

**A new Monodontidae (Cetacea, Delphinoidea) from the early Pliocene of Italy supports a warm-water origin for narwhals and white whales**

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3 A new Monodontidae (Cetacea, Delphinoidea) from the early Pliocene of Italy supports a  
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5 warm-water origin for narwhals and white whales  
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24 RH: BIANUCCI ET AL.—NEW MONODONTID FROM ITALY  
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3 ABSTRACT—A new taxon of monodontid cetacean, *Casatia thermophila* gen. et sp. nov., is  
4 here described on the basis of a partial skull from lower Pliocene (5.1-4.5 Ma) marginal-  
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6 marine deposits of Tuscany (central Italy). This new taxon belongs to Monodontidae owing to  
7  
8 the presence of a medial exposure of the maxillae anterior and lateral to the external bony  
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10 nares; it mainly differs from all other named monodontids by the presence of a median  
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12 depression of the premaxillae anterior to the premaxillary sac fossae and by a medial margin  
13  
14 of the premaxillary-maxillary suture that does not parallel the anterolateral profile of the  
15  
16 external bony nares. Our phylogenetic analysis, the first including all taxa of Monodontidae,  
17  
18 recovers *Casatia* as a crown monodontid, more closely related to *Delphinapterus* than to  
19  
20 *Monodon* and sister group of an unnamed taxon from the North Sea. The holotype of *Casatia*  
21  
22 represents the first and only fossil monodontid from the Mediterranean Basin. Taking place  
23  
24 besides abundant fossils of strongly thermophilic marine vertebrates such as the bull shark  
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26 *Carcharhinus leucas*, the tiger shark *Galeocerdo cuvier*, and the extinct sirenian  
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28 *Metaxytherium subapenninum*, our finding represents the strongest evidence supporting the  
29  
30 hypothesis that monodontids once thrived in low-latitude, warm-water habitats. In the light of  
31  
32 our phylogenetic reconstruction, the early relatives of the extant monodontids might have  
33  
34 adapted independently to the high-latitude, cold-water environments they currently master.  
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36 The definitive disappearance of the Neogene thermophilic monodontids could be attributed to  
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38 the cooling episode that accompanied the onset of long-term Northern Hemisphere glaciation  
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40 around 3 Ma.  
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## 51 INTRODUCTION

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56 The narwhal (*Monodon monoceros*) and the white whale or beluga (*Delphinapterus*  
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3 *leucas*), two of the most charismatic marine mammal species, are the sole extant members of  
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5 the toothed whale family Monodontidae, living exclusively in arctic and subarctic cold waters  
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7 (e.g., O'Corry-Crowe, 2018; Heide-Jørgensen, 2018). Unlike other modern cetacean families,  
8  
9 the fossil history of monodontids is much fragmentary, and only three extinct species  
10  
11 (*Bohaskaia monodontoides*, *Denebola brachycephala*, and *Haborodelphis japonicus*) have  
12  
13 been described so far, each of them being known by the sole holotype (Barnes, 1984; Vélez-  
14  
15 Juarbe and Pyenson, 2012; Ichishima et al., 2019). Here we report on a newly found early  
16  
17 Pliocene (5.1-4.5 Ma) monodontid fossil from shallow-marine deposits of the Mediterranean  
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19 Basin whose fossil content depict warm-water paleoclimatic conditions. Recognized as  
20  
21 representative of a new genus and species of crown monodontids, this finding strongly  
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23 supports the hypothesis that extant narwhals and white whales have warm-water, near-tropical  
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25 evolutionary roots.  
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30 **Institutional Abbreviations**—**IRSNB**, Institut royal des Sciences naturelles de  
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32 Belgique, Bruxelles, Belgium; **MACUB**, Museo di Anatomia Comparata dell'Università di  
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34 Bologna, Italy; **MACUP**, Museo di Anatomia Comparata dell'Università di Pavia, Italy;  
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36 **MCSNT**, Museo Civico di Storia Naturale di Trieste, Italy; **MLSUF**, Museo di Storia  
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38 Naturale, La Specola, Università di Firenze, Italy; **MSNB**, Museo di Scienze Naturali di  
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40 Bergamo “E. Caffini”, Italy; **MSNUP**, Museo di Storia Naturale dell'Università di Pisa, Italy;  
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42 **MZUN**, Museo Zoologico dell'Università degli Studi di Napoli “Federico II”, Italy; **USNM**,  
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44 National Museum of Natural History, Smithsonian Institution, Washington, USA.  
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## 51 SYSTEMATIC PALEONTOLOGY

### 52 53 54 55 56 57 58 59 60 CETACEA Brisson, 1762

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3 ODONTOCETI Flower, 1867

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5 DELPHINOIDEA Gray, 1821

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7 MONODONTIDAE Gray, 1821

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9 *CASATIA*, gen. nov.

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14 **Type and Only Known Species**— *Casatia thermophila* gen. et sp. nov.

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16 **Diagnosis**—Same as for the type species until other species are described.

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18 **Etymology**—The genus name honors Simone Casati, prominent amateur paleontologist  
19 who discovered most of the fossil vertebrates from Arcille (the locality where the holotype of  
20 *Casatia thermophila* was found) and author of several academic and popularizing works on  
21 the Pliocene marine vertebrates of Tuscany (Casati, 2007; Bianucci et al., 2009; Oddone et al.,  
22 2009; Casati and Oddone, 2011; Cigala Fulgosi et al., 2009; Collareta et al., 2017, 2018).

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33 *CASATIA THERMOPHILA*, sp. nov.

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35 (Figs. 2–4)

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39 **Holotype**—MSNUP I-17602, partial skull.

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41 **Etymology**—The species name is from the Greek *thermós* (=hot) and *philos* (=loving),  
42 considering the warm-water habits of this extinct cetacean.

