

## **A cetotheriid whale from the Miocene of the Mediterranean**

(Running title: **Cetotheriid from the Mediterranean**)

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With 3 figures

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### **Abstract**

Cetotheriids are a once diverse clade of baleen whales with a rich fossil record across the  
30 entire Northern Hemisphere, except the Mediterranean Basin. Here, we describe a partial  
mandible from the upper Miocene Arenaria di Ponsano Formation exposed near Pisa  
(Tuscany, Italy), which unequivocally represents a cetotheriid based on its low, broadly  
triangular coronoid process, obliquely oriented condyle, deeply excavated subcondylar  
furrow, and posteriorly elongated angular process. Our new specimen highlights the apparent  
35 rarity of this family in the Mediterranean, which may reflect competition with ecologically  
similar grey whales. The latter, in turn, may explain the geographical isolation and disparate  
anatomy of the seemingly endemic Paratethyan cetotheriines.

**Key words:** Arenaria di Ponsano Formation, Cetotheriinae, Eschrichtiinae, mandible,  
40 Mysticeti, Italy, palaeobiogeography, Paratethys, Tortonian, Tuscany.

## 1. Introduction

Cetotheriids are a mostly extinct clade of small to medium-sized baleen whales with a highly distinctive skull anatomy (BOUETEL & DE MUIZON 2006; WHITMORE & BARNES 2008; EL ADLI et al. 2014; GOL'DIN et al. 2014; MARX et al. 2019). Their feeding strategy may have involved suction (EL ADLI et al. 2014; GOL'DIN et al. 2014; TARASENKO 2014; MARX et al. 2017a), with aspects of their skull architecture resembling grey whales (STEEMAN 2007; BISCONTI 2008).

Cetotheriids first appeared in the middle Miocene in the form of *Tiucetus* and *Ciuciulea* (MARX et al. 2017b; GOL'DIN 2018; BOSIO et al. 2020), and attained a seemingly global distribution during the Tortonian (BOUETEL & DE MUIZON 2006; WHITMORE & BARNES 2008; BOESSENECKER 2011; BISCONTI 2015; GOL'DIN & STEEMAN 2015; MARX et al. 2016; DI CELMA et al. 2017; GOL'DIN & STARTSEV 2017; MARX et al. 2019). During the Pliocene, they became restricted to various species of *Herpetocetus* and then finally disappeared – except, perhaps, for the pygmy right whale *Caperea* – during the early Pleistocene (BOESSENECKER 2013; FORDYCE & MARX 2013; EL ADLI et al. 2014).

Despite cetotheriids being clearly present in both the North Atlantic and the Paratethys (a former epicontinental sea stretching from Eastern Europe to Central Asia), no unambiguous occurrences have been described from the Mediterranean (but see BISCONTI et al. 2020c). This gap is striking both from a biogeographical point of view and given the widespread local occurrence of cetacean-bearing formations (BIANUCCI & LANDINI 2002; BISCONTI 2009). Here, we provide the first detailed description of a cetotheriid from the Mediterranean Basin, and discuss possible causes and consequences of the rarity of the family in this region.

## 2. Stratigraphic and palaeoecological framework

The new specimen comes from the upper portion of the Arenaria di Ponsano Formation, a

65 mostly sandy, marine sedimentary unit exposed at various sites around the Tuscan village of Ponsano, central Italy (FORESI et al. 1997; FORESI et al. 2004) (Fig. 1). It was discovered by two of the authors (S.C. and A.D.C.) just west of Podere Orgiaglia, 1.5 km west-northwest of Ponsano (locality 28 of MENESINI 1967b). Foraminifera and nannoplankton suggest an upper Miocene (lower Tortonian) age (MAZZANTI et al. 1981; BIANUCCI & LANDINI 2005).

