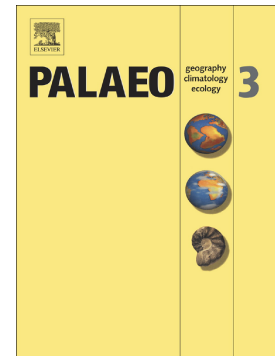


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Direct evidence of trophic interaction between a large lamniform shark, *Cretodus* sp., and a marine turtle from the Cretaceous of northeastern Italy

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Abstract

In the nineties of the 20th century, a large and partially articulated skeleton of a lamniform shark was discovered in Upper Cretaceous hemipelagic beds of the Venetian Prealps of northeastern Italy. The shark, dating back to the middle Turonian, is here ascribed to *Cretodus* and represents the first record of this genus in Italy. The fossil is the most complete specimen of *Cretodus* so far discovered and includes 120 teeth, 86 vertebral centra and many placoid scales. Closely associated with the remains of the shark (estimated total length over 6.5 meters) is a pellet-like accumulation of partially broken bones belonging to a large chelonoid turtle (about 2 m of estimated total length). Some of the bones show evidence of damages referable to bites and possible acid etching. Because of this, and because of their position in correspondence of the abdominal region of the shark, the turtle remains are interpreted as stomach content. The taphonomy of this association is discussed

and compared with other fossil records of shark predation/scavenging and with lamniform shark-chelonioid turtle interactions in modern marine environment. The Italian fossil represents the second evidence of a turtle swallowed by a shark in the fossil record and a direct evidence of the possible dietary preference of *Cretodus*, adding some evidence for discerning scavenging from predatory lifestyle.

Keywords: Lamniform shark; Swallowed marine turtle; Predation/Scavenging; Trophic interaction; Taphonomy; Cretaceous

1. Introduction

The Upper Cretaceous-lower Eocene Scaglia Rossa Formation widely crops out in the Venetian Prealps of northeastern Italy. It mainly consists of pink to reddish limestones, marly limestones and marls rich in planktonic foraminifera and deposited in hemipelagic setting (Channell and Medizza, 1981; Massari et al., 1983). This formation is generally poor in macrofossils, but it is renowned since the 19th century for findings of echinoids, mollusks and rarer marine vertebrates (e.g., Astolfi and Colombara, 2003; Cigala Fulgosi et al., 1980; Dalla Vecchia et al., 2005; Giusberti et al., 2005 and references therein; Palci et al., 2013; Trevisani and Cestari, 2007). Fossil vertebrates come almost exclusively from the Cretaceous portion of Scaglia Rossa and are mainly represented by isolated teeth and vertebrae of chondrichthyans (e.g., Bassani, 1877; Bassani, 1886; Cigala Fulgosi et al., 1980; D'Erasmus, 1922; De Zigno, 1883; Lioy, 1865; Nicolis, 1882; Pellegrini, 1883; Sirna et al., 1994). However, some almost complete vertebral columns of lamniform sharks, often associated with teeth, were discovered between the end of 19th century and the beginning of 21st century during quarrying activities in peculiar lithofacies of Scaglia Rossa (called 'lastame' and 'pietra di Castellavazzo'). These important finds have been mostly referred to *Cretoxyrhina mantelli*, but after the pioneering paper by Bassani (1888), they were only briefly mentioned in short notes (e.g., Cigala Fulgosi et al., 1980; Roghi, 2010; Trevisani, 2011), remaining practically unknown to the scientific community.

Here we report a previously undescribed large lamniform shark associated with remains of a large turtle coming from the Upper Cretaceous of Lessini Mountains, near the village of Sant'Anna d'Alfaedo (Verona Province, northeastern Italy; Fig. 1). The goal of this paper is to describe in detail and identify this exceptional fossil discussing the taphonomic and paleoecological implications of the shark-turtle association. This study, including precise dating of the fossil through calcareous plankton analysis, was carried out in the context of a broader project aimed to

describe and revise the entire vertebrate marine fauna from the Scaglia Rossa Formation of northern Italy.

2. Geological and paleontological context

The specimen comes from the ‘Giovanni and Gianfranco Benedetti's Quarry’ that is located on the western slope of Mt. Loffa, near the village of Sant'Anna d'Alfaedo (Fig. 1), which is approximately 30 km N of Verona and 50 km W of the famous Eocene *Lagerstätten* of Bolca (Papazzoni et al., 2014). The hemipelagic limestone of the Scaglia Rossa is extensively quarried around Sant'Anna d'Alfaedo and in other localities of western Lessini Mountains for building stone (e.g., Cigala Fulgosi et al., 1980; Ginevra et al., 2000; Massari and Savazzi, 1981). The quarried interval, which is locally known as ‘lastame’, is a peculiar lithofacies of Scaglia Rossa (‘lithozone’ 2 of Scaglia Rossa; Lozar and Grosso, 1997) and ranges from lower Turonian to lower Santonian (Lozar and Grosso, 1997; Palci et al., 2013). ‘Lastame’ is about 7-8 meters thick and comprises 70 layers of flaser-nodular whitish to reddish limestones that are laterally continuous with a thickness ranging from 4 to 35 cm (Lozar and Grosso, 1997; Massari and Savazzi, 1981; Roghi and Romano, 2009). According to the finder, Gianfranco Benedetti, the slab that contains the specimen forming the focus of this study comes from the middle of the section. The strata of ‘lastame’ are subhorizontal and planar and are separated by thin, dark red and shaly layers (marls and clays). The bedding surfaces are firmgrounds, representing long intervals of non-deposition (Trevisani and Cestari, 2007). Large echinoid burrows occur on some bedding surfaces (Trevisani and Cestari, 2007). Early lithification of the nodules of ‘lastame’ has been inferred from their lack of compactional deformation, while the matrix suffered compaction, as suggested by the presence of solution seams (Massari and Savazzi, 1981). The ‘lastame’ facies is highly reminiscent of the nodular Rosso Ammonitico Formation of Middle-Late Jurassic age (Massari and Savazzi, 1981). It deposited on the ‘Trento Plateau’, which was a basinal high (Winterer and Bosellini, 1981) some hundred kilometers away from an emergent area drained by rivers that was located to the north/north-west, probably in the Upper Austroalpine domain (Cigala Fulgosi et al 1980; Massari and Medizza, 1973; Massari and Savazzi, 1981).

In strict analogy with ‘Rosso Ammonitico’, ‘lastame’ shows clear evidence of low sedimentation rates, such as reduced thickness compared to its temporal range, local invertebrate macrofossil concentrations and local hardgrounds or incipient hardgrounds (Massari and Savazzi, 1981; Trevisani and Cestari, 2007). Paleodepth interpretation of Lessinian ‘lastame’ is quite controversial

and debated (ranging from 50-100 meters to full bathyal; Trevisani and Cestari, 2007; Venturini, 2012) and is in need of a careful revision based on integrated sedimentological and macro-micropaleontological studies.

Fossil macroinvertebrates from 'lastame' consist of ammonites, inoceramids, rudists and irregular echinoids. Skeletons of large marine vertebrates were occasionally recovered from different levels within the quarried interval (Cigala Fulgosi et al., 1980). They include several condrichthyans (*Cretoxyrhina mantelli*, *Ptychodus* spp. and a sclerorhynchid, Amalfitano et al., 2017; Cigala Fulgosi et al., 1980; Trevisani and Cestari, 2007); marine turtles (*Protosphargis veronensis* and other taxa, Chesi, 2008; Villa et al., 2014) and mosasaurs (*Romeosaurus fumanensis* and *R. sorbinii*; Palci et al., 2013). Despite the importance of these finds, recent paleontological studies have been occasional, including just the revisions of the rudists (Trevisani and Cestari, 2007) and mosasaurs (Palci et al., 2013). Most of the vertebrate remains recovered from the quarries of 'lastame' near Mt. Loffa are housed in the Museum of Prehistory and Paleontology of Sant'Anna d'Alfaedo and, subordinately, in the Museum of Natural History of Verona and the Geo-Paleontological Museum of Camposilvano.

3. Materials and Methods

All necessary permits were obtained from the Italian Ministry of Cultural Heritage and Activities and Tourism (Veneto Region Superintendence for Archaeological Heritage) for the described study, which complied with all relevant regulations (prot. no. 156 08/01/2016).

The unique identification number of the specimen studied is IGVR 91032 (it is a State number because fossils in Italy are State property). The photographs of IGVR 91032 are printed and made available under permission of the Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage. All rights reserved.

