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Large deadfalls of the 'ginsu' shark *Cretoxyrhina mantelli* (Agassiz, 1835) (Neoselachii, Lamniformes) from the Upper Cretaceous of northeastern Italy

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ABSTRACT

Cretoxyrhina mantelli was a large pelagic lamniform shark geographically widespread during the Late Cretaceous, and well known because of several nearly complete skeletons from the Western Interior Seaway of North America. Here we report 15 partial skeletons belonging to lamniform sharks from the 'lastame' lithozone of the Upper Cretaceous Scaglia Rossa Formation of the Lessini Mountains (northeastern Italy). Seven partial but articulated skeletons include tooth sets that allow a confident attribution to *Cretoxyrhina mantelli* based on dental morphologies. We review the taxonomic history of *C. mantelli*, evidencing that the taxon was erected by Agassiz (1835) and tracing back four of the original syntypes. Based on calcareous plankton biostratigraphy, the rock in which the Italian skeletal remains are embedded is constrained to the middle-upper Turonian. Total length estimates of the specimens suggest that the sample includes the largest specimen of *Cretoxyrhina mantelli* (615–650 cm estimated total length) known to date. The placoid scale morphology indicates that *C. mantelli* most likely was a fast swimmer with a similar ecology as the extant white shark, *Carcharodon carcharias*. The associated skeletal elements of the specimens represent large chondrichthyan deadfalls and the cadavers decayed on the seafloor where they remained exposed for several months, as indicated by bioerosional traces, some of which are interpreted as a product of bone-eating worm activities and other bioerosional traces with *Gastrochaenolites*-like structure. The *Cretoxyrhina mantelli* remains described herein provide new information about the 'lastame' vertebrate assemblage, which seemingly was strongly dominated by chondrichthyans, especially lamniform sharks.

1. Introduction

The 'ginsu' shark, *Cretoxyrhina mantelli* (Agassiz), is probably one of the best known and ecologically relevant top predators of the Late Cretaceous seas. Isolated teeth of this shark have been reported from many localities all around the world (Africa, Asia, Europe, North and South America; Cappetta, 2012). Some nearly complete skeletons were discovered in the Smoky Hill Chalk Member of the Niobrara Chalk in the Western Interior Seaway of North America (Bourdon, Everhart, 2011; Shimada, 1993a,b, 1994a–c, 1997a–e, 2008; Shimada et al., 2006). These skeletons indicate that *Cretoxyrhina mantelli* had a general morphology close to that of the white shark (*Carcharodon carcharias* Linnaeus, 1758) (Shimada, 1997b; Shimada et al., 2006), being similar or even larger in size.

Isolated teeth are so far the most common remains of *C. mantelli* reported from Italy (e.g., Bassani, 1876; D'Erasmo, 1922), although

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some partial skeletons were found in the Scaglia Rossa Formation of Lessini Mountains (Verona Province, Veneto Region) during the 1970s (Amalfitano et al., 2017b,c; Cigala Fulgosi et al., 1980; Dalla Vecchia et al., 2005; Ginevra et al., 2000). The majority of these skeletal remains consist of teeth associated with calcified vertebral centra and fragments of calcified cranial cartilage; in some cases, they include also placoid scales.

The goal of this paper is to provide an overview of all the skeletal remains of *C. mantelli* discovered in northeastern Italy, and to discuss their paleobiological, stratigraphic and taphonomical implications. The historical record of the genus *Cretoxyrhina* in northeastern Italy is also discussed and we propose a solution to the nomenclatural conundrum of the exact date of the original erection of *Cretoxyrhina mantelli.*

2. Geological background

All of the articulated skeletons of *Cretoxyrhina mantelli* discovered in northeastern Italy come from the Scaglia Rossa Formation, which crops out and is extensively quarried in several localities of the western Lessini Mountains (Verona Province; Massari and Savazzi, 1981; Amalfitano et al., 2017a; Ginevra et al., 2000) and the Piave Valley (Belluno Province; Colombara, 2013). Quarries are opened into two peculiar lithofacies (one in the Lessini Mountains and the other in the Piave Valley) that yielded the totality of the skeletons. They are named ‘lastame’ (or ‘Pietra di Prun’) and ‘Pietra di Castellavazzo’.

The ‘lastame’ (‘lithozone’ 2 of the Scaglia Rossa Formation of Lozar and Grosso, 1997) crops out in the surroundings of S. Anna d'Alfaedo village (Verona Province) (Fig. 1), on Loffa Mount (western Lessini Mountains). It consists of a 7-8 m-thick package of limestone that is subdivided into 72 flaser-nodular whitish to reddish layers, rich in planktonic foraminifera and calcareous nannofossils (Amalfitano et al., 2017b). Such layers are laterally continuous with a thickness ranging from 4 to 35 cm and are separated by thin, dark red and shaly layers (marls and clays; Amalfitano et al., 2017b). According to Lozar, Grosso (1997), the ‘lastame’ spans from the lower Turonian to the lower Santonian, while other authors assigned a Turonian-Coniacian age to it (e.g., Cigala Fulgosi et al., 1980). A stratigraphic revision of the whole lithozone, however, is currently in progress. The macrofossils of the ‘lastame’ include several remains of large marine vertebrates (chondrichthyans, bony fishes, marine turtles, and mosasaurs; Amadori et al., 2019; Amalfitano et al., 2017a-c; Capellini, 1884; Chesi, Delfino, 2007; Dalla Vecchia et al., 2005; Cigala Fulgosi et al., 1980; Palci et al., 2013).

The ‘Pietra di Castellavazzo’ crops out in the surroundings of Castellavazzo village (near Longarone, Belluno Province) in the Piave Valley (Fig. 1). The facies resembles the ‘lastame’, being a 6–7 m thick section of micritic nodular limestones, with laterally continuous layers ranging in thickness from a few cm to 40 cm, separated by dark red clay interlayers (Trevisani, 2009, 2011). Moreover, the ‘Pietra di Castellavazzo’ is subdivided into two sub-units, the lower reddish portion and the upper grey-greenish portion (Trevisani,

Fig. 1. Location of the sites. The sites that yielded the skeletal remains of *Cretoxyrhina mantelli* described herein (Sant'Anna D'Alfaedo, Verona province) and Castellavazzo, near Longarone (Belluno province) are the only other site that yielded *Cretoxyrhina mantelli* skeletons. Scale bar = 100 km [single-column width].

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2009, 2011). Some authors referred the 'Pietra di Castellavazzo' to the early-middle Coniacian based on correlation with the 'lastame' (Coleselli et al., 1997; Trevisani, 2011), pending revisions, which are currently being carried out (Federico Fanti, pers. comm.). The fossil content of the 'Pietra di Castellavazzo', is similar to that of the 'lastame', including chondrichthyans and bony fishes, mostly represented by isolated teeth, and occasionally by more complete remains (e.g., Bassani, 1876, 1888; Trevisani, 2009, 2011).

3. Historical background

The first report of isolated teeth of *Cretoxyrhina mantelli* from the Upper Cretaceous Scaglia Rossa Formation of the Lessini Mountains was that by Bassani (1876). However, teeth of this species have been found in northern Italy from at least the first half of the 19th century, as testified by the presence of four specimens in the collection of Tommaso Antonio Catullo (1782–1869) housed in the Museum di Geology and Paleontology of the University of Padova (pers. obs.; see Table 1 for details and D'Erasmo, 1922; Fig. 2 and supplementary material Fig. A.1θ-λ). Other teeth from the 'Pietra di Castellavazzo' were initially misidentified as *Lamna* (=*Sphenodus*) *longidens* (Bassani, 1876; D'Erasmo, 1922). De Zigno (1883: p. 9) reported several localities of the Scaglia Rossa Formation yielding isolated teeth of *C. mantelli*, including the Valpolicella, Agno Valley, Follina Hills, and the surroundings of the towns of Feltre and Belluno.

The first Italian specimen of *C. mantelli* with articulated vertebral centra and associated teeth was recovered in 1878 from the 'Pietra di Castellavazzo' at the Olantreghe quarry near Longarone (Bassani, 1888). The fossil, consisting of 122 vertebral centra and 55 teeth, is housed in the collection of the Museum of Natural History, University of Pavia and is currently under review (Paolo Guaschi and Federico Fanti, pers. comm.).

D'Erasmo (1922) published the last synopsis on the *C. mantelli* record from the Veneto Region as part of a review about fossil fishes of northeastern Italy. Since then, studies on this lamniform shark in Italy have been neglected, despite the recovery of new relevant specimens during the second half of the 20th century. In particular, well-preserved vertebral column segments, often associated with teeth, were discovered during quarrying into the 'lastame' in the Lessini Mountains. These important findings were only briefly mentioned in short notes (e.g., Cigala Fulgosi et al., 1980), remaining virtually unknown to the scientific community. The oldest stratigraphic record of *Cretoxyrhina mantelli* from the study area reported in the literature refers to isolated teeth coming from the upper Cenomanian Bonarelli Level (Sorbini, 1976; Dalla Vecchia et al., 2005).

4. Material and methods

4.1. Institutional abbreviations

CE.A.S.C.: Centro di Analisi e Servizi Per la Certificazione, University of Padova, Padova, Italy; **FHSM:** Sternberg Museum of Natural History, Hays, Kansas, USA; **NHM:** The Natural History Museum, London, UK; **MCSNV:** Museo Civico di Storia Naturale di

Table 1
List of the specimens examined during the study. Institutional abbreviations: **MCSNV:** Civic Museum of Natural History of Verona, Italy; **MGC:** Geopaleontological Museum of Camposilvano, Italy; **MGP-PD:** Museum of Geology and Paleontology, University of Padova, Italy, C: Catullo's Collection, Z: De Zigno's Collection; **MPPSA:** Prehistoric and Paleontological Museum of S. Anna d'Alfaedo, Italy. The provenance locality reported in the historical labels of MGP-PD 14029 and 14034–14039 is 'Forni di Zoldo' (Belluno) but the lithology of the matrix embedding the specimens indicates that they come from the surroundings of Castellavazzo ('Pietra di Castellazazzo').

Inventory number	Preservation	Provenance locality
MPPSA-IGVR 36371	partial skeleton (teeth, articulated vertebrae, cranial cartilage fragments, placoid scales)	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45305	partial skeleton (teeth, articulated vertebrae, cranial cartilage fragments, placoid scales)	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45308	disarticulated vertebrae	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45319-45320	portion of vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45321-45322	portion of vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45323	portion of vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45324	teeth associated with a portion of the vertebral column and fragments of cranial cartilage	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45326	teeth associated with a portion of the vertebral column and fragments of cranial cartilage	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45334	teeth associated with a portion of the vertebral column and fragments of cranial cartilage	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45337	portion of vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MPPSA-IGVR 45344-45345	teeth associated with a portion of the vertebral column and fragments of cranial cartilage	Loffa Mount (S. Anna d'Alfaedo)
MGC-IGVR 47789	articulated vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MGC-IGVR 81375-81376	partial anterior portion of skeleton (teeth, articulated vertebral centra, cranial cartilage fragments, placoid scales)	Loffa Mount (S. Anna d'Alfaedo)
MGP-PD 3805	isolated tooth	Castellavazzo?
MGP-PD 5404	isolated tooth	Spilecco (Verona)
MGP-PD 6721 Z	isolated tooth	Mazzurega (Verona)
MGP-PD 6736 Z	isolated tooth	Mazzurega (Verona)
MGP-PD 7342C	isolated tooth	Castellavazzo (Belluno)
MGP-PD 7343C	isolated tooth	Castellavazzo (Belluno)
MGP-PD 7372C	isolated tooth	Mt. Belvedere (Belluno)
MGP-PD 8498C	isolated tooth	Castellavazzo (Belluno)
MGP-PD 8889	isolated tooth	Cerè Alto-Valdagno (Vicenza)
MGP-PD 14020	isolated tooth	Valle del Cismon (Belluno)
MGP-PD 14029	isolated tooth	Castellavazzo (Belluno)
MGP-PD 14034-14039	isolated teeth	Castellavazzo (Belluno)
MGP-PD 14042	isolated tooth	Castellavazzo (Belluno)
MGP-PD 22401-22470	isolated teeth	Castellavazzo (Belluno)
MGP-PD 23527-23529	isolated teeth	Belluno province
MGP-PD 31960	portion of vertebral column	Loffa Mount (S. Anna d'Alfaedo)
MCSNV V. 1094	isolated tooth	Spilecco (Verona)
MCSNV V. 1095	isolated tooth	Spilecco (Verona)
MCSNV V. 11798	isolated tooth	Spilecco (Verona)
MCSNV V. 12518	isolated tooth	Caprino Valley (Lubiara, Verona)
MCSNV V. 12519	isolated tooth	Prun (Verona)

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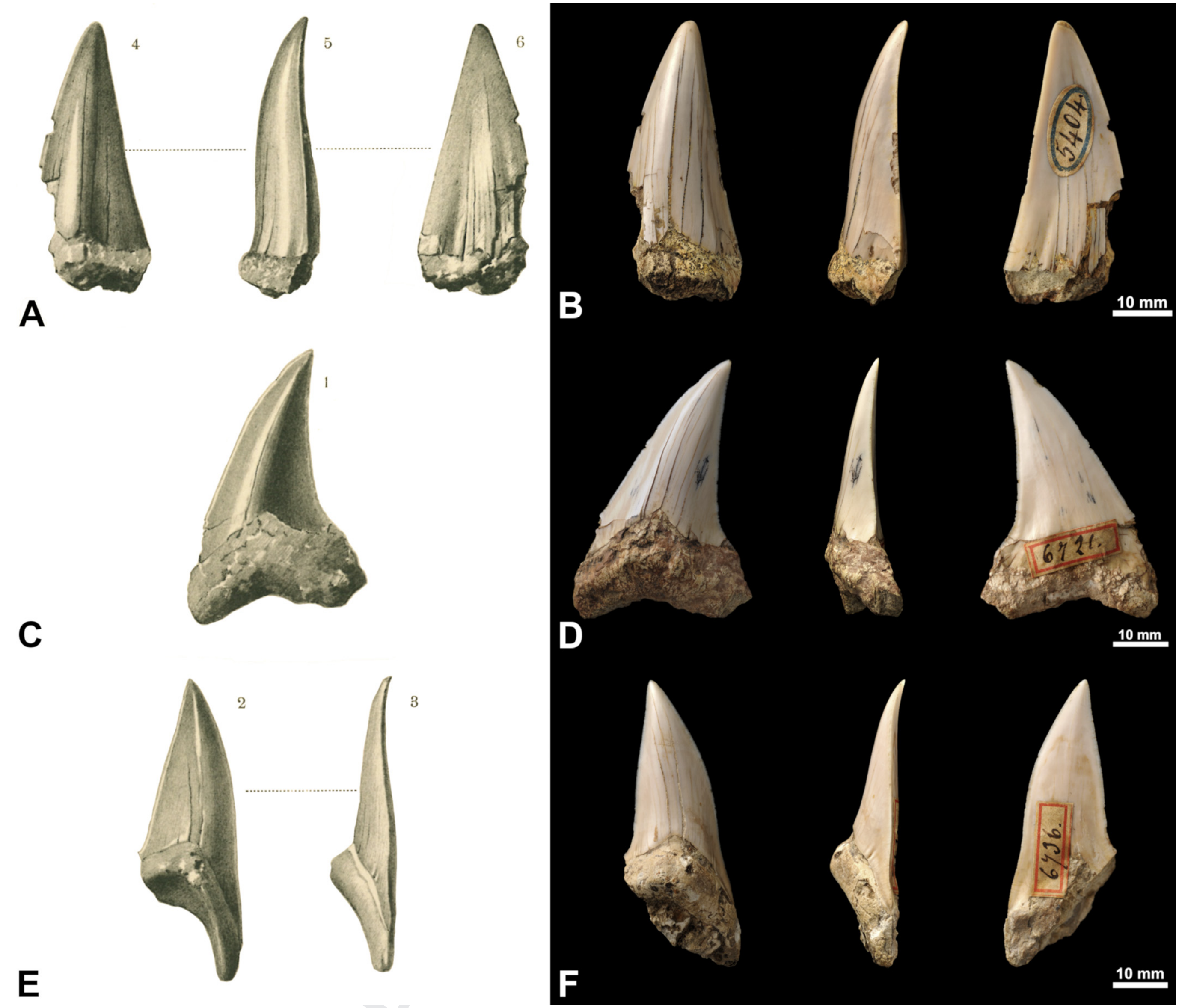

Fig. 2. ***Cretoxyrhina mantelli*** **(Agassiz, 1835). Isolated teeth housed in the historical collections of the Museum of Geology and Paleontology of the University of Padova. A.** MGP-PD 5404 as figured by D'Erasmo (1922: pl. 3, figs. 4-6), coming from Spilecco (VR) and erroneously attributed to the Eocene. **B.** photos of MGP-PD 5404 in lingual, lateral and labial view. **C.** MGP-PD 6721 as figured by D'Erasmo (1922: pl. 3, Fig. 1). **D.** photos of MGP-PD 6721 in lingual, lateral and labial view (Achille De Zigno's collection). **E.** MGP-PD 6736 as figured by D'Erasmo (1922: pl. 3, figs. 2-3). **F.** photos of MGP-PD 6736 in lingual, lateral and labial view (Achille De Zigno's collection). Scale bars = 10 mm [2-column width].

