Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 128(1): 229-240. **March 2022**

NEW REMAINS OF *CASATIA THERMOPHILA* (CETACEA, MONODONTIDAE) FROM THE LOWER PLIOCENE MARINE VERTEBRATE-BEARING LOCALITY OF ARCILLE (TUSCANY, ITALY)

MARCO MERELLA[1,2]*, ALBERTO COLLARETA[2], VALERIO GRANATA[2], SIMONE CASATI[3] & GIOVANNI BIANUCCI[2]

Dottorato Regionale "Pegaso" in Scienze della Terra, Università di Pisa, via Santa Maria 53, 56126 Pisa, Italy. E-mail: marco.merella@phd.unipi.it
[2]Dipartimento Scienze della Terra, Università degli Studi di Pisa, Via S. Maria 53, 56126 Pisa, Italy. E-mails: alberto.collareta@unipi.it; v.granata2@studenti.unipi.it; giovanni.bianucci@unipi.it
[3]Gruppo Avis Mineralogia e Paleontologia Scandicci, Piazza Vittorio Veneto 1, Badia a Settimo, 50018 Scandicci, Italy.
E-mail: sim.casati@gmail.com
*Corresponding author.

Associate Editor: David M. Alba

To cite this article: Merella M., Collareta A., Granata V., Casati S. & Bianucci G. (2022) - New remains of *Casatia thermophila* (Cetacea, Monodontidae) from the Lower Pliocene Marine vertebrate-bearing locality of Arcille (Tuscany, Italy). *Riv. It. Paleontol. Strat.*, 128(1): 229-240.

Keywords: Baccinello-Cinigiano Basin; Delphinoidea; Odontoceti; osteoanatomy; palaeocetology; palaeoecology, toothed whales; Zanclean.

Abstract. An incomplete cranium, three cervicals (including the axis) and two likely lumbars of a monodontid cetacean are here described from lower Pliocene (ca. 5.1–4.5 Ma) marine sandstones cropping out at Arcille (Grosseto Province, Tuscany, Italy). This fossil find comes from the same locality as the holotype of *Casatia thermophila*, which it resembles in terms of overall size and cranial morphology, and especially, by displaying a similarly depressed portion of the dorsal surface of the premaxillae anterior to the premaxillary sac fossae and medial to the anteromedial sulci. Our new find is thus assigned to *C. thermophila*, and significant anatomical parts that are missing in the holotype are described in order to improve the diagnosis of this monodontid species. Some dentigerous fragments of the maxillae hint at a homodont and polydont dentition, which in turn suggests a ram prey capture method that differs from the highly derived suction method that is proper of extant monodontids. This second find of *C. thermophila* from the warm-water Arcille palaeoenvironment lends further support to the hypothesis that monodontids once thrived in tropical and subtropical habitats.

INTRODUCTION

The marine vertebrate-bearing locality of Arcille is located about 10 km NE of Grosseto (Tuscany, central Italy) (Fig. 1A). Here, a Lower Pliocene succession is exposed in a sand quarry and in the surrounding rural area (Benvenuti et al. 2001, Tinelli 2013) (Fig. 1B). This important fossil locality was discovered in 2007 by one of us (S.C.), and continuous field prospections have since then led to the discovery of an impressive number of fossil remains that are now kept in the Museo Geopaleontologico GAMPS, Scandicci, Italy, as well as in the Museo di Storia Naturale dell'Università di Pisa, Calci, Italy.

The macrofossil assemblage of Arcille includes several skeletal remains of marine tetrapods and fishes. The former are represented by the holotype cranium of the extinct monodontid cetacean *Casatia thermophila*, five partial skeletons of the extinct dugongid sirenian *Metaxytherium subapenninum*,

Received: April 19, 2021; accepted: September 16, 2021

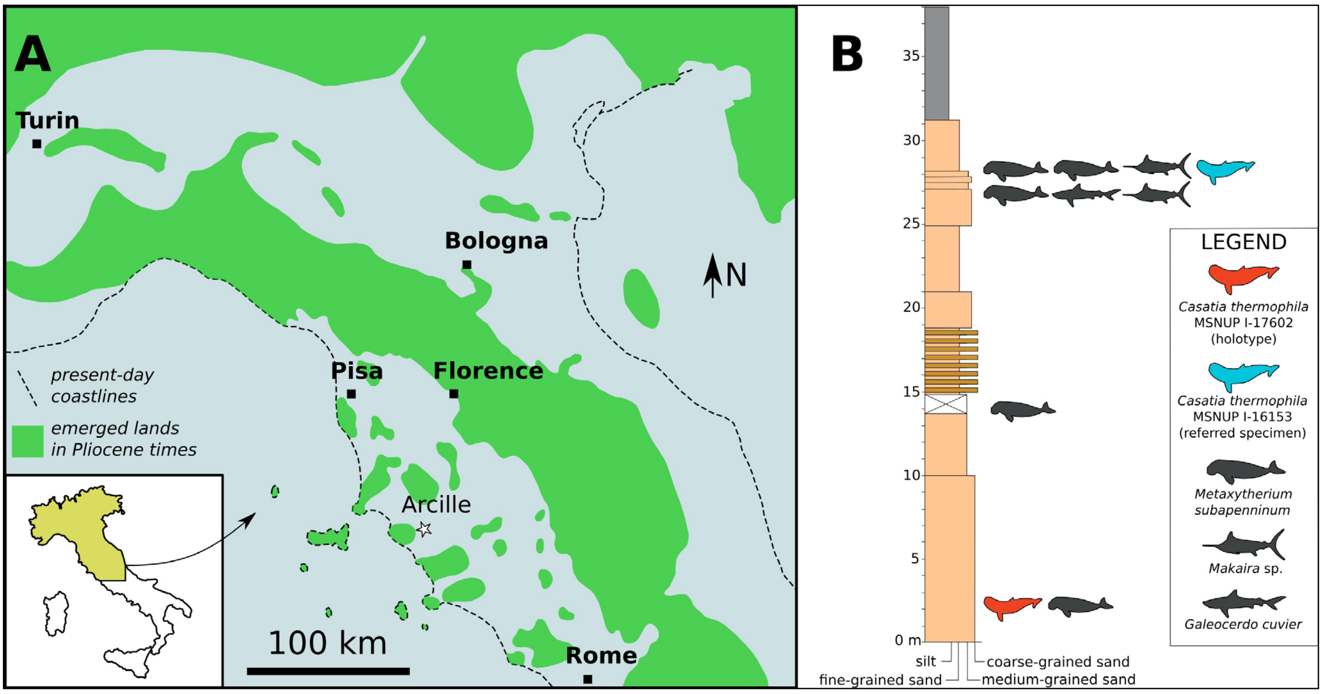

Fig. 1 - Geographic and geological setting. A) Schematic palaeogeographic map of central and northern Italy in the Pliocene. The star indicates the geographic location of the site of Arcille where both the holotype and the referred specimen of *Casatia thermophila* were found. Palaeogeographical reconstruction after Collareta et al. (2021b) and the references therein. B) Stratigraphic section of the Lower Pliocene deposits exposed at Arcille.

and several fragmentary bones of sea turtles (Cheloniidae indet.) (Sorbi et al. 2012; Tinelli 2013; Bianucci et al. 2019; pers. obs.). Fishes are mostly represented by isolated elasmobranch teeth and spines referred to *Aetomylaeus bovinus*, *Carcharhinus brachyurus*, *Carcharhinus* cf. *falciformis*, *Carcharhinus leucas*, *Carcharhinus limbatus*, *Carcharias taurus*, *Cosmopolitodus plicatilis*, *Dasyatis* sp., *Galeocerdo cuvier*, *Hexanchus griseus*, *Himantura* sp., *Megascyliorhinus miocaenicus*, *Myliobatis* sp., *Nebriimimus wardi* (including the holotype tooth), *Pachyscyllium dachiardii*, *Rhinobatos* sp., *Rostroraja olisiponensis* and *Squatina* sp.; the bony fish assemblage includes fragmentary skeletons of *Makaira* sp., bony and dental remains of *Sphyraena* sp., and isolated teeth of Labridae and Sparidae (Merella et al. 2020, 2021, 2022; Collareta et al. 2021b,c). In addition to these vertebrate remains, the macrofossil assemblage of Arcille also features bivalves, such as pectinids and venerids (e.g., the extinct large-sized clams *Callista italica* and *Pelecyora gigas*), and subordinately ahermatypic corals, barnacles, crabs, echinoids, gastropods and scaphopods (Tinelli 2013; Bianucci et al. 2019; Merella et al. 2020; Collareta et al. 2021b).