3.1. Materials

The specimen IGVR 91032 (Fig. 2) is housed in the Museum of Prehistory and Paleontology of Sant'Anna d'Alfaedo. It consists of the main slab (slab A; Fig. 2), which preserves the teeth, the proximal segment of the vertebral column and the partial cranial calcified cartilages of the shark and the remains of the turtle, and another slab (slab B; Fig. 2), which contains a distal portion of the shark vertebral column. Slab A is made of three pieces that were glued together.

The specimen was found between 1996 and 1997 by the quarry owners Giovanni and Gianfranco Benedetti and it was prepared by Giovanni Benedetti in 2003. According to the latter, the two slabs

come from the same layer and were separated only by a karst fissure; thus, the skeletal remains in slab A and B should belong to the same individual. Nevertheless, the two slabs slightly differ in color; furthermore, the different sizes between the last vertebral centrum on slab A and the first on the slab B suggest that several vertebrae are missing in between the two segments. Most of the teeth (70%) detached from the slab A when it was exposed by quarry works or remained attached to the counterslab (now missing); they were glued to the slab later and sometimes not in their exact original position. However, there is no doubt that the glued teeth belong to this specimen because they are similar to the *in situ* teeth and because this is the first report of such a kind of shark teeth from the Scaglia Rossa in 140 years of discoveries. On slab A, the vertebrae are *in situ*, except for 12 centra that detached as the teeth were glued to the slab. The association of the latter is proven by a photograph taken before preparation. All centra on slab B were glued to the slab. The maximum length of slab A is 305 cm, the maximum width is 172 cm. Its thickness is 10 cm. Slab B has a maximum length of 204.9 cm and a maximum width of 164.9 cm. Its thickness is 13 cm.

3.1.1. Lithology and microfacies of the slab A of IGVR 91032

Slab A is a portion of a single bed of nodular pinkish limestone in which every calcareous nodule is surrounded by veeners of dark reddish marl or clay (Fig. 3A). Deformation by compaction has formed stylolithes in the internodular matrix. Both upper and lower bedding surfaces of the slab present consistent traces of the reddish calcareous marl that originally separated it from overlying and underlying beds of nodular limestone. The vertebrate remains are preserved within the reddish calcareous marl and do not go inside the limestone. The microfacies of a limestone nodule removed from IGVR 91032 (sample A7) is a planktonic foraminiferal wackestone with marginotruncanids, *Dicarinella hagni*, heterohelcidids and hedbergellids (Fig. 3B).

3.2. Methods

3.2.2. Micropaleontology

Foraminifera. Semiquantitative analysis of planktic and small benthic foraminifera was performed in washed residues of the $>63\ \mu\text{m}$ fraction obtained from a sample removed from slab A (A3 sample), and processed following the cold acetholysate method of Lirer (2000) as described in Luciani et al. (2007).

The studied residues are deposited in the micropaleontological collections of the Department of Geosciences, Padua University (Italy) and labeled with the sample number assigned during the sampling from slab A of IGVR 91032.

Calcareous nannofossils. The sample IGVR91032 was prepared from unprocessed material as smear slide and examined using a light microscope at 1250x magnification. In order to check the presence or absence of index species, the semi-quantitative counting of the number of useful species in a prefixed area of about 8-7 mm² (roughly equivalent to 4 vertical traverses; modified after Gardin and Monechi, 1998) was performed. The studied smear slide is deposited in the micropaleontological collections of the Department of Geosciences of the Padua University (Italy) and labelled with the sample number assigned during the specimen matrix extraction.

3.2.2. *Shark and turtle.*

The specimen was photographed with several digital cameras: Nikon Coolpix L120, Sony α 200 mounting 18-70mm lens and Fuji XE1 mounting 18-55mm lens. The specimen was subjected to orthophotography and macrophotographs. The images were edited using Adobe Photoshop CS6. Drawings were also produced using the Adobe Photoshop CS6. Many works (e.g. Applegate, 1965; Applegate and Espinosa-Arrubarrena 1996; Cappetta, 1987, 2012; Leriche, 1905; Purdy, 2006; Shimada, 2002; Welton and Farish, 1993) were used as reference for tooth terminology, morphology and comparison. Dental measurements were taken following Shimada (2007: fig. 4). A number was arbitrarily assigned to each tooth ranging from 1 to 120 (Appendix A). Vertebral centra are referred to as 'v1' through 'v85', counting sequentially starting from the cranialmost centrum. Matrix samples for placoid scale extraction were taken from six different points of the slab A (see Fig. 4) and were labeled 'A1' to 'A6'. The placoid scales were picked and counted from the residues >63 μ m of the six samples processed following the cold acetolysis method of Lirer (2000). The placoid scales are deposited in the micropaleontological collections of the Department of Geosciences, Padua University (Italy) and labeled with the sample number assigned during the sampling from slab A of IGVR 91032.

Representative specimens of main morphologies of placoid scales were imaged using a SEM (JSM Jeol 6490) at the CE.A.S.C. The height of the scales (base to apex of the central cusp measurement) and the width of their cusp in anterior view were taken by a micrometer mounted on a Leica MZ16 stereomicroscope. Capellini (1884, 1898), Hay (1908), Hirayama (1992, 1994, 1997 and 1998), Kapuścińska and Machalski (2015), Lehman and Tomlinson (2004), Młynarsky (1976), Mulder (2003), Parris et al. (2014), Villa et al. (2014), Wieland (1900, 1906), Wyneken (2001, 2003),

Zangerl and Sloan (1960) were used for the comparison and taxonomic identification of the turtle remains. Shark body length (TL) was estimated from individual vertebral centrum diameter (CD) using the following formulas taken from Shimada (2008) and Gottfried et al. (1996), respectively:

$$TL \text{ (cm)} = 0.281 + 5.746[CD(\text{mm})]$$

$$TL \text{ (m)} = 0.22 + 0.058[CD(\text{mm})]$$

All measurements were taken with a caliper P/M vernier scale.

3.2.3. *Institutional abbreviations.* IGVR, Inventario Generale di Verona, Soprintendenza Archeologica del Veneto, Verona, Italy; MGGC, Museo Geologico ‘Giovanni Capellini’, Bologna, Italy; MGPC, Geo-Paleontological Museum of Camposilvano (Verona), Italy; MPPS, Museum of Prehistory and Paleontology of Sant’Anna d’Alfaedo (Verona), Italy; MSNV, Museum of Natural History of Verona, Italy; OMNH, Sam Noble Oklahoma Museum of Natural History, Oklahoma City, USA.

4. Dating IGVR 91032: calcareous microfossils analysis

Calcareous nannofossils. The analyzed samples contain few calcareous nannofossils, having a moderate/poor state of preservation. The assemblage is dominated by different species of *Watznaueria* (116 specimens). *Quadrum eptabrachium* and *Retecapsa crenulata* (9 specimens) are the more common species after *Watznaueria*, whereas *Eiffelithus eximius* and *Lucianorhabdus maleformis*, which are biostratigraphically useful, are poorly represented (2 and 4 specimens, respectively). A questionable specimen referable to *Lucianorhabdus quadrifidus* has been also detected.

The presence of *E. eximius* and *L. maleformis* and the concomitant absence of *Marthasterites furcatus* and *Lithastrinus septenarius* allow assigning the sample to the calcareous nannofossil Zone CC12 of Sissingh (1977) or to the ZoneUC8 of Burnett (1998). Hence, on this basis the age of the sample is middle Turonian according to Ogg and Hinnov (2012).

Foraminifera. The residue (fraction >63 µm) contains over 95% of planktic foraminifera. Rare benthic foraminifera are dominated by calcareous-hyaline morphotypes and, secondarily, by agglutinants. As well as foraminifera, several placoid scales were also found in the residue, of average size >250 µm (for details see below). The high value of planktic/benthic foraminifer ratio in the residue is indicative, at least, of the upper bathyal zone (>200 m). The planktic assemblage is diversified and dominated by marginotruncanids with common dicarinellids and

muricohedbergellids, rare praeglobotoruncanids and globigerinelloidids. The Cretaceous zonal schemes and the taxonomy of Cretaceous planktic foraminifera are in a flux state; here, we refer to Coccioni and Premoli Silva (2015). Our assemblage is confidentially attributable to the *Dicarinella primitiva*/*Marginotruncana sigali* Zone (or *Marginotruncana schneegansi* Zone according to Sliter, 1989) due to the absence of *Helvetoglobotruncana helvetica* and *Dicarinella concavata* markers of the underlying and overlying zones respectively. This zone is referable to the middle-upper Turonian (Coccioni and Premoli Silva, 2015; Ogg and Hinnov, 2012).