Verona (Civic Museum of Natural History), Verona, Italy; **MGC:** Museo Geopaleontologico di Camposilvano (Geopaleontological Museum), Camposilvano, Italy; **MGP-PD:** Museo di Geologia e Paleontologia (Museum of Geology and Paleontology), University of Padova, Padova, Italy; **MPPSA:** Museo Preistorico e Paleontologico di S. Anna d'Alfaedo (Prehistoric and Paleontological Museum), S. Anna d'Alfaedo, Italy.

4.2. Material

The material reported herein is part of the collections of the Prehistoric and Paleontological Museum of S. Anna d'Alfaedo, the Geopaleontogical Museum of Camposilvano, the Museum of Geology and Paleontology, University of Padova, and the Civic Museum of Natural History of Verona. Most of the specimens come from the 'lastame' quarries of Loffa Mount. Limestone slabs of different size contain calcified vertebral centra, teeth, and, in some cases, fragments of calcified cranial cartilage and placoid scales. The isolated teeth come from several localities of Veneto Region. In Table 1, a detailed list of the examined material is provided, reporting the specimen number and its repository, a concise description of its state of preservation, and its locality of provenance.

4.3. Methods

The specimens were documented with different photographic techniques depending on the size of the slabs (e.g., MPPSA IGVR 36371 and MPPSA IGVR 45305 were photographed with the photogrammetric technique and then the images were elaborated to obtain an orthophoto) using digital cameras (a Canon PowerShot SX720 HS and a Fuji X-E1 mounting 18–55 mm lens). Images and interpretative drawings of the specimens were obtained using the freewares GIMP (v. 2.10.2) and ImageJ (v. 1.47). The synonymy list

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and open nomenclature follow the standards proposed by Matthews (1973), Bengston (1988) and Sigovini et al. (2016).

We refer to papers concerning *Cretoxyrhina* dentition (e.g., Bourdon, Everhart, 2011; Cappetta, 2012; Shimada, 1997a, 2002) for tooth position identification, general dental characters and technical terms. The identification of tooth position in lamniform sharks is a debated matter related to the tooth rows arrangement on the palatoquadrate and Meckel's cartilage, as well as to the structure of these cranial elements (e.g., presence/absence of intermediate bar *sensu* Shimada, 2002 and the two hollows present on each side of the jaw *sensu* Siverson, 1999). 'Intermediate teeth' is probably the most controversial term. Siverson (1999) and Shimada (2002) proposed two alternative indications, based on homologous/non-homologous tooth positions. Later on, Cook et al. (2011: p. 9–10) summarized the arguments discussed in the debate. We refer to Cook et al. (2011) and Kriwet et al. (2015). We follow Shimada (1997d) for general skeletal anatomy and Newbrey et al. (2015) for the vertebral morphology of *C. mantelli*. The terminology used for placoid scales follows Reif (1985).

As for other fossil chondrichthyans (see Cappetta, 1987, 2012), the diagnosis of *Cretoxyrhina mantelli* is essentially based on dental characters. Herein, we propose an emended diagnosis of *C. mantelli* that integrates all of the dental characters reported by Bourdon, Everhart (2011), Cappetta (2012) and Shimada (1997a), in order to complete and better formalize it.

Significant measurements for teeth and vertebral centra were taken using the image analysis software ImageJ or directly on the specimens; in particular, the maximum diameter of the largest vertebral centra (posterior precaudal centra, especially mid-trunk, when available), the maximum and minimum height of the teeth and the maximum height of the crown measured on the labial side (see supplementary material for further measurements, Tables. A.1–A.2). Maximum tooth height was measured in the anterior teeth when possible. We used the equations proposed by Shimada (2008) to estimate the maximum body size of the specimens. The count of incremental bands on vertebral centra for individual age estimation was performed on the more complete preserved centra of the two better preserved specimens (MPPSA-IGVR 36371 and 45305). It was not possible to perform any vertebral section because all the vertebral centra are embedded in the limestone slabs and could not be removed. Only a single vertebra from the specimen MGP-PD 31960 was removed and sectioned, although it did not provide any significant result because of diagenetic alteration. Small limestone nodules detached from selected specimens (MPPSA-IGVR 36371, 45305 and MGC-IGVR 81375–81376) were processed for micropaleontological analyses. Some nodules were processed following the cold acetolysis method of Lirer (2000) for isolating planktonic foraminifera and placoid scales of the >63 μm fraction, whereas some other nodules were utilized for thin sections and for preparation of smear slides for calcareous nannofossil analysis. Placoid scales were picked and counted from the residues >63 μm from selected specimens (MPPSA-IGVR 36371 and MGC-IGVR 81375–81376). Representative specimens of the main morphologies of placoid scales were selected and imaged using a SEM (JSM Jeol 6490) at the CE.A.S.C. structure of Università degli Studi di Padova. Additionally, we described bioerosional structures that occur on two specimens, MPPSA IGVR 36371 and MGP-PD 31960, following the ichnotaxonomy of Pirrone et al. (2014).

5. Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Superorder Galeomorphii Compagno, 1973
Order Lamniformes Berg, 1937
Family Cretoxyrhinidae Glikman, 1958

Genus *Cretoxyrhina* Glikman, 1958
Type species: Oxyrhina mantelli (Agassiz, 1835) from the Chalk of the Lewes area, East Sussex, England (UK).

Remarks. The taxonomic status of the genus *Cretoxyrhina* was discussed by Siverson et al. (2013). The authors rejected Zhelzko's (2000) synonymy of *Cretoxyrhina* with *Pseudoisurus*. Glikman (1958) erected the new genus *Cretoxyrhina* with *Oxyrhina mantelli* (Agassiz) as type species (Siverson, 1996; Siverson et al., 2013). Later, Glikman (1964) replaced *Oxyrhina mantelli* with *Isurus denticulatus* (Glickman, 1957) as type species of the genus *Cretoxyrhina* without explanation. As implied by Siverson (1996) and Siverson et al. (2013), this represents an invalid taxonomic amendment (see Ride et al., 2000, Art. 68.2). The genus *Cretoxyrhina* currently includes four species: *C. mantelli*, *C. denticulata*, *C. vraconensis* and *C. agassizensis*.

Cretoxyrhina mantelli (Agassiz, 1835).
Figs. 2–12, 15, supplementary material Figs. A.1α-δ, θ-λ.

(selected synonyms).
v1822 Squalus *mustelus* - Mantell, p. 226, pl. 32, fig. 11.
v1822 Squalus *zygaena?* - Mantell, p. 227, pl. 32, figs. 4, 7, 8, 10, 26, 28.
†1835 *Lamna Mantellii* Ag. - Agassiz, p. 54.
p.1838 *Oxyrhina Mantellii* Agass. - Agassiz, pl. 33, figs. 1-5,7-9 (*non* 6).
1843 *Oxyrhina Mantellii* Agass. - Agassiz, p. 280.
1876 *L.* (*Sphenodus*) *longidens* Agass. - Bassani, p. 296.
1876 *Ox. Mantellii* Agass. - Bassani, p. 298.
1876 *Ox. subinflata* Agass. - Bassani, p. 299.
1886 *Oxyrhina Mantellii* Agassiz - Bassani, p. 144, figs. 1-5.
v1886 *Oxyrhina subinflata* Agassiz - Bassani, p. 145.
1888 *Oxyrhina Mantellii* Agassiz - Bassani, p. 1, pl. 1–3.
1889 *Oxyrhina mantelli* Agassiz - Woodward, p. 376, pl. 17, figs. 9–21.
1894 *Oxyrhina mantelli* - Eastman, p. 151, pl. 16–18.
1911 *Oxyrhina mantelli* Agassiz - Woodward, p. 202, text-fig. 60, 61, pl. 43, figs. 10-15 (*cum syn.*).
v1922 *Oxyrhina Mantelli* Ag. - D'Erasmo, p. 36, pl. 3, figs. 1-3 (*cum syn.*).
v1922 *Oxyrhina* cfr. *Mantelli* Ag. - D'Erasmo, p. 37, pl. 3, figs. 4-6.
1957 *Cretoxyrhina mantelli* - Glickman, p. 569.
v1976 *Isurus mantelli* (Agassiz) 1843 - Sorbini, p. 481, pl. 1.
1977 *Cretoxyrhina mantelli* (Agassiz L.) 1843 - Herman, p. 219, pl. 9, fig. 6 (*cum syn.*).
v1978 *Isurus mantelli* - Sorbini, p. 69, fig. 9.
v1980 *Cretoxyrhina mantelli* - Cigala Fulgosi et al., p. 126, text-fig. p. 125 (*cum syn.*).
v1984 *Isurus mantelli* - Aspes, Zorzin, p. 14, text-figure p. 15.
1987 *Cretoxyrhina mantelli* (Agassiz, 1843) - Cappetta, p. 99, figs. 87e–i.
1992 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson, p. 526, pl. 1, figs. 18–19 (*cum syn.*).
1993 *Cretoxyrhina mantelli* (Agassiz, 1843) - Welton, Farish, p. 101, text-figs. 1–12 p. 101, 1–2 p. 102.
1996 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siversson, p. 819, pl. 1, figs. 1-18.
1997a *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 269, figs. 1-10.
1997b *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 926, figs. 1-2, 5-6.
1997c *Cretoxyrhina mantelli* - Shimada, p. 233, fig. 1.

1997d *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 642, figs. 1-11.
1997e *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 139, fig. 1.
v2000 *Cretoxirina mantelli* (*sic*) - Ginevra et al., p. 31, fig. 6.1.
v2000 Denti di squalo - Ginevra et al., p. 33, fig. 6.3.
v2001 *Cretoxyrhina mantelli* - Zorzin, p. 98 (including text-fig.).
v2003 *Isurus mantelli* (Agassiz) - Astolfi, Colombara, p. 144, fig. 205.
2005 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson, Lindgren, p. 303, fig. 2.
v2005 *Cretoxyrhina mantelli* - Dalla Vecchia et al., p. 108, fig. 81.
2006 *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada et al., p. 185, figs.1-6.
2008 *Cretoxyrhina mantelli* (Agassiz) - Shimada, p. 21, figs. 1-2, 6-7.
2011 *Cretoxyrhina mantelli* Agassiz - Bourdon, Everhart, p. 15, figs. 2, 4-7.
2012 *Cretoxyrhina mantelli* (Agassiz, 1838) - Cappetta, p. 236, figs. 216E—I.
2013 *Cretoxyrhina mantelli* (Agassiz, 1843) - Cook et al., p. 568, fig. 10.
2013 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson et al., p. 3, fig. 10.
vp.2013 Vertebre di selaceo squaloideo (*sic*) - Colombara, p. 40 (text-fig.)
2014 *Isurus denticulatus* Glickman (1957) - Diedrich, p. 8, figs. 4, 5A-D, 7A-F, N—V.
2015 *Cretoxyrhina mantelli* (Agassiz, 1843) - Newbrey et al., p. 878, figs. 7A-C, 8.
2017 *Cretoxyrhina mantelli* - Everhart, fig. 13.3.

Nomenclatural notes. *Cretoxyrhina mantelli* was originally erected by Louis Agassiz in his paleoichthyological treatise ‘Recherches sur les poissons fossiles’ (hereinafter ‘Recherches’). The ‘Recherches’ were published in a series of installments (‘Livraisons’) over a span of eleven years (1833—1844; Brignon, 2015; Woodward, Sherborn, 1890) and it caused considerable confusion and ambiguity in establishing the correct years of erection of several taxa and *Cretoxyrhina mantelli* is no exception. The date of erection of this species was considered to be either 1838 or 1843 according to various authors (e.g, Cappetta, 1987, 2012; Herman, 1977; Shimada, 1997a-e). In fact, the plate 33 was published in Agassiz (1838, Volume III), whereas the description of the taxon was published in Agassiz (1843, Volume III, text: p. 280), both reporting the name "*Oxyrhina Mantellii*" and, thus, creating confusion for nowadays nomenclatural rules. Furthermore, Agassiz published 72 supplementary sheets (‘Feuilletons additionnel’) in addition to several ‘Livraisons’, which were later removed from the five volumes on the advice of the author, because they contained redundant information in his opinion (see Brignon, 2015). A few copies of the “Recherches” still containing these ‘Feuilletons’, nevertheless survived, which are pivotal for nomenclatural purposes because they contain the first mentions of numerous new valid taxon names created by Agassiz (Brignon, 2015). In the ‘Feuilleton additionnel’ published with the 4th ‘Livraison’ in January 1835, Agassiz (1835: p. 54) listed several new taxa identified from the Mantell’s collection (NHM) and that were previously described and figured by Mantell (1822). Namely, Agassiz (1835: p. 54) unambiguously referred isolated shark teeth from this collection (Mantell, 1822: plate 32, figs. 4, 7, 8, 10, 11, 26, 28) to the new taxon *Lamna Mantellii* (Fig. 3A). According to Article 12.1 of the ICZN Code (Ride et al., 2000), the name *Lamna Mantellii*, associated by Agassiz (1835) with previously

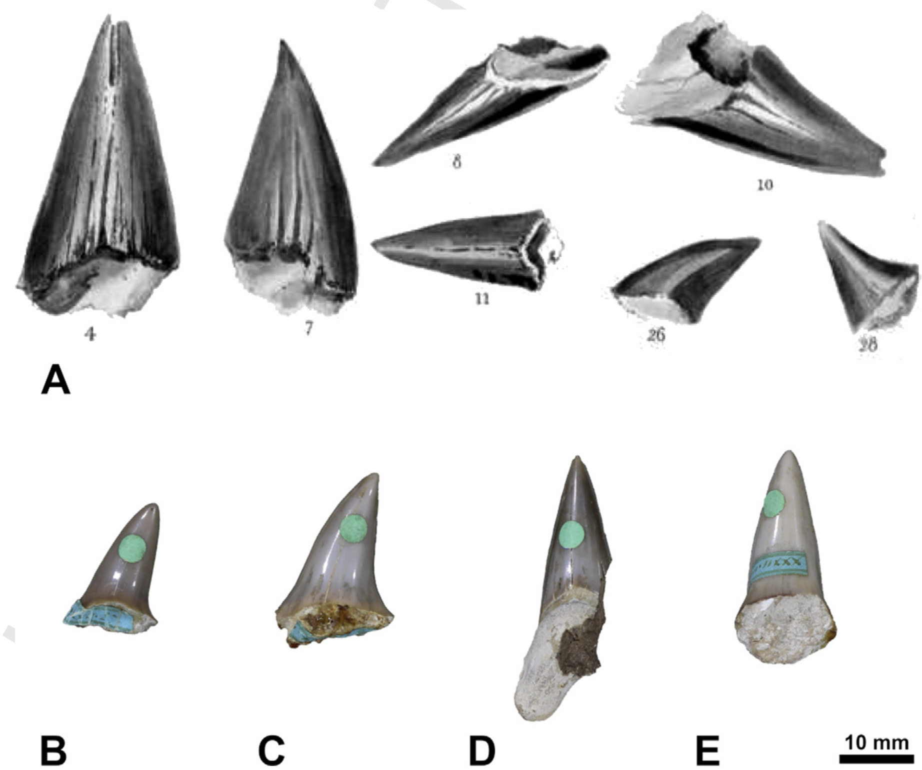

Fig. 3. Syntypes of *Cretoxyrhina mantelli* (Agassiz, 1835). **A.** Isolated teeth figured by Mantell (1822: pl. 32, figs. 4, 7, 8, 10, 11, 26, 28) to which Agassiz (1835, p. 54) referred when created *Lamna Mantellii* (subsequently *Oxyrhina mantelli* and *Cretoxyrhina mantelli*). Woodward (1889) identified the teeth illustrated by Mantell (1822) in Fig. 8 (NHM PV OR 4539), 11 (NHM PV OR 4540), 26 (NHM PV OR 4527) and 28 (NHM PV OR 4524) of plate 32. Excerpt of the plate 32 of Mantell (1822). ETH-Bibliothek Zürich, Rar 2452, http://doi.org/10.3931/e-rara-16021/Public Domain Mark. **B-E.** Photos of four of the seven original syntypes of *Cretoxyrhina mantelli* (Agassiz, 1835). **B.** NHM PV OR 4524. **C.** NHM PV OR 4527. **D.** NHM PV OR 4539. **E.** NHM PV OR 4540. Scale bar = 10 mm. Collections of the Natural History Museum, London (CC-BY). Photos courtesy of Natural History Museum, London. Dataset: Collection specimens. Resource: Specimens. Natural History Museum Data Portal (data.nhm.ac.uk). https://doi.org/10.5519/0002965. Retrieved: 10:32 25 Jul 2018 (GMT). [single-column width].