70 Besides our new fossil, the Arenaria di Ponsano Formation has yielded molluscs, echinoids, barnacles, cartilaginous and bony fishes, sirenians, and other cetaceans (MENESINI 1963; TAVANI & TONGIORGI 1963; MENESINI 1966, 1967a, b; MAZZANTI et al. 1981; BIANUCCI & LANDINI 2002; 2003; 2005). Sedimentological and fossil assemblage data suggest a subtropical infralittoral to circalittoral shelf setting, possibly close to a river mouth (MENESINI 75 1967b; MAZZANTI et al. 1981; BIANUCCI & LANDINI 2005).

### 3. Systematic palaeontology

Cetacea BRISSON, 1762

Neoceti FORDYCE & MUIZON, 2001

80 Mysticeti GRAY, 1864

Cetotheriidae BRANDT, 1872

Cetotheriidae gen. et sp. indet.

(Figure 2)

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**Referred material:** Posterior portion of a mandible, stored at Badia a Settimo (Scandicci, Italy) as part of the permanent exhibition “Gruppo AVIS Mineralogia e Paleontologia Scandicci” (GAMPS; accession number 00970).

**Occurrence:** Lower Tortonian portion of the Arenaria di Ponsano Formation (Tuscany,  
90 central Italy); 43°22'03.6" N, 10°58'11.1" E.

**Description:** Incomplete left mandible (355 mm long) preserving the ramus and proximal  
portion of the body. In medial view (Fig. 3a), the coronoid process is low and roughly  
triangular, with its tip being located 215 mm anterior to the end of mandible. The mandibular  
fossa rivals the body in height and ventrally terminates in a broad, deeply excavated  
95 subcondylar furrow. The angular process is robust, gently descends below the level of the  
neck, and extends well posterior to the mandibular condyle. Its medial surface bears an  
elongate, flattened platform likely marking the insertion of the medial pterygoid muscle.

In lateral view (Fig. 3b), the condyle forms an angle of ca 70° with the horizontal and rises  
almost to the level of the coronoid process. Posteroventrally, it joins the angular process via a  
100 thick ridge obscuring the posterior termination of the subcondylar furrow. Anterior to the  
condyle, the ramus is excavated by a shallow fossa for the deep masseter muscle.

In dorsal view (Fig. 3c), the ramus is flattened medially but convex laterally. The tip of the  
coronoid process is strongly bent outwards. The postcoronoid elevation is well developed and  
overhangs the mandibular fossa along the relatively straight mandibular neck. The condyle is  
105 narrow and somewhat offset laterally from the remainder of the ramus.

**Comparisons and remarks:** GAMPS-00970 belongs to Cetotheriidae based on its low and  
broadly triangular coronoid process; obliquely oriented, dorsally raised mandibular condyle;  
trough-like subcondylar furrow; and elongated angular process with a well-defined  
attachment area for the medial pterygoid muscle (EL ADLI et al. 2014; GOL'DIN et al. 2014;  
110 MARX et al. 2019).

The pronounced development of these features distinguishes it from early-diverging  
cetotheriids like *Joumocetus* and, possibly, *Diorocetus* and *Thinocetus* (MARX et al. 2017b;

KIMURA & HASEGAWA 2021). Likewise, the angular process is too elongate and the condyle too oblique and low to permit an assignment to cetotheriines (sensu GOL'DIN & STARTSEV 115 2017). Among the remaining cetotheriids, both herpetocetines and several genera of uncertain subfamilial affinity (e.g. *Herentalia*, *Piscobalaena*, *Tranatocetus*) provide a possible match, although the elongation of the angular process in herpetocetines tends to be more obvious (BOESSENECKER 2011; EL ADLI et al. 2014; COLLARETA et al. 2015; TANAKA et al. 2018).

#### 120 **4. Taphonomic observations**

Like other previously described cetotheriid mandibles (e.g. DEMÉRÉ & CERUTTI 1982; COLLARETA et al. 2017), GAMPS-00970 preserves several shark bite marks. The latter are located on the ventrolateral surface of the mandibular neck (Fig. 3a) and take the form of centimetre-sized, shallow, subvertical, roughly parallel grooves matching types I or II of 125 CIGALA FULGOSI (1990). Absence of serration suggests a large shark with smooth-edged teeth like *Cosmopolitodus hastalis*, which is known from the same outcrop as GAMPS-00970 (MENESINI 1967b). The shallowness of the incisions and the lack of type III-V bite marks (sensu CIGALA FULGOSI 1990, and COLLARETA et al. 2017) may suggest low-motivation scavenging.