4.1. Age of IGVR 91032.

The biozonal assignments, based on the calcareous plankton, allow ascribing the studied specimen IGVR 91032 to the middle Turonian (Fig. 5), according to the zonal integrated scheme of Ogg and Hinnov (2012). Furthermore, the presence of a questionable specimen of the calcareous nannofossil *L. quadrifidus* would suggest assigning IGVR 91032 to the Subzone UC8b of Burnett (1998), hence further constraining the age of the fossil to the middle part of middle Turonian *sensu* Ogg and Hinnov (2012).

5. Systematic Paleontology

5.1. The shark

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902

Subcohort NEOSELACHII Compagno, 1977

Superorder GALEOMORPHII Compagno, 1973

Order LAMNIFORMES Berg, 1958

Family *incertae sedis*

Genus *CRETODUS* Sokolov, 1965

Type species. *Otodus semiplicatus* Münster in Agassiz, 1843 (see Cappetta, 2012).

Stratigraphic and geographic distribution. Albian-Santonian of North America (U.S.A: Alabama, Georgia, Minnesota, New Mexico, Texas; Canada: Alberta), Africa (Angola; Egypt), Asia (Kazakhstan); Europe (Belgium, Czech Republic, England, Germany, Italy [this paper], Portugal, Spain); Near East (Lebanon) (for more details see Cappetta, 2012 and references therein).

Remarks. Fossil shark taxonomy is dramatically chaotic due mainly to the fact that lower taxa were mostly erected on single or few isolated teeth instead of adequately complete dentitions. Furthermore, those taxon names were later referred to specimens that are quite unlike the original teeth on which they were based. In some cases, the type specimens were lost and only drawings remain of them. Finally, authors considered local association for their comparisons without considering the whole available sample from different regions of the world. Now, it is extremely difficult to disentangle the puzzle.

Cretodus sp.

(Figs 2, 4, 6-10 and 15)

Description

Teeth. The specimen preserves 120 teeth, at different growth stages (Figs. 6-7), from immature growing teeth with a thin enameloid cap, no crown-filling dentine and without root to mature functional teeth with fully developed crown and root (see Welton and Farish, 1993). At least 18 immature growing teeth can be identified; at least 24 are mature functional teeth and 30 teeth have roots but without well-formed lobes, thus are considered as an intermediate stage. Teeth occur in a crescent-shaped accumulation roughly perpendicular to the vertebral column and about 110 cm wide. However, most of the teeth are fixed to the slab by resin (see Fig. 6). Many of these teeth are damaged, lacking mainly the root. Probably they detached from the counterslab and the root remained there and was not collected. Thus, the present arrangement of the glued teeth could simply be an artefact produced by the person who did it, although the teeth are all from this specimen as we explained in the Materials and Methods section.

Teeth vary in size (see Appendix A), with the maximum tooth height of 69 mm and the minimum tooth height of 16 mm, and morphology suggesting monognathic heterodonty and 'lamnoid tooth pattern' (Shimada, 2002) in the dentition. Crowns have a large central (main) cusp and mesial and distal cusplets. The central cusps have a variable outline in labiolingual view according to their position (from erect in anterior teeth to strongly inclined in latero-posterior teeth) and are slightly sigmoid in mesiodistal view. Numerous, regularly spaced, well-marked, and very short basoapical grooves occur on both the labial and lingual sides of crown bases on the central cusp and cusplets of all mature, intermediate-stage and immature teeth (Fig. 7). Those grooves extend also to the upper part of the dental bands in mature teeth. The labial face of the central cusp is barely convex, often with a distinct median flattening. It presents two to five basoapical enameloid plications (foldings separated by deep grooves). They start from the base of the crown and have a different extent

according to the height of the tooth considered. They are especially marked and long in the larger crowns. The lingual face is strongly convex and smooth except for the short and thin basal grooves. The cutting edges are sharp and continuous, without serrations. Usually, each shoulder of the central cusp bears a triangular, broad, and strongly divergent cusplet of the same size (Fig. 7); in some cases the cusplet are broken off. The cusplets have sharp and continuous cutting edges, without serrations. Their heights range three to 17 mm and is directly proportional to the height of the central cusp.

The roots are U-shaped, holaulacorhizous, with a prominent lingual protuberance. The extent of the lobes is variable as well as the angle they form each other, according with the tooth position (see Purdy, 2006).

Vertebrae. The vertebral column consists of 86 vertebral centra, 51 on slab A and 35 on slab B. Measurements are provided in Appendix B. Centra on slab A represent a semiarticulate segment of the anterior part of the vertebral column (Fig. 8A). Centra on slab B form a semiarticulate segment of the posterior part of the vertebral column with central diameter decreasing backward (Fig. 8B). As already reported in the Materials section, they were all glued to the slab, so their semi-articulation may be artificial. The different diameters of the last centrum on slab A (9.3 cm) and the first one on slab B (7.9 cm) suggest that a portion of the vertebral column between the two segments is missing. This is also indicated by the low vertebral count (86) compared with that of another lamniform shark (*Cretoxyrhina*) from the 'lastame' of Sant'Anna d'Alfaedo, which has a count (155; Cigala Fulgosi et al., 1980) that is closer to the 216 vertebrae estimated for *Cretoxyrhina* specimens from Kansas (Shimada et al., 2006). Living lamniform sharks have a count ranging from 156 to 170 vertebrae in *Carcharias*, from 187 to 197 in *Isurus*, from 153 to 162 in *Lamna* and from 172 to 187 in *Carcharodon* (Springer and Garrick, 1964). The diameter of the centra on slab A ranges from 11.5 cm (vertebra 16) to 5.3 cm (vertebra 1) (see Appendix B); that on slab B ranges from 7.9 cm (first centrum of the slab) to 2.8 cm (last three centra) (see Appendix B). The centra are well-calcified and structurally match the definition of 'lamnoid vertebrae' (*sensu* Applegate, 1967: p. 62) exhibiting concentric lamellae around the primary calcification that is amphicoelous, imperforate and double-cone-shaped (Shimada, 2007) (Fig. 8C-D). They are asterospondylic with many, tightly spaced and radiating calcified lamellae (Fig. 8C). Many centra suffer a slight taphonomic distortion and some are incomplete.

Tessellated calcified cartilage remains. Seven main fragments of tessellated calcified cartilage are identified on the slab (each main fragment is actually divided into smaller fragments). Four occur all close to each other at one extremity of the tooth accumulation (Fig. 6) and three are glued within

the turtle remains. The latter probably splitted away from the slab during the removal of the counterslab and were erroneously glued to the turtle remains by the preparators of the specimen who considered them as fragments of the turtle shell. The fragments are flat and range from 5.5 to 13 cm in length and from 4 to 8.5 cm in width. Their exposed surface shows the characteristic tesserae (Dean and Summers, 2006; Dingerkus et al., 1991) (Fig. 10). One of the fragments close to the teeth accumulation bears a lateral tooth. The presence of a tooth rooted into one of the fragments further supports this interpretation and indicates that the fragment is part of the palatoquadrate or Meckel's cartilage.

Placoid scales. Placoid scales are common in the reddish calcareous marl all around the tooth accumulation and vertebral column of the shark and the turtle remains. They appear as whitish submillimetric dots in the reddish rock. A total of 412 placoid scales were picked up from the >63 μm residues of the seven samples collected from slab A (Fig. 4). They are usually composed of a base and a crown, the first bearing a nutrient foramen on its basal face (Fig. 9). Sometimes they lack the base because it is delicate and is easily damaged by the action of the acid used to dissolve the limestone. Their height ranges from 1 to 0.3 mm and their width from 0.6 to 0.3 mm. We could not determine how the placoid scales were originally distributed. All the scales are ornamented with fine parallel basoapical ridges on their crown and have different sizes (from broad to slender) and general shapes (rhomboid, e.g., Fig. 9A-C, F, H; rounded or drop-like, e.g., Fig. 9D, G; cuneiform, e.g., Fig. 9E). In addition, the cusp varies from rounded (e.g., Fig. 9D, G) to pointed (with a single cusp) (e.g., Fig. 9B, C, E, F, H), in some cases also tricuspid (Fig. 9A). The prominent basoapical ridges resemble the deep enameloid plications on the labial face of the central cusp of the teeth.