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47 **Type Locality, Horizon, Age and Associated Fossils**—MSNUP I-17602 was  
48 discovered and collected from a quarry at Arcille (Campagnatico, Grosseto Province,  
49 Tuscany, central Italy; 42°47'12.18" N, 11°17'6.13" E). The finding site (Fig. 1A) is located in  
50 the Baccinello-Cinigiano Basin, one of the post-collisional basins of the northern Apennines.  
51 This basin is filled by Neogene and Quaternary continental and marine deposits (Benvenuti et  
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3 al., 2001) that host rich and diverse fossil vertebrate assemblages. The succession exposed at  
4  
5 the Arcille quarry (Fig. 1B) is comprised of shallow marine siliciclastic deposits dominated  
6  
7 by yellowish fossiliferous sandstones with subordinate conglomeratic horizons overlain by  
8  
9 greyish mudstones (Tinelli et al., 2012). These deposits can be entirely referred to the “S2  
10  
11 Synthem” recognized in the Neogene sedimentary succession of Tuscany by Dominici et al.  
12  
13 (2018). The “S2 Synthem” is a large-scale, stratigraphically complex, and lithologically  
14  
15 diverse lower Pliocene (i.e., Zanclean) depositional unit which includes fluvial  
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17 conglomerates, fluvio-deltaic sandstones, and shelfal mudstones (Dominici et al., 2018). The  
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19 fossiliferous sandstones from which the *Casatia* holotype was collected were deposited in a  
20  
21 deltaic to shoreface shallow-water setting (Tinelli, 2013) and feature a planktic foraminiferal  
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23 assemblage that indicates the lower part of the Zanclean, i.e. the Mediterranean Pliocene  
24  
25 (=MPI) zone 2 of Cita (1975), whose bounding bioevents have been calibrated by Lourens et  
26  
27 al. (2004) at 5.08 and 4.52 Ma, respectively (Sorbi et al., 2012). Other vertebrate remains  
28  
29 from this deposit include five skeletons of the extinct dugongid sirenian *Metaxytherium*  
30  
31 *subapenninum*, two skeletons of billfish (*Makaira* sp.), and several teeth of *Carcharias*  
32  
33 *taurus*, *Carcharhinus* spp. (including *Carcharhinus leucas*), *Galeocerdo cuvier*, *Hexanchus*  
34  
35 *griseus*, *Sparus* sp., and *Squatina* sp. (Sorbi et al., 2012; Tinelli, 2013, and our personal  
36  
37 observations (2012-2019) on the fossil assemblage of Arcille); in particular, a sirenian  
38  
39 specimen was collected from the same horizon as MSNUP I-17602 (Fig. 1B). Macro-  
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41 invertebrate remains are commonly found in the vertebrate-bearing strata of Arcille; they are  
42  
43 dominated by bivalves (mostly pectinids and venerids, including the extinct large-sized clam  
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45 *Pelecypora gigas*) with subordinate gastropods, scaphopods, echinoids, bryozoans, and corals.  
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54 **Diagnosis**—MSNUP I-17602 is unambiguously assigned to Monodontidae owing to the  
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56 presence of a medial exposure of the maxillae anterior and lateral to the external bony nares  
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3 (Muizon, 1988). It differs from all other named monodontids by the following characters: 1-  
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5 presence of a median depression, anterior to the premaxillary sac fossae, made by the  
6  
7 depressed medial part of the two premaxillae; 2-medial part of the premaxillary-maxillary  
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9 suture not paralleling the anterolateral profile of the external bony nares, rather diverging  
10  
11 posterolaterally. It shares with *Bohaskaia*, *Delphinapterus*, and *Denebola* a U-shaped outline  
12  
13 of the anterior margin of the external bony nares. It shares with *Bohaskaia*, *Delphinapterus*,  
14  
15 and *Haborodelphis* the posterior end of the premaxillae reaching about the mid-level of the  
16  
17 external bony nares. It shares with *Delphinapterus* a triangular shape of the nasals and a U-  
18  
19 shaped outline of the anterior margin of the exposure of the maxillae medial to the  
20  
21 premaxillae anterior to the external bony nares. It shares with *Monodon* the convex and  
22  
23 inflated premaxillary sac fossae and the presphenoid bone filling completely the posterior  
24  
25 portion of the mesorostral groove and not exceeding dorsally the level of the medial margin of  
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27 the maxillae.  
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## 35 DESCRIPTION

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40 **Preservation State**—The fragmentary cranium consists of well-preserved, rather  
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42 mineralized bones that appear as not deformed. The best-preserved portion of the cranium is  
43  
44 the dorsal surface of the neurocranium (Fig. 2A, B), including both premaxillae, part of the  
45  
46 left maxilla, a smaller portion of the right maxilla, the right nasal bone, and the presphenoid.  
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48 The rostrum is completely missing. In posterior view (Fig. 3C, D), most of the exoccipitals  
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50 and the internal sagittal crest can be observed, whereas most of the supraoccipital is missing.  
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52 In right (Fig. 2C, D) and left lateral views, parts of both the squamosal and the parietal are  
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54 visible. The ventral surface of the skull (Fig. 4) is partially covered by a concretion that  
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3 cannot be removed due to its hardness. However, a CT-scan analysis did not reveal any  
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5 significant anatomical feature beneath this nodule and highlighted the lack of the right and left  
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7 ear bones.  
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10 **General Features**—In lateral view (Fig. 2C, D), the vertex is quite elevated and  
11  
12 rounded (although to a lesser degree than observed in *Denebola*). As in all extant odontocetes  
13  
14 and in many extinct species (MacLeod et al., 2007), the cranium is asymmetrical, having the  
15  
16 vertex shifted leftwards and the right premaxillary sac fossa transversely wider than the left  
17  
18 (Fig. 2A, B). The anterior margin of the external bony nares exhibits a U-shaped outline as in  
19  
20 *Bohaskaia*, *Delphinapterus*, and *Denebola*.  
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24 **Ontogeny**— Given the well-sutured skull bones, the complete ossification of the  
25  
26 ethmoid bone, and the limited dorsal exposure of the supraoccipital, we hypothesize the  
27  
28 holotype of *Casatia thermophila* to be an adult animal. Nevertheless, the lack of vertebrae and  
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30 forelimb bones does not allow to verify if the epiphyses are fused to the corresponding centra  
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32 or diaphyses, which would represent a better clue to the ontogenetic status of the specimen  
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34 (e.g., Galatius and Kinze, 2003).  
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40 **Premaxilla**—Only the posterolateral portions of the premaxillae are preserved. In  
41  
42 dorsal view, both premaxillae exhibit a transverse narrowing at the level of the dorsal  
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44 infraorbital foramina, where the premaxilla-maxilla suture appears as markedly concave  
45  
46 laterally (Figs. 2A, B, 3A, B), a condition also observed in several skulls of *Monodon*. The  
47  
48 premaxillary sac fossa is particularly swollen (Fig. 2C, D), as in *Monodon*, *Haborodelphis*,  
49  
50 and in an unnamed skull of monodontid from the early Pliocene of the North Sea (IRSNB M  
51  
52 1922; Lambert and Gigase, 2007), whereas in *Bohaskaia* and *Delphinapterus* the premaxillary  
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54 sac fossae appear as almost completely flat. The premaxillary sac fossa is bordered laterally  
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3 by a deep posterolateral sulcus, whereas the posteromedial sulcus is barely identifiable (Fig.  
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5 2A, B). Both sulci depart from the premaxillary foramen. The latter is elliptical and  
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7 anteroposteriorly elongated. The anteromedial sulcus is far less excavated than the  
8  
9 posterolateral sulcus and forms the lateral border of a nearly flat and partly depressed region  
10  
11 of the premaxilla (Fig. 3A, B), only observed in IRSNB M 1922 (Lambert and Gigase, 2007)  
12  
13 among other monodontids. Throughout its preserved length, the margins of the mesorostral  
14  
15 groove are slightly risen, but not as much as in extant monodontids and *Bohaskaia*, where  
16  
17 they are protuberant and the area along the groove is convex. The groove itself is very narrow  
18  
19 transversely, never wider than 10 mm (Fig. 2A, B). The premaxillae end posteriorly at  
20  
21 roughly mid-length of the external bony nares, with the caudal termination of the right  
22  
23 premaxilla being located slightly posterior to the corresponding feature on the left side of the  
24  
25 cranium.