Most of the fossil vertebrates from Arcille were discovered within the quarry area, during the activities of sand excavation. However, a partial skeleton of *M. subapenninum*, including the skull, rib cage and parts of a forelimb, was discovered under different circumstances, in a cultivated area some tens of meters NW of the Arcille quarry. Here, few bones from the sirenian skeleton emerged after the plowing of a field. By using a Ground Penetrating Radar (GPR) system, other bones from the same specimen were discovered a few tens of centimetres below the ground level (Tinelli et al. 2012). The sirenian fossil was collected and transported to the MSNUP for the subsequent preparation and study, but an unexpected discovery occurred while cleaning some bones inside a block of sandstone collected near the *Metaxytherium subapenninum* skeleton. In fact, these bones do not belong to a sirenian, but rather to a cetacean and in particular to *C. thermophila*, the monodontid delphinoid whose holotype (the sole specimen known to date) had been previously discovered in the lowermost layers of the Arcille quarry (Bianucci et al. 2019).

The aim of the present work is to describe this second specimen of *C. thermophila*, thus providing new clues on the skeletal anatomy of this extinct monodontid species while also contributing to our knowledge of the palaeoecology of the Arcille marine vertebrate assemblage.

MATERIAL AND METHODS

Discovery and preparation. The monodontid specimen described herein was found during the cleaning and preparation of MNSUP I-15892, a partial skeleton of *Metaxytherium subapenninum* contained in several blocks of sandstone.

The fossil was prepared by one of us (V.G.) by using pneumatic hand-tools and was later consolidated by means of Paraloid B-72 (5% to 10%).

3D model. A 3D model (Fig. 2) of the monodontid cranium was created by means of a SHINING 3D EinScan Pro HD handheld scanner. The 3D model of the skull is available as Supplementary Material file.

Institutional abbreviations. IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MSNUP, Museo di Storia Naturale dell'Università di Pisa, Pisa, Italy; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

List of specimens directly examined for comparison. *Bohaskaia monodontoides* (USNM 25819); *Casatia thermophila* (MSNUP I-17602); *Delphinapterus leucas* (MSNUP C276, MSNUP C277); *Monodon monoceros* (MSNUP C274, MSNUP C275); Monodontidae indet. (IRSNB M 1922).

Anatomical terminology. The anatomical terminology used herein follows Mead & Fordyce (2009) and Bianucci et al. (2019) for the skull, and Evans & Lahunta (2013) and Ramassamy et al. (2018) for the postcranial skeleton.

SYSTEMATIC PALAEONTOLOGY

CETACEA Brisson, 1762
Odontoceti Flower, 1867
Delphinoidea Gray, 1821
Monodontidae Gray, 1821
Casatia Bianucci, Pesci, Collareta & Tinelli, 2019

Casatia thermophila Bianucci, Pesci, Collareta & Tinelli, 2019

Figs. 2, 3, 4, 5, 6

Referred material: MSNUP I-16153, a fragmentary cranium including a large portion of the neurocranium, the base of the rostrum and some detached rostral fragments of the maxillae, together with the axis, two additional cervical vertebrae and two likely lumbar vertebrae.

Locality*:* MSNUP I-16153 was collected at the marine vertebrate-rich locality of Arcille (Grosseto Province, Tuscany, central Italy), at a distance of some tens of metres from the Arcille sand quarry, near and in the same horizon of MSNUP I-15892, a partial skeleton of *Metaxytherium subapenninum* (Tinelli et al. 2012). The geographic coordinates of the Arcille quarry are the following: 42°47'12.2" N, 11°17'06.1" E (Fig. 1A).

Horizon and age*:* The sediments exposed at the find locality are part of the marine deposits filling the southwestern portion of the post-collisional Baccinello-Cinigiano Basin of southern Tuscany (Benvenuti et al. 2001). These are referred to the S2 Synthem recognised by Dominici et al. (2018) in the upper Neogene to lower Quaternary marine and paralic successions of Tuscany. The Lower Pliocene deposits of Arcille are referred to the MPl2 biozone of Cita (1975), which is dated between 5.08 and 4.52 Ma in light of the orbital tuning calibration by Lourens et al. (2004) (Sorbi et al. 2012). The succession cropping out at Arcille includes marine detrital sediments dominated by yellowish, fossil-rich sandstones with intervening conglomeratic lenses passing upwards to greyish shelfal mudstones (Tinelli et al. 2012). MSNUP I-16153 was collected from a shell bed located about 3 m below the top of the sandstones and some 26 m above the type horizon of *Casatia thermophila* (Fig. 1B). Three shark teeth, referred to *Carcharhinus brachyurus*, *Carcharhinus* cf. *falciformis* and *Chaenogalaeus affinis*, have been found in close association with the MSNUP I-16153 cranium.

Emended diagnosis*:* *Casatia thermophila* is assigned to Monodontidae based on the presence of i) a medial exposure of the maxillae anterior and lateral to the external bony nares and ii) a lateral lamina of the palatine that passes anterior to the posterolateral edge of the frontal groove (Muizon 1988). It differs from all other named monodontids by displaying the following characters: (1) presence of a flattened median depression, anterior to the premaxillary sac fossae and medial to the anteromedial sulci, formed by the depressed medial part of the two premaxillae; (2) medial part of the premaxillary-maxillary suture not paralleling the anterolateral profile of the external bony nares, but rather diverging posterolaterally; and (3) palatine bones greatly elongated anteroposteriorly. It shares with *Bohaskaia*, *Delphinapterus* and *Denebola* a 'U'-shaped outline of the anterior margin of the external bony nares. It shares with *Bohaskaia*, *Delphinapterus* and *Haborodelphis* the posterior end of the premaxillae reaching about the mid-level of the external bony nares. It shares with *Bohaskaia* and *Denebola* the palatines that do not contact each other medially and the maxillary dental alveoli that are small and closely spaced. It shares with *Monodon* and some specimens of *Delphinapterus* an antorbital notch that is deeply excavated medially. It shares with *Delphinapterus* a triangular shape of the nasals and a 'U'-shaped outline of the anterior margin of the exposure of the maxillae medial to the premaxillae anterior to the external bony nares. It shares with *Haborodelphis* and with some specimens of *Delphinapterus* a bifurcated falciform process of the squamosal. It shares with *Monodon* the convex and inflated premaxillary sac fossae and the presphenoid bone completely filling the posterior portion of the mesorostral groove and dorsally not exceeding the level of the medial margin of the maxillae.