Size estimate. Using the two formulae to estimate total body length based on the diameter of the vertebral centra that are reported in the Materials and Methods section and the vertebral diameter of 115 mm (which refers to the largest undeformed and completely exposed centrum, A46), the total length of the individual results to be 6.61 m and 6.89 m. However, that is not the largest centrum in the sample (see Appendix B). There are some larger vertebrae but they are slightly distorted. Using the maximum diameter measured in the sample (about 130 mm), the maximum total length would be 7.47 m and 7.76 m. According to these estimates, IGVR 91032 would rival with the largest specimens of *Cretoxyrhina mantelli* (6-7 m) and other fossil specimens of lamniform shark, like OMNH 68860 from the Lower Cretaceous of Texas (6.3-6.6 m; Frederickson et al., 2015). Comparing the estimate length with the maximum length of extant predaceous sharks, like *Carcharodon carcharias* (maximum assumed length: 7.8 m; Randall, 1973), *Sphyrna mokarran* (maximum reported length: 6 m; Compagno, 1984; Gilbert, 1967;) and *Galeocerdo cuvieri*

(maximum size reported: 7.4 m; Compagno, 1984; Randall, 1992; Simpfendorfer et al., 2001), IGVR 91032 could be considered a very large predaceous shark, with a similar ecology to these extant sharks due to its size and dental morphology. A direct estimate of the total length for IGVR 91032 is impossible, because the vertebral column is not complete. Shark vertebral counts can vary significantly from species to species with no specific evolutionary trend (Springer and Garrick, 1964). Therefore, the original count cannot be reconstructed by comparison with similar extant lamniform sharks.

Discussion

The presence of the ‘lamnoid tooth pattern’ (Shimada, 2002) and of ‘lamnoid’ vertebrae (Applegate, 1967) confidently indicates that the shark under examination belongs to the Lamniformes (Compagno, 1990; Shimada, 2002; Shirai, 1996).

The examined specimen shares the following characters with the genus *Cretodus sensu* Cappetta (2012): large-sized teeth with a triangular, rather narrow central cusp in anterior files and never very broad in lateral files; labial face barely convex, while the lingual one is more strongly cambered often with a distinct median flattening; pair of broad, triangular, sharp and lightly divergent lateral cusplets; the root has a well-marked lingual protuberance. The Italian specimen matches also the description of Schwimmer et al. (2002), especially for ‘short vertical grooves’ on lingual and labial face at the base of the crown (different from the description of Cappetta, 2012: p. 253 and fig. 233) and also for the ‘deep vertical plications’ on the labial face, which is however present in almost all teeth of IGVR 91032, not only in larger ones (see Schwimmer et al., 2002: p. 704). Furthermore, the lingual face of the Italian teeth is smooth, except for the short grooves at the crown base. According to Cappetta (2012), *Cretodus* teeth are up to 4 cm high, while the largest in our sample is 69 mm high. However, Schwimmer et al. (2002) report *Cretodus* teeth from North America that are up to 66 mm high.

The Late Cretaceous lamniform *Archaeolamna* has also labial enameloid plications at the base of the crown, but only in lateral teeth (Siversson, 1996) and in the distalmost latero-posterior teeth (Siversson, 1992). One tooth has strong and short folds only below the cusplets. Possibly, some of *Archaeolamna* teeth with plications reported by Siversson (1992; 1996) belong to *Cretodus* (Cappetta, 2012). *Cretalamna* is another Cretaceous lamniform taxon with a general tooth morphology similar to that of the teeth under examination, but its central cusps have smooth faces (Cappetta, 2012) and the teeth are less robust and of smaller size. Large-toothed Late Cretaceous

Lamniformes include also *Cretoxyrhina* (Shimada, 1997b), *Cardabiodon* and *Dwardius* (Siversson, 1999), but their teeth are very different from those of IGVR 91032, which are broader, have bigger and divergent cusplets and enameloid plications. Based on all these features, the Italian specimen matches better the description of *Cretodus*. Cappetta (2012) reports four species included in the genus (*C. semiplicatus* Münster in Agassiz, 1843; *C. crassidens* Dixon, 1850; *C. longiplicatus* Werner, 1989 and *C. gigantea* Case, 2001), while Schwimmer et al. (2002) consider *C. crassidens* a junior synonym of *C. semiplicatus*. Considering that the taxonomy of *Cretodus* and related species is strongly debated and in need of a global revision including also the specimen under study, we limit the identification of Italian specimen to an indeterminate species of the genus *Cretodus*, pending further taxonomic investigation.

The placoid scales, which are reported for the first time in the genus *Cretodus*, have limited or no taxonomic value and cannot help in establishing its taxonomic affinity (Reif, 1985). However, their general morphology can be used to infer the swimming behavior and the ecological niche occupied by a shark (Reif, 1985). In living sharks, the placoid scales with narrowly spaced ridges (0,04-0,08 mm) occur in fast hunting pelagic sharks (*sensu* Reif, 1985), such as *Isurus oxyrinchus*, *Lamna nasus* and *Carcharodon carcharias*. The scales of IGVR 91032 resemble those of the aforementioned sharks, especially those of *Isurus* and *Lamna*. Therefore, *Cretodus* might have had a similar swimming behavior. Comparing IGVR 91032 placoid scales with those of other Cretaceous lamniform sharks, some scales (Fig. 9B, D, E) are similar to those described in a cardabiodontid shark by Dickerson et al. (2013), sharing a drop-like crown. Other scales (Fig. 9F) show some resemblance with the placoid scales of the anacoracid *Squalicorax* (Shimada and Cicimurri, 2005). The placoid scales of the shark under examination are quite different from those of *Cretoxyrhina mantelli* figured by Shimada et al. (2006) and Diedrich (2014). *C. mantelli*, which is by far the most common lamniform shark in the 'lastame', has placoid scales with parallel ridges that are thinner and less prominent than those of IGVR 91032. The presence of the same placoid scales in different samples from slab A is further evidence that slab A is not a composite made of different shark parts and that the association with the turtle remains is not an artifact.

5.2. The turtle

Class REPTILIA Laurenti, 1768

Subclass DIAPSIDA Osborn 1903

Order TESTUDINES Linnaeus, 1758

Superfamily CHELONIOIDEA Baur, 1893

Chelonioidea indet.

(Figs. 2, 11-12 and 14)

Description

A pellet-like accumulation of turtle bones occurs on slab A alongside the shark vertebral column (Fig. 2). It is roughly elliptical in outline with main and lesser diameters that are 1564 mm and 1080 mm long, respectively. Skeletal elements are totally disarticulated, but they are grouped together and sometimes closely packed. Parts of some bones split away when the slab was extracted and removed; some of them were lost, but others have been reattached to the accumulation (Fig. 11B). Some of the latter have clearly been pasted in their original position (for example, half of a large shell fragment; Fig. 11B). Others are set on a base of glue, so it is impossible to know whether their position is the original or not (for example, the large shell fragments associated with the calcified cartilage fragments). Finally, a few metapodials, phalanges and fragmentary long bones are clearly not in their original seat. As noted above, also three fragments of tessellated calcified cartilage belonging to the shark were mistakenly added. A lateral tooth of the shark occurs at the periphery of the accumulation (Fig. 15). Although the fragmentarity and the overlapping by other elements prevent the identification of many bones, some can reliably identified and others can be tentatively referred. They include a hyoid, six or seven cervical vertebrae, many plates and fragments of the plates from the shell, possible fragmentary thoracal ribs, possible fragments of the shoulder and pelvic girdles, a left humerus, two femurs, a tibia and a fibula, a possible ulna, a few possible basipodials, and several elongated metapodials and phalanges.

At least seven very elongated and narrow peripheral plates can be identified at the margins of the accumulation. They range from 198 to 212 mm in length. Most of them are associated in two groups of three elements (Fig. 11). At least 13-15 flat and broad bone fragments can be referred to the other shell plates (carapace or plastron). They have irregular shapes and often jagged margins, so they are clearly parts of broken plates of the shell. They range from 6 to 34 cm in length and show different patterns of ornamentation on the exposed surface: pits and irregular grooves forming a vermicular texture, scattered small pits and thin grooves, or short and parallel grooves and elongated pits that probably were arranged in a radial pattern in the complete element. No scute sulci can be identified. The external surface of the carapace and plastron elements of some sea

turtles has a similar texture and poorly developed or absent scute sulci (Mulder, 2003; Lehman and Tomlinson, 2004; Zangerl and Sloan, 1960).