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published figures, is available by indication (and Article 12.2.7), and the nominal species therefore takes authorship and date from Agassiz (1835). Furthermore, the seven teeth figured by Mantell (1822) are the original figured syntypes of *C. mantelli* (*non* the 'type specimens' of Woodward, 1889: p. 377). Woodward (1889) listed specimens NHM PV OR 4524, 4527, 4539, 4540 (Figs. 3B–E) as those specimens figured by Mantell (1822: figs. 8, 11, 26, 28); furthermore, there is a reference of Mantell's corresponding plate and figure on the label stuck on the specimens (Amalfitano J., Giusberti L., pers. obs.). For these reasons, these specimens are surely four of the seven figured syntypes originally designated by Agassiz (1835), while the remaining figured syntypes (Mantell, 1822: figs. 4, 7, 10) are possibly lost or not easily detectable among the teeth of the Mantell's collection.

Referred material. MPPSA-IGVR 36371*, 45305*, 45324*, 45326*, 45334*, 45344-45345*, MGC-IGVR 81375–81376*; MGP-PD 3805, 5404, 6721, 6736, 7342, 7343, 7372, 8498, 8889, 14020, 14029, 14034-14039, 14042, 22401-22470, 23527-23529; MCSNV V. 1094, 1095, 11798, 12518, 12519 (starred specimens indicate those including other skeletal elements associated with teeth).

Emended diagnosis. Lamniform shark unique in having the following apomorphic combination of dental characters: dental

Table 2

Biostratigraphic data from *Cretoxyrhina mantelli* specimens. Main calcareous plankton taxa and biostratigraphic classification of samples obtained from three partially articulated specimens of *Cretoxyrhina mantelli* (Agassiz, 1835).

				PLANKTON BIOSTRATIGRAPHY			
SAMPLE	DESCRIPTION	LOCALITY	LITHOFACIES	Calcareous nannofossil assemblage	NANNOs (Burnett, 1998)	Planktic foraminiferal assemblage	FORAMs (Coccioni & Premoli Silva, 2015)
MPPSA-IGVR 36371	Partially articulated skeleton	**Monte Loffa** (S. Anna d'Alfaedo, Verona)	**Lastame** (Scaglia Rossa Fm.)	*Watznaueria* spp. **(C)**; *Chiastozygus* spp. **(RR)**; *Eiffellithus* spp. **(RR)**; *Eprolithus octopetalus* **(RR)**; ***Quadrum gartneri* (R)** *Quadrum intermedium* **(RR)**; *Prediscosphaera* spp. **(RR)**	**UC7-UC9 Zone.** Concomitant presence of *Q. gartneri* and absence of *Micula staurophora*. The scarcity in calcareous nannfossil content makes it hard to constrain even more the biostratigraphic interval	*Marginotruncana sigali* (RR); *M. schneegansi* (RR); *M. renzi* (F); *M. pseudolinneiana* (RR); *M coronata* (RR); *M. marianosi* (RR); *Dicarinella limbricata* (RR); *Heterohelix* spp. (C); *Muricohedbergella* spp. (R); *Macroglobigerinelloides* spp. (R); Calcisphaerulids (A)	***Dicarinella primitiva/ Marginotruncana sigali Zone:*** occurrence of marginotruncanids and dicarinellids in absence of *Helvetoglobotruncana helvetica* and *Dicarinella concavata*, markers of the total range zones underlying and overlying.
MPPSA-IGVR 45305	Partially articulated skeleton	**Monte Loffa** (S. Anna d'Alfaedo, Verona)	**Lastame** (Scaglia Rossa Fm.)	*Watznaueria* spp. **(C/A)**; *Zeugrhabdotus bicrescenticus* **(R)**; *Eprolithus octopetalus* **(RR)**; *Chiastozygus* spp. **(RR)**; *Retecapsa* spp. **(R)**; *Rhagodiscus achlyostaurion* **(RR)**; ***Lucianorhabdus quadrifidus*** **(RR)**; *Quadrum gartneri* **(RR)**; *Prediscosphaera* spp. **(F)**	**UC8b-UC9 Zone.** Concomitant presence of *L. quadrifidus* and absence of *Micula staurophora*. The vacancy of *Lithastrinus septenarius* could be an ecological exclusion. Hence, its stratigraphical absence cannot be confirmed.	*Marginotruncana sigali* (R); *M. schneegansi* (R); *M. renzi* (F); *M coronata* (RR); *Dicarinella imbricata* (RR); *D. canaliculata* (F); *Whiteinella* sp. (RR) *Heterohelix reussi*(C); *H. moremani* (RR); *Muricohedbergella planispira* (R); *M. delrioensis* (F); *Macroglobigerinelloides* spp. (C) Calcisphaerulids (AA)	***Dicarinella primitiva/ Marginotruncana sigali Zone:*** occurrence of marginotruncanids and dicarinellids in absence of *Helvetoglobotruncana helvetica* and *Dicarinella concavata*, markers of the total range zones underlying and overlying.
MGC-IGVR 81375	Cephalic portion of partially articulated skeleton	**Monte Loffa** (S. Anna d'Alfaedo, Verona)	**Lastame** (Scaglia Rossa Fm.)	*Watznaueria* spp. **(C)**; *Chiastozygus* spp. **(RR)**; *Retecapsa* spp. **(R)**; ***Quadrum gartneri*** **(RR)**; *Prediscosphaera* spp. **(F)** *Eiffellithus* spp. **(RR)**;	**UC7-UC9 Zone.** Concomitant presence of *Q. gartneri* and absence of *Micula staurophora*. The scarcity in calcareous nannfossil content makes it hard to constrain even more the biostratigraphic interval	*Marginotruncana sigali* (R); *M. schneegansi* (R); *M. renzi* (F); *M. marianosi* (C) *M. pseudolinneiana* (RR); *M. coronata* (RR); *M. undulata* (R); *Dicarinella imbricata* (C); *D. canaliculata* (R); *Heterohelix* reussi (R); *H. moremani (RR);* *Muricohedbergella planispira* (RR); *M. delrioensis* (C) *M. delrioensis* (C); *Macroglobigerinelloides* spp. (RR) Calcisphaerulids (C)	***Dicarinella primitiva/ Marginotruncana sigali Zone:*** occurrence of marginotruncanids and dicarinellids in absence of *Helvetoglobotruncana helvetica* and *Dicarinella concavata*, markers of the total range zones underlying and overlying.

A = abundant; C = common; F = few; R = rare; RR = very rare.

formula: 4S-2A-4I-11(+x)L/1s?-2a-1i-15(+x)l; monognatic heterodonty, strongly disjunct in upper teeth, slightly gradational in lower teeth; teeth with usually narrow, blade-like, asymmetrical and distally curved or sloped crown, extending above the mesial branch of root (especially in anterior teeth); cusp sharply pointed; symphyseal teeth strongly asymmetrical, with crown higher than wide, and distal root lobe generally more developed than the mesial one; first symphyseal teeth distally inclined, other symphyseal teeth mesially curved; anterior teeth nearly symmetrical; lower anterior teeth with very high cusp, higher than wide, particularly the second lower anterior tooth; first anterior teeth (upper and lower) usually the most symmetrical, with the second anterior tooth characterized by a slight distal inclination; crown tending to be labiolingually thicker and more sigmoidal (labially directed) in lower than in upper teeth, which are flatter and thinner, with the point of the cusp labially curved; lower teeth with more massive roots than uppers; intermediate teeth with crown height greater or similar to crown width, cusp inclined distally,

Fig. 4. ***Cretoxyrhina mantelli*** **(Agassiz, 1835). Orthophotos of the specimens MPPSA-IGVR 36371 and 45305. A.** MPPSA-IGVR 36371. **B.** MPPSA-IGVR 45305. Scale bar = 100 cm [2-column width].

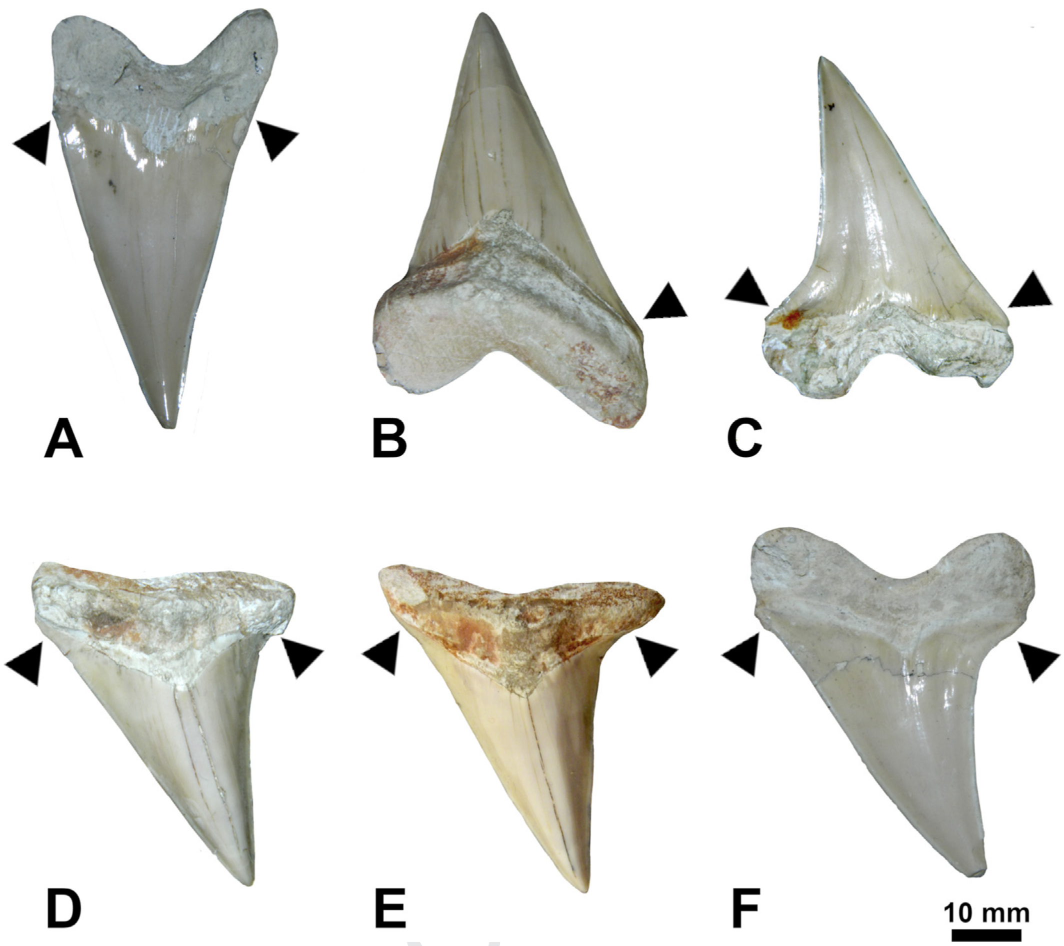


Fig. 5. ***Cretoxyrhina mantelli*** **(Agassiz, 1835). Teeth of the specimen MPPSA-IGVR 36371. A.** First upper anterior tooth (A1) (left palatoquadrate), labial view. **B.** Second lower anterior tooth (a2) (left Meckel's cartilage), lingual view. **C.** Intermediate tooth/third lower anterior? tooth (i?/a3), labial view. **D.** First upper lateral tooth (L1) (right palatoquadrate), lingual view. **E.** Second upper lateral tooth (L2) (right palatoquadrate), lingual view. **F.** Lateral tooth (L/l?), labial view). Arrows indicate the small oblique heel (or shoulders). Scale bars = 10 mm [2-column width].

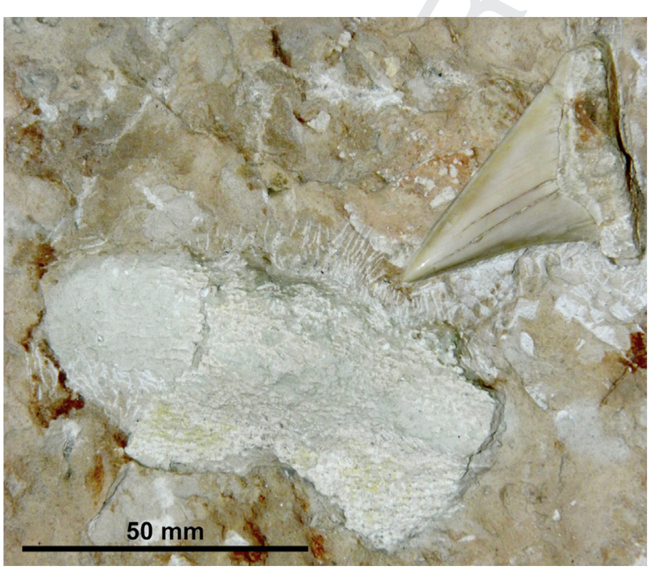
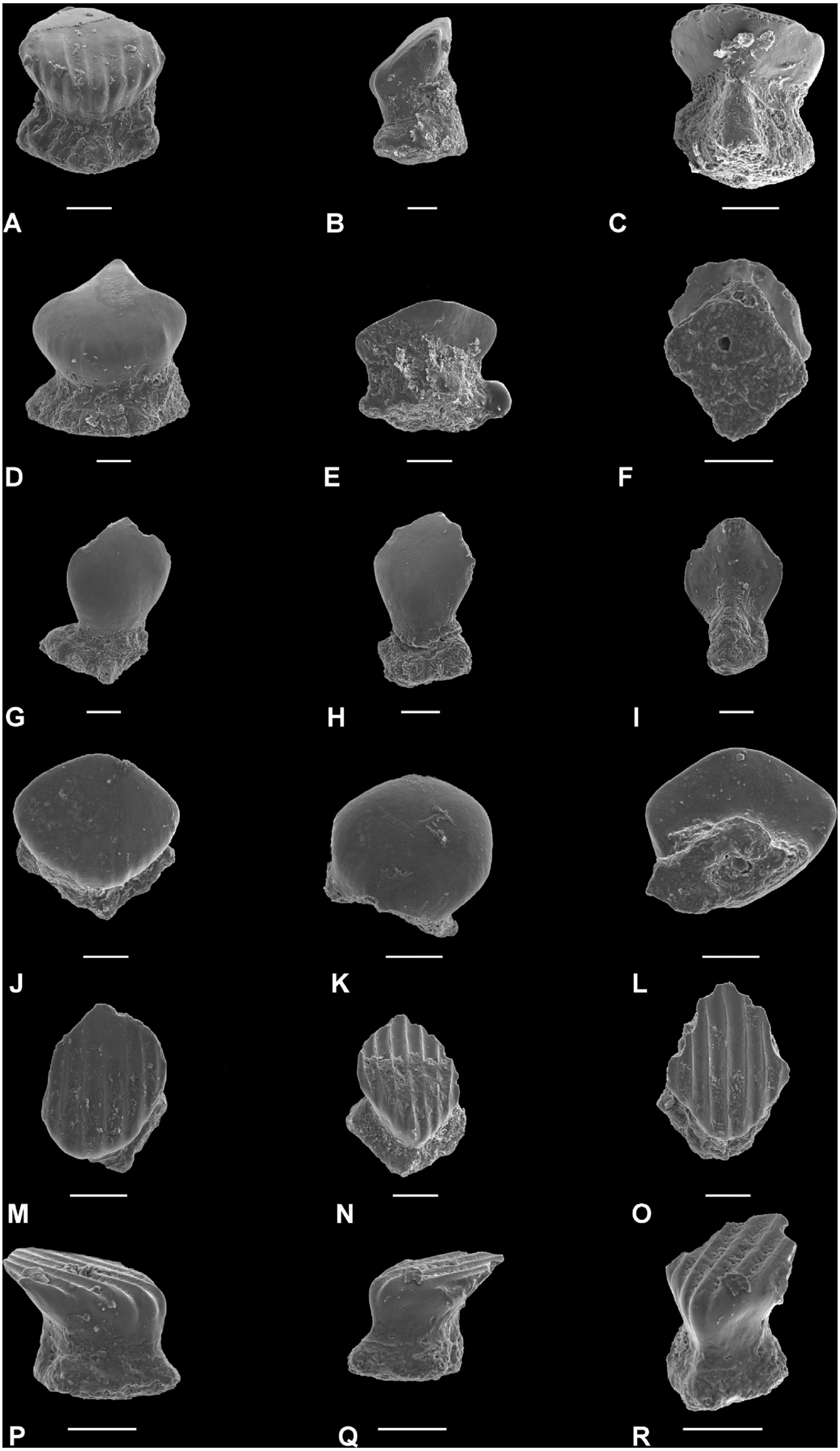