Description. *Ontogeny.* The unfused caudal epiphyses of the two preserved postcervical vertebrae, and the dislocation of the occipital bones due

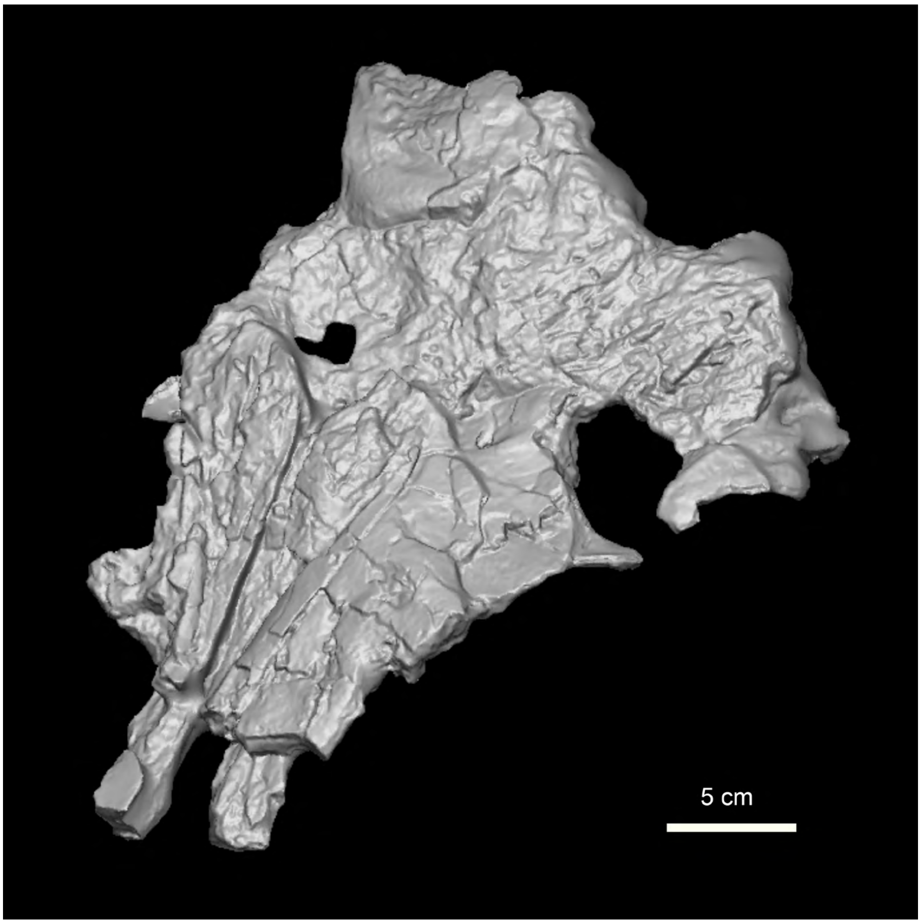

Fig. 2 - 3D model of the skull of MSNUP I-16153, partial skeleton of *Casatia thermophila* from the Lower Pliocene of Arcille. the skull is portraited in left anterodorsolateral view. The 3D model of the skull is available as a Supplementary Material file.

to the incompletely fused cranial sutures allow for hypothesising that MSNUP I-16153 was a sexually mature but physically immature animal (Yoshida et al. 1994; Galatius et al. 2011; Tsai 2017; pers. obs.).

Cranium

Preservation state. The fragmentary cranium exhibits a remarkable dorsoventral compression. The dorsal surface of the anterior portion of the partial cranium is well preserved, including conspicuous portions of the premaxillae and left maxilla, a small portion of the right maxilla, and a portion of the left supraorbital process of the frontal that is dorsally exposed due to the breakage of the left maxilla. Posterior to the external bony nares, most of the dorsal surface of the neurocranium is damaged and/or covered by sediment, and the posterior margin of the external bony nares, the well diagnostic area of the cranial vertex and the right squamosal are missing. Several superimposed bone fragments cluster in the posterior portion of the ventral surface of the skull. In ventral view, the left squamosal, a fragment of the exoccipital, the supraoccipital, parts of the right parietal and frontals, the presphenoid, part of the left lacrimojugal, the palatines, the poorly preserved pterygoids, several portions of the vomer, and part of the premaxillae can be observed. Two isolated rostral fragments of the maxillae, featuring distinct dental alveoli, are also preserved.

Premaxilla. Although the posteriormost portions of both the premaxillae are largely worn out along the dorsal surface of the neurocranium, their outline can be easily reconstructed by observing the underlying sutural surface of the maxillae (Fig. 3). The overall morphology of the preserved dorsal surface of the premaxillae is definitively consistent with that of the holotype of *Casatia thermophila.* Shared features include: (1) the bulging and swollen shape of the premaxillary sac fossae; (2) the occurrence of a flattened depression anterior to the premaxillary sac fossae and medial to the anteriomedial sulcus; (3) the presence of a single anteroposteriorly elongated (measuring 8×4 mm) premaxillary foramen; and (4) the shallow anteromedial sulcus and the narrow and deep posterolateral sulcus (Fig. 3).

The only significant difference between the premaxillae of MSNUP I-16153 and those of the holotype is the absence in the former of a trans-

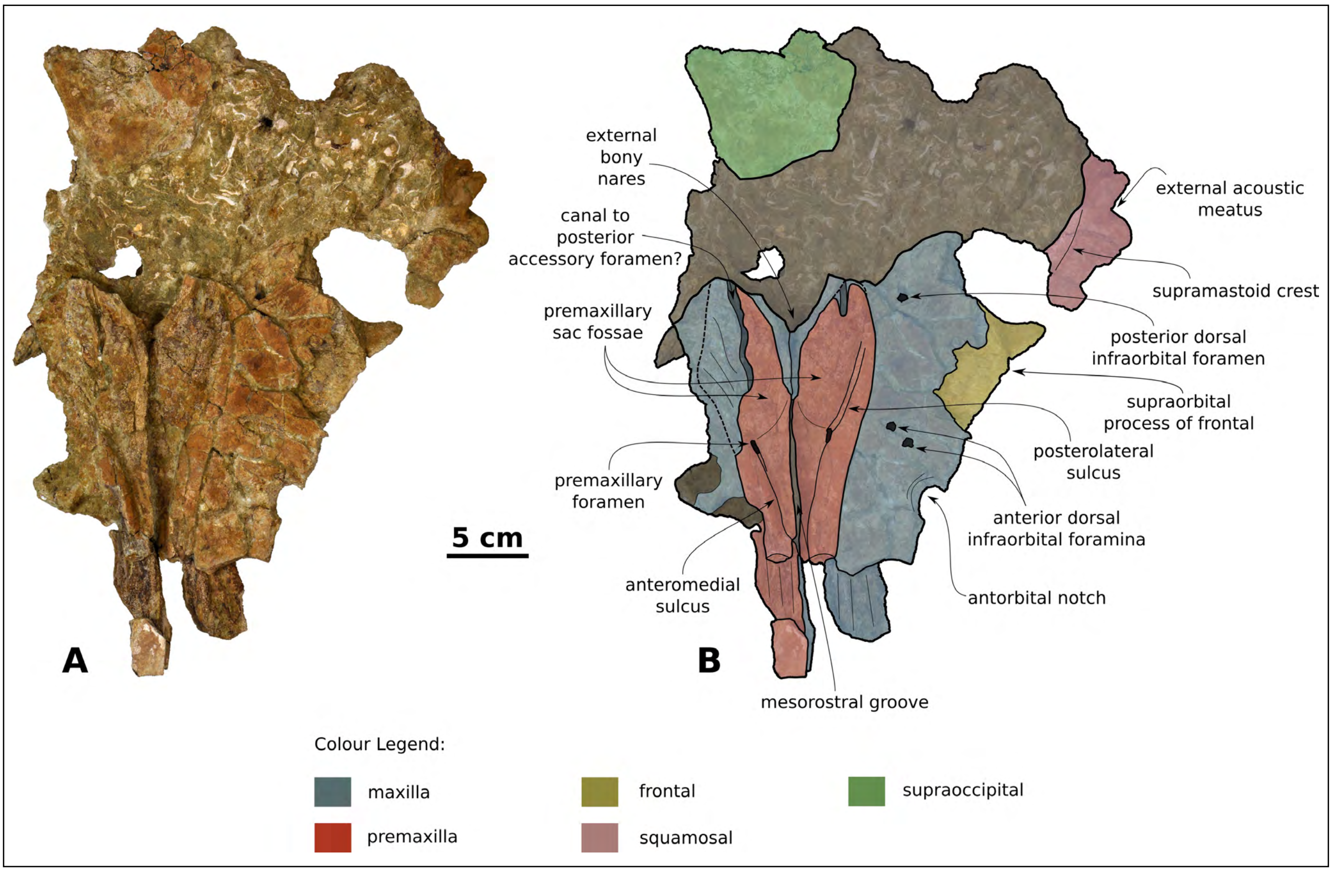

Fig. 3 - Dorsal view of the skull of MSNUP I-16153, partial skeleton of *Casatia thermophila* from the Lower Pliocene of Arcille. A) Photograph; B) corresponding explanatory line drawing.

verse narrowing at the level of the anterior dorsal infraorbital foramina, a condition subject to intraspecific variation in the extant monodontids.