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30 **Maxilla**—Only the medial portions of the ascending processes of both maxillae are  
31  
32 preserved, with the left maxilla being preserved to a greater degree than the right. On the  
33  
34 dorsal surface of the left maxilla, three anterior dorsal infraorbital foramina open  
35  
36 anterolaterally. The diameter of these foramina is ca 8 mm and they are 7 mm apart from each  
37  
38 other forming on the whole an anteriorly convex curved line (Fig. 2A, B). The posteriormost  
39  
40 of these foramina lies at the same level as the left premaxillary foramen. This configuration is  
41  
42 reminiscent of that observed on the left maxilla of *Monodon*. On the right side of the  
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44 neurocranium, at the same level as the left anterior infraorbital foramina, the dorsal portion of  
45  
46 the maxilla is broken and the large (i.e., having a transverse diameter of ca 15 mm) right  
47  
48 infraorbital canal is exposed. A narrower sulcus departs from this canal and runs  
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50 posterolaterally up to the preserved posterolateral margin of the right maxilla. Close to this  
51  
52 broken margin, a posterolateral dorsal infraorbital foramen probably lied.

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3 The preserved posterior portion of the ascending process of the right maxilla surrounds  
4 the lateral margin of the right nasal and ends a little more posterior to the posterior margin of  
5 the right nasal. The right posterior accessory foramen (*sensu* Vélez-Juarbe and Pyenson, 2012  
6 the right nasal. The right posterior accessory foramen (*sensu* Vélez-Juarbe and Pyenson, 2012  
7 = posterior maxillary foramen *sensu* Barnes, 2006) takes place on the right maxilla just  
8 posterior to the end of the right premaxilla. The left posterior accessory foramen is more  
9 posteriorly located, being placed about 10 mm posterior to the end of the left premaxilla. Both  
10 the right and the left foramina measure 5 mm in transverse diameter and are followed  
11 posterodorsally by a deep and elongated sulcus, a condition observed in all extinct and extant  
12 monodontids (Lambert and Gigase, 2007; Vélez-Juarbe and Pyenson, 2012; Ichishima et al.,  
13 2019) as well as in many species of phocoenids (Muizon, 1988; Barnes, 2006). Medial to the  
14 premaxilla, the maxilla is also exposed anterior and lateral to the external bony nares (Fig.  
15 2A, B), a feature observed in all the fossil skulls referred to this family and regarded as a  
16 synapomorphy of Monodontidae (Muizon, 1988). This portion of the maxilla is laterally  
17 delimited by the medial margin of the premaxilla that, unlike in other monodontids, does not  
18 run parallel to the anterolateral profile of the external bony nares, but rather diverges  
19 posterolaterally. Anterior to the bony nares, the medial exposure of the maxilla extends  
20 anteriorly for 45 mm and terminates just posterior to the level of the premaxillary foramina.  
21 The outline of the anterior margin of the medial exposure of the maxillae is U-shaped as in  
22 *Delphinapterus*, thus differing from all other monodontids that display a V-shaped exposure.  
23 The anterolateral margins of the external bony nares are formed by the maxillae and have a U-  
24 shaped outline, as observed in *Bohaskaia*, *Delphinapterus*, and *Denebola*.