Fig. 6. ***Cretoxyrhina mantelli*** **(Agassiz, 1835). Tessellated calcified cartilage of MPPSA-IGVR 36371.** Photo of a fragment of cranial calcified cartilage associated to a tooth. Scale bar = 50 mm [single-column width].

with the sole first upper intermediate tooth distally curved; lateral teeth generally with crown wider than high, slightly to strongly distally inclined, decreasing in size distally, their inclination increases distally; enameloid smooth and cutting edges continuous; enameloid may form weak basoapical ripples, mainly on the labial side; lingual face convex, labial face nearly flat or only weakly convex; basal part of crown characterized by small oblique heels (shoulders), with continuous cutting edges on the sides of the cusp; both heels may occasionally bear a lateral cusplet in distolateral and commissural teeth; tooth neck marked; root strongly bilobated, becoming more splayed distally; concavity of the basal margin of the root low (lateral teeth) to high (anterior-intermediate teeth); mesial branch of the root usually pointed, the distal one rounded and expanded; lingual protuberance developed, lacking a nutrient groove and usually bearing one nutrient foramen.

Locality and horizon. All the specimens described here come from the 'lastame' lithofacies of the Scaglia Rossa Formation of Mt. Loffa and other surrounding sites (Lessini Mountains of Verona Province, Italy).

Based on calcareous nannofossils and planktic foraminifera biostratigraphy, the specimens are dated to the middle-late Turonian (for more details see Table 2) according to the correlation between calcareous plankton zones and stages by Ogg, Hinnov


A
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(2012) (UC7-UC9 Zones, Burnet, 1998 and *Dicarinella primitiva*/*Marginotruncana sigali* Zone, Coccioni, Premoli Silva, 2015).

Description. We provide below a brief description of the skeletal remains of *C. mantelli* found in the 'lastame' quarries. The most complete and best-preserved specimens are MPPSA-IGVR 36371 and 45305 (Fig. 4).

Specimen MPPSA-IGVR 36371 (Fig. 4A) is preserved on nine limestone slabs of different size, which were originally part of a single bigger slab. The specimen exhibits 37 teeth (23 totally or partially preserved and 14 preserved as impression only), 157 vertebral centra and some fragments of tessellated cartilage, whose original skeletal position is impossible to identify due to the partial preservation. Teeth are scattered on different slabs, and therefore do not provide any evidence of the original tooth arrangement. Most of the teeth are localized in what appears to be the cranial region, although some of them are scattered along the vertebral column. The teeth (Fig. 5) display the characteristic features of *C. mantelli*. There are no lateral cusplets in any preserved tooth. Most of teeth are embedded in the rock, exposing only the labial or lingual side, thereby rendering difficult to establish their original position. At least 16 teeth have complete crowns and roots (e.g., Figs. 5A–B, F). Other teeth are fragmentary. The highest tooth measures 67 mm in total height (52 mm in crown height on the labial side), while the lowest tooth is ca. 28 mm high.

The vertebral centra show the typical lamnoid structure (see Applegate, 1967: p. 67), with well-calcified asterospondylic, amphicoelous, and imperforated centra. All centra suffered a taphonomic anteroposterior compression; some show a slight taphonomic distortion and some others are incomplete or broken. Most of the vertebral centra are disarticulated, moderately scattered near the longitudinal axis of the skeleton and laying on the anterior or posterior articular face. Part of the vertebral column, including more or less 40 posterior caudal centra, is accumulated in a pile along the vertebral column axis. At least twenty-five vertebral centra are extremely fragmentary or preserved as impressions only. The largest vertebral centrum has a maximum diameter of 107 mm, while the smallest one has a maximum diameter of ca. 40 mm. The antero-posterior length ranges from 14 mm to ca. 40 mm.

Remains of tessellated calcified cartilage are very fragmentary (Fig. 6) and show a mosaic texture and rough surfaces. Specimen MPPSA-IGVR 36371 was sampled near the cranial region for investigating placoid scales and a total of 526 placoid scales were found. The placoid scales (Figs. 7A-R) consist of a rhomboidal root and a crown (covered with enameloid) with different shapes depending on the position along the body of the shark. Their size does not exceed 500 μm in height and width. The root may preserve a nutrient foramen at the base (Fig. 7F) and one or two foramina along the posterior side. The crown is constricted near the base, forming a neck. The shape of the crown can be stubby (e.g., Figs. 7A-F, 7J-L) or slender (e.g., Figs. 7G-I), with a rounded (e.g., Figs. 7A-C, 7E-F, 7J-L) or pointed cusp (e.g., Figs. 7D, 7G-I, 7M-R). No scales with multiple cusps were found. The anterior face of the crown can be characterized by a more or less expanded, flattened or weakly inclined and swollen superior shelf (Figs. 7J, 7M–O), forming a hooked profile in lateral view (Figs. 7B, 7P-Q). The anterior face can be smooth (Figs. 7D, 7G-H, 7J-K) or crossed by thin parallel ridges (or riblets) that are divided by grooves running antero-posteriorly towards the cusp, which can reach the posterior margin of the cusp (Figs. 7A, 7M-R). Ridges, in some cases, may be restricted to the anterior part of the scale, extending apically from the neck up to midway the cusp, while the remaining apical part of the cusp is smooth (Fig. 7A). The posterior face of the crown is convex and smooth, crossed by a central vertical weak keel (Figs. 7C, 7E, 7I, 7L).

Specimen MPPSA-IGVR 45305 (Fig. 5B) is preserved on four slabs and comprises 131 vertebral centra, 55 teeth, and is associated with fragments of tessellated calcified cartilage. All teeth are scattered around the cranial region and totally displaced, without any evidence of their original arrangement, but are morphologically similar to those of MPPSA-IGVR 36371 (Figs. 8–9). In two cases (e.g., Fig. 9A), the teeth are still articulated to tessellated calcified cartilage, thereby confirming that these fragments were part of the jaws. It was not possible to identify whether these fragments were part of the palatoquadrate or of the Meckel's cartilage, because one of them represents a lateral tooth and the other a commissural one, both not readily identifiable as upper or lower. The crown height of the highest tooth measures 42 mm on the labial side, while the smallest one measures only 5 mm. The maximum diameter of the largest centrum is 98 mm, while that of the smallest one is ca. 42 mm. The antero-posterior length ranges from 20 to ca. 35 mm. In all teeth, the root is poorly preserved or completely lacking (e.g., Figs. 9B-D). Most vertebral centra are still connected to each other lying on their lateral side along the axis of the vertebral column, forming an arch. The posterior-most centra show a moderate degree of disarticulation. The centra are of the lamnoid type and show the same taphonomic alterations as observed in MPPSA-IGVR 36371. No placoid scales were found in the samples extracted from this specimen.

Other skeletal remains include segments of partially articulated vertebral columns associated with teeth and cranial cartilage fragments (MPPSA-IGVR 45324, MPPSA-IGVR 45326, MPPSA-IGVR 45334, MPPSA-IGVR 45344–45345, MGC-IGVR 81375–81736). All of these specimens have dental and vertebral features that are identical to those of MPPSA-IGVR 36371 and 45305, and the teeth are still embedded in the limestone, partially or totally exposed only in labial or lingual views. The vertebral column segments show various degrees of disarticulation, from totally displaced centra (MPPSA-IGVR 45344–45345) to almost articulated sets (e.g., MGC-IGVR 81375–81376). The majority of the vertebral centra lie facing up exposing the articular surfaces, while few others expose the lateral side, as in MPPSA-IGVR 36371 and 45305.

Specimen MPPSA-IGVR 45324 (see supplementary material Fig. A.1β) includes five teeth, a single vertebral centrum, and small fragments of tessellated cartilage. The highest complete tooth has a total height of ca. 52 mm, and a crown height measured on the labial side of 37 mm.

Specimen MPPSA-IGVR 45326 (see supplementary Fig. A.1γ) comprises 16 teeth, two vertebral centra and some fragments of tessellated cartilage. Most of the teeth are almost totally embedded in the rock. The crown height of the highest tooth (preserved as impression only), measured on the labial side, is ca. 53 mm. The maximum diameter of the largest vertebral centrum is ca. 97 mm.

Specimen MPPSA-IGVR 45334 (see supplementary Fig. A.1δ) consists of a slab containing two teeth, 14 vertebral centra, and a fragment of tessellated cartilage. The total height of the highest tooth measures ca. 37 mm, and the crown height measured on the labial face 28 mm. The maximum diameter of the largest vertebral centrum is 97 mm.

Fig. 7. *Cretoxyrhina mantelli* (Agassiz, 1835). SEM images of placoid scale from MPPSA-IGVR 36371. A. Frontal view. **B.** Lateral view. **C.** Posterior view. **D.** Anterior view. **E.** Posterior view. **F.** Inferior view. **G.** Anterior view. **H.** Anterior view. **I.** Posterior view. **J.** Superior view. **K.** Frontal view. **L.** Posterior view. **M.** Superior view. **N.** Superior view. **O.** Superior view. **P.** Lateral view. **Q.** Lateral view. **R.** Anterior view. Scale bars = 100 μm [single-column width].

Specimen MPPSA-IGVR 45344–45345 (Fig. 10) includes slab and counterslab that contain 16 teeth, 15 vertebral centra, and a fragment of tessellated cartilage. The teeth solely preserved the crown (e.g., Figs. 10B–D). The crown height of the highest tooth measured on the labial side reaches 46 mm, while that of the smallest one measures ca. 20 mm. The maximum diameter of the largest vertebral centrum is 76 mm, while that of the smallest vertebral centrum measures ca. 60 mm.

Specimen MGC-IGVR 81375–81376 (Fig. 11) is preserved on a slab and its counterpart with 80 teeth, 33 vertebral centra, and many fragments of tessellated cranial cartilage. The total height of the highest tooth is 67 mm, whereas the smallest one measures 12 mm. In this tooth set, the maximum crown height on the labial side is 47 mm. The maximum diameter of the largest vertebral centrum is 86 mm, while that of the smallest one is 45 mm. A total of 142 placoid scales was found in a sample extracted from

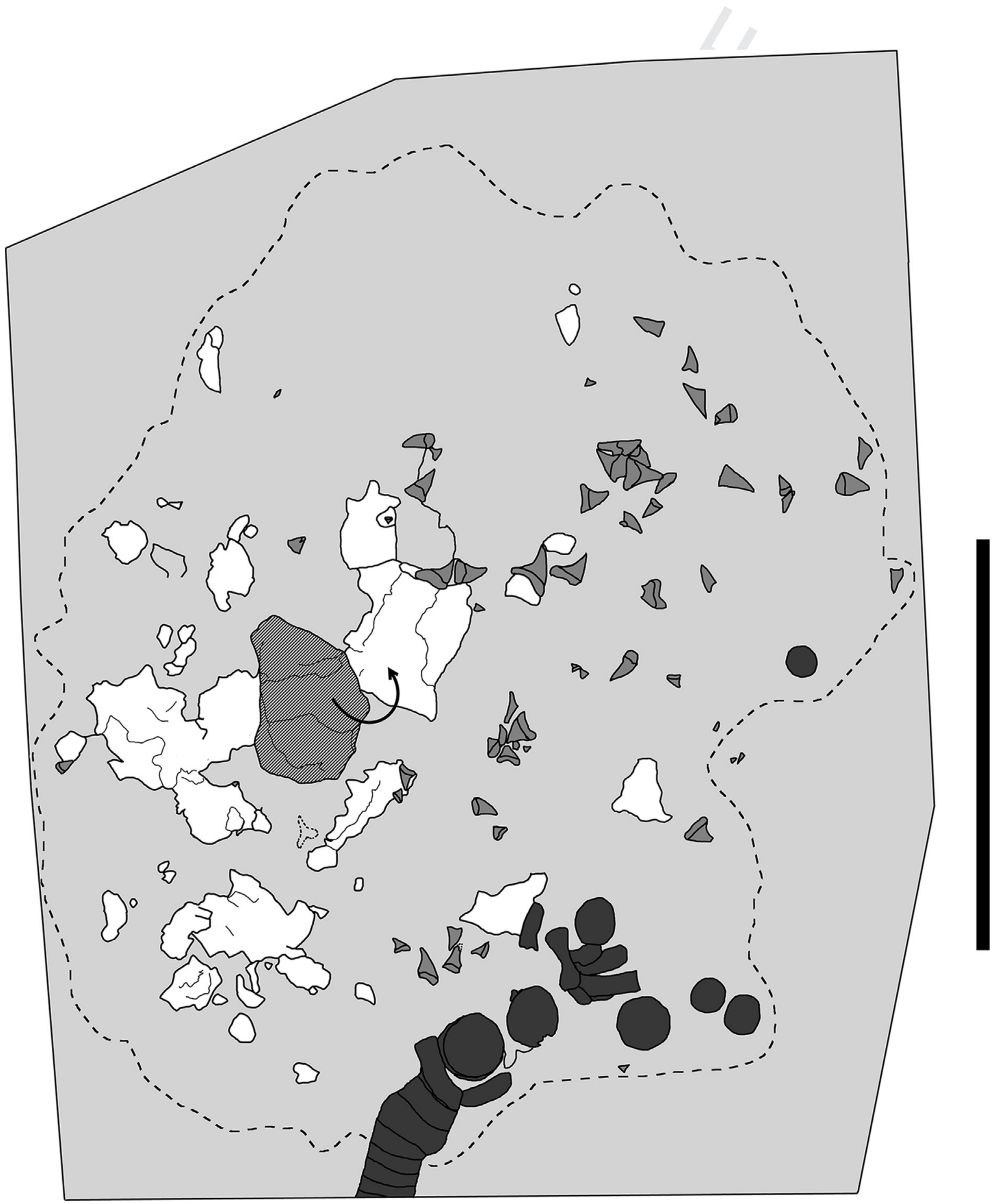

Fig. 8. Line drawing of the head region of the specimen of *Cretoxyrhina mantelli* (Agassiz, 1835) MPPSA-IGVR 45305. Colors map: dark gray = vertebral centra; gray = teeth; light gray = rocky matrix; white = fragments of tessellated cartilage. The barred area represents a glued fragment which contains the counterpart of the cranial cartilage indicated by the arrow. The dashed line delimits the area where can be detected the fragments (tesserae) of cranial calcified cartilage. Scale bar = 100 cm [2-column width].