The right and left premaxillary foramina are respectively located 25 and 30 mm posterior to the anteroposterior level of the left antorbital notch (the antorbital notches are not preserved in the holotype). The premaxillary foramen being located behind the corresponding antorbital notch represents a condition shared with all other monodontids.

Maxilla. A large, C-shaped indentation in the lateral margin of the left maxilla represents the partly preserved left antorbital notch (Fig. 3). It appears as deeply excavated medially, thus recalling the condition observed in *Monodon monoceros* and, to a lesser extent, *Haborodelphis japonicus* and some specimens of *Delphinapterus leucas*. No excavation at all is instead observed in *Bohaskaia monodontoides* and in the unnamed monodontid (IRSNB M 1922) from the Pliocene of Belgium (Lambert & Gigase 2007), both of which have a L-shaped antorbital notch, whereas the antorbital notches of *Denebola brachycephala* are too poorly preserved to properly evaluate this character.

At the level of the left premaxillary foramen, two roughly circular dorsal infraorbital foramina, having a maximum diameter of 8 mm, are observed on the dorsal surface of the left maxilla. Roughly in the same area, three foramina are present on the left maxilla of the *C. thermophila* holotype, suggesting some degree of intraspecific variability as regards this character. A single posterior dorsal infraorbital foramen opens posterior to the level of the postorbital process in the posterior preserved part of the left maxilla, at a distance of about 20 mm from the lateral margin of the premaxilla. This foramen is anteromedially elongated and exhibits a maximum length of 8.5 mm. No posterior dorsal infraorbital foramina are discernible on the preserved maxillary portions of the holotype. Medial to the premaxilla, the maxilla is exposed anterior and lateral to the external bony nares, and consequently, the preserved anterior and anterolateral margins of the external bony nares are solely formed by the maxillae. Regarded as a synapomorphy of Monodontidae

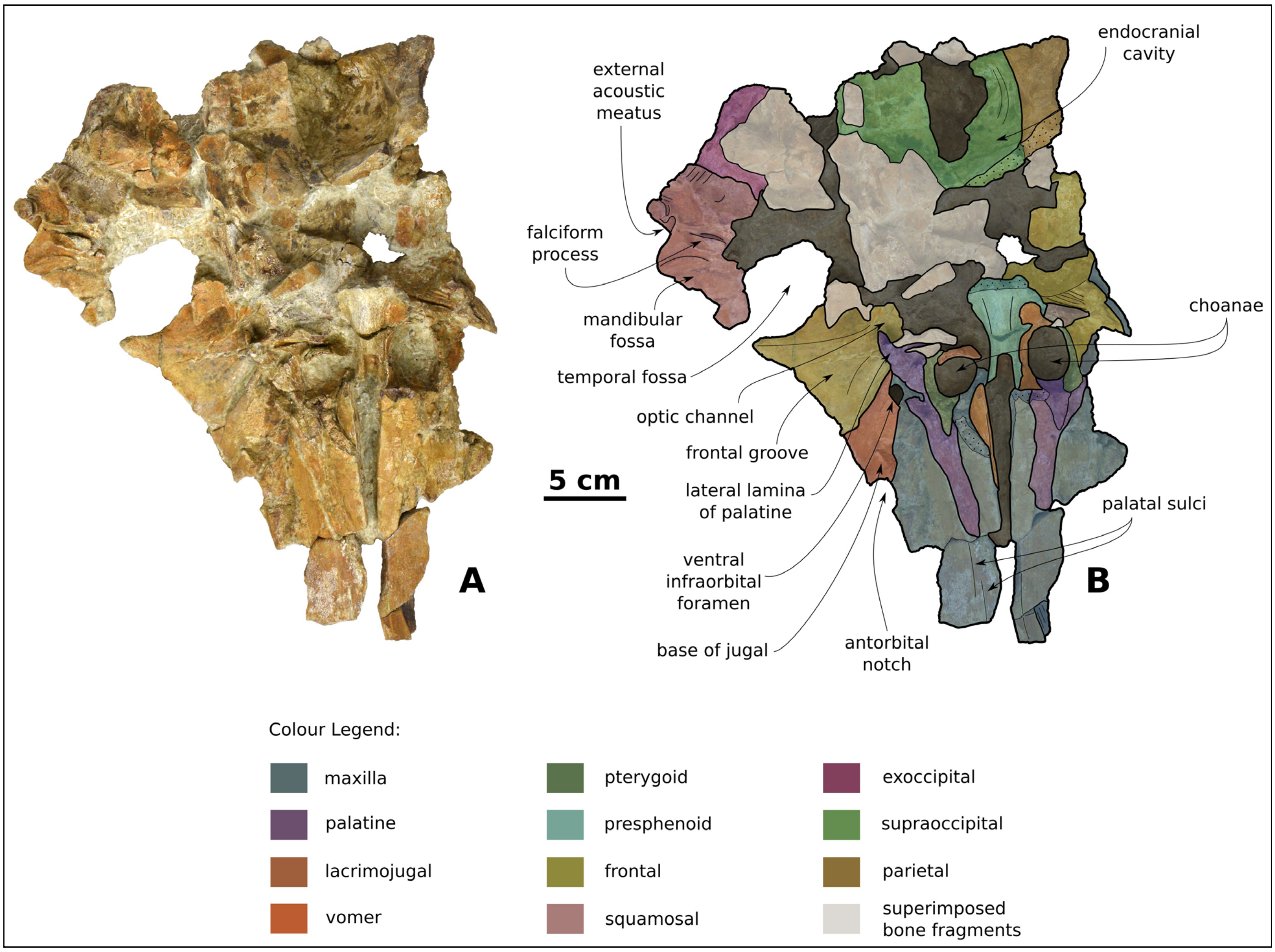

Fig. 4 - Ventral view of the skull of MSNUP I-16153, partial skeleton of *Casatia thermophila* from the Lower Pliocene of Arcille. A) Photograph; B) corresponding explanatory line drawing.

(Muizon 1988), this character is observed also in the holotype.

The posterior accessory foramina, which are well discernible in the holotype, are not preserved in MSNUP I-16153. However, along the sutural surface of the right maxilla (and subordinately of the left maxilla), a canal takes its place at the maxilla-premaxilla interface. This canal runs anteroposteriorly, describing a slightly sinuous path. It probably represents a branch of the infraorbital canal that led to the posterior accessory foramen.

The ventral surface of the maxilla (Fig. 4) comprises most of the preserved portion of the palate, which is deformed and incomplete. Anterior to the palatines, three palatal sulci – one on the right maxilla and two on the left maxilla – run anteroposteriorly. The left ventral infraorbital foramen is elliptical and opens on the maxilla, at the lateral end of the lacrimojugal; its measures are 22×13 mm.