The left humerus is exposed in ventral view and is 320 mm long but it is incomplete distally (Fig. 12). Taking as reference the humerus of *Atlantochelys mortoni* (see below), the minimum length of the complete element would be about 370 mm. The short shaft is relatively slender, straight, and waisted in the middle (minimum width is 55 mm). Its extremities are much expanded, the proximal more than the distal one. The medial process is large and long; its extremity is slightly expanded and apically rounded. The caput is hemispherical, slightly offset, and about as broad as the medial process. It is set in a broad depression and is distinctly separated from the adjoining processes. The well-developed lateral process is immediately distal to the caput. Its outline is trapezoidal but its worn surface suggests that its original shape could have been slightly different. The distal part of the humerus is broken and does not preserve the distal condyles.

The right and left femora are exposed in ventroposterior and anterior view, respectively. They are 340-350 mm long, only slightly shorter than the humerus. The major trochanter of the right femur is not highly elevated compared to the femoral head, but its apical part is probably damaged and worn. The minor trochanter is comma-shaped, broad but low and smaller than the major trochanter. The huge caput is necked and strongly offset forming a high angle with the axis of the diaphysis (ca. 145°). In dorsoventral view, the diaphysis is comparatively slender and slightly sigmoid; in anteroposterior view, it is straight and markedly waisted in the middle. The distal part of the element is much expanded dorsoventrally.

Metapodials and phalanges of digits II-IV of chelonoid turtle manus have a similar slender and elongated shape. As metapodials and elongated and slender phalanges have an overall similar morphology, they cannot be distinguished in the disarticulated specimen IGVR 91032. At least 13 slender and straight bones expanded at both extremities; with flat articular surfaces and ranging in length 80-120 mm are probably metapodials or slender phalanges. Other six stouter or shorter bones (length ranges 4-5.8 cm) of similar morphology are phalanges, probably from the pes and manual digit I. Two very robust and large bones (the complete one is 8.5 cm long), much expanded at the proximal extremity and with a well-formed distal articular condyle (the complete one) can be the metacarpals I, while two other bones with a similar morphology, but less expanded proximally and smaller (5.1-5.2 cm long) could be the metatarsals I (under the assumption that elements of the hind limb flippers are smaller than those of the forelimb as in *Protostega gigas*, *Archelon ischyros* and living chelonoids). Long bones show a preferential orientation of their axes, which are in many cases aligned with the axis of the shark vertebral column (Fig. 11C). This alignment is evident in

the long bones preserved in the core of the accumulation (Fig. 11C1), while it is not apparent in those preserved at its periphery (Fig. 11C2).

Discussion

A detailed taxonomic study of the turtle remains associated with the shark is beyond the scope of this paper and it is still in progress and will be published elsewhere (Rabi et al., in prep.). Only some preliminary comparisons with *Protosphargis veronensis* Capellini, 1884, the only taxon described to date from 'lastame', is attempted here. Nevertheless, a high taxonomic diversity of marine turtles from Scaglia Rossa is actually present (Chesi, 2008; Dalla Vecchia et al., 2005; Villa et al., 2014; Márton Rabi, pers. comm.) and an extensive revision is underway. Villa et al. (2014) briefly described the turtle specimen of IGVR 91032, with the identification of some skeletal elements, in the ambit of a preliminary note on the chelonoid turtles from 'lastame'. They did not attempt any further taxonomic attribution. The morphology of the humerus of IGVR 91032 is typical for the Chelonioidea (the thalassic type humeri as described by Weiland, 1900; see also Młynarsky, 1976; Hirayama, 1994, 1997; Wyneken, 2001; Parris et al., 2014): longer than femur, with a nearly straight shaft, and with the lateral process located distal to the caput humeri (Chesi and Delfino, 2007; Hirayama, 1994). Other features supporting the referral to the Chelonioidea, besides the fact that the specimen is preserved in marine deposits, are elongated metapodials and phalanges of digits I-III lacking movable articulations and scute *sulci* on plastron absent (Chesi and Delfino, 2007; Hirayama, 1994, 1998; Lehman and Tomlinson, 2004). The humerus is poorly preserved in the holotype of *P. veronensis* to allow comparisons (see Capellini, 1884). The large specimen MSNV V.10670 was referred to *P. veronensis* by Cigala Fulgosi et al. (1980) and preserves both humeri resembling that of IGVR 91032 (JA pers. obs., *contra* Villa et al. 2014). However, the attribution of MSNV V. 10670 to *P. veronensis* is not supported by any published comparison with the holotype and the latter must be considered the only unequivocal specimen of this species. Tibia, fibula and peripheral plates of IGVR 91032 are similar to those of the holotype of *P. veronensis* (see Capellini, 1884). However, the femora are less massive than those of this taxon (see Capellini, 1884: Pl.VII, figs 1-3). The femur is just slightly shorter than the humerus like in a few marine turtles (e.g., *Protosphargis* and other taxa as *Toxochelys* and *Desmatochelys*; Lehman and Tomlinson, 2004); this is also considered a plesiomorphic feature (Lehman and Tomlinson, 2004).

As noticed by Villa et al. (2014), the turtle IGVR 91032 was a large individual. Taking as model the skeleton of *Desmatochelys lowi* figured in Hirayama (1994) and using the minimum humeral length

estimate as reference for proportions, the anteroposterior length of the carapace is 1830 mm, but taking as model the skeleton of *Protostega gigas* (same source) it is 1260 mm, because its carapace is less elongate than that of *Desmatochelys lowi*. Using the femoral length of *Protostega gigas* as reference for proportions, the length of the snout-tip of the tail of the turtle IGVR 91032 is 2320 mm and the anteroposterior length of the carapace 1470 mm. Capellini (1884) estimated the total length of *Protosphargis veronensis* as about three meters taking as model the living leatherback turtle (*Dermochelys coriacea*), but its femur is only 297 mm long and that estimate is probably exaggerated. The femur and humerus of a specimen of *Protostega gigas* are 270 and 340 mm long, respectively (Wieland, 1906).

6. Turtle-shark association: taphonomic and paleoecological inferences

The shark-turtle association is mostly preserved within a thin calcareous marly layer between two limestone strata, so it is now lying at the top of the underlying stratum or at the base of the overlying one. According to the finder and quarry owner, IGVR 91032 occurs at the top of the underlying stratum. This is the case of most vertebrate remains found in the 'lastame'. As far as we know, no vertebrates have been found inside a limestone bed.

The shark tooth set can be considered a 'disturbed associated tooth set' (*sensu* Shimada, 2005) because there is no way to know whether the detached teeth (Fig. 6) have been glued into their original position or not; probably, this is not always the case. The vertebral count is not complete because a karst cavity existed between the two slabs A and B, according to the discoverer and quarry owner. Therefore, a segment of the vertebral column originally present between the two preserved ones was lost. Part of the vertebral column was possibly lost also during the extraction of the fossil-bearing slab. The vertebral centra on slab A are arranged in a rectilinear row (although undulating) with the teeth occurring to its left extremity; disarticulation of the vertebral column is moderate. Vertebral centra 20-31 probably detached from the slab when it was removed and were later glued into their original place. At least 14 other specimens of lamniform sharks (most of them belonging to *Cretoxyrhina*) were collected from the 'lastame' in the area of Sant'Anna d'Alfaedo, consisting of vertebral column segments, often associated with teeth and sometimes preserving also traces of calcified cartilage (Cigala Fulgosi et al., 1980; Dalla Vecchia et al., 2005; pers. obs.). The extent of the segments of the vertebral column is clearly limited by the impossibility of extracting or preserving larger slabs. Originally, all segments were probably more complete than they appear but part of them was destroyed, lost or remained *in situ*. The longest recovered segment preserves 155 vertebrae associated with 34 teeth (IGVR 36371; Cigala Fulgosi et al., 1980). The vertebral columns show various degrees of disarticulation. It ranges from nearly perfectly articulated segments (IGVR 47789), to long segments of articulated centra with local disarticulation and a tooth accumulation at the end of the vertebral column (IGVR 45305), short segments of articulated centra alternated with zones of disarticulated centra, but always scattered around the longitudinal axis of the shark body (also with a tooth accumulation at one end of the vertebral column; e.g., IGVR 81375, IGVR 36371), to an elongate set of disarticulated centra (IGVR 45308). There is no evidence of preferential orientation of the skeletal elements, embrication or accumulation in piles caused by tractive currents or extreme dispersal due to water turbulence. The remains seem to represent various degrees of disarticulation of slowly decaying bodies exposed for a long time on the sea bottom under low energy conditions. No other shark but IGVR 91032 is associated with

other vertebrate remains. The state of preservation of IGVR 91032 (slab A) is not unlike that of the other sharks of the 'lastame'. The arrangement in a line of the vertebrae on slab B is possibly artificial (they are all glued to the slab) and their association to those of slab A is made *fide* the quarry owner and discoverer of the specimen.