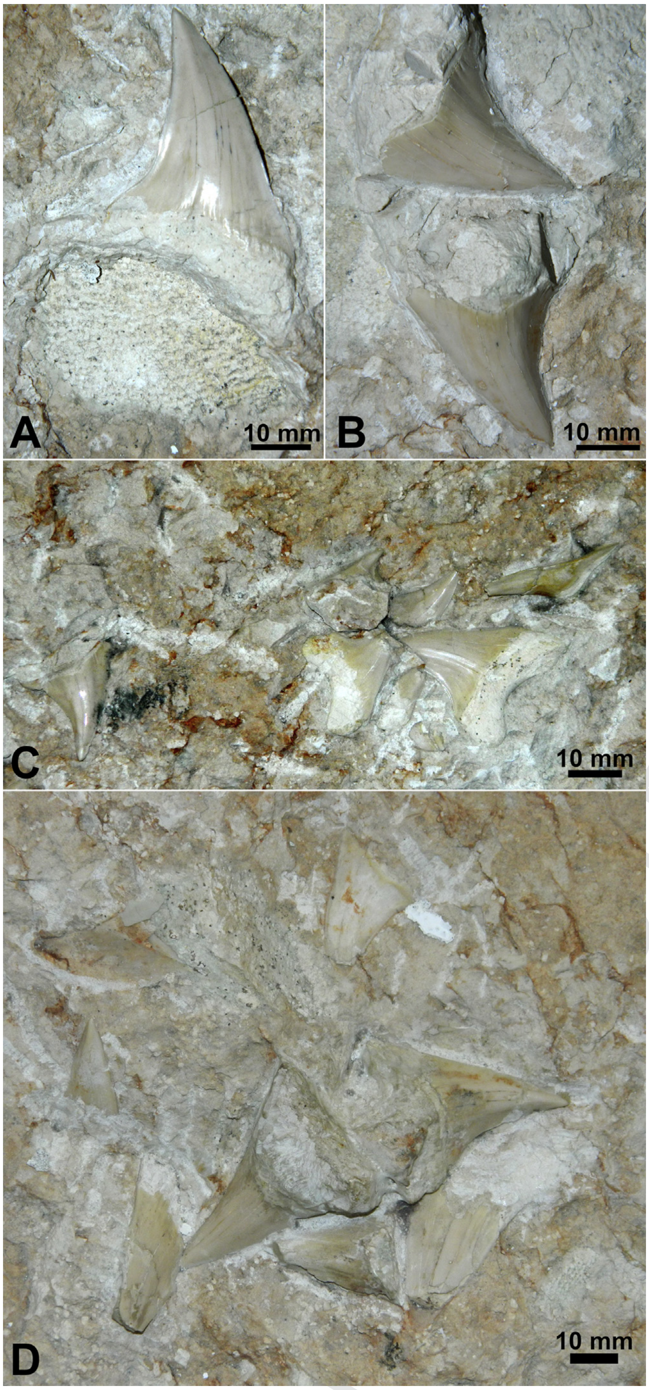

Fig. 9. *Cretoxyrhina mantelli* (Agassiz, 1835). Teeth from MPPSA-IGVR 45305. A. Teeth articulated to a fragment of tessellated mandibular cartilage. **B.** Two lateral teeth with poorly preserved roots. **C-D.** Partially associated tooth sets. Scale bars = 10 mm [single column width].

specimen MGC-IGVR 81375, exhibiting morphologies very similar to those observed in MPPSA-IGVR 36371 (Fig. 12).

Discussion. The shark specimens from the 'lastame' lithozone of the Scaglia Rossa Formation can be unquestionably referred to the genus *Cretoxyrhina*, because of the presence of narrow and blade-like crowns. The oblique heels on the side of the cusp, the absence of the lateral cusplets, and the asymmetric, sharp pointed and rather robust crown (if compared to other congeneric species) support the assignment of the specimens to *Cretoxyrhina mantelli*. *Cretoxyrhina mantelli* had a cosmopolitan distribution, since it has been reported in Europe, Russia, Africa, North America and Brazil (Cappetta, 2012). The genus *Cretoxyrhina* includes also the species *C. denticulata* (Glickman, 1957) and *C. agassizensis* (Underwood, Cumbaa, 2010), both of which are diagnosed by the presence of lateral cusplets (with sharp apices in *C. agassizensis*, and rounded apices in *C. denticulata*) in many of the lateroposterior teeth (see Underwood, Cumbaa, 2010; Newbrey et al., 2015). *C. agassizensis* teeth also exhibit a slender and generally straight cusp (also in lateroposterior teeth) than *C. mantelli* and *C. denticulata* (see Underwood, Cumbaa, 2010), and incomplete cutting edges on small juvenile anterior teeth (Newbrey et al., 2015). The latter character, however, cannot be taken into account to compare and differentiate adult teeth from the other species. Some associated dentitions of *C. mantelli* exhibit almost upright crown on lateroposterior teeth (e.g., Eastman, 1894), but this condition may be related to gynandric heterodonty (Siverson M., pers. comm.). Two of the three species have partially overlapping stratigraphic distributions, because *C. denticulata* ranges from the lower Cenomanian to the lower middle Cenomanian, *C. agassizensis* ranges from the upper middle Cenomanian to lower middle Turonian (Newbrey et al., 2015), whereas *Cretoxyrhina mantelli* is reported globally from the upper Cenomanian to the Campanian (Bourdon, Everhart, 2001; Cappetta, 2012; Shimada, 1997e). Another species of *Cretoxyrhina*, the upper Albian-lower Cenomanian *C. vraconensis* (Zhelezko, 2000), was revised by Siverson et al. (2013) and clearly differs from *C. mantelli* in having cusplets and different tooth morphologies in corresponding dental positions (for details see Siverson et al., 2013: p. 14). The species of the genus *Cretoxyrhina* might possibly represent chronospecies of a single evolutionary lineage (see Newbrey et al., 2015). This evolutionary lineage was characterized by the progressive reduction of lateral cusplets and the progressive increasing size and robustness of teeth throughout its temporal range (see Underwood, Cumbaa, 2010; Cook et al., 2013; Siverson, Lindgren, 2005). An increase in tooth size (probably corresponding to an increase in body size; see "Paleobiological Remarks" for individual length estimates), a significant decrease of crown height-crown width ratio and a loss of lateral cusplets are recorded in the upper Cenomanian-Coniacian interval (see Shimada, 1997e; Siverson, Lindgren, 2005) and the size of the teeth of the Italian specimens indicates that the teeth from the middle-upper Turonian had already reached a size similar to those of the Coniacian specimens.

Specimens MPPSA-IGVR 36371 and 45305 are among the most complete remains of *Cretoxyrhina mantelli* in the world. Most of the *Cretoxyrhina mantelli* skeletons were recovered from the Coniacian-lower Campanian Niobrara Chalk in Kansas (USA) and include very well-preserved articulated remains (e.g., FHSM VP-323, FHSM VP-2187; Newbrey et al., 2015; Shimada, 1997d). Eastman (1894) reported the first nearly complete skeleton from Kansas, which belonged to the collections of the Bayerische Staatssammlung für Paläontologie und Geologie of Munich, Germany, but was unfortunately destroyed during World War II (Diedrich, 2014).

Additional incomplete skeletons were found in Europe. These include a set of about 57 teeth associated with vertebral centra of a single individual from the Upper Chalk (Coniacian-lower Campanian) of Grays, southeastern England (NHM PV OR 32346–32347, 39434; Woodward, 1889, 1911: fig. 60). Diedrich (2014: fig. 5) described partial skeletal remains of "*Isurus denticulatus*" (= *Cretoxyrhina mantelli*) consisting of 149 vertebral centra that are mostly disarticulated and associated with five teeth, coming from the upper Turonian of Halle/Westphalia in Germany.

In northeastern Italy, *Cretoxyrhina mantelli* was reported from the upper Cenomanian Bonarelli Level (Sorbini, 1976) up to the

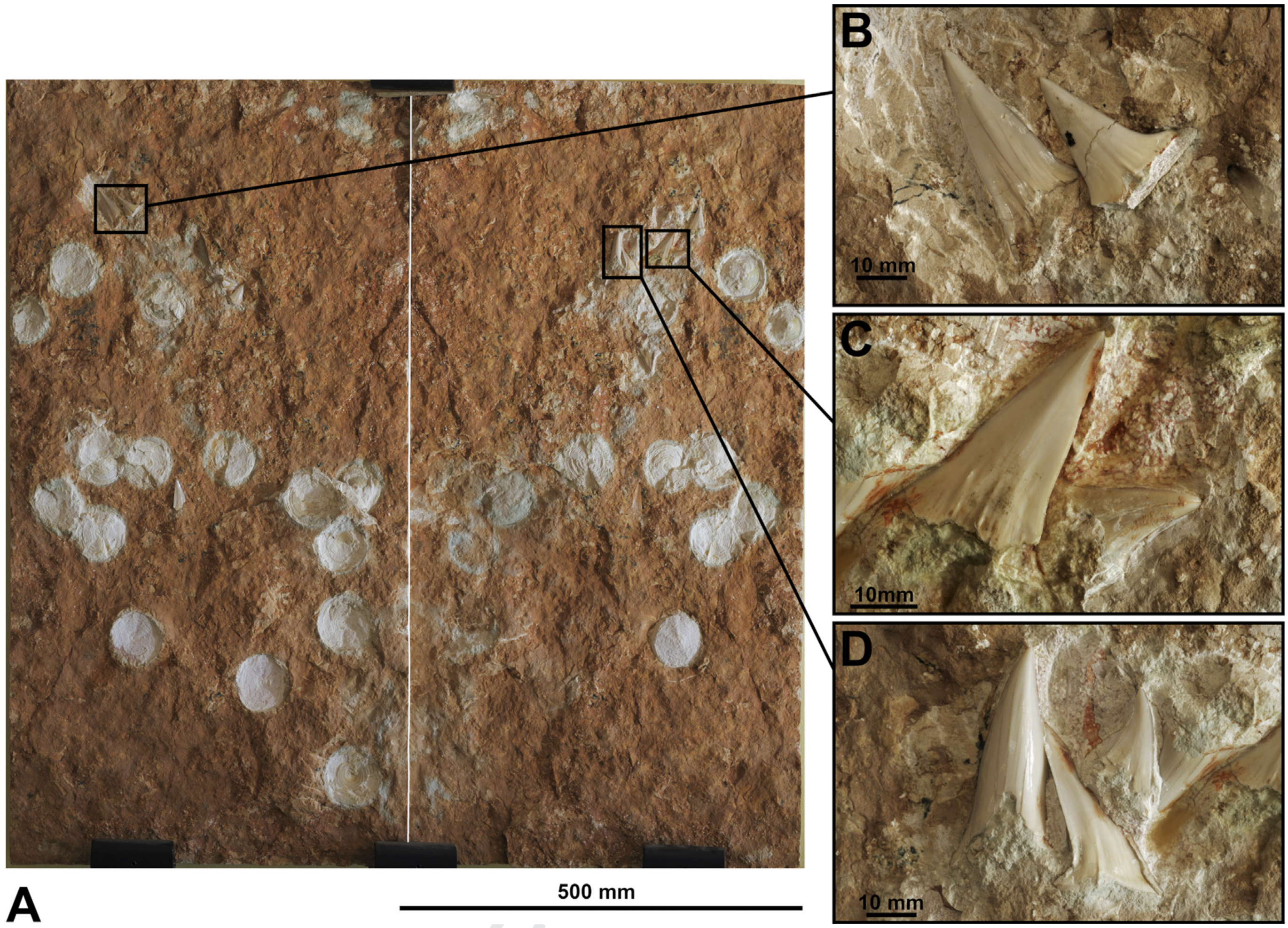

Fig. 10. ***Cretoxyrhina mantelli*** (Agassiz, 1835). **MPPSA-IGVR 45344–45345. A.** MPPSA-IGVR 45345 (left slab) and MPPSA-IGVR 45344 (right counterslab). Scale bar = 500 mm. **B.** Detail of the labial side of the teeth. Scale bar = 10 mm. **C.** Detail of the labial side of teeth. Scale bar = 10 mm. **D.** Detail of teeth on the lingual side. Scale bar = 10 mm [2-column width].

uppermost middle and upper Turonian ‘lastame’ of the Scaglia Rossa Formation as documented herein (see Table 2). The teeth from the Bonarelli Level are currently under revision, but at least two teeth among those reported by Sorbini (1976) exhibit a series of characters that allow to refer them to *C. mantelli* (Amalfitano J., pers. obs.). The Italian specimens reported herein represent some of the oldest associated skeletal remains of *C. mantelli.*

Specimens MPPSA-IGVR 36371 (with 157 preserved centra over an estimated total count of 216 vertebrae given by Shimada et al., 2006) and MPPSA-IGVR 45305 (with 131 vertebrae) are considered two partial vertebral columns associated with disarticulated teeth and fragments of tessellated calcified cartilage. The specimen MGC-IGVR 81375–81376 is interpreted as the anterior portion of the vertebral column with associated teeth and fragments of tessellated cartilage. The remaining specimens (MPPSA-IGVR 45324, 45326, 45344-45345) are short anterior portions of the vertebral column associated with disarticulated teeth. MPPSA-IGVR 45334 is distinct because it probably includes posterior precaudal vertebral centra. Mid-trunk vertebral centra are usually the largest in the vertebral column (see Newbrey et al., 2015). The maximum vertebral diameter is 97 mm in MPPSA-IGVR 45334, which is similar to the maximum vertebral diameter in MPPSA-IGVR 36371 (107 mm) and therefore are most likely large posterior precaudal centra. Further taphonomic inferences are provided in the paragraph “Taphonomic Remarks”.

?Cretoxyrhina sp
Figs. 13–14, supplementary material Figs. A.1ε-η

vp.2013 Vertebre di selaceo squaloideo (*sic*) - Colombara, p. 40 (text-fig.)

Referred material. MPPSA-IGVR 45308, MPPSA-IGVR 45319–45320, MPPSA-IGVR 45321–45322, MPPSA-IGVR 45323, MPPSA-IGVR 45337, MGC-IGVR 47789, MGP-PD 31960.
Locality and horizon. All these specimens come from the ‘lastame’ of Scaglia Rossa Formation of Loffa Mount and other surrounding sites (Lessini Mountains, Verona Province, Italy).
Description. The material described here consists of portions of vertebral columns of lamniform sharks with different degrees of disarticulation. The vertebral centra are of lamnoid type *sensu* Applegate (1967).

Specimen MPPSA-IGVR 45308 (Fig. 13A) consists of 55 scattered vertebral centra with diameters ranging from 38 to 81 mm.

Specimens MPPSA-IGVR 45319 and 45320 (Fig. 13B) are preserved on two slabs with portions of vertebral columns that included a total of 25 vertebral centra (12 and 13 centra, respectively). Centra are partially embedded in the rock and are moderately articulated, arranged in a nearly linear row mostly showing the lateral side. These elements likely belong to a single individual as the vertebral diameter gradually decreases along the vertebral rows.

Specimens MPPSA-IGVR 45321 and MPPSA-IGVR 45322 (see supplementary material Figs. A.1ε-ζ) represent two portions of the vertebral column containing 17 and 12 centra, respectively. Centrum diameters range from 92 to 98 mm. The portions probably belong to two distinct individuals, because all centra have similar diameters and there is no decrease in diameter along the vertebral rows.

Specimen MPPSA-IGVR 45323 (Fig. 13C) is a slab with 52 articulated vertebral centra arranged in a linear row except for eight centra that are slightly displaced from the row. The row shows a slight bend toward one extremity. The diameter of the centra ranges from 40 to 85 mm.

Specimen MPPSA-IGVR 45337 (see supplementary material Fig. A.1η) is preserved on a small slab with seven vertebral centra arranged in two clusters of three articulated centra plus a single centrum separated from the clusters. Centra are embedded in the rock and measurements cannot be taken.

Specimen MGC-IGVR 47789 (Fig. 14) consists of a partial vertebral column comprising ca. 122 vertebral centra that are arranged in an arched row. The maximum diameter of the vertebral centra is 84 mm.