Squamosal. In the *C. thermophila* holotype most of the squamosal is missing; in turn, the left squamosal is well preserved in MSNUP I-16153 (Figs. 3-5). This bone has been dislocated from its anatomical position due to the dorsoventral compression of the cranium. Because of such distortion, the temporal fossa is completely visible in dorsal view (Fig. 3). The zygomatic process is well preserved and, in lateral view, it appears as gently bent dorsally. It measures 55 mm in length (measured from the postglenoid process to the anteriormost tip of the process). The dorsal surface of the zygomatic process is smooth and the supramastoid crest is well defined. When viewed ventrally (Fig. 4), the ventral face of the zygomatic process is smooth and, on its tip, the articular facet of the jugal is preserved (Fig. 5). The mandibular fossa is smooth and gently concave, with poorly defined medial and anterior margins. This fossa is bordered posteriorly by the postglenoid process, which is followed further posteriorly by the postglenoid notch. The anterior

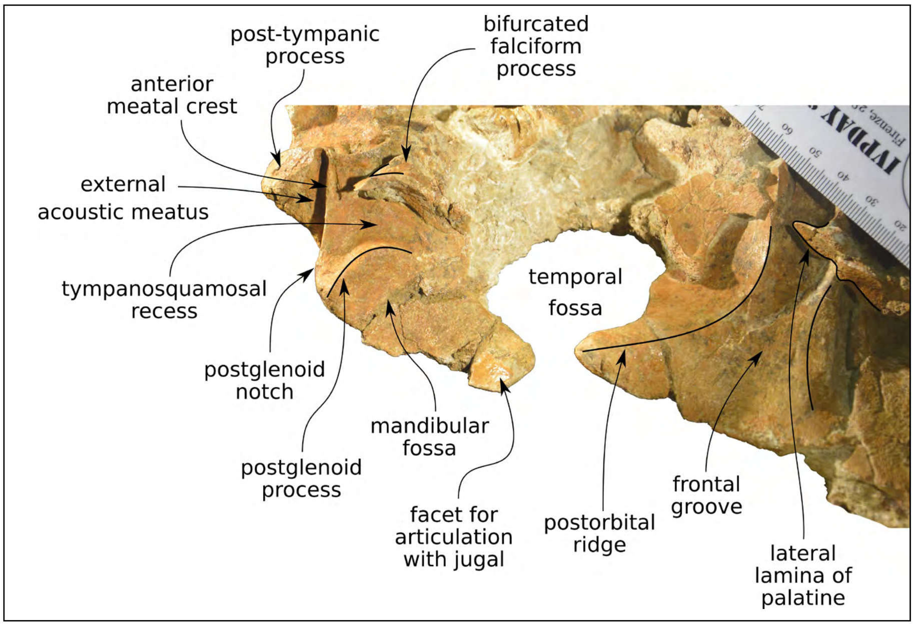

Fig. 5 - Close-up, in left anteroventrolateral view, of the orbital, temporal and zygomatic regions of the skull of MSNUP I-16153, partial skeleton of *Casatia thermophila* from the Lower Pliocene of Arcille.

meatal crest comprises the anterior margin of the well-preserved external acoustic meatus (Fig. 5). The latter consists of a deep, 4 mm wide, anterolaterally directed groove. The post-tympanic process and the tympanosquamosal recess are almost completely preserved. The falciform process, which is located medial to the tympanosquamosal recess, is partly broken except for its base, which appears as bifurcated. A bifurcated falciform process is common in some individuals of *Delphinapterus leucas* and is present in the holotype of *Haborodelphis japonicus* (Ichishima et al. 2019).

Vomer. Shreds of the vomer are locally recognisable in ventral view (Fig. 4). One of these fragments forms the left wall of the mesorostral groove. Along the mesorostral groove, the vomer is broken longitudinally due to the displacement of the left maxilla relative to its right antimere. A thin, sheet-like, largely abraded portion of the vomer coats the right face of the presphenoid and constitutes the posteromedial margin of the right choana. Another fragment of the vomer comprises of a thin bony lamina that defines the posterior wall of the left choana (which is smaller than the right one).

Palatine. Visible in ventral view (Fig. 4), the palatine bones are greatly elongated anteroposteriorly and compressed transversely. This morphology of the palatine is not consistent with those of the other extinct and extant species of Monodontidae known to date. In all monodontid genera, the palatines are poorly elongated anteroposteriorly. This is particularly true for *Bohaskaia* and *Denebola*, in which the palatines are stocky and their anterior terminations do not even reach the base of the rostrum. *Casatia* displays a unique morphology of the palatines: (1) their anterior termination exceeds the anteroposterior level of the posterior margin of the antorbital notch by at least 40 mm; and (2) their transversal maximum width does not exceed 15 mm. Similar to the condition observed in *Denebola* and *Bohaskaia*, in *Casatia* the palatines do not contact each other medially.

The right palatine separates the right pterygoid from the maxilla. The lateral lamina of the left palatine is preserved. This sheet-like bone formation projects posterolaterally, partly flooring the optic channel; its posterior preserved termination is located somewhat anterior to the posterolateral edge of the frontal groove (Figs. 4, 5). The observation of the lateral lamina of the palatine ventral to the optic channel is currently regarded as a synapomorphy of Monodontidae (Muizon 1988).

Pterygoid. Two small, poorly preserved remnants of the pterygoids are observed in ventral view (Fig. 4). They constitute the lateral margin of the choanae.

Lacrimojugal. A small portion of the lacrimojugal, bordered anteromedially by the maxilla and posterolaterally by the frontal, is preserved (Fig. 4). The anterior margin of the lacrimojugal contributes to the posterior margin of the antorbital notch. The base of the jugal is preserved ca. 10 mm posterior to the antorbital notch. The posteromedial corner of the lacrimojugal apparently contributes to the ventral infraorbital foramen. The posteromedial end of the lacrimojugal seemingly contacts the palatine, in occurrence of the posterior border of the ventral infraorbital foramen.

Presphenoid. Only visible in ventral view (Fig. 4), the presphenoid comprises the bony septum that separates the choanae from each other. This consists of a massive bone that moderately flares posterolaterally. The ventral aspect of the presphenoid is strongly convex transversely, and its right ventrolateral surface is partially coated by the vomer.

Frontal. A broad part of the partially preserved left supraorbital process of the frontal is visible in dorsal view due to the lack of a remarkable anterolateral portion of the ascending process of the left maxilla (Fig. 3). The postorbital process is well preserved and laterally bent; it defines the anterior margin of the temporal fossa. In ventral view, as in the other extinct monodontid genera, a broad frontal groove runs obliquely, being bordered posteriorly by the postorbital ridge (Fig. 4). The optic channel is found at the medial end of the frontal groove and is partly floored by the underlying lateral lamina of the palatine (Fig. 5).

Supraoccipital. The occipital region of the neurocranium is comprised of several dislocated and fragmentary bones. In dorsal view, part of the supraoccipital is recognisable (Fig. 3). The dorsal surface of the dislocated supraoccipital shield comprises the posteriormost portion of the cranium (Fig. 4). It is flattened as a consequence of the dorsoventral compression of the skull. In turn, the dorsal surface of the remaining posterior part of the neurocranium is covered by sediments. In ventral view, the dislocated, smooth, and fractured endocranial cavity is observed. It is strongly concave and partly covered by sediment and bone fragments.

Parietal. A 65-mm-long part of the parietal in connection with the supraoccipital shield is preserved. In lateral view the parietal is ventrally elongated and its surface is strongly abraded. The suture surface with the squamosal is visible.

Dentition. Two detached fragments of the rostral portion of the maxillae preserve several dental alveoli along their ventral surface (Fig. 6A, B), providing important information on the otherwise unknown dentition of *Casatia.* In particular, a 77-mm-long fragment of the left maxilla features nine alveoli (Fig. 6A) whereas three alveoli are preserved along the 27-mm-long lateral margin of a fragment of the right maxilla (Fig. 6B). All the preserved dental alveoli are small (diameter about 5.5 mm), elliptical, closely spaced, and – as in *Bohaskaia*, *Delphinapterus* and *Denebola* – anteroventrally and laterally oriented. The large number of the alveoli counted in these maxillary fragments and their invariant size and shape suggests that *Casatia* had a homodont and polydont dentition. In this respect, *Casatia* recalls the fossil monodontid genera *Bohaskaia* and *Denebola*, both of which have about 15 upper teeth in each upper quadrant (Barnes 1984; Vélez-Juarbe & Pyenson 2012). In turn, *Delphinapterus* has nine large teeth in each upper quadrant (Jefferson et al. 1993), *Haborodelphis* has an alveolar row without distinct alveoli (Ichishima et al. 2019), and *Monodon* has no functional teeth, except for males that bear a single tusk rooted within the maxilla (Nweeia et al. 2012; Post & Bosselaers 2017; Berkovitz & Shellis 2018).