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51 **Frontal**—Both frontals have their lateral portions missing, preventing any possible  
52 reconstruction of the orbit area (Fig. 2). As in *Bohaskaia*, at the cranial vertex the frontals  
53 exhibit a slightly wedge-like anteromedial projection that separates the nasals  
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3 posteromedially.  
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5       **Lacrima**—A poorly preserved portion of the right lacrimal is exposed dorsally, due to  
6 the breakage of the overlying antorbital process of the maxilla (Fig. 2A, B). It tapers  
7 posteriorly and wedges between the frontal (laterally) and the maxilla (medially).  
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10       **Parietal**—Small and flat portions of the parietals, making contact with the squamosals,  
11 are visible on both lateral surfaces of the cranium (Fig. 2C, D). The suture line between the  
12 squamosal and the parietal takes place mid-height within the temporal fossa, running  
13 subhorizontally for about 20 mm, then turning downwards. The dorsoventral level of this  
14 suture is comparable to that observed in *Delphinapterus*, whereas in *Monodon* it is far higher,  
15 taking place close to the top of the temporal fossa.  
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18       **Nasal**—Only the right nasal is preserved (Fig. 2A, B). It is fragmented in three parts, its  
19 dorsal surface being partially eroded. In dorsal view, the right nasal is triangular and  
20 longitudinally elongated. Although the left nasal is missing, the preserved sutural surface of  
21 this bone with the underlying left frontal exhibits a triangular outline, similar to that of the  
22 right nasal. Based on this reconstruction, the nasals contacted each other for a short tract,  
23 being separated posteriorly by the frontals. This architecture of the nasals, recalling the shape  
24 of a stylized butterfly, is similar to that of *Delphinapterus*, being in turn different from the  
25 chevron-shaped nasals of *Denebola* and from the rounded, button-like, and anteroposteriorly  
26 constricted nasals of *Bohaskaia*, *Haborodelphis*, and *Monodon* (Vélez-Juarbe and Pyenson,  
27 2012; Ichishima et al., 2019). In lateral view, the vertex of the cranium appears rounded and  
28 comprised of both nasals and the eroded frontals (Fig. 2C, D).  
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50       **Presphenoid**—Following Ichishima (2016), we identify the bony septum that separates  
51 the external nares medially as the presphenoid rather than the mesethmoid. In MSNUP I-  
52 17602, this bone extends at the anterior margin of the external bony nares and between the  
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3 maxillae, filling the posteriormost portion of the mesorostral groove (Fig. 2A, B). The  
4  
5 presphenoid does not exceed dorsally the margin of the mesorostral groove, thus differing  
6  
7 from *Bohaskaia*, *Monodon*, and IRSNB M 1922. The cribriform plate of the ectethmoid,  
8  
9 which forms the posterior wall of the external bony nares, is transversely narrow (similar to  
10  
11 *Delphinapterus*) and almost vertical. The plate is divided in two portions by a sharp medial  
12  
13 keel. A similar keel is also present in *Monodon* and IRSNB M 1922 (Lambert and Gigase,  
14  
15 2007). At the triple contact between the maxilla, the nasal, and the presphenoid, there is a  
16  
17 fossa bordering the posterolateral region of the external bony nares. This fossa represents a  
18  
19 character shared by monodontids and phocoenids, although in the latter the fossa appears as  
20  
21 less conspicuous (Muizon, 1988).  
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26 **Supraoccipital**—The external surface of the supraoccipital is not preserved and the  
27  
28 only preserved portion of this bone is an internal section of the sagittal crest consisting of  
29  
30 spongy tissue (Fig. 3C, D). This allows to compare the size of the cerebral hemispheres.  
31  
32 Differing from the condition of strong asymmetry observed in several Delphinidae (e.g.,  
33  
34 *Tursiops* and *Stenella*; Ridgway and Brownson, 1984), in this specimen the cerebral  
35  
36 hemispheres are similar to each other in size, in agreement with the condition observed in  
37  
38 *Delphinapterus* (Marino et al., 2001). By relating the position of the occipital condyles to that  
39  
40 of the vertex, it can be hypothesized that the supraoccipital was almost vertically oriented, as  
41  
42 in *Delphinapterus* and *Monodon*.  
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46 **Exoccipital**—Both exoccipitals are partially preserved (Figs. 2C, D, 3C, D, 4). The  
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48 paraoccipital processes are broken but the right and left hypoglossal foramina (4 mm in  
49  
50 diameter) are visible on the bottom of the preserved portions of the jugular notches. Both the  
51  
52 right and left occipital condyles are broken and only their ventral portions are preserved.  
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54 Based on their size, the width of the occipital condyles can be estimated at around 100 mm.  
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3 This value is very low if compared to that measured in adults of extant monodontids (Heide-  
4 Jørgensen and Reeves, 1993). The ventral condyloid fossa is deeper than observed in extant  
5 monodontids. Very deep ventral condyloid fossae are seemingly related to conditions of great  
6 neck mobility (Mead and Fordyce, 2009; Racicot et al., 2014).  
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12 **Basioccipital**—The wide ventral surface of the basioccipital is almost completely  
13 covered by a hard concretion (Fig. 4). Both basioccipital crests are visible, but they are badly  
14 preserved and their margins are eroded in several points (Fig. 2A, B). The maximum distance  
15 between them is 135 mm, measured at their posterior end. Moving anteriorly, the distance  
16 between the basioccipital crests reduces to 100 mm, then increases to 110 mm to their anterior  
17 end.  
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26 **Squamosal**—Both squamosals lack the zygomatic process and their ventral surface is  
27 partially covered by the hard concretion (Fig. 4). In ventral view, from front to back, the  
28 partially preserved left squamosal exhibits a prominent postglenoid process, a deep  
29 posterolateral portion of the tympanosquamosal recess, a narrow and obliquely oriented  
30 external auditory meatus, and a robust post-tympanic process. In lateral view (Fig. 2C, D), the  
31 preserved portions of both the squamosal and the parietal allow to follow the posterior profile  
32 of the temporal fossa; the latter appears to be quite vertically elevated, more similar to  
33 *Delphinapterus* and *Denebola* than to *Monodon*.  
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## 47 PHYLOGENETIC ANALYSIS

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51 The phylogenetic relationships of the new genus and species *Casatia thermophila* were  
52 investigated by means of a matrix of 21 characters (Supplemental Data). The selected  
53 outgroup is the extinct Kentriodontidae *Kentriodon pernix*, whereas the extant Delphinoidea  
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3 *Tursiops truncatus* and *Phocoena phocoena* are included in the analysis as representatives of  
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5 Delphinidae and Phocoenidae, respectively. Our analysis includes all the monodontid genera  
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7 known to date (the extant *Delphinapterus* and *Monodon*, and the extinct *Bohaskaia*, *Casatia*,  
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9 *Denebola*, and *Haborodelphis*, together with the unnamed monodontid from the early  
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11 Pliocene of the North Sea IRSNB M 1922).

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14       Considering that all the fossil and extant monodontids exhibit clear distinctive  
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16 synapomorphies supporting the monophyly of this family, we limited the number of taxa  
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18 included in our phylogenetic analysis to monodontids and a few other delphinidans. However,  
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20 investigating the relationships of monodontids with other delphinoids among delphinidans is  
21  
22 beyond the scope of this work. Moreover, we considered a limited number of characters  
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24 because many parts of the skeleton (including ear bones, mandibles, and teeth) are still  
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26 unknown for most of the fossil monodontids and, consequently, the addition of other  
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28 characters in the matrix would most likely not cause significant changes in the results of the  
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30 analysis.  
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35       The twenty-one morphological characters (partially taken from previous analyses:  
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37 Fordyce, 1994; Muizon, 1988; Geisler and Sanders, 2003) were coded for the 10 analyzed  
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39 taxa. All characters are binary with the exception of one multistate character (char. 8). All  
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41 characters are parsimony-informative in this analysis. The analysis was run on PAUP\*  
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43 (version 4.0b10; Swofford, 2003) considering all the characters as non-additive (unordered)  
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45 and unweighted, using the heuristic search option, optimized by ACCTRAN and using the  
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47 tree bisection and reconnection (TBR) algorithm. Bootstrap analyses were carried out with  
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49 5000 replicates.  
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54       The cladistic analysis produced two equally parsimonious trees, with tree length = 33,  
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56 consistency index (CI) = 0.67, and retention index (RI) = 0.74. The most parsimonious trees  
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3 (Fig. 5) support the referral of *Casatia* to the family Monodontidae, in a more derived position  
4 than *Haborodelphis* and *Denebola*, and sister group of the coeval North Sea monodontid  
5 IRSNB M 1922. The monophyly of Monodontidae is supported by a bootstrap value of 90  
6 and by the following three synapomorphies: (1) presence of an exposure of the maxillae  
7 between the premaxillae, lateral and anterior to the external bony nares (char. 2, state 1); (2)  
8 absence of fossae for the pterygoid sinus in the orbital region (char. 3, state 1); and (3) lateral  
9 lamina of the palatine passing anterior to the lateral edge of the frontal groove (char. 4, state  
10 1). Based on this analysis, the earlier diverging *Haborodelphis* and *Denebola* form the stem  
11 Monodontidae, whereas the clade formed by (*Monodon* + *Bohaskaia*) + ((*Casatia* + IRSNB  
12 M 1922) + *Delphinapterus*)) represents the crown Monodontidae, supported by a bootstrap  
13 value of 54 and by the following two synapomorphies: (1) absence of functional premaxillary  
14 teeth (char. 11, state 1); and (2) rostrum displaying a dorsally convex outline, given by the  
15 raised premaxillae (char. 15, state 1). Within the crown Monodontidae, the clade formed by  
16 *Delphinapterus* + (*Casatia* + IRSNB M 1922) is supported by the following synapomorphy:  
17 U-shaped anterior margin of the exposure of the maxillae medial to the premaxillae and  
18 anterior to the external bony nares (char. 9, state 1).  
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## 42 DISCUSSION