The mega-pellet made of turtle bones is interpreted as the last meal of the shark that was still in its stomach when the shark carcass deposited at the sea bottom. The following evidences support this interpretation.

1) The close association of shark and turtle remains.

The Scaglia Rossa of the Trento Plateau is interpreted as a hemipelagic deposit without contributions by gravity resedimentation (turbidites and debris flow) (Massari and Savazzi, 1981). The slabs IGVR 91032A-B do not contain evidences of direct or inverse gradation, centimeter-long clasts floating in the matrix, channeling, tractive structures, embrication or preferred orientation of skeletal elements and other objects, which are related to turbidity currents, debris flows and tractive currents. Those structures were never reported from the 'lastame'. Therefore, there is no evidence that the shark-turtle association as well as the pellet-like accumulation were produced by marine currents, turbidites or debris flows. It is intuitive that turbulence, currents and high environmental energy in general would totally disarticulate both the turtle skeleton and the shark vertebral column, scattering the skeletal elements.

The overall density of macrovertebrate fossils within the 'lastame' is low and vertebrates are very rare. The relatively high number of available specimens is due to the intensive quarrying since at least mid-1850ies. The fortuitous deposition of two different and large vertebrates in the same spot is unlikely. Thus, a casual association of the shark and turtle remains is highly improbable.

2) The arrangement of the turtle bones.

The shape of the accumulation supports its identification as a gastric content because processes affecting the carcass of a vertebrate are dispersive: it loses pieces up to the complete disarticulation (Davis and Briggs, 1998; Schäfer, 1972). Abiotic processes usually lead to the dispersal of the skeletal elements, not to their accumulation. Accumulation is sometimes caused by high-energy processes (e.g., running waters), predator activity (e.g., in caves), mass deaths, or presence of traps, but it regards more individuals in most cases, not the clumping of the disarticulated and partial skeleton of a single individual (Behrensmeyer, 1991). As seen above, IGVR 91032 is preserved in a fine-grained and low energy deposit and the elements of the shark are either articulated or closely associated (even the small placoid scales), which indicates little abiotic post-mortem disturbance.

At least other nine specimens of marine turtles have been collected from the ‘lastame’ (Chesi 2008; Villa et al., 2014; pers. obs.). None is preserved as a pellet-like accumulation and the only very disarticulated specimen is that associate with a mosasaur (IGVR 45299; under study). Four specimens with a size comparable to that of the turtle under examination (IGVR 45300, IGVR 91051, MSNV V.10670 and the holotype of *Protosphargis veronensis*, MGGC 8841) suffered only moderate disarticulation (Fig. 13), in agreement with the conditions of slow decaying of carcasses exposed for a long time at the sea bottom under low energy conditions, as supposed for the sharks.

The turtle bone accumulation under examination closely resembles fossil gastric pellets and ejecta produced by vertebrates and containing vertebrate remains (Dalla Vecchia and Chiappe, 2002; Holgado et al., 2015; Myhrvold, 2011; Sanz et al., 2001; Schweigert et al., 2001). The preferential orientation of long bones within the accumulation (Fig. 11C) suggests that it formed in a constrained space as the esophagus (Holgado et al., 2015). Many long bones of the turtle are parallel to the long axis of the vertebral column, which is also the axis of the esophagus. This orientation is observed mainly in the core of the accumulation (compare Fig. 11C1-2), because the dismemberment of a pellet-like gastric content that is slowly rotting in still water plausibly starts from its periphery.

The stomach of a great white shark (*Carcharodon carcharias*) is about 20% of its body length, it can expand to accomodate large preys and its maximum capacity is about 10% of the shark's total weight (Aidan Martin, 2003). A 6.4 meter-long white shark is reported to weight about 3,300 kg (Ellis and McCosker, 1995); a 1.8 m-long leatherback sea turtle weights 360 kg (Nahill, 2014). Therefore, we consider the size of the turtle bone accumulation not to be too large for the stomach of a 6.61-7.76 m-long shark.

3) The position of the accumulation with respect to the shark.

The stomach of the great white shark is located just posterior to the gills (Aidan Martin, 2003; for general anatomy of elasmobranch digestive system see Holmgren and Nilsson, 1999). Based on the distance between the first vertebra and the last gill slit, the stomach should begin 1085 mm distal to the first vertebra in 6.6 m-long white sharks. This is approximately the same distance between the first preserved vertebra of IGVR 91032 and the closer margin of the turtle bones accumulation. Furthermore, the latter is as close to the vertebral column of the shark as it was the stomach. Thus, the mega-pellet is located in the place of the shark stomach.

4) The presence of broken bones.

Several skeletal elements of IGVR 91032 turtle (i.e., many bones of the shell, the humerus, the tibia, and the presumed ulna, scapular processes and proximal part of the coracoid) are evidently

broken (Fig. 14). Damage was not produced during the extraction and transfer of the slab, because the fractured surface is not as sharp and light in color as in a freshly broken fossil bone and it is locally covered by a veneer of rock. No plausible alternative to predation or scavenging can be found to explain a high number of broken bones in a marine turtle deposited in a open marine and low energy environment. Our observation is further supported by the fact that one of the diagnostic features of gastric pellets is the presence of bones that have been broken by the bites of the predator/scavenger (e.g., Holgado et al., 2015; Myrhvold, 2001).

5) A shark tooth embedded within the accumulation.

A lateral *Cretodus* tooth is embedded within the turtle bone accumulation (Figs 11 and 15). This tooth differs from the other 120 teeth found in the slab in having a blunt apex and margins and an opaque surface. This suggests that the tooth was etched by the hydrochloric acid produced by secretory cells in the shark stomach, which helps soften and break-down the bones of the swallowed preys or carcasses. In addition, many bones show edge rounding, finely pitted surfaces and exposure of the cancellous bone that could be caused by corrosion produced by the digestive acid (Sanz et al., 2001; Myrhvold, 2011). However, a similarly worn surface occurs in other turtle remains from 'lastame' that are only moderately disarticulated (e.g., IGVR 91051) and could be related to a long exposure of the skeleton on the sea bottom in absence of sedimentation. Nevertheless, the state of preservation of the tooth indicates that digestive acid etching mostly caused the features of the turtle bones listed above. This is also supported by the good state of preservation of the shark vertebral centra. Because of the extreme rarity of *Cretodus* in the Scaglia Rossa Formation, it is highly unlikely that the tooth belongs to another individual. The most parsimonious hypothesis is that the tooth was lost by the shark while biting the turtle and was then swallowed with it.

6) Living sharks use to feed on marine turtles.

A large Cretaceous shark feeding on a marine turtle is not unexpected. The literature dealing with the presence and even dominance of chelonoid turtles in the diet of large living sharks (e.g., *Carcharhinus leucas*, *Carcharhinus longimanus*, *Negaprion brevirostris*, *Galeocerdo cuvieri*, *Sphyrna* sp. and *Carcharodon carcharias*) is vast (e.g., Fergusson et al., 2000; Heithaus, 2001; Long, 1996; Stanczyk, 1981; Witzell 1987; Simpfendorfer et al., 2001). Long (1996) reports the attack of adult individuals of *Carcharodon carcharias* (the great white shark) with an estimated length of 5-5.5 m on two specimens of leatherback turtles with a total carapace length of 1580 and 1620 mm. A shark with an estimate length ranging 6.61-7.76 m could afford to predate or scavenge a turtle with a carapace that could be 1230 to 1830 mm long.

Evidence of shark predation or scavenging on marine turtles is reported in the Cretaceous fossil record, although most of it consists of bite or tooth marks and teeth embedded in the bones (Schwimmer et al., 1997; Shimada and Hooks, 2004). Only in one case, shark remains were found associated with probably digested toxochelyid turtle elements, together with remains of a mosasaur and an ichthyodectid fish (Druckenmiller et al., 1993). The here reported specimen is the second fossil record of a marine turtle ingested by a shark and the first evidence of possible dietary preference of *Cretodus*.