Specimen MGP-PD 31960 (Fig. 13D) is a slab containing a segment of a vertebral column with 52 centra. The centra lie on the articular faces and are slightly scattered along the original axis of the vertebral column, with only a few centra that are articulated to each other. The diameter of the centra is nearly consistent throughout the segment, with a maximum value of 67 mm.

Discussion. The segments of vertebral columns described above can be unambiguously assigned to lamniform sharks because of the vertebral centra of lamnoid type (Applegate, 1967; Shimada, 2007; see also MPPSA-IGVR 36371 above for a brief description of the vertebral type). At least seven shark specimens of the 'lastame' sample with associated teeth and vertebral centra allow a reliable specific attribution to *Cretoxyrhina mantelli*. The only other lamniform shark from the 'lastame' is *Cretodus* (Amalfitano et al., 2017b), which is represented therein by a single specimen. Furthermore, most of the isolated teeth from the 'lastame' belong to *Cretoxyrhina mantelli*. Therefore, *Cretoxyrhina mantelli* is so far the most common lamniform shark from the 'lastame' and the additional vertebral column portions described here are tentatively referred to as ?*Cretoxyrhina* sp.

The arrangement of the vertebral centra on the slabs does not allow determining the original position of the preserved portions within the original vertebral column, with the exception of MGC-IGVR 47789, which is the most complete segment (see Fig. 14). However, the variability of the diameter of the centra along the vertebral column provides some information. MPPSA-IGVR 45308 seems to include both caudal and precaudal centra, because of the high range of vertebral diameters from 38 to 81 mm. A similar range in vertebral diameter occurs in MPPSA-IGVR 43323; here the original arrangement of the vertebral column is partly retained, so that the caudal flexion of the vertebral column, in correspondence of the upper lobe of the caudal fin, is still evident (Fig. 13C). The remaining specimens (MPPSA-IGVR 45319, 45320, 45321, 45322, MGP-PD 31960) show more constant values in vertebral diameter, and probably represent transitional segments between the anterior abdominal and the precaudal portions or between the precaudal sector and the caudal extremity.

6. Paleobiological Remarks

6.1. Length and longevity estimates

Qualitative and quantitative data provided by fossil remains of extinct sharks can be useful to infer various parameters related to aspects of their paleobiology. Such inferences are often hampered by the fact that complete shark skeletons are rare in the fossil record due to low fossilization potential of cartilaginous skeletal elements (Shimada, 2008). Shimada (1997c) provided a general analysis on the periodic marker bands of *Cretoxyrhina mantelli* vertebral centra and, later, Shimada (2008) expanded his study through a quantitative exploration of the ontogenetic parameters of *C. mantelli* (e.g., length at birth, growth rate, and longevity). Other authors addressed this issue, comparing the data from *C. mantelli* skeletons with those of other sharks in order to hypothesize the length at birth, total length, and longevity in various extinct lamniform sharks (e.g., *Cretalamna hattini* in Shimada, 2007; *Archaeolamna kopingensis* in Cook et al., 2011; and *Cardabiodon ricki* in Newbrey et al., 2015). The specimens described herein, especially MPPSA-IGVR 36371 and MPPSA-IGVR 45305 provide some significant data for the estimation of their total length (TL) and longevity. Using the equations of Shimada (2008) on the specimen MPPSA-IGVR 36371, that has a maximum crown height measured on the labial side (EH in Shimada, 2008) of 52 mm and a maximum vertebral diameter (CD in Shimada, 2008) of 107 mm, results in estimated TLs of 650 cm and of 615 cm, respectively. These estimated TLs suggest that MPPSA-IGVR 36371 represents one of the largest individuals of *Cretoxyrhina mantelli* ever found. The size is comparable to the asymptotic (= maximum) length for *Cretoxyrhina mantelli* (691 cm) proposed by Shimada (2008), and to the estimated range (640–700 cm) for the largest individual described to date (represented by a well-preserved caudal fin; Shimada et al., 2006). MPPSA-IGVR 45305 (42 mm of maximum EH and 98 mm of maximum CD) has an estimated total length of 525 cm based on EH, and 563 cm based on CD. Other relevant specimens are MPPSA-IGVR 45344–45345 and MGC-IGVR 81375–81376, with the maximum EH of 46 and 47 mm corresponding to TLs of 575 cm and 587.5 cm, respectively. The other specimens exhibit a comparatively smaller size or are more fragmentary and do not include the largest precaudal vertebra or the highest tooth, and for this reason these are not used for size estimates.

The incremental bands of the vertebral centra (couplets of translucent and opaque bands that correspond to annual growth) allow the estimation of the individual longevity in extant and extinct elasmobranchs (e.g., Cailliet, Goldman, 2004; Shimada, 2007; Shimada, 2008; Goldman et al., 2012; Newbrey et al., 2015; Amalfitano et al., 2017c). These bands can be observed in the vertebral centra of specimens IGVR 36371 and 45305. Other than the birth band, it is possible to observe 26 incremental bands in MPPSA-IGVR 36371 (Fig. 15A) and 21 in MPPSA-IGVR 45305 (Fig. 15B), thereby suggesting an estimated age of at least 26 and 21 years, respectively. The incremental band counting is consistent with the results obtained from the equation by Shimada (2008) that uses the number of bands to estimate the individual total length. The equation, $TL = 119(BN+1)^{0.522}$, in which BN refers to the band number (with 0 referring to the birth band and the outermost band assumed to represent the maximum BN), provides total length estimates (ca. 665 cm for MPPSA-IGVR 36371, 597 cm for MPPSA-IGVR 45305) that are only slightly larger than those obtained using the vertebral and dental measurements (615–650 cm for MPPSA-IGVR 36371 and 525–565 cm for MPPSA-IGVR 45305).

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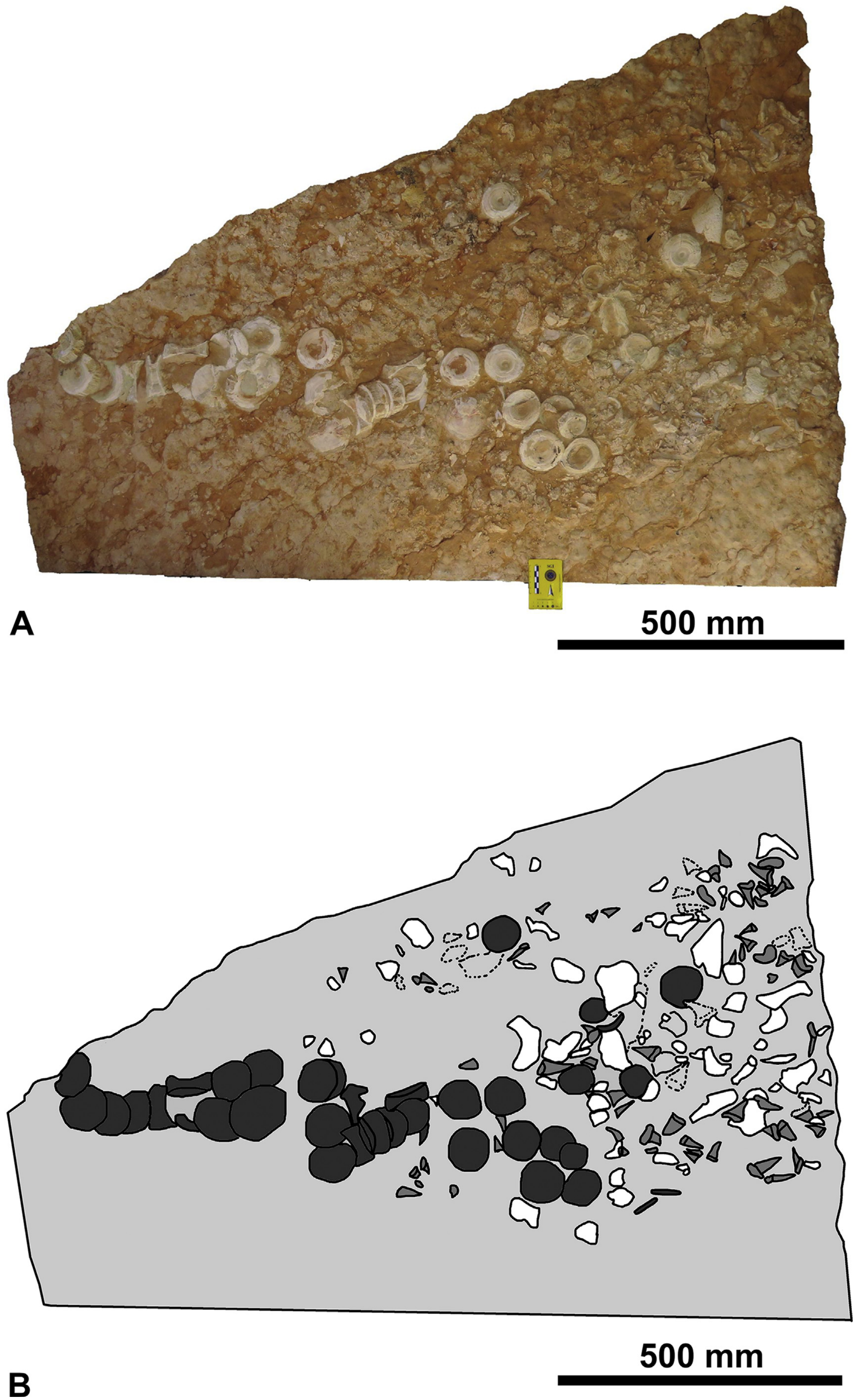
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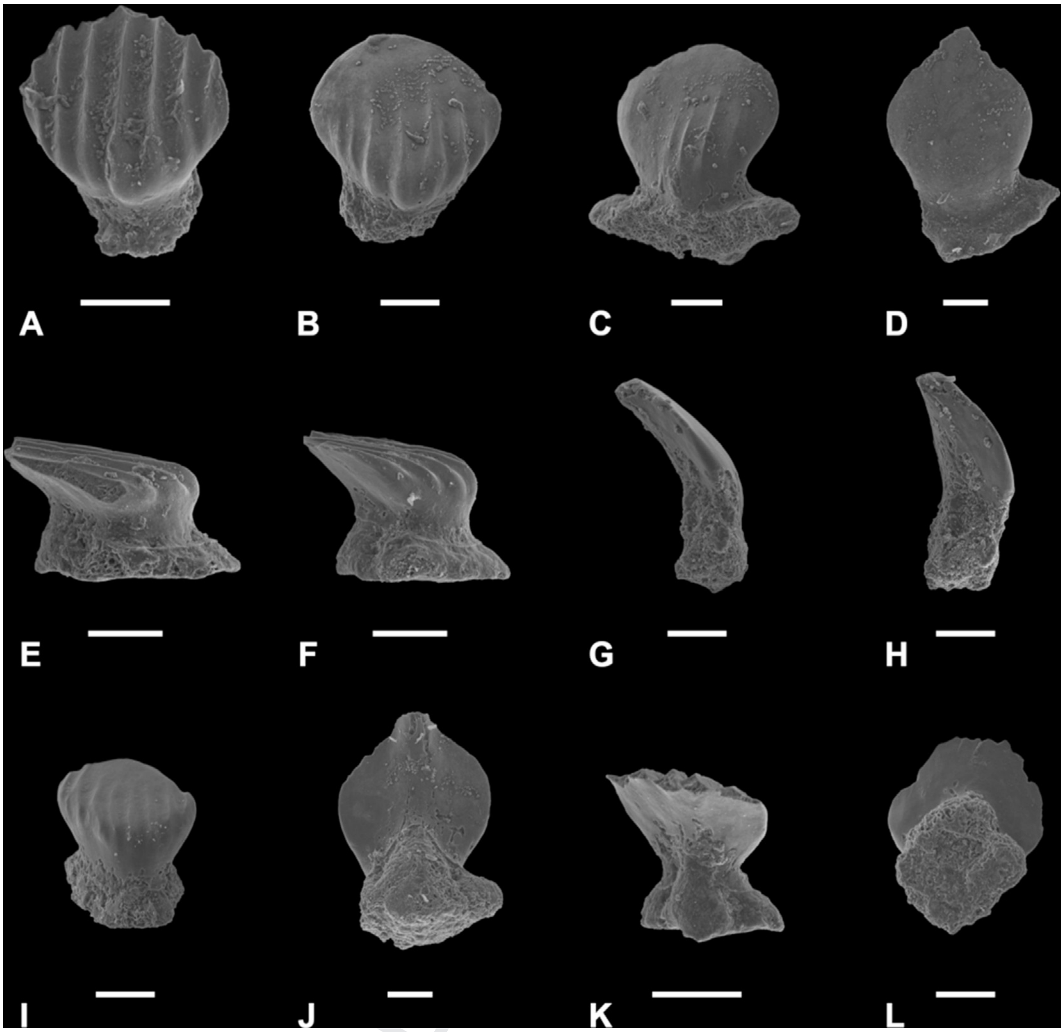

Fig. 12. *Cretoxyrhina mantelli* (Agassiz, 1835). Placoid scale from MGC-IGVR 36371. SEM imaging of selected placoid scales, from different views, coming from the residual of detached samples. **A-D.** Anterior views. **E-H.** Lateral views. **I.** Anterior view. **J-K.** Posterior views. **L.** Inferior view. [single column width].

6.2. Swimming behavior and paleoecology

Newbrey et al. (2015) observed that the vertebral centra of *Cretoxyrhina mantelli* are relatively antero-posteriorly compressed when compared to those of other fossil and extant lamniform sharks. The short vertebral centra and the high vertebral count led Newbrey et al. (2015) to hypothesize a carangiform swimming mode for *Cretoxyrhina mantelli*, implying that it was a moderately fast swimmer with high maneuverability.

The swimming capabilities of sharks can be estimated also through the morphological analysis of the placoid scales (e.g., Reif, 1985). Scale morphology suggests that *Cretoxyrhina mantelli* was a fast swimming shark (Shimada, 1997d). According to Reif and Dinkelacker (1982), keels (= ridges or riblets) and grooves on the scales that run approximately parallel to the body axis, as observed in *Cretoxyrhina mantelli*, are characteristic of fast swimming sharks (see also Shimada, 1997d). Reif (1985) recognized six ecological groups of sharks based on their locomotory habits, in which placoid scales have different functions that correlate to the ecology of the various shark species. Only in two groups, the fast swimming pelagic sharks and the large near-shore predators/moderate speed pelagic predators, the morphology of the placoid scales shows an evident hydrodynamic function. Fast swimming pelagic sharks have flat, usually overlapping scale crowns that form a dense pavement (Reif, 1985). Crowns exhibit a rounded posterior end or short cusps. The surface of the crown in this group of sharks is ornamented with fine parallel ridges that have average distances between 40 and 80 μm with U-shaped grooves separating the ridges. The placoid scales of *Cretoxyrhina mantelli* show all of these features. When found articulated, such as those figured in Shimada (1997d: fig. 8), they have a pavement-like arrangement to reduce hydrodynamic drag. As far as the scale ornamentation is concerned, placoid scales from MPPSA-IGVR 36371 and MGC-IGVR 81375 exhibit a pattern of ridges and grooves nearly identical to that observed by Shimada (1997d), Shimada et al. (2006) and Diedrich (2014) in *Cretoxyrhina mantelli* from other localities. The distance between the ridges in the specimens described herein ranges between 33 μm and 60 μm, with the mean value falling within the range of fast swimming sharks