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47 MSNUP I-17602 is the first and only fossil monodontid recorded from the  
48 Mediterranean Basin. As such, it significantly expands the paleobiogeographical extent of  
49 Monodontidae and increases our knowledge on the Pliocene Mediterranean biodiversity,  
50 suggesting that the current understanding of the Pliocene cetacean paleocommunities of this  
51 area is still far from being exhaustive.  
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3 As reported above, the fossil-bearing sandstones exposed at the Arcille quarry depict a  
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5 deltaic to shoreface shallow-water setting. Supporting this interpretation, the holotype of  
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7 *Casatia thermophila* occurs besides several skeletons of the extinct sea cow *Metaxytherium*  
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9 *subapenninum* (Fig. 6), which has been interpreted as a coastal to estuarine species that shared  
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11 the ecological and environmental preferences of extant sirenians (Sorbi et al., 2012). A  
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13 marginal-marine shallow-water paleoenvironment close to a river mouth is also suggested by  
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15 the presence of some littoral fish such as the sand tiger shark (*Carcharias taurus*) and the bull  
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17 shark (*Carcharhinus leucas*); in particular, bull sharks commonly extend their habitat to  
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19 transitional environments (e.g., mangrove swamps and estuaries) and even penetrate far up in  
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21 rivers (Pollard and Smith, 2009; Simpfendorfer and Burgess, 2009). In turn, strong  
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23 connections with open-sea, deep-water environments are supported by the presence of  
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25 remains of the bluntnose sixgill shark (*Hexanchus griseus*) and marlin (*Makaira* sp.) (Cook  
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27 and Compagno, 2009; Collette et al., 2011). Nowadays, during summertime, white whales can  
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29 be found in coastal waters as shallow as 1 to 3 meters deep, and they typically enter estuaries,  
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31 occasionally moving upstream into rivers (Lowry et al., 2017). Although floating cetacean  
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33 carcasses can suffer substantial transport before depositing on the seafloor (Schäfer, 1972), it  
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35 seems reasonable to hypothesize that, at least on a seasonal basis, *C. thermophila* inhabited  
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37 shallow-water, marginal-marine paleoenvironmental settings such as the Arcille area during  
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39 deposition of the nearshore sandstones from which MSNUP I-17602 was collected.  
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47 Extant narwhals and white whales, as well as their Quaternary fossil remains, are  
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49 invariably associated to low seawater temperatures (Deinse, 1944; Post and Kompanje, 1995;  
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51 Harrington, 2008; Post and Bosselaers, 2017; O'Corry-Crowe, 2018; Heide-Jørgensen, 2018);  
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53 by contrast, during the early Pliocene, the Mediterranean Basin in which *Casatia* lived was  
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55 characterized by warmer than today, tropical to subtropical climate conditions (e.g., Prista et  
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3 al., 2015). In this respect, an appraisal of the vertebrate and macro-invertebrate taxa that occur  
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5 besides MSNUP I-17602 at the Arcille quarry strongly supports typical tropical conditions for  
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7 the paleobiotope in which *Casatia* lived. Among vertebrates, the extant bull shark and tiger  
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9 shark (*Galeocerdo cuvier*) are known as warm-water species that are no longer featured in the  
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11 present-day Mediterranean Sea, but still inhabit the coasts of western tropical Africa  
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13 (Simpfendorfer and Burgess, 2009; Ferreira and Simpfendorfer, 2019). *Dugong dugon*, the  
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15 closest living relative of *M. subapenninum*, is found in warm coastal waters of the Indo-  
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17 western Pacific realm, between latitudes of about 26° North and South of the Equator (Marsh  
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19 et al., 2002). The extinct venerid clam *Pelecypora gigas* belongs to a stock of thermophilic  
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21 mollusk taxa, categorized as the Mediterranean Pliocene Molluscan Unit (=MPMU) 1, whose  
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23 most eurythermic members (including *P. gigas*) did not survive the pulse of climate cooling  
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25 recorded in the Mediterranean basin at about 3 Ma (Raffi and Monegatti, 1993; Monegatti and  
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27 Raffi, 2001). Recent oxygen-isotope analyses of a shell of *P. gigas* from the lower Pliocene of  
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29 Tuscany (Ragaini et al., in press) have resulted in estimating an average temperature of  
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31 23.0°C for the water where the shell lived, whereas calculated temperature extremes range  
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33 between 18.5°C (for winter) and 27.6°C (for summer). These temperature estimates are in  
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35 very good agreement with those proposed on the basis of the lower Pliocene Mediterranean  
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37 mollusk taxa, which nowadays live along the western African shores, south of latitude N 22-  
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39 20° (surface seawater temperature over 24°C for at least 5-6 months per year and never below  
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41 19°C) (Ragaini et al., in press). Given these considerations, *Casatia* should be regarded as  
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43 inhabiting a typically tropical paleoenvironment that strikingly contrasts with the habitat  
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45 preferences of extant monodontids. Recently, Ichishima et al. (2019) interpreted the Neogene  
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47 genera *Denebola*, *Bohaskaia*, and *Haborodelphis* as cool-temperate taxa, possibly reflecting  
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49 some physical or behavioral predisposition in favor of cool climates in the ancestral  
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3 monodontids (Fig. 7A). Taking place besides abundant fossil remains of strongly thermophilic  
4 marine organisms such as *C. leucas*, *G. cuvier*, *M. subapenninum*, and *P. gigas*, our finding  
5 represents the strongest, definitive evidence supporting the hypothesis that early monodontids  
6 thrived in warm-water habitats, as already evoked elsewhere (Barnes, 1984; Vélez-Juarbe and  
7 Pyenson, 2012).  
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12 Our phylogenetic analysis, the first including all taxa of Monodontidae, contributes to  
13 further shed light on the evolutionary history of narwhals and white whales (Figs. 5, 7B). In  
14 the light of our results, monodontids appear to be comprised of a stem group (formed by the  
15 Pacific genera *Haborodelphis* and *Denebola*) and a crown group whose extinct  
16 representatives (i.e., *Bohaskaia*, *Casatia*, and IRSNB M 1922) come from North Atlantic and  
17 Mediterranean localities. It is thus reasonable to hypothesize that monodontids originated in  
18 the North Pacific and then dispersed to the North Atlantic. The latter appears to be the area  
19 where the crown monodontids (i.e., the clade that includes the new genus described herein, as  
20 well as the extant narwhal and white whales) emerged not later than the early Pliocene.  
21  
22 Furthermore, recovering *Casatia* as a crown monodontid, more closely related to  
23 *Delphinapterus leucas* than *Monodon monoceros*, suggests that the early relatives of the  
24 extant narwhal and white whale might have adapted independently to the cold-water high-  
25 latitude environments they currently inhabit. Therefore, the ancestors of the living species *D.*  
26 *leucas* and *M. monoceros* might have found refuge in the periarctic region via the parallel  
27 evolution of surprising adaptations to extreme thermal conditions.  
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32 What did happen to *Casatia* and other Neogene lineages of warm-water monodontids,  
33 leading to their eventual extirpation from low latitudes? As proposed for several thermophilic  
34 lower Pliocene Mediterranean vertebrates and invertebrates, including the latest  
35 Mediterranean sirenian *M. subapenninum* (Sorbi et al., 2012) and the bivalve *P. gigas*  
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3 (Ragaini et al., in press), they might have gone extinct following the pulse of climate  
4 degradation that accompanied the onset of long-term Northern Hemisphere glaciation around  
5 3 Ma (De Schepper et al., 2014; Pimiento et al., 2017) (Fig. 7B). If monodontids, as a whole,  
6 tell us an evolutionary tale of habitat plasticity and multiple adaptations to a changing world  
7 climate, that might not be sufficient for warranting their survival in the present times of  
8 human-induced global warming and ice loss, which are believed to threaten cryophilic marine  
9 mammals in an especially worrying way (Simmonds and Isaac, 2007).  
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13  
14 of MSNUP I-17602 was included in F.P.'s M.Sc. thesis.  
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## FIGURE CAPTIONS