The preservation of ingested vertebrates in predatory fishes is unusual, but not rare in the fossil record. For example, an high percentage of the fossils of the small to medium-sized osteichthyan *Prionolepis* from the Cenomanian of Lebanon have one and even two smaller osteichthyans (usually around one third the total length of the predator) in their stomach (FMDV, pers. obs.). Sharks were (and are) among the most active predators and scavengers in the seas. Martin and Rothschild (1989) reported a specimen of *Cretolamna* with remains of the osteichthyan *Xiphactinus* as stomach content; Shimada (1997a) described a nearly complete specimen of *Cretoxyrhina mantelli* associated with many bones of *Xiphactinus audax* scattered along its body remains; and Kriwet et al. (2008) reported a Paleozoic xenacanth shark with two amphibians preserved in its stomach. It is impossible to establish whether the last meal caused the death of the predator/scavenger or not in those cases as well as in the case of IGVR 91032. As feeding is usually the principal activity of fish everyday life, it is plausible that death could sometimes catch them with a full stomach. Furthermore, sharks can store food in their stomachs for prolonged periods of the order of months (like the great white shark; see Aidan Martin, 2003)

As a general rule, it is impossible to establish whether the turtle was attacked when alive or it was scavenged as a carcass (Shimada, 1997). However, the elements of the hyoids and the distal elements of the limbs are among the first to detach and get lost in a rotting and floating carcass (Schäfer, 1972). In fact, the other better-articulated turtles from 'lastame' preserve very few metapodials and phalanges or none. Therefore, the presence of those elements in the accumulation would support predation rather than scavenging of a floating carcass. If the turtle was already dead when the shark attacked it, it was not in an advanced stage of decomposition.

The large size of *Cretodus* and its robust teeth could be a specialization for feeding upon the large chelonoid turtles with reduced carapaces that diversified and spread in the Late Cretaceous seas all over the world (Everhart, 2005; Hirayama, 1997).

5. Conclusions

A large, over 6.5 meters-long lamniform shark *Cretodus* from middle Turonian of Italy is preserved with closely associated remains of a big cheloniod turtle (estimated length about 2 meters) alongside its articulated vertebral column. The fossil is the most complete specimen of *Cretodus* described to date in literature and represents the first record of the genus in Italy. The strict analogy of placoid scales of IGVR 91032 with those of extant sharks like *Isurus* and *Carcharodon* indicates that *Cretodus* was probably a fast hunting pelagic shark.

The accumulation of the turtle bones in a circular pellet, their state of preservation, the bite marks, the presence of a shark tooth embedded among the remains and the shark's articulated vertebral column alongside the turtle pellet allow to interpret these remains as stomach content of *Cretodus*. This shark-cheloniod turtle fossil association is an exceptional find, because only few reported records of predation/scavenging of sharks on turtles exist and none including so large and well-preserved specimens. The stomach content offers direct evidence about the diet of *Cretodus*, but also offers some evidence for discerning a scavenging or predatory lifestyle of the animal. The preservation of some elements of the turtle skeleton, usually easily movable and lost in a rotting carcass (e.g., hyoid, phalanges and metapodials), is in favour of predation rather than scavenging.

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Figures captions

Fig. 1. Location of the site. The quarry that yielded the specimen IGVR 91032 in the surrounding of Sant'Anna D'Alfaedo (Verona) is indicated by an asterisk. [single column size]

Fig. 2. The specimen IGVR 91032. Above: orthophoto; below: interpretative drawing. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 3. Lithology of the slab IGVR 91032A. A) Transverse section of the slab showing the flaser-nodular texture that is characteristic of the 'lastame' interval of the Scaglia Rossa from Lessini Mountains. The vertebrate remains are preserved at the upper surface of the slab within a layer of reddish calcareous marl. B) Thin section of sample A7 showing the microfacies of a calcareous nodule: planktonic foraminiferal wackestone with marginotruncanids, *Dicarinella hagni*, heterohelcidids and hedbergellids (the photo is taken with parallel nicols). Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [1.5 column size]

Fig. 4. Location of the samples on slab IGVR 91032A. Samples (from A1 to A6) were collected for placoid scales extraction and micropaleontological analyses. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 5. Age of IGVR 91032. Turonian-Santonian biostratigraphy of calcareous plankton after (Ogg and Hinnov (2012)) and the stratigraphic position of IGVR 91032, which is indicated by the grey band. [single column size]

Fig. 6. Teeth of *Cretodus* sp. (IGVR 91032). Graphic sketch of the specimens indicative of the position of the skeletal elements. Color code: blue, calcified cartilage remains; yellow, *in situ* teeth. Non-colored teeth were glued to the slab. Numbers are progressive from no. 1 to no. 120. Tooth no. 111 (box) is preserved within the turtle remains. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig 7. Representative teeth of *Cretodus* sp. (IGVR 91032). A) anterior tooth (no. 3), labial view; B) anterior tooth (no. 11), lingual view; C) anterior tooth (no. 9), labial view; D) lateral tooth (no. 61), labial view; E) lateral tooth (no. 59); F) lateral tooth (no. 20), lingual view; G) latero-posterior tooth (no. 94), labial view; H) latero-posterior tooth (no. 103), lingual view. Numbers match those in Fig. 6. Scale bar equals 2 cm. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 8. Vertebral column of *Cretodus* sp. (IGVR 91032). Drawing of the shark remains on slab A (A) and slab B (B) with the vertebrae glued to the slab that are highlighted in yellow. Particular of vertebra A30 in anterior view (C) and segment of vertebral column A21-29 (D). Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities

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Fig. 9. Placoid scales of *Cretodus* sp. (IGVR 91032). (A1-3) tricuspid scale, with broad rhomboid crown, anterior, posterior and lateral views; (B1-3) single cusp scale, with rhomboid crown, anterior, lateral and posterior views; (C1-3) single cusp scale, with slender rhomboid crown, anterior, lateroposterior and anterolateral views; (D1-3) scale with broad rounded crown, lateral and posterior views; (E1-3) single cusp scale, with cuneiform crown, anterior, lateral and posterior views; (F1-2) single cusp scale, with broad rhomboid crown, upper and lateral views; (G) scale with drop-like crown, anterior view; (H) single cusp scale, with broad rhomboid crown, anterior view. Scale bar equals 100 μ m. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [1.5 column size]

Fig. 10. Calcified cartilage of *Cretodus* sp. (IGVR 91032). (A) fragment glued within the turtle remains (B) the largest fragment close to the teeth accumulation (C). Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 11. Chelonioid turtle remains of IGVR 91032. A) Photo of the specimen. B) drawing and identified bones. C) rose diagram showing the long bone axis orientation with respect to the axis of the shark vertebral column (axis 90-270° in the diagram) in the core of the accumulation (C1), at the periphery (C2) and in both of them altogether (C3). Colors: red = the lateral tooth of the shark embedded within the turtle remains; blue = fragments of the shark's calcified cartilage erroneously glued to the turtle remains; green = the glued turtle remains. Abbreviations: as, astragalus; co, coracoid; cdv, caudal vertebrae; cv, cervical vertebra; fe, femur; fi, fibula; h, humerus; hy, ceratobranchial I of the hyoid apparatus; mcl, metacarpal I; mph, metapodial or phalanx; mtI, metatarsal I; mtV, metatarsal V; ph, phalanx; pp, peripheral plate of the carapace; pu, pubis; sc, scapula; sh, fragment of the shell (carapace or plastron); svc, vertebral centra of the shark; th, tooth; ti, tibia; tr, thoracal rib; u, ulna. Abbreviations in brackets indicate left elements. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 12. Chelonioid turtle of IGVR 91032, left humerus in ventral view. A) photo of specimen; B) drawing. Abbreviations: ch, caput humeri; lph, lateral process; mph, medial process. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [1.5 column size]

Fig. 13. Marine turtles from the 'lastame' of Sant'Anna d'Alfaedo (Verona). A) MGGC 8841, holotype of *Protosphargis veronensis* (from Capellini, 1884, pl. 2), the slab measures 150x185 cm; B) MSNV V.10670, Chelonioidea indet. Scale bar = 1 m. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 14. Damages on the turtle bones referable to shark bites of IGVR 91032. A) Peripheral plate with a long and acute notch; B) one of the bones tentatively identified as scapular processes

with a clearly broken extremity; C) a relatively flat and large bone with a jagged margin, possibly a fragment of the shell; D) the broken distal end of the humerus; E) the fragmentary bone tentatively identified as the proximal part of a coracoid (compare its superficial texture with that of the nearby metapodial/phalanx); F) the bone tentatively identified as an ulna, with a clearly broken distal extremity; G) the tibia with a broken distal extremity. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [full width size]

Fig. 15. Lateral tooth of *Cretodus* sp. (IGVR 91032) preserved with the turtle bones. The scale bar is in millimetres. Photographs printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved. [single column size]