130 The mandible is associated with two bivalves: an encrusting oyster just beside the postcoronoid crest (Fig. 3) and an articulated pectinid shell inside the collapsed mandibular canal. Whereas the presence of the pectinid is likely fortuitous, the oyster attached itself to the bare bone and thus implies decomposition of the overlying integument prior to burial.

#### 135 **5. Discussion**

Cetotheriid fossils are common across the North Atlantic but surprisingly not in the

Mediterranean. Previous studies reported specimens from Spain and Italy, but the available material is either too incomplete to allow a clear identification (PILLERI 1990; BIANUCCI & LANDINI 2005; BIANUCCI & SORBINI 2014), uncertainly related (TSAI et al. 2017), or remains  
140 largely undescribed (BISCONTI et al. 2020c). GAMPS-00970 represents the first unequivocal, fully described cetotheriid from the Mediterranean basin. Even so, the almost complete absence of this family from the otherwise rich local mysticete record (BISCONTI 2009, 2010; BIANUCCI et al. 2019; BISCONTI et al. 2020a; BISCONTI et al. 2020b; BISCONTI et al. 2020c) is remarkable.

145 During the early Tortonian, the Mediterranean connected the North Atlantic with the remnants of the Paratethys (RÖGL 1999; POPOV et al. 2006) (Fig. 3). Cetotheriids were common in the Eastern Paratethys during this time, but generally belonged to an endemic lineage (cetotheriines) characterised by small size and pachyosteosclerosis (GOL'DIN & STARTSEV 2017). Judging from the scarcity of Mediterranean fossils, cetotheriines had little  
150 contact with their North Atlantic cousins, which – along with the localised conditions of the Paratethys itself – may explain their peculiar anatomy.

The scarcity of cetotheriids in the Mediterranean may reflect competition with grey whales, which are thought to have a superficially similar feeding ecology (EL ADLI et al. 2014; GOL'DIN et al. 2014; TARASENKO 2014), as well as a deep history in the region (BISCONTI  
155 & VAROLA 2006; BISCONTI 2008; MARX & FORDYCE 2015). On the other hand, grey whales seemingly overlapped with herpetocetines in the North Atlantic for much of the Pliocene (WHITMORE & KALTENBACH 2008; TSAI et al. 2020), casting doubt on the idea of competitive exclusion. A better understanding of the Mediterranean history (or lack thereof) of both clades is required to elucidate this question.

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## Figure captions

320 [Possible positions for the three figures: Fig. 1 between lines ... and ...; Fig. 2 between  
lines ... and ...; Fig. 3 between lines ... and ...]

**Fig. 1.** Position of the fossil locality (white star) on a schematic regional geological map. B-  
CI = Baccinello-Cinigiano Basin; CA = Casino Basin; RD = Radicofani Basin; SI = Siena  
325 Basin; VC = Val di Chiana Basin; VE = Valdelsa Basin; VO-RA-CH = Volterra-  
Radicondoli-Chiusdino Basin. Modified from SPADINI & MANGANELLI (2015).

**Fig. 2.** Posterior portion of a left cetotheriid mandible (GAMPS-00970) from the upper  
Miocene Arenaria di Ponsano Formation, in A – medial, B – lateral, and C – dorsal views.  
Vertical arrowheads indicate the location of bivalve specimens (downward pointing  
330 arrowheads: encrusting oyster; upward pointing arrowhead: pectinid). The horizontal  
arrowhead points to shark tooth marks.

**Fig. 3.** Palaeogeographical reconstruction of the Mediterranean and the Eastern Paratethyan  
during the Tortonian, modified from RÖGL (1999: fig. 12).