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8 FIGURE 1. Locality and horizon of MSNUP I-17602, holotype of *Casatia thermophila* gen.  
9 et sp. nov. **A**, location of the site where MSNUP I-17602 was found (black star) and  
10 schematic regional geological map. CA = Casino Basin; EL = Elsa Basin; VC = Val di Chiana  
11 Basin; VO-RA-CH = Volterra-Radicondoli-Chiusdino Basins; RD = Radicofani Basin; SI =  
12 Siena Basin. Modified after Collareta et al. (2018). **B**, stratigraphic section of the lower  
13 Pliocene sedimentary succession exposed at Arcille, showing the position of MSNUP I-17602  
14 and fossil vertebrates having extant relatives that live in warm waters (isolated teeth of  
15 Elasmobranchii are not considered). Stratigraphic section modified after Tinelli (2013).  
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33 FIGURE 2. *Casatia thermophila*, gen. et sp. nov, MSNUP I-17602, holotype. Skull in **A**, **B**,  
34 dorsal and **C**, **D**, right lateral views. **Abbreviations:** **bn**, bony nares; **cc**, concretion; **cp**,  
35 cribriform plate; **ns**, nasal; **psf**, premaxillary sac fossa; **soc**, supraoccipital. Diagonal lines  
36 represent broken surfaces.  
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49 FIGURE 3. *Casatia thermophila*, gen. et sp. nov, MSNUP I-17602, holotype. Skull in **A**, **B**,  
50 anterior and **C**, **D**, posterior views. **Abbreviations:** **bn**, bony nares; **cc**, concretion; **cp**,  
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10 FIGURE 4. *Casatia thermophila*, gen. et sp. nov, MSNUP I-17602, holotype. Close-up of the  
11 basicranium in ventral view.  
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19 FIGURE 5. Consensus of two most parsimonious trees from the cladistic analysis showing the  
20 phylogenetic relationships of *Casatia thermophila* gen. et sp. nov. with all the officially  
21 named monodontid species known to date and an unnamed taxon from the early Pliocene of  
22 the North Sea. Numbers associated with the nodes are bootstrap values. †, extinct taxon.  
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33 FIGURE 6. Life reconstruction of *Casatia thermophila* gen. et sp. nov. swimming in the  
34 coastal waters off present-day Tuscany in early Pliocene times (5.1-4.5 Ma). Behind the  
35 cetacean, two individuals of the sirenian *Metaxytherium subapenninum* are approaching the  
36 shallow sea floor, likely attracted by the presence of abundant seagrasses. The coexistence of  
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38 waters of the central Mediterranean basin during the early Pliocene reflects the composition of  
39 the fossil vertebrate assemblage from Arcille, where a sirenian specimen was collected from  
40 the same horizon as the holotype of *C. thermophila*.  
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3 FIGURE 7. Cold- and warm-water monodontid cetaceans from the Neogene and the  
4 Quaternary. **A**, map of the Northern Hemisphere showing the distribution of extant  
5 *Delphinapterus* (pink area) and congeneric Quaternary fossils (pink squares), extant  
6 *Monodon* (blue area) and congeneric Quaternary fossils (blue squares), the extinct *Casatia*  
7 (red square) and other Neogene monodontid genera (green squares). **B**, global sea-level  
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9 sea level-drop linked to the Northern Hemisphere Glaciation (NHG). See Supplemental Data  
10 for data sources.  
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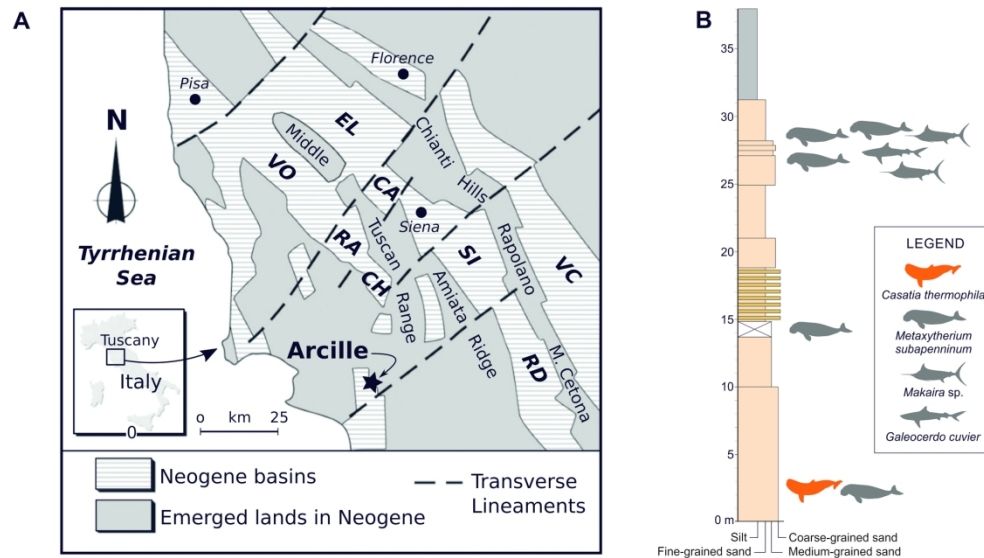