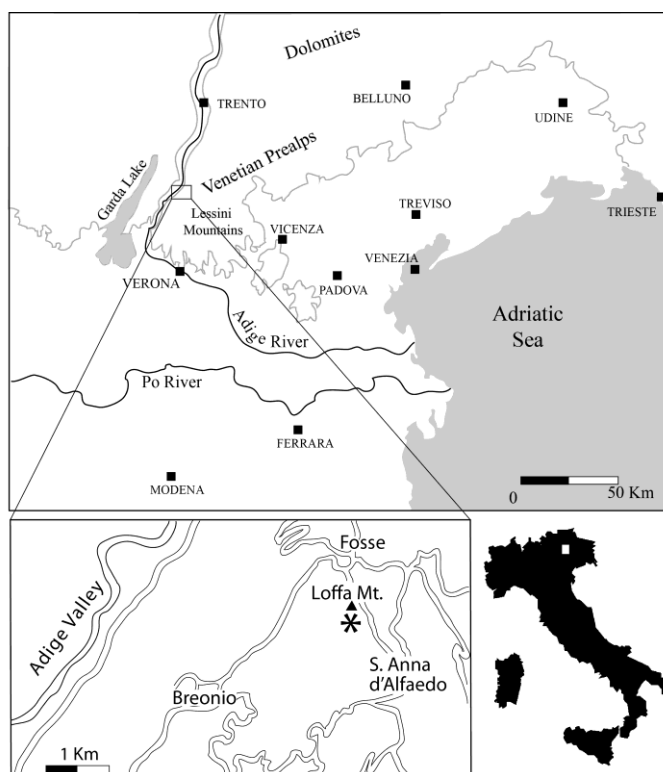


Figure 1



Figure 2

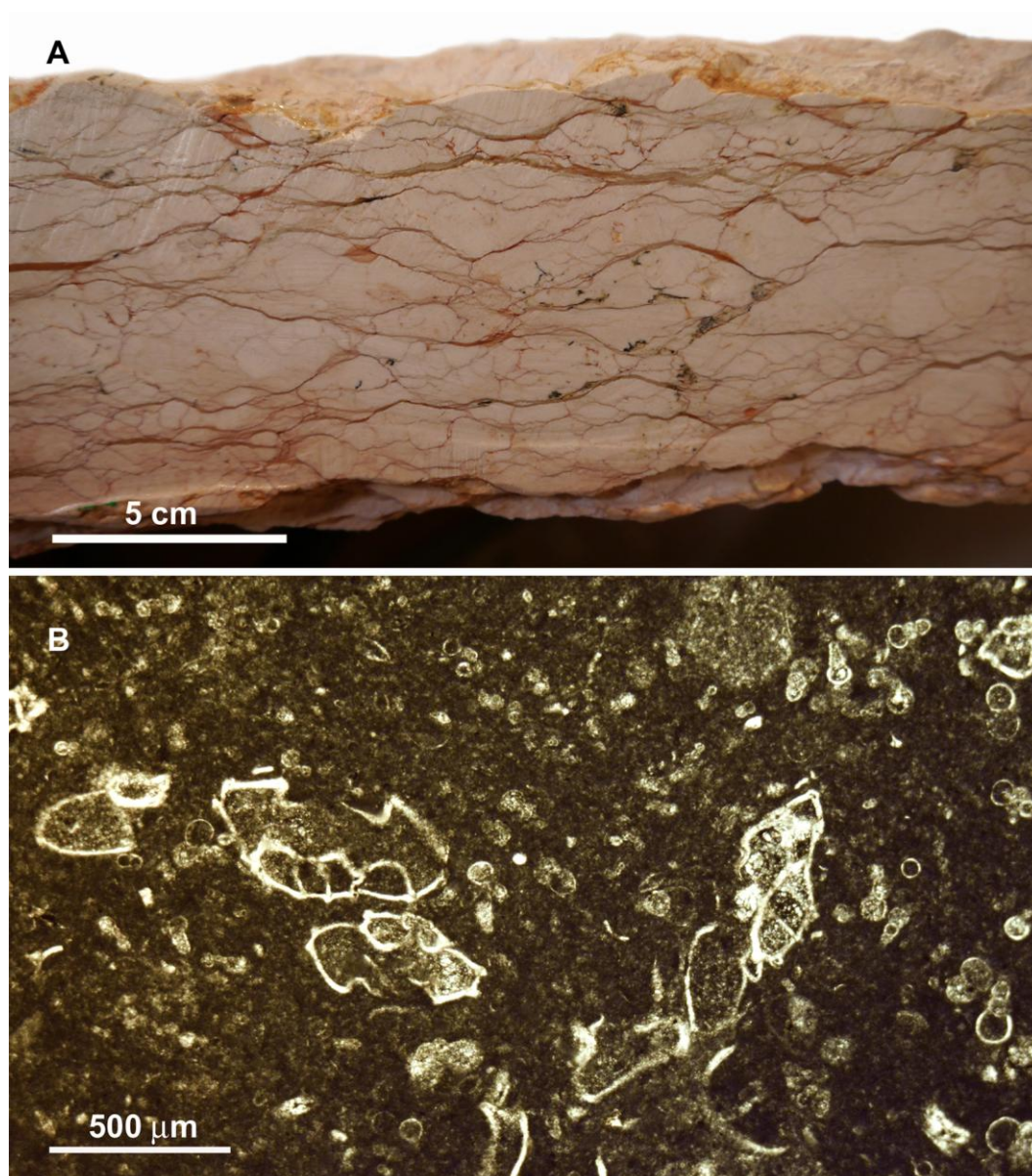


Figure 3

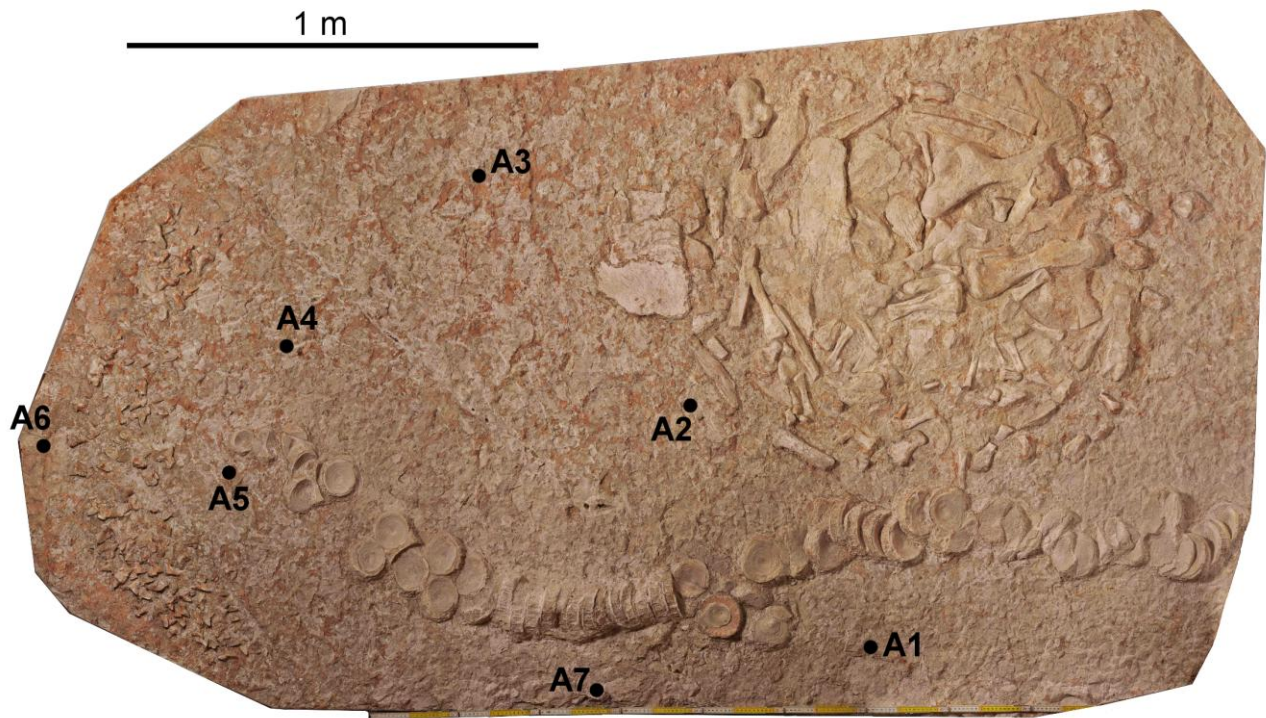


Figure 4



Figure 5

