between supraoccipital shield length vs. total skull length is plotted. A linear regression (equation: $y = 0.3937x - 62.803$) predicts a 3.95 m total skull length for the Ricavo specimen (Text-fig. 4). The value is within the range provided by Tomilin (1967) and True (1904). Tomilin (1967) suggests that in *Eubalaena glacialis* the total body length is around 3-3.5 times the total skull length; this leads to a total body length of about 11.86-13.84 m (approximately 12-14 m) for the Ricavo specimen that is within the range of an adult living right whale. From both these estimates and morphology it is impossible to assess the sex of the specimen. However, judging from the complete fusion of the supraoccipital with both exoccipitals, the marked supraoccipital dome, and the high development of the squamosal crests, it can be said that the specimen represents a mature individual.

DISCUSSION

Pilleri (1987) described two fragmentary specimens from the Italian Pliocene attributed to the genus *Eubalaena*. They are a 70-cm-long radius from Emilia and a lumbar vertebra from Tuscany. The age



Text-fig. 4 - Linear regression to infer the total skull length of the *Eubalaena* sp. from Ricavo (Tuscany, Central Italy). Data from Tomilin (1967). Regression equation: $y = 0.3937x - 62.803$ ($R^2 = 0.5967$). Black triangles are extant *E. glacialis*; white square is the Ricavo specimen. The position of the Ricavo specimen onto the regression line is inferred for the x-axis from the regression equation.

of the specimens is unclear (Pliocene *s.l.*). Unfortunately, Balaenidae lumbar vertebrae do not bear apomorphies at the species level and the radius is exceptionally large to belong to the genus *Eubalaena*. Morphology of the radius reveals that the curvature of internal and external borders are not marked as it is observed in extant Balaenidae, and this makes it possible the radius belongs to a large odontocete like *Physeter*. According to the advice expressed by Fordyce (1989) and Fordyce and Barnes (1994) to use just apomorphies to state both diagnoses of new taxa and identifications of specimens, the systematic identifications by Pilleri (1987) of *Eubalaena glacialis* are not acceptable. About the radius, Pilleri himself is doubtful (1987, p. 123: the radius "shape does not match any of the recent species completely"; the radius "bears the greatest resemblance to a *Eubalaena glacialis*, although the rear (ulnar) edge of both recent species is unequivocally concave, whereas in the fossil radius it is straight"; and radius "dimensions are considerably in excess of those of the radii of northern and southern right whales"). In light of this discussion, the Ricavo specimen is the oldest known individual belonging to the genus *Eubalaena*.

It is impossible to state if the Ricavo skull belongs to the extant taxon *Eubalaena glacialis* or another putative species of the genus *Eubalaena*. Lacking other morphological evidence, the characteristics shared by the Ricavo specimen and all the stocks belonging to the extant *Eubalaena* could be synapomorphies of the genus and these are the following: presence of supraoccipital dome, and a discontinuous sagittal crest is present on the supraoccipital shield. Other discoveries are needed to evaluate the past and present morphological diversity of *Eubalaena*.

The Ricavo skull traces back the history of *Eubalaena* to 3.5-3.3 Ma partly filling the gap in the fossil record of this genus. The early Late Pliocene (~3.5 Ma) is also the proposed age of the small balaenid *Balaenula astensis* from northern Italy (Bisconti, 2000). Through the phylogenetic analyses shown by Bisconti (2000) it is possible to assess the time of divergence between the genus *Balaena* and the *Balaenula-Eubalaena* clade at 5.0-4.8 Ma. That is the date proposed for the fossil *Balaena montalioni*, presently the only extinct member of the genus *Balaena* whose phylogenetic relationships are known. This hypothesis is corroborated by the fossil record of the small-sized genus *Balaenula* and other large balaenids. In fact, Barnes (1977) cites an early occurrence of *Balaenula* and Whitmore (1994) mentioned a balaenid whale very close to the extant *Balaena mysticetus* in latest Miocene/early Pliocene (10-5 Ma) sediments from East and West U.S. This data supplement the phylogenetic analyses provided by Bisconti (2000) in supporting the hypothesis of a late Miocene radiation of *Balaenula*, *Balaena* and *Eubalaena*.

There are not right whale populations in the present Mediterranean Sea; the last sighting of an

Eubalaena in Italian waters is from 19th century (Capellini, 1877). The presence of a fossil right whale in Central Italy suggests that the Pliocene *Eubalaena* distribution comprised also the Mediterranean basin. However, other data are needed to estimate both its Pliocene abundance and Plio-Pleistocene exclusion from that basin.

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