FIGURE 1. Locality and horizon of MSNUP I-17602, holotype of *Casatia thermophila* gen. et sp. nov. A, location of the site where MSNUP I-17602 was found (black star) and schematic regional geological map. CA = Casino Basin; EL = Elsa Basin; VC = Val di Chiana Basin; VO-RA-CH = Volterra-Radicondoli-Chiusdino Basins; RD = Radicofani Basin; SI = Siena Basin. Modified after Collareta et al. (2018). B, stratigraphic section of the lower Pliocene sedimentary succession exposed at Arcille, showing the position of MSNUP I-17602 and fossil vertebrates having extant relatives that live in warm waters (isolated teeth of Elasmobranchii are not considered). Stratigraphic section modified after Tinelli (2013).  
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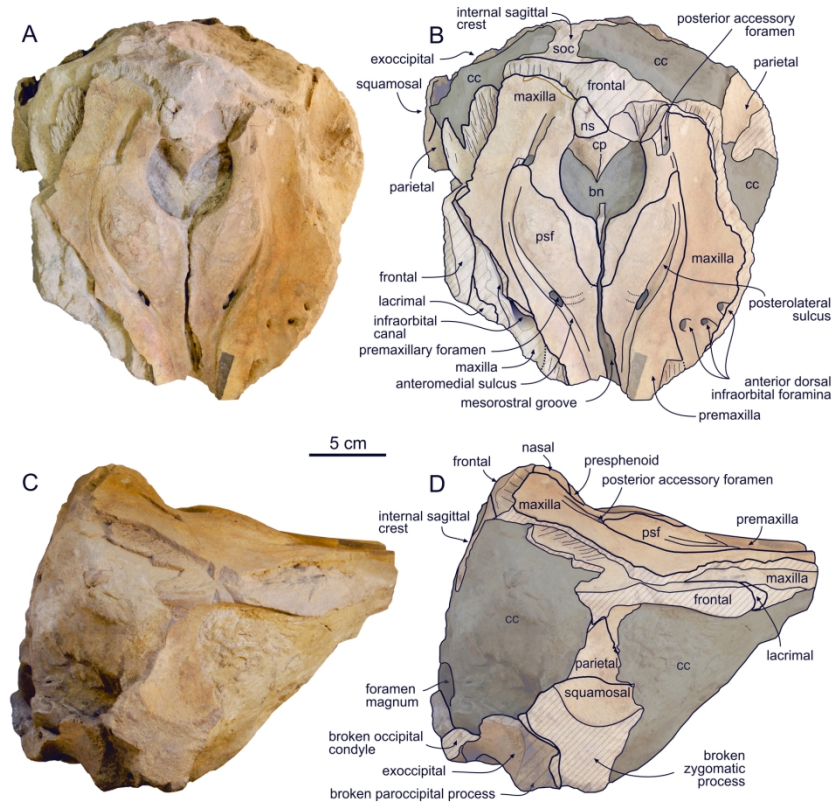


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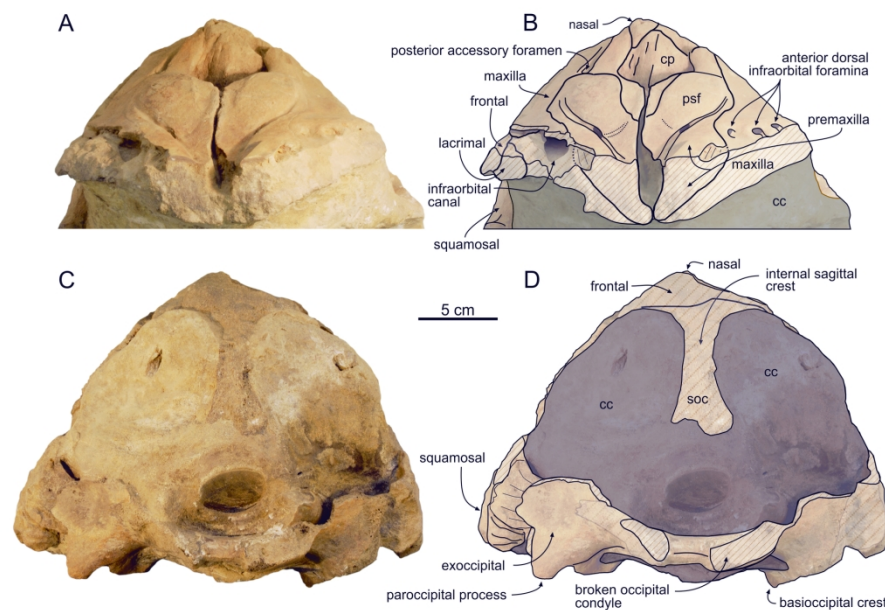


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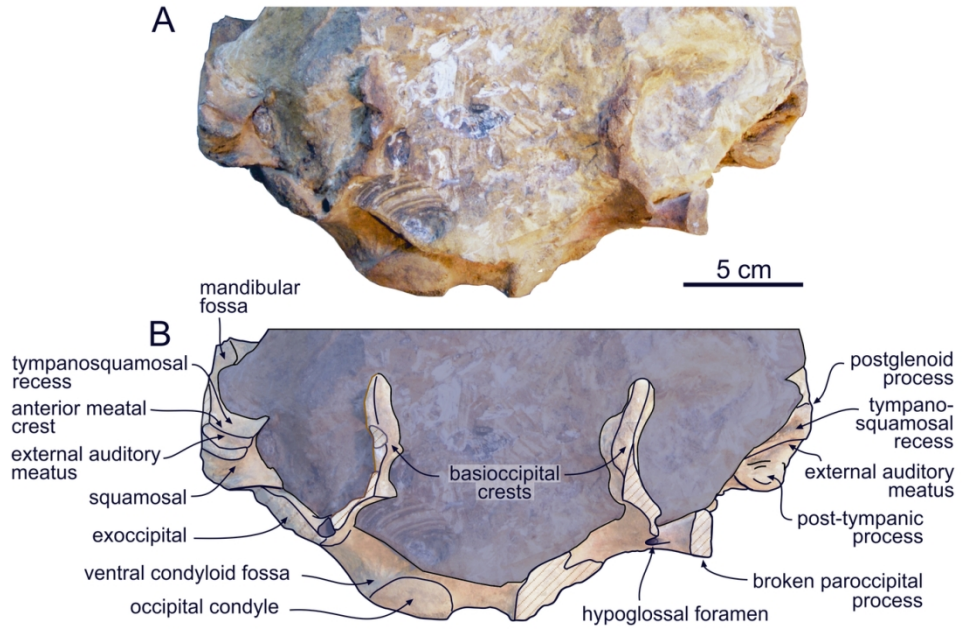