Postcranial bones

Cervical vertebrae. The free axis is well preserved with only its ventrolateral portion missing (Fig. 6C-F). Unfused atlas and axis are also observed in the extant *Delphinapterus* and *Monodon* (O'Corry-Crowe 2018; Racicot et al. 2018; pers. obs.) and in *Haborodelphis*, the only other fossil monodontid for which the axis has been described (Ichishima et al. 2019), whereas the axis is fused to the third cervical in at least some adult individuals of *Monodon* (pers. obs.). The preserved left anterior articular facet for the atlas is weakly concave and reniform. The preserved left transverse process is very short and has a rounded lateral margin in anterior and posterior views (Fig. 6C, D). As in *Delphinapterus*, *Haborodelphis* and *Monodon*, the odontoid process is robust (Fig. 6E). The neural canal is almost circular; it measures 32 mm in height and 41 mm in transverse width. The posterodorsally oriented neural spine measures 42 mm in length; as also observed in *Delphinapterus*, it is ventrally incised by a deep groove. Two small and rounded postzygapophyses are preserved (Fig. 6D); they are visible on the posterior surface of the neural arch. A narrow but evident medial hypapophysis is present on the ventral surface of the centrum.

Two additional damaged cervicals are preserved. They are strongly compressed anteroposteriorly. The body of one of these vertebrae measures 35 mm in dorsoventral height, 41 mm in transverse width and 12 mm in anteroposterior length; the body of the other vertebra measures 33 mm in dor-

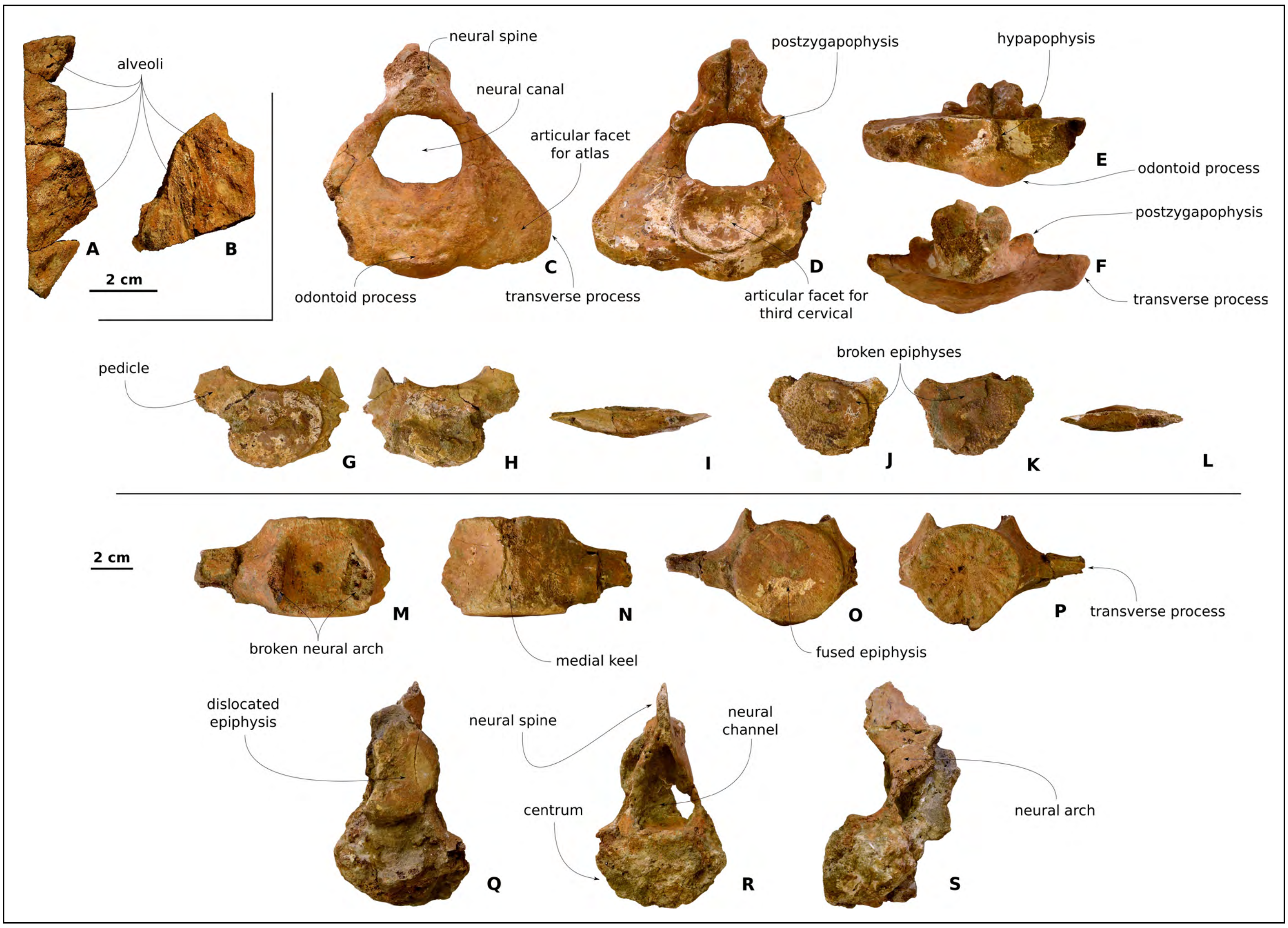

Fig. 6 - Cranial (A, B) and postcranial (C-S) elements of MSNUP I-16153, partial skeleton of *Casatia thermophila* from the Lower Pliocene of Arcille. (A, B) Dentigerous fragments of the left (A) and right (B) maxillae, in ventral view; (C-F) axis in (C) cranial, (D) caudal, (E) ventral and (F) dorsal views; (G-I) cervical vertebra in (G) cranial, (H) caudal and (I) dorsal views; (J-K) cervical vertebra in (J) cranial, (K) caudal and (L) dorsal views; (M-P) lumbar? vertebra in (M) dorsal, (N) ventral, (O) cranial and (P) caudal views; (Q-S) lumbar? vertebra in (Q) cranial, (R) caudal and (S) lateral views.

soventral height, 39 mm in transverse width and 12 mm in anteroposterior length (Fig. 6G-L). One of the cervicals preserves a proximal portion of the anteroposteriorly compressed pedicles. The heavily abraded epiphyses are fused to the corresponding centra.

Postcervical vertebrae. Both the post-cervical vertebrae are damaged and partially preserved. Owing to their incompleteness, these vertebrae are here tentatively identified as anterior lumbars, though an origin from the posterior thoracic region cannot be excluded. One of the putative lumbars (Fig. 6M-P) has an anteroposteriorly short, wider than high vertebral body measuring 45 mm in height, 49 mm in transverse width and 42 mm in anteroposterior length. The base of the neural arch is rather wide transversely. Its cranial epiphysis is fused to the centrum, which in turn displays a well preserved articular surface for the unfused (and unpreserved) caudal epiphysis. An abraded medial keel is present on the ventral surface of the centrum. The other putative lumbar is comprised of part of the centrum, a dislocated (cranial?) epiphysis and most of the neural arch; the latter is broadly triangular in cross section and roughly twice as long as it is wide (Fig. 6Q-S).