Fig. 11. *Cretoxyrhina mantelli* (Agassiz 1835). MGC-IGVR 81375. A. Photo of MGC-IGVR 81375. **B.** Line drawing of MGC-IGVR 81375. Colors map: dark gray = vertebral centra; gray = teeth; light gray = rocky matrix; white = fragments of tessellated cartilage. Dashed lines delimit imprints of teeth and vertebral centra. Scale bars = 500 mm [1,5-column width]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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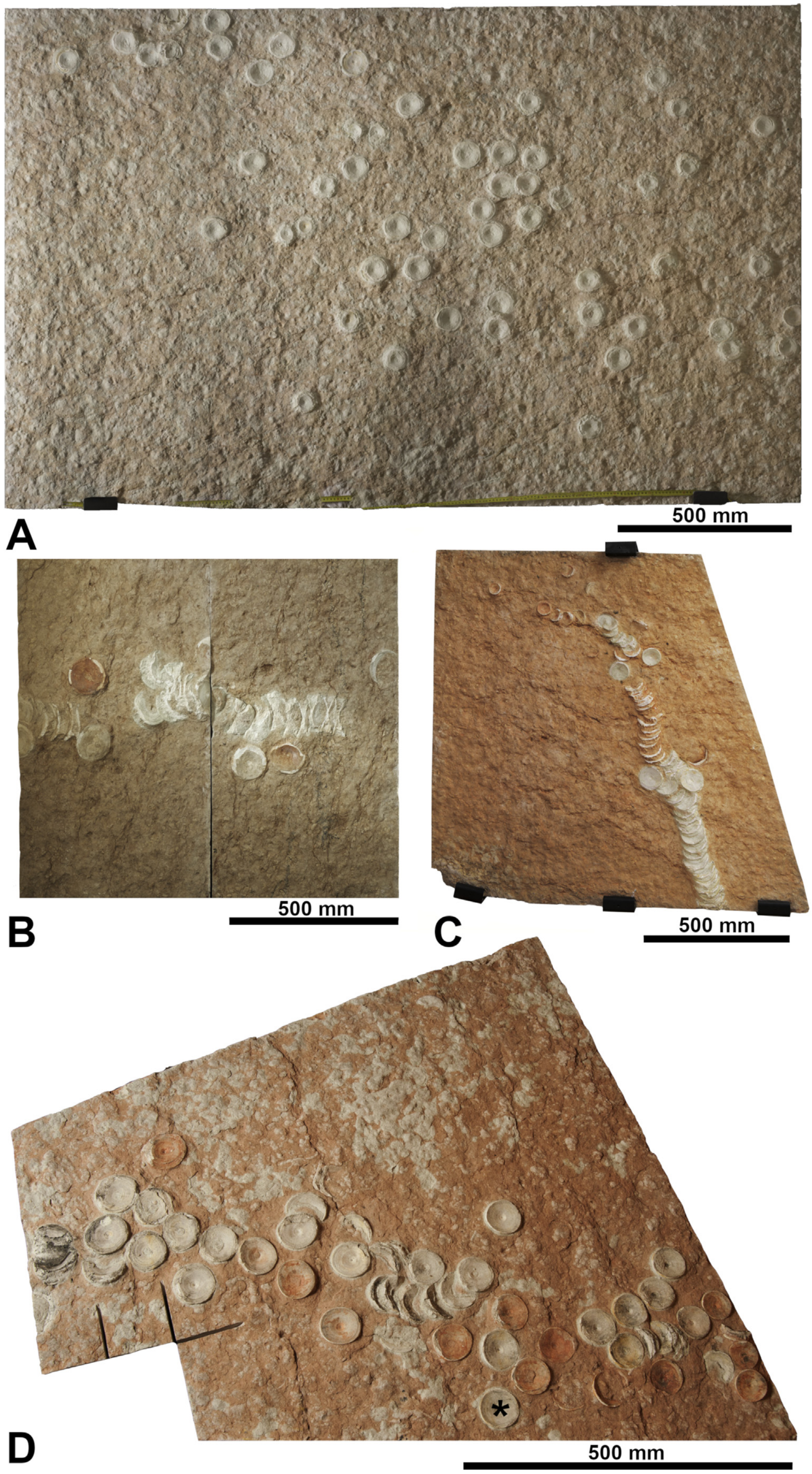
500 mm
A
500 mm
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*

Fig. 14. ?*Cretoxyrhina* sp. Vertebral column. Photo of MGC-IGVR 47789. Scale bar = 100 cm [single column width].

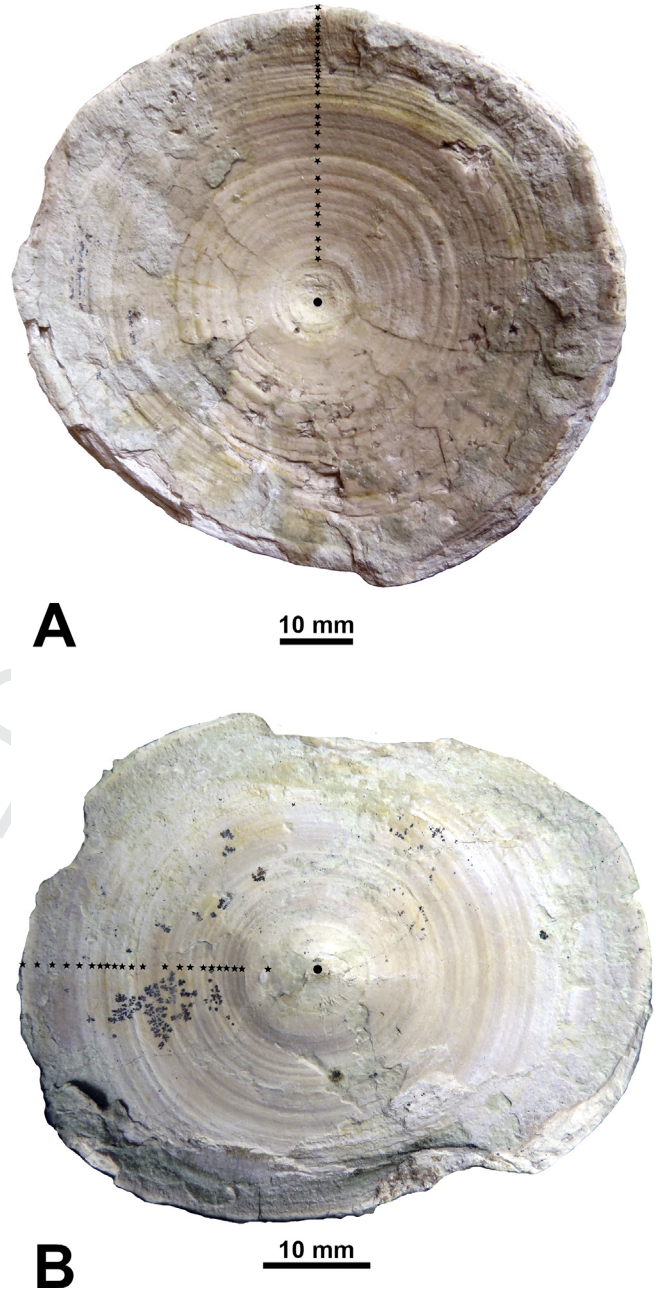

Fig. 15. *Cretoxyrhina mantelli* (Agassiz, 1835). Count of incremental bands of individuals MPPSA-IGVR 36371 and 45305. A. Vertebral centrum from MPPSA-IGVR 36371. The black dot indicates the vertebral fulcrum, the black stars indicate the incremental bands (26). **B.** Vertebral centrum from MPPSA-IGVR 45305. The black dot indicates the vertebral fulcrum, the black stars indicate the incremental bands (21). Scale bars = 10 mm [1,5-column width].

(Reif, 1985). Moreover, we employed a method utilized by Reif (1985) that was recently used for other fossil sharks (e.g., Marramà et al., 2017), which takes into account the ridge spacing and the scale width. We plotted the average ridge spacing and average crown width from a few individuals (FHSM VP-2187, MPPSA-IGVR 36371, MGC-IGVR 81375; see Tab. A.3) and compared the results with those of fast pelagic hunting sharks and large near-shore hunters/pelagic predators of moderate speed (see Reif, 1985). The results are shown in Fig. 16, in which *Cretoxyrhina mantelli* clearly falls within the fast pelagic hunting shark group, in particular the ridge spacing is very similar to that of *Isurus oxyrhinchus* and *Sphyrna tudes*. The average crown width, however, differs from those observed in these two taxa, but it is more similar to that of

Fig. 13. ?*Cretoxyrhina* sp. Incomplete vertebral columns. A. Orthophoto of MPPSA-IGVR 45308. **B.** Photo of MPPSA-IGVR 45319 (right) and MPPSA-IGVR 45320 (left). **C.** Photo of MPPSA-IGVR 45323. **D.** Orthophoto of MGP-PD 31960. The asterisk indicates the vertebral centrum removed and showing bioerosive fossil traces (see Taphonomic Remarks and Fig. 18E-F). Scale bars = 500 mm [1,5-column width].

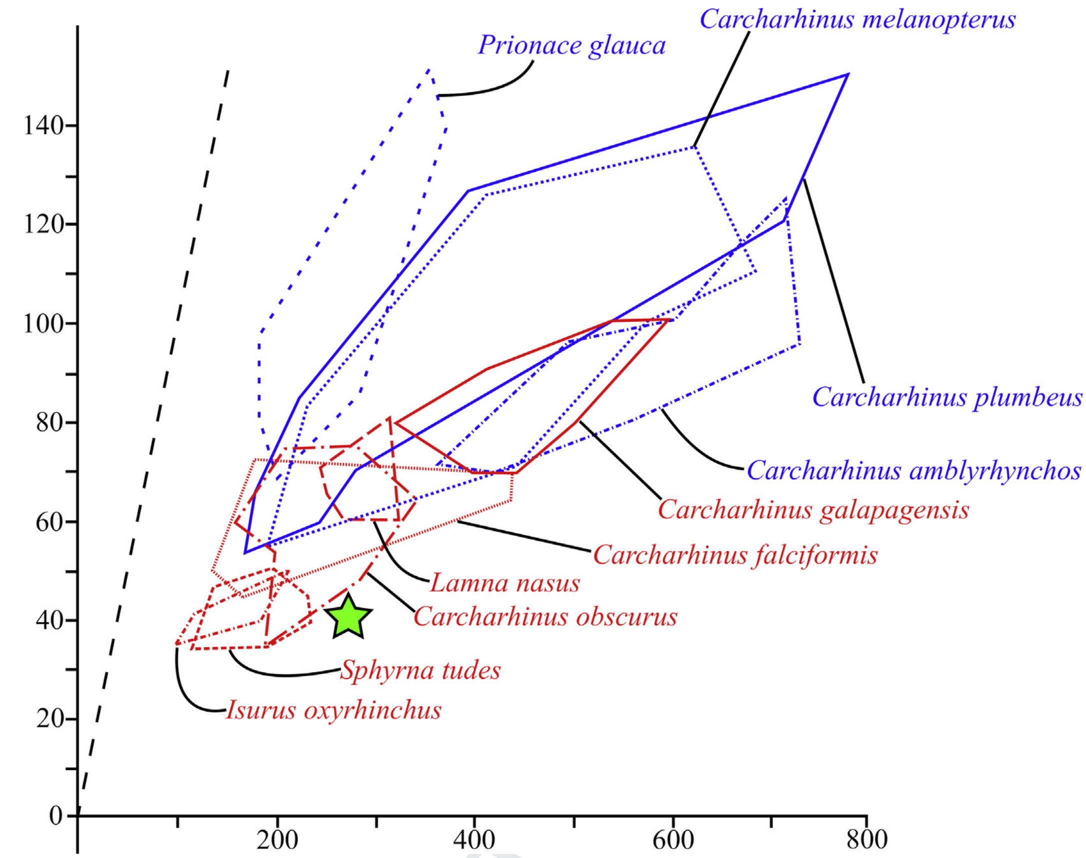

Fig. 16. Correlation diagram of scale crown width (x axis) and ridge distance (y axis) (in μm). The black dashed line indicates the slope of 1,0. The red labeled taxa are from the group of fast pelagic hunting sharks, while the blue labeled taxa are from the group of large nearshore predators/moderate speed pelagic predators. Note that the *Cretoxyrhina mantelli* average (green star) falls in the clouds of correlation of fast pelagic hunting sharks, in the lower part of the diagram. The diagram is modified after Reif (1985). [single column width]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Lamna nasus. Comparing the morphology and arrangement of placoid scales of *Cretoxyrhina mantelli* and those of extant lamniform sharks, the scales of *Cretoxyrhina mantelli* (see Shimada, 1997d: fig. 8) nevertheless differ from those of *Isurus oxyrhinchus* (see Reif, 1985: pl. 20, 21), which is a very fast hunter adapted to chasing fast moving fishes, such as swordfishes and tunas, in that the placoid scales have a looser arrangement. Actually, the placoid scales arrangement in *C. mantelli* is more similar to that in *Carcharodon carcharias* (see Reif, 1985: pl. 23). However, the number of ridges in the scales of *C. mantelli* (up to nine; Shimada, 1997d) is greater than that observed in *I. oxyrhinchus* (up to five ridges; Reif, 1985) and *Carcharodon carcharias* (up to three ridges). Reif (1985) hypothesized that new ridges were added with the expansion of the crown width to maintain constant the distance between the ridges.

Fig. 17. ?*Cretoxyrhina* sp. MGP-PD 31960. Photo of a section of a vertebral centrum fully embedded in the rocky matrix. Scale bar = 50 mm [single column width].

Considering all the aspects discussed herein, the conclusions drawn by other authors about caudal fin morphology and metabolic rate estimates (e.g., Kim et al., 2013; Ferron, 2017), and the fossil record of predation attributed to *C. mantelli* (see Shimada, 1997b; Shimada, Hooks III, 2004; Hone et al., 2018), this Cretaceous lamniform shark was likely a fast swimmer with an ecology in some ways similar to that of the living *Carcharodon carcharias* (see Shimada, 1997d).

7. Taphonomic Remarks

7.1. General features of the C. mantelli deadfall from ‘lastame’

All of the specimen from the ‘lastame’ documented herein are preserved within the limestone beds or on their bedding surfaces, sometimes draped with calcareous marly sediments. Lamniform sharks represent the most represented taxonomic group within associated or at least partly articulated vertebrate skeletal remains found in the ‘lastame’, with 15 specimens out of a total of at least 39 determined specimens, including four other chondrichthyans (Ptychodontidae, *Cretodus*, and *Onchosaurus*), 13 marine turtles, six mosasaurs and a bony fish. Other skeletal remains of lamniform

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sharks consisting of segments of vertebral columns (at least three) are housed in the collections of the MCSNV and probably come from the 'lastame' lithozone (Zorzin R., pers. com.), thereby confirming the great abundance of lamniform shark remains.

Skeletal remains of lamniform sharks include mainly portions of vertebral columns, which in many cases are associated with disarticulated tooth sets (*sensu* Shimada, 2005), and sometimes also with fragments of tessellated calcified cartilage and placoid scales. Teeth in some specimens are accumulated at the anterior end of the vertebral column; sometimes they are associated with tessellated cartilage of the mandibular arch, sometimes they are totally displaced and scattered along the vertebral column. Most of the teeth show fissures on the enameloid produced by compression, and, in many cases, have broken cusps or roots, or may be preserved as impression only.

Mineralized cranial elements are not well-preserved, because the cranial skeleton consists of tessellated cartilage, formed by a mosaic of tesserae (composed of both prismatic and globular calcification) overlaying a core of extracellular matrix that is not mineralized (Dean, Summers, 2006). The decay of the extracellular matrix causes the disarticulation and displacement of the tesserae. Only multilayered elements, which are considerably stiffer (e.g., jaws; Dean, Summers, 2006; Maisey, 2013), are characterized by a better state of preservation and occur in some of the specimens described herein (e.g., MPPSA-IGVR 45305).

Most vertebral centra described herein show antero-posterior compression; some suffered a slight taphonomic deformation and some others are incomplete, broken or fragmented. Some centra also show diagenetic alteration, such as oxidation (e.g., manganese dendrites; see Fig. 15B). The completeness of the skeletons is clearly biased by the technical difficulty of extracting larger slabs in the quarries, indicating that most of the skeletons were probably more complete when buried (Amalfitano et al., 2017b). The most complete vertebral column available, MPPSA-IGVR 36371, includes 157 vertebral centra and was fully extracted, as reported by the quarrymans, and subdivided into smaller slabs to facilitate the transport and the preparation (Fig. 4A).