Figure 1

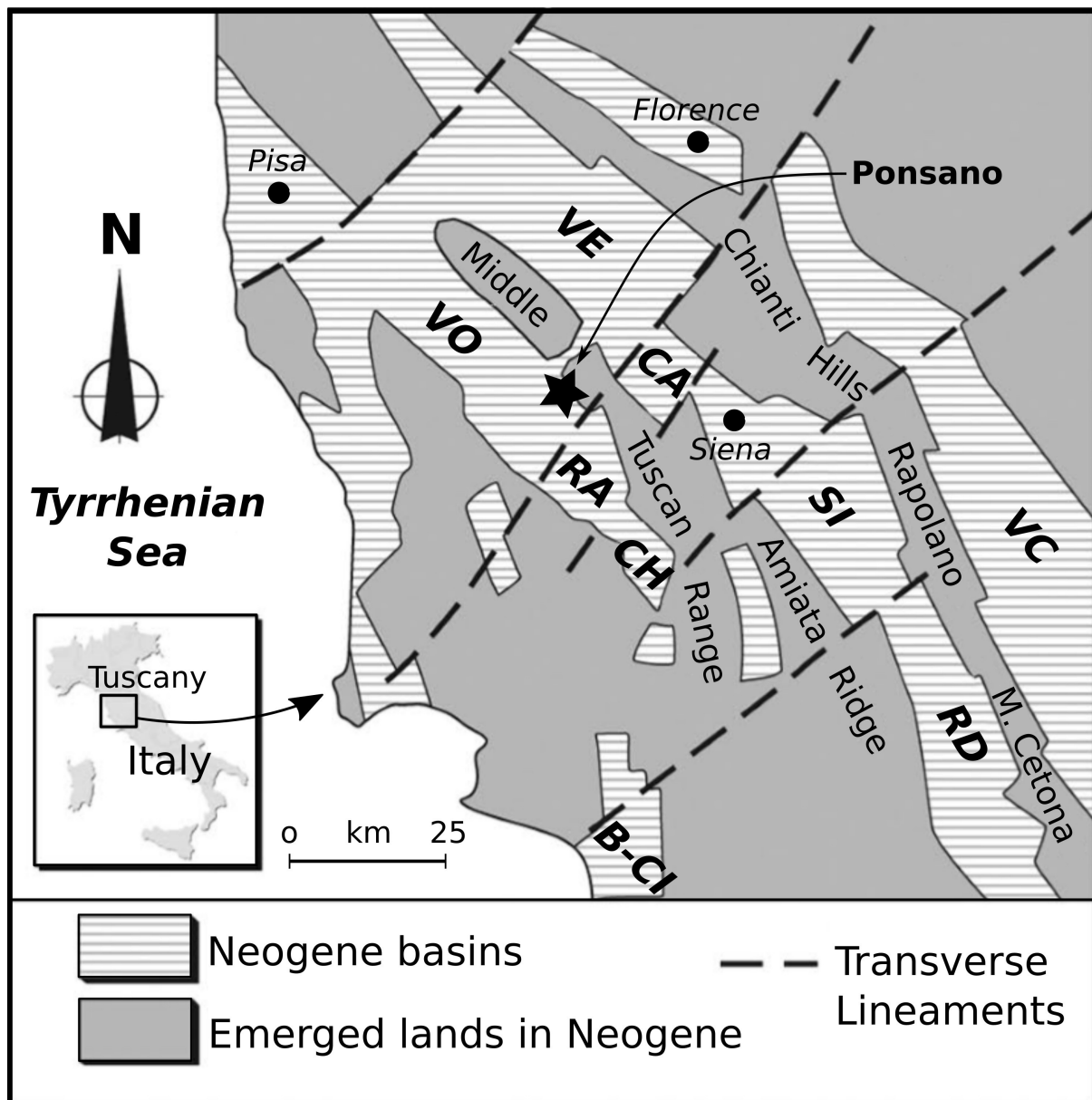