Discussion and conclusions

Although the skull of MSNUP I-16153 is incomplete and dorsoventrally compressed, it allows for gathering new data on the osteological anatomy of *Casatia thermophila* and consequently improving the diagnosis of this extinct monodontid species. In particular, the well preserved ventral surface of the cranium allows for pointing out the following characters that were not observed in the *C. thermophila* holotype: (1) a lateral lamina of the palatine that passes anterior to the posterolateral edge of the frontal groove – a synapomorphy shared with all other monodontids known to date (Muizon 1988); (2) palatine bones that are greatly elongated anteroposteriorly – a distinctive character of *C. thermophila*; (3) palatines that do not contact each other medially, (4) small and closely spaced dental alveoli on the maxilla – the same condition as in *Bohaskaia monodontoides* and *Denebola brachycephala*; and (5) a bifurcated falciform process of the squamosal – a character shared with *Haborodelphis japonicus* and some specimens of *Delphinapterus leucas*. Moreover, as in *Monodon monoceros,* some specimens of *D. leucas* and *Haborodelphis japonicus*, the partially preserved left antorbital notch features a deep medial excavation.

The maxillary fragments that preserve dental alveoli allow for some inferences about the feeding style of *C. thermophila*. Extant monodontids capture their food items by means of suction, i.e., by reducing the intraoral pressure to generate an inward flow of water that draws the prey into the mouth (Werth 2006; Hocking et al. 2017; Berkoviz & Shellis 2018). As highlighted by Werth (2006), suction feeding in cetaceans correlates with a reduction in tooth numbers (with some exceptions, as exemplified by the killer whale *Orcinus orca*). Reduced tooth counts are indeed observed in the extant monodontids *D. leucas* and *M. monoceros*. A suction-based prey capture method might have also been used by *H. japonicus*, which displays a vestigial alveolar row without distinct alveoli. By contrast, a high number of functional teeth, inferred on the basis of the observation of several well individualised, regularly shaped, similarly sized upper dental alveoli, suggests that *C. thermophila*, *B. monodontoides* and *D. brachycephala* captured their prey by using a ram feeding method (i.e., one that involves a rapid forward movement of the body aimed at engulfing prey), maybe coupled with a snapping action as in other polydont cetaceans (Hocking et al. 2017).

MSNUP I-16153 represents the second find of *C. thermophila* as well as the second fossil monodontid specimen ever recorded from the Mediterranean Basin. As such, it supports the notion that the occurrence of the holotype of *C. thermophila* in present-day Italy does not testify an Atlantic vagrant individual whose remains serendipitously fossilised in the Mediterranean Sea. Recent palaeoclimatic reconstructions for the Early Pliocene Mediterranean Sea suggest surface seawater temperatures about 2–3°C higher than today (e.g., Prista et al. 2015; Ragaini et al. 2019; Coletti et al. 2021), as also supported by a conspicuous fossil record of thermophilic marine vertebrates (e.g., Mora Morote 1996, 1997; Collareta et al. 2017, 2021a). Besides several specimens of the purportedly thermophilic sirenian *Metaxytherium subapenninum* (Sorbi et al. 2012), the deposits in which MSNUP I-16153 was found feature a high concentration of fossil teeth belonging to tropical or subtropical elasmobranch species, such as the bull shark *Carcharhinus leucas* and the tiger shark *Galeocerdo cuvier* (Simpfendorfer & Burgess 2009; Ferreira & Simpfendorfer 2019). These fossils also indicate a marginal-marine, shallow-water setting for the Arcille palaeo-area; that said, several remains referred to marlins (*Makaira* sp.) and bluntnose six-gill sharks (*Hexanchus griseus*) suggest strong connections with open-sea settings (Cook & Compagno 2009; Collette et al. 2011). Therefore, the discovery of a second specimen of *C. thermophila* at its Tuscan Pliocene type locality suggests that this extinct monodontid species was a regular inhabitant of the tropical, marginal-marine Arcille palaeoenvironment. Furthermore, it further corroborates the hypothesis that early monodontids thrived in warm-water habitats, in agreement with previous reflections on the same topic by Barnes (1984), Vélez-Juarbe & Pyenson (2012) and Bianucci et al. (2019).

Acknowledgements and funding. The discovery and collection of the fossil specimen described herein were made possible by a concession for excavation and palaeontological research of the Italian Ministero per i Beni e le Attività Culturali, Direzione Generale per le Antichità to the MSNUP (scientific supervisor: G.B.). Special thanks are due to M. Turchetti, L. Tondo and P. Volpe (Soprintendenza per i Beni Archeologici della Toscana) for their institutional support. We are grateful to all the volunteers of GAMPS for their crucial cooperation in excavating these and other Arcille fossil vertebrates. P. Agnelli, D. Bohaska, N. Bressi, S. Farina, V. Franceschini, O. Lodovici, S. Maretti, N. Pyenson, O. Lambert, and C. Sorbini provided access to museum collections. O. Lambert is also thanked for fruitful discussion about the fossil record of Monodontidae.

The excavation and recovery of MSNUP I-15892 and MSNUP I-16153 was generously funded by the MSNUP. Acquisition of the scanner used for creating the 3D model of MSNUP I-16153 was possible thanks to a funding grant from Università di Pisa (PRA_2020_25). Not least, we are sincerely indebted to H. Ichishima, K. Post, C. Lombardo and David M. Alba, whose thorough reviews greatly contributed to improve an early draft of this paper.

REFERENCES

Barnes L.G. (1984) - Fossil odontocetes (Mammalia: Cetacea) from the Almejas Formation, Isla Cedros, Mexico. *PaleoBios*, 42: 321-343.

Benvenuti M., Papini M. & Rook L. (2001) - Mammal biochronology, IBSU and palaeornvironment evolution in a post-collisional basin: evidence from the Late Miocene Baccinello-Cinigiano basin in southern Tuscany, Italy. *Bollettino della Società Geologica Italiana*, 120: 97-118.

Berkovitz B.K. & Shellis R.P. (2018) - The teeth of mammalian vertebrates. Academic Press.

Bianucci G., Pesci F., Collareta A. & Tinelli C. (2019) - A new Monodontidae (Cetacea, Delphinoidea) from the lower Pliocene of Italy supports a warm-water origin for narwhals and white whales. *Journal of Vertebrate Paleontology*, 39: e1645148.

Cita, M.B. (1975) - Biodynamic effects of the Messinian Salinity Crisis on the evolution of planktonic foraminifera in the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 20: 23-42.

Coletti G., Bosio G. & Collareta A. (2021) - Lower Pliocene barnacle facies of western Liguria (NW Italy): a peek into a warm past and a glimpse of our incoming future. *Rivista Italiana di Paleontologia e Stratigrafia*, 127: 103-131.

Collareta A., Casati S., Catanzariti R. & Di Cencio A. (2017) - First record of the knifetooth sawfish *Anoxypristis* (Elasmobranchii: Rhinopristiformes) from the Pliocene of Tuscany (central Italy). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 284: 289-297.

Collareta A., Merella M., Casati S., Coletti G., Di Cencio A. (2021a) - Another thermophilic "Miocene survivor" from the Italian Pliocene: a geologically young occurrence of the pelagic eagle ray *Aetobatus* in the Euro-Mediterranean region. *Carnets de Geologie*, 21: 203-214.

Collareta, A., Merella, M., Casati, S., & Di Cencio, A. (2021b). First fossils of the extant blacktip shark Carcharhinus limbatus from Europe and the Mediterranean Basin. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 301: 109-118.

Collareta A., Mollen F.H., Merella M., Casati S. & Di Cencio A. (2021c) - Remarkable multicuspid teeth in a new elusive skate (Chondrichthyes, Rajiformes) from the Mediterranean Pliocene. *Paläontologische Zeitschrift*, 95: 117-128.

Collette B., Acero A., Amorim A.F., Boustany A., Canales Ramirez C., Cardenas G., Carpenter K.E., de Oliveira Leite Jr. N., Di Natale A., Die D., Fox W., Fredou F.L., Graves J., Guzman-Mora A., Viera Hazin F.H., Hinton M., Juan Jorda M., Minte Vera M., Miyabe N., Montano Cruz R., Nelson R., Oxenford H., Restrepo V., Salas E., Schaefer K., Schratwieser J., Serra R., Sun C., Teixeira Lessa R.P., Pires Ferreira Travassos P.E., Uozumi Y. & Yanez E. (2011) - *Makaira nigricans*. The IUCN Red List of Threatened Species 2011:e.T170314A6743776. Available at www.iucnredlist.org/species/170314/6743776. Accessed April 16, 2021.