The vertebral column segments within the 'lastame' sample show different degrees of disarticulation, ranging from totally disarticulated and scattered vertebral centra (e.g., MPPSA-IGVR 45308, Fig. 13A) to nearly perfectly articulated segments (e.g., MPPSA-IGVR 45305, Fig. 4B; MGC-IGVR 47789, Fig. 14), in some cases preserving anatomical details like the caudal flexion (e.g., MPPSA-IGVR 43323, Fig. 13C). Other skeletal remains consist of segments of articulated vertebral centra alternated with sectors of disarticulated vertebral centra that, however, are always scattered around the longitudinal axis of the shark body. There is no evidence of preferential orientation of the skeletal elements, imbrication or accumulation caused by tractive currents or remarkable displacement due to water turbulence (Amalfitano et al., 2017b). Therefore, these skeletal remains can be interpreted as representing various degrees of disarticulation of slowly decaying deadfall exposed for more or less long-lasting time intervals on the sea bottom under low energy conditions (see in analogy Amalfitano et al., 2017b).

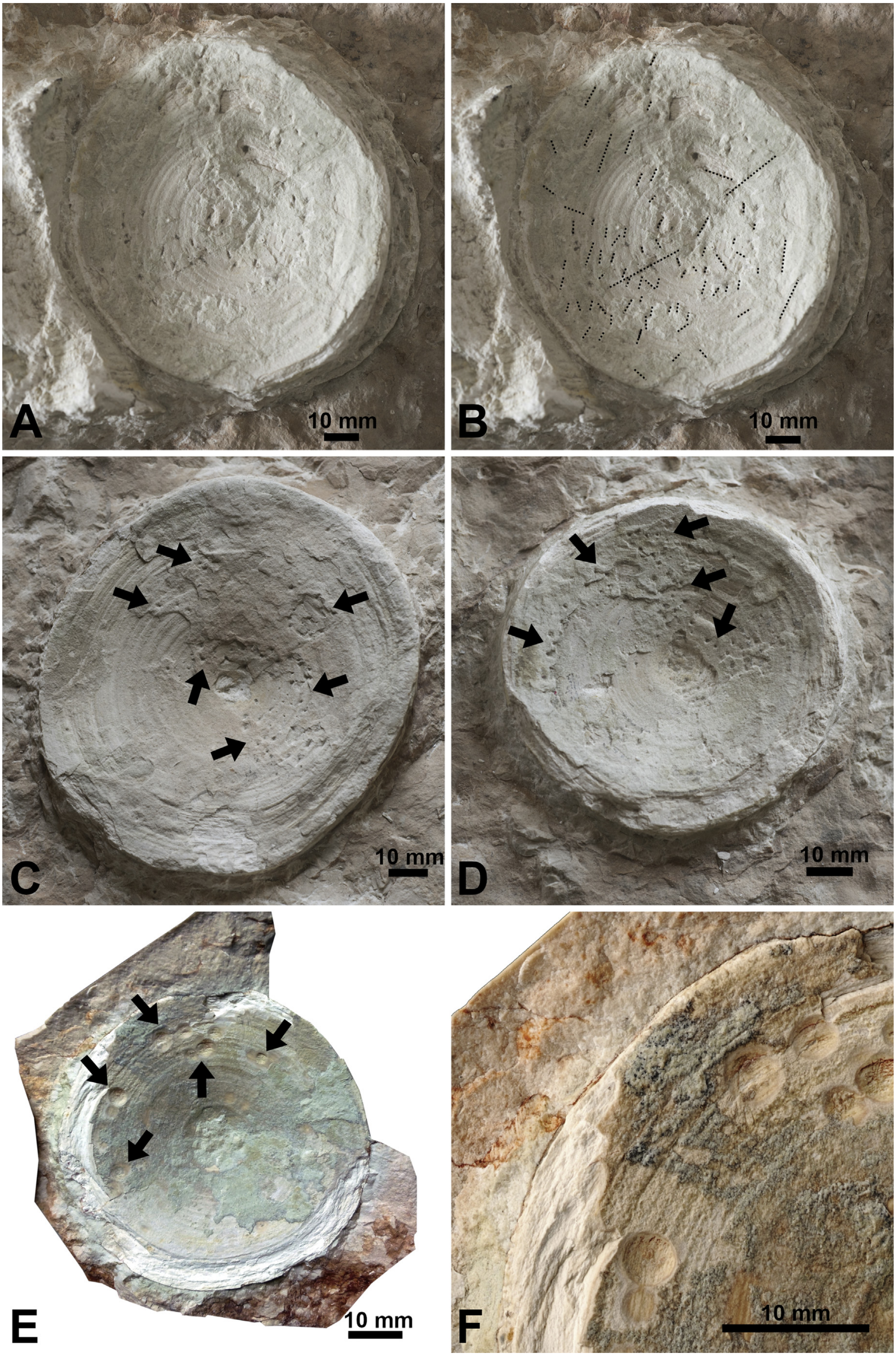
The more or less rapid decay of non-mineralized tissues, differential sinking in the unconsolidated calcareous nannoplankton-foraminiferal ooze that characterized the sea floor during the deposition of the 'lastame' and the different exposure intervals on the seafloor before burial could explain the different conditions of the skeletal remains, from the better preserved and fully articulated vertebral columns, MPPSA-IGVR 45305 and MGC-IGVR 47789, to the largely disarticulated vertebral column of MPPSA-IGVR 45308. Some articulated specimens, such as IGVR 36371, 45305 and 47789 (Figs. 4, 14), show an arched arrangement of the vertebral column, which could be explained as a possible product of tetany of the carcasses. The limited displacement of adjacent vertebral centra in partially articulated skeletons was probably caused by the limited decay of the thin fibrous intervertebral cartilages that firmly connect consecutive centra (Cappetta, 1987). Such limited disarticulation of the chondrichthyan axial structures was observed in cases of experimental taphonomy of chondrichthyan material (e.g., Samson et al., 2013). Fully disarticulated skeletons were probably exposed to the biological activity on the seafloor for longer periods. The partial sinking of the carcasses in the carbonate ooze is supported by the presence of centra and teeth partially or totally embedded in the rock and slightly displaced from the main plane of arrangement of the skeletal remains on the bedding surface (e.g., MGP-PD 31960, Fig. 17, and supplementary material Fig. A.1η). The centra exposing one of the articular surfaces may have had slower sinking, floating for hydrostatic thrust, because they exposed the largest surface to the underlying calcareous nannoplankton-foraminiferal ooze, and did not totally sink because of the precocious lithification of the underlying substrate.

7.2. Bioerosive fossil traces

The prolonged exposure of the carcasses on the seafloor discussed above is also supported by the occurrence of bioerosional trace fossils on the vertebral centra. They were produced by the activity of organisms that colonized or fed on the deadfalls after partial or total consumption of their soft tissues either by scavengers and/or bacteria. These traces have different morphologies and sizes and are detectable only in two specimens, MPPSA-IGVR 36371 and MGP-PD 31960 (Fig. 18). The traces on MPPSA-IGVR 36371 are located on the articular surfaces of some vertebral centra and consist of very short, sharp and narrow grooves, V– or U-shaped in cross-section (length 1.5–26 mm and width 0.4–0.9 mm; Figs. 18A–B), with a lined or overlapping pattern, and clustered small circular openings (diameter 0.2–1.4 mm; Figs. 18C–D), with a cylindrical section. The borings on MGP-PD 31960 (Figs. 18E–F) are larger and different from those in MPPSA-IGVR 36371, with a lenticular shape (diameter 1.4–3.7 mm), showing different depths, from superficial to 0.8 mm-deep holes; they are also evidently clustered.

The short, sharp, and narrow grooves on some vertebral centra of the specimen MPPSA-IGVR 36371 (e.g., Figs. 18A–B) could be interpreted as tooth marks produced by the scavenging activity of other sharks or fishes on the deadfall. Many chondrichthyans or bony fishes usually feed on deadfall, being the first stage of ecological succession in a deadfall community - the mobile-scavenger stage (see Smith et al., 2015) - and there are several reports of such activity also in the fossil record (e.g., Schwimmer et al., 1997). Damage on the vertebral centra due to preparation of the specimen can be excluded, because the marks do not exhibit fresh fractures or scratches typically caused by a preparation tool.

Small circular borings on MPPSA-IGVR 36371 vertebral centra are similar to the fossil traces of *Osedax*, a marine worm (Siboglinidae, Anellida) thriving on vertebrate deadfalls (Rouse et al., 2004). Among siboglinids, *Osedax* has developed a unique metazoan-bacteria symbiosis that exploits the organic material sequestered within the bones of dead vertebrates as an energy source (Danise, Higgs, 2015). *Osedax* and *Osedax*-like fossil traces were found on diverse vertebrate remains (e.g., whales, marine birds, bony fishes, marine turtles, and plesiosaurs; Danise, Higgs, 2015; Muñiz et al., 2010; Kiel et al., 2010; Kiel al., 2011; Kiel et al., 2013); the oldest one dates back to the Albian-Cenomanian (Danise, Higgs, 2015). There is no record of *Osedax* borings in chondrichthyans, and also experimental studies on extant


A
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vertebrate remains (e.g., Rouse et al., 2011) did not report colonization by *Osedax* on chondrichthyan remains. However, the use of juvenile *Isurus oxyrhinchus* vertebrae (diameter 5 mm) in the experiment carried out by Rouse et al. (2011) does not provide a definitive support to exclude any possible colonization of adult chondrichthyan deadfalls, which show more calcified skeletal components and, thereby, represent a potential site for *Osedax* colonization. However, it is not possible to demonstrate whether these borings were actually produced by *Osedax* worms or not, mostly because the vertebral centra of the larger slabs are still embedded in the rock, thereby preventing a tomographic analysis (like that carried out on other fossil vertebrate remains, e.g. Danise and Higgs, 2015). In any case, coalescent *Osedax* borings originating from colonization of multiple individuals may often collapse into small irregular pits (Danise S., pers. comm.) surrounded by some individual borings. This feature is evident in two vertebral centra, supporting a tentative attribution to *Osedax* colonization and likely representing the first one reported from chondrichthyan remains.

The borings on the bioeroded vertebra of specimen MGP-PD 31960 have a *Gastrochaenolites*-like structure, representing only a superficial boring stage. In fact, these borings resemble the borings produced by pholadid bivalves reported from fossil whale bones affected by clavate bivalve borings (see Belaústegui et al., 2012 and references therein). *Gastrochaenolites* borings were also described in coprolites and fish bones from Cretaceous-Paleogene phosphatic conglomerates from Northeastern Mali (Tapanila et al., 2004). All the occurrences known so far record borings on transported bone clasts. Belaústegui et al. (2012) provided evidence of the only examples of putative pholadid colonization and borings on an autochthonous carcass after its deposition on the sea bottom and the removal of the soft tissue cover. However, all the considered fossil traces come from shallow marine environments, while the fossil specimen described herein comes from a basinal setting. Moreover, the borings described here have no traces of the bioglyphs typical of the *Gastrochaenolites* structures. As a consequence, we cannot ascertain the *Gastrochaenolites* affinities of the borings in the bioeroded vertebral centrum of specimen MGP-PD 31960, but it is the most similar ichnotaxon among those reported on vertebrate bones (see Belaústegui et al., 2012, for a review about bioerosive traces on fossil vertebrate remains). It is evident that these traces were produced by opportunistic organisms that colonized the bones or the organically enriched sediments surrounding the carcass.

8. Concluding remarks

Skeletal remains of lamniform sharks from the Upper Cretaceous of the Lessini Mountains (Verona Province, northeastern Italy) are described. Seven of these skeletal remains can be reliably referred to the 'ginsu' shark *Cretoxyrhina mantelli* based on the associated tooth sets. The remaining specimens are tentatively attributed to ?*Cretoxyrhina* sp. because of the morphology of the available skeletal elements and information on the fossil assemblage.

Three specimens (MPPSA-IGVR 36371, 45305, MGC-IGVR 81375–81376) were dated in detail through calcareous plankton analysis. The specimens date back to the latest middle-upper Turonian and represent some of the most complete remains of *Cretoxyrhina mantelli* reported from northeastern Italy, previously known only from isolated teeth and a single partial skeleton reported by Bassani (1888) from the Castellavazzo locality.

The estimated total lengths of the *C. mantelli* specimens have revealed that MPPSA-IGVR 36371 is probably the largest individual known to date of this taxon, attaining a maximum length of 615–650 cm. The longevity of two individuals was estimated by counting the incremental bands on the vertebral centra resulting in values of about 26 years for the specimen MPPSA-IGVR 36371 and 21 years for the specimen MPPSA-IGVR 45305.

The analysis of the morphology of the placoid scales supports the ecological niche of *C. mantelli* as a fast pelagic hunting shark (*sensu* Reif, 1985) similar to the extant white shark *Carcharodon carcharias*.

The specimens of *C. mantelli* from the 'lastame' lithofacies of the Scaglia Rossa Formation show features that allow to interpret the taphonomic processes that affected the carcasses before their final burial. The disarticulation patterns and degree of preservation of some components more prone to degradation (e.g., calcified cartilage) demonstrate that the deadfalls slowly decayed exposed on the seafloor under low energy conditions for relatively long time and were visited by different communities of scavenger and colonized by opportunistic feeders as demonstrated by the bioerosive fossil traces. On IGVR 36371 vertebral centra, it is possible to observe what appears to be the first putative *Osedax* borings on a chondrichthyan skeleton as well as some bite marks made by scavengers, while MGP-PD 31960 vertebral centra contain some peculiar lenticular borings reminiscent of *Gastrochaenolithes* structures. The evidence of at least two stages of ecological succession of deadfall community, the mobile-scavengers stage (testified by the bite marks) and the enrichment-opportunist stage (i.e. the putative *Osedax* and lenticular borings) (see Smith et al., 2015), demonstrate that the *C. mantelli* deadfalls could have acted like modern whale deadfalls and supported an heterotrophic community like other vertebrate carcasses did, as testified by other cases in the Mesozoic fossil record (e.g., Kaim et al., 2008).

We also reviewed the nomenclatural history of *C. mantelli*, establishing that Agassiz (1835) originally erected the species (under the name *Lamna Mantellii*) when referring to previously published figures by Mantell (1822, plate 32). We also traced back four (PV OR 4524, 4527, 4539, 4540) of the original syntypes by comparing the figures of pl. 32 of Mantell (1822) with specimens from the Mantell's Collection of The Natural History Museum, London. The *Cretoxyrhina mantelli* skeletal remains described herein provide new relevant data to the knowledge of the 'lastame' vertebrate assemblage, which is dominated by chondrichthyan remains (15 skeletal remains out of a total of 39 associated or articulated skeletal remains known so far), mostly *Cretoxyrhina* specimens. Recent studies (e.g., Amadori et al., 2019; Amalfitano et al., 2017a-c; Palci et al., 2013) have revealed the diverse composition of this still poorly studied vertebrate fauna of the marine Upper Cretaceous of Italy, which is the object of a detailed in progress revision.

Author contribution statement Q3

Jacopo Amalfitano conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, prepared figures and/or tables, approved the final draft.

Fig. 18. *Cretoxyrhina mantelli* (Agassiz, 1835) and ?*Cretoxyrhina* sp. bioerosive fossil traces on vertebral centra. A. Photo of a vertebra with short grooves from MPPSA-IGVR 36371. **B.** Same as in A, with the grooves highlighted by dashed lines. **C.** Photo of small circular openings and collapsed areas on a vertebra from IGVR 36371, indicated by the black arrows, here interpreted as putative *Osedax* borings. **D.** Another photo of a vertebral centrum from MPPSA-IGVR 36371 with putative *Osedax* borings. **E.** Photo of a vertebra from MGP-PD 31960, with lenticular borings with a *Gastrochaenolites*-like structure. **F.** Detail of the lenticular borings from the vertebra of MGP-PD 31960. Scale bars = 10 mm [2-column width].

Luca Giusberti conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Eliana Fornaciari performed the micropaleontological analyses, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, prepared supplementary tables, approved the final draft.

Fabio Marco Dalla Vecchia authored or reviewed drafts of the paper, approved the final draft.

Valeria Luciani performed the micropaleontological analyses, analyzed the data, authored or reviewed drafts of the paper, prepared supplementary tables, approved the final draft.

Giorgio Carnevale authored or reviewed drafts of the paper, approved the final draft.

Jürgen Kriwet authored or reviewed drafts of the paper, approved the final draft.

Uncited reference

Q5 Agassiz, 1833–1844, Lioy, 1865.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.02.003.

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