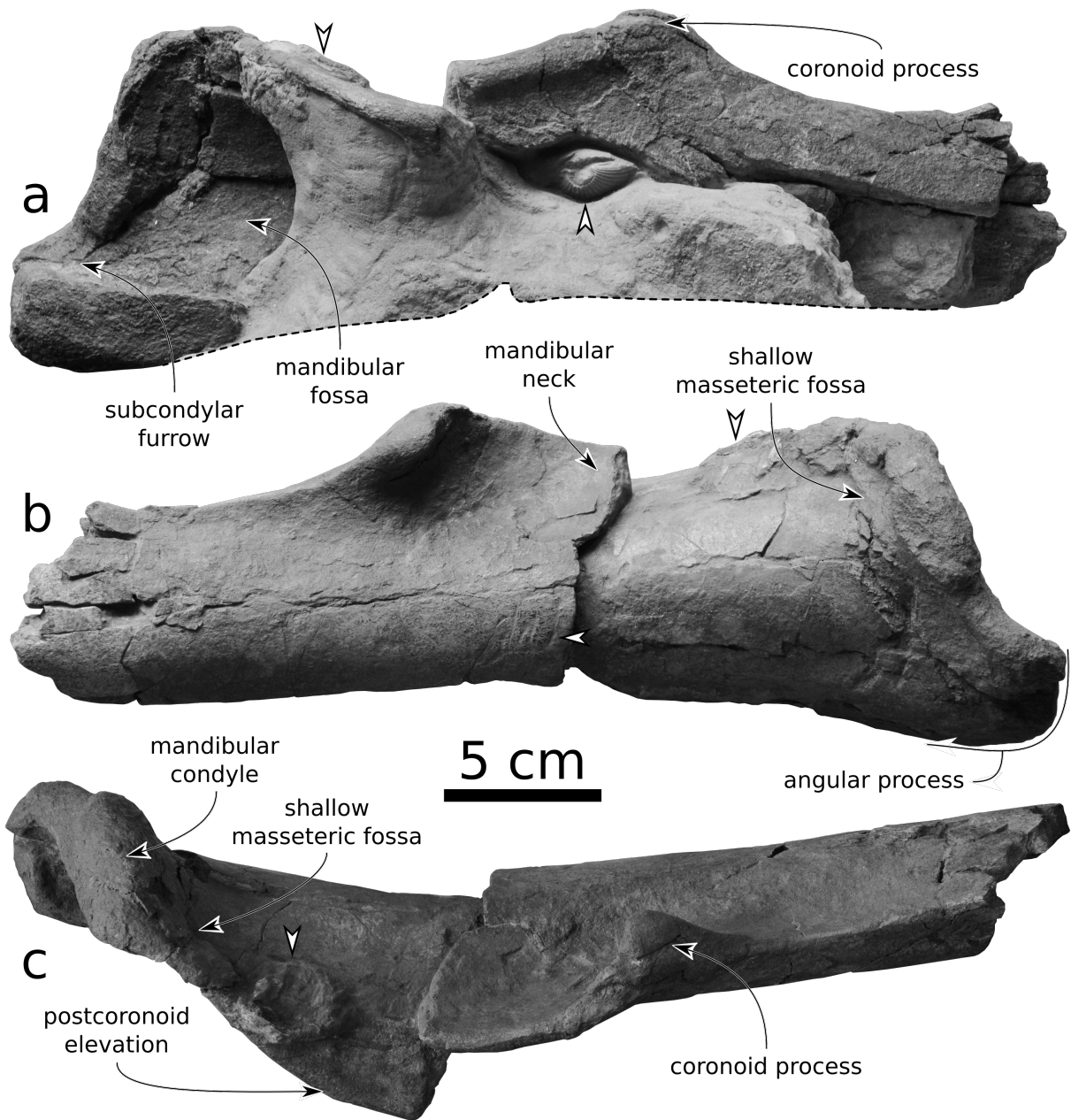


Figure 2



**Figure 3**