Cook S.F. & Compagno L.J.V. (2009) - *Hexanchus griseus*. The IUCN Red List of Threatened Species 2009:e.T10030A3155348. Available at www.iucnredlist.org/species/10030/3155348. Accessed April 16, 2021.

Dominici S., Danise S. & Benvenuti M. (2018) - Pliocene stratigraphic palaeobiology in Tuscany and the fossil record of marine megafauna. *Earth-Science Reviews*, 176: 277-310.

Evans H.E. & Lahunta A. de (2013) - Miller's Anatomy of the Dog. Saunders, St Louis, 850 pp.

Ferreira L.C. & Simpfendorfer C. (2019) - *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2019:e.T39378A2913541. Available at www.iucnredlist.org/species/39378/2913541. Accessed April 16, 2021.

Galatius A., Berta A., Frandsen M. S. & Goodall R.N.P. (2011) - Interspecific variation of ontogeny and skull shape among porpoises (Phocoenidae). *Journal of Morphology*, 272: 136-148.

Hocking D.P., Marx F.G., Park T., Fitzgerald E.M. & Evans A.R. (2017) - A behavioral framework for the evolution of feeding in predatory aquatic mammals. *Proceedings of the Royal Society B: Biological Sciences*, 284: 20162750.

Ichishima H., Furusawa H., Tachibana M. & Kimura M. (2019) - First monodontid cetacean (Odontoceti, Delphinoidea) from the early Pliocene of the north-western Pacific Ocean. *Papers in Palaeontology*, 5: 323-342.

Jefferson T.A., Leatherwood S. & Webber M.A. (1993) - FAO species identification guide. Rome, FAO. 320 p. 587 figs.

Lambert O. & Gigase P. (2007) - A monodontid cetacean from the early Pliocene of the North Sea. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 77: 197-210.

Lourens L.J., Hilgen F.J., Laskar J., Shackleton N.J. & Wilson D. (2004) - Appendix 2. Orbital tuning calibrations and conversions for the Neogene period, 469-484. In: Gradstein F., Ogg J. & Smith A.(Eds) - A Geologic Time Scale 2004. Cambridge University Press, Cambridge, U.K.

Mead J.G. & Fordyce R.E. (2009) - The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology*, 627:1-261.

Merella M., Collareta A., Casati S., Di Cencio A., Landini W. & Bianucci G. (2020) - The lower Pliocene elasmobranch assemblage from Arcille (Campagnatico, Grosseto Province): palaeoecological and palaeoenvironmental significance. *Fossilia*, 2020: 41-43.

Merella M., Collareta A., Casati S., Di Cencio A. & Bianucci G. (2021) - An unexpected deadly meeting: deep-water (hexanchid) shark bite marks on a sirenian skeleton from Pliocene shoreface deposits of Tuscany (Italy). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 301 (3): 295-305.

Merella M., Collareta A., Casati S., Di Cencio A. & Bianucci G. (2022) - Erratum: Merella, M., Collareta, A., Casati, A., Di Cencio, A. & Bianucci, G. (2021): An unexpected deadly meeting: deep-water (hexanchid) shark bite marks on a sirenian skeleton from Pliocene shoreface deposits ofTuscany (Italy). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 301 (3): 295–305. doi: 10.1127/njgpa/2021/1012. *Neues Jahrbuch für Geolo-*

gie und Paläontologie-Abhandlungen, 303: 1-3.

Mora Morote P. (1996) - Peces Galeomorfos y Squatinomorfos en el Plioceno de Guardamar del Segura (Alicante). *Cidaris*, 5: 98-124.

Mora Morote P. (1997) - Peces Myliobatiformes y Pristiophoriformes en el Plioceno de Guardamar del Segura (Alicante). *Cidaris*, 11-12: 48-63.

Muizon C. de. (1988) - Les relations phylogénétiques des Delphinida (Cetacea, Mammalia). *Annales de Paléontologie*, 74: 159-227.

Nweeia M.T., Eichmiller F.C., Hauschka P.V., Tyler E., Mead J.G., Potter C.W., Angnatsiak D.P., Richard P.R., Orr J.R. & Black S.R. (2012) - Vestigial tooth anatomy and tusk nomenclature for *Monodon monoceros*. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, 295: 1006-1016.

O'Corry-Crowe, G.M. (2018) - Beluga Whale: *Delphinapterus leucas*; pp. 93-96 in B. Würsig, J.G.M. Thewissen, and K. Kovacs (Eds) - Encyclopedia of Marine Mammals, third edition. Academic Press, London, U.K.

Post K. & Bosselaers M. (2017) - Cetacean fossils from a 1961 expedition at the Schelde estuary, province of Zeeland, The Netherlands. *Cainozoic Research*, 17: 11-21.

Prista G.A., Agostinho R.J. & Cachão M.A. (2015) - Observing the past to better understand the future: a synthesis of the Neogene climate in Europe and its perspectives on present climate change. *Open Geosciences*, 7: 65-83.

Racicot R.A., Darroch S.A. & Kohno N. (2018) - Neuroanatomy and inner ear labyrinths of the narwhal, *Monodon monoceros*, and beluga, *Delphinapterus leucas* (Cetacea: Monodontidae). *Journal of anatomy*, 233: 421-439.

Ragaini L., Ficini F., Zanchetta G., Regattieri E., Perchiazzi N. & Dallai L. (2019) - Mineralogy and oxygen isotope profile of *Pelecyora gigas* (Veneridae, Bivalvia) from Tuscan Pliocene. *Alpine and Mediterranean Quaternary*, 32: 5-13.

Ramassamy B., Lambert O., Collareta A., Urbina M. & Bianucci G. (2018) - Description of the skeleton of the fossil beaked whale *Messapicetus gregarius*: searching potential proxies for deep-diving abilities. *Fossil Record*, 21: 11-32.

Simpfendorfer C. & Burgess G.H. (2009) - *Carcharhinus leucas*. The IUCN Red List of Threatened Species 2009:e. T39372A10187195. Available at www.iucnredlist.org/species/39372/10187195. Accessed April 16, 2021.

Sorbi S., Domning D.P., Vaiani S.C. & Bianucci G. (2012) - *Metaxytherium subapenninum* (Bruno, 1839) (Mammalia, Dugongidae), the latest sirenian of the Mediterranean Basin. *Journal of Vertebrate Paleontology*, 32: 686-707.

Tinelli C., Ribolini A., Bianucci G., Bini M. & Landini W. (2012) - Ground penetrating radar and palaeontology: The detection of sirenian fossil bones under a sunflower field in Tuscany (Italy). *Comptes Rendus Palevol*, 11: 445-454.

Tinelli C. (2013) - Marine Vertebrates from Pliocene Shell Beds from Tuscany (Italy): Prospecting, Taphonomy, Palaeoecology and Systematic Palaeontology. Ph.D. Dissertation, Università di Pisa, Pisa, 164 pp.

Tsai C.H. (2017) - A Miocene breeding ground of an extinct baleen whale (Cetacea: Mysticeti). *PeerJ*, 5: e3711.

Vélez-Juarbe J. & Pyenson N.D. (2012) - *Bohaskaia monodontoides*, a new monodontid (Cetacea, Odontoceti, Delphinoidea) from the Pliocene of the western North Atlantic Ocean. *Journal of Vertebrate Paleontology*, 32: 476-484.

Werth A.J. (2006) - Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *Journal of Mammology*, 87: 579-588. (doi:10.1644/05-mamma-279r1.1)

Yoshida H., Shirakihara M., Takemura A. & Shirakihara K. (1994) - Development, sexual dimorphism, and individual variation in the skeleton of the finless porpoise, *Neophocaena phocaenoides*, in the coastal waters of western Kyushu, Japan. *Marine Mammal Science*, 10: 266-282.