FIGURE 4. *Casatia thermophila*, gen. et sp. nov, MSNUP I-17602, holotype. Close-up of the basicranium in ventral view.  
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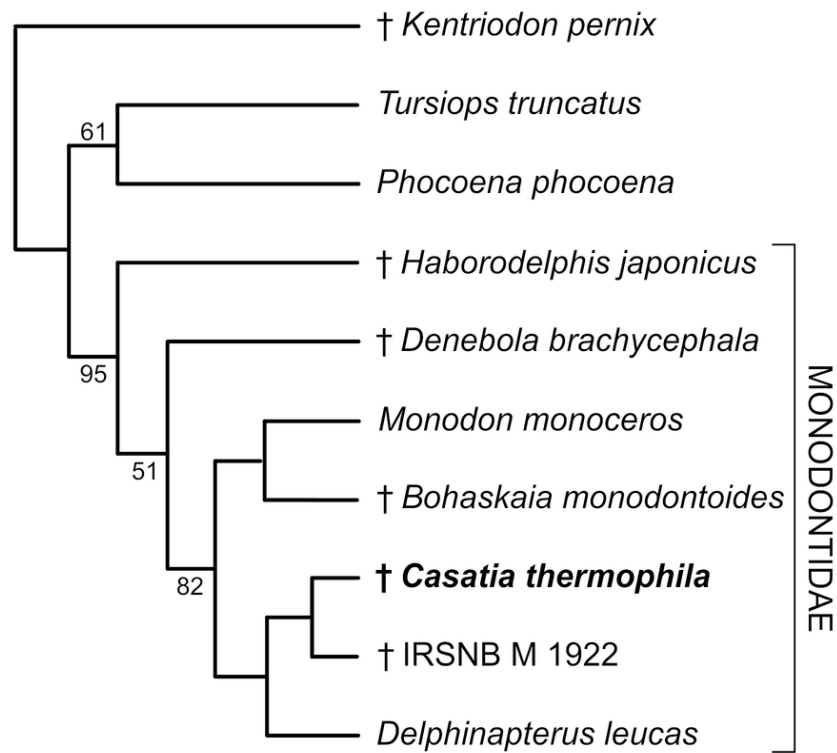


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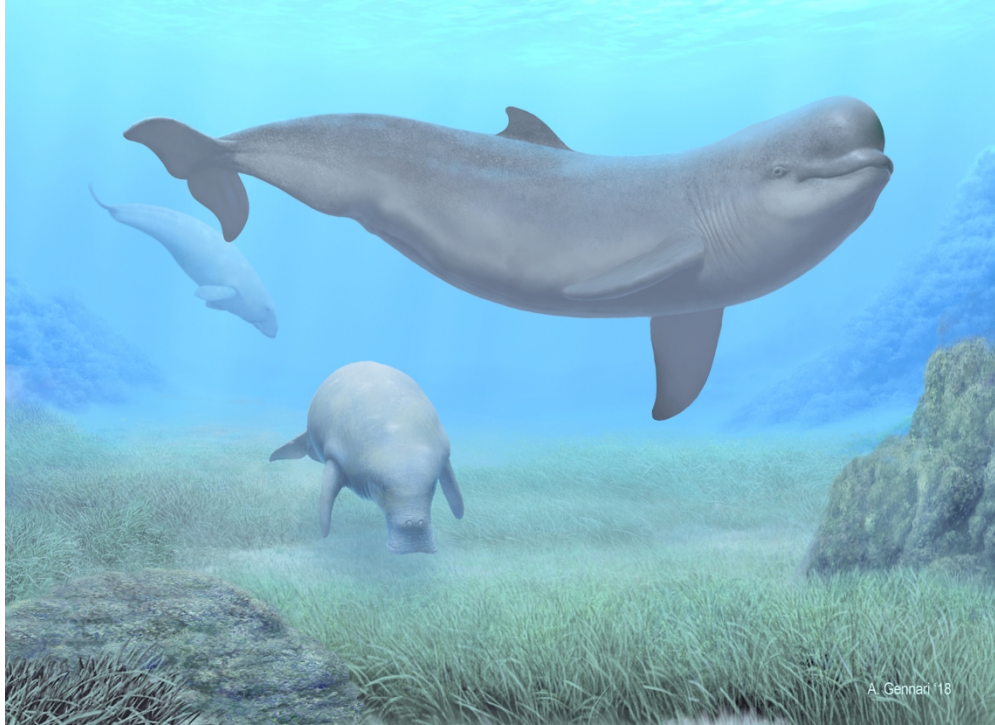


FIGURE 6. Life reconstruction of *Casatia thermophila* gen. et sp. nov. swimming in the coastal waters off present-day Tuscany in early Pliocene times (5.1-4.5 Ma). Behind the cetacean, two individuals of the sirenian *Metaxytherium subapenninum* are approaching the shallow sea floor, likely attracted by the presence of abundant seagrasses. The coexistence of monodontids (*C. thermophila*) and sea cows (*M. subapenninum*) in the warm marginal-marine waters of the central Mediterranean basin during the early Pliocene reflects the composition of the fossil vertebrate assemblage from Arcille, where a sirenian specimen was collected from the same horizon as the holotype of *C. thermophila*.

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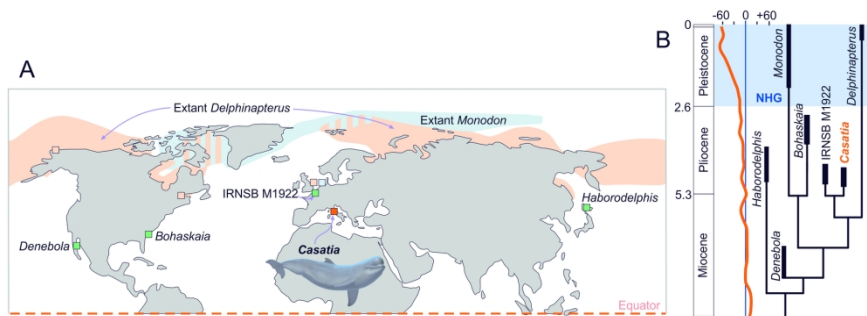


FIGURE 7. Cold- and warm-water monodontid cetaceans from the Neogene and the Quaternary. A, map of the Northern Hemisphere showing the distribution of extant *Delphinapterus* (pink area) and congeneric Quaternary fossils (pink squares), extant *Monodon* (blue area) and congeneric Quaternary fossils (blue squares), the extinct *Casatia* (red square) and other Neogene monodontid genera (green squares). B, global sea-level change over time compared to the age of the fossils shown in A, highlighting the Quaternary sea-level-drop linked to the Northern Hemisphere Glaciation (NHG). See Supplemental Data for data sources. [Planet for full page width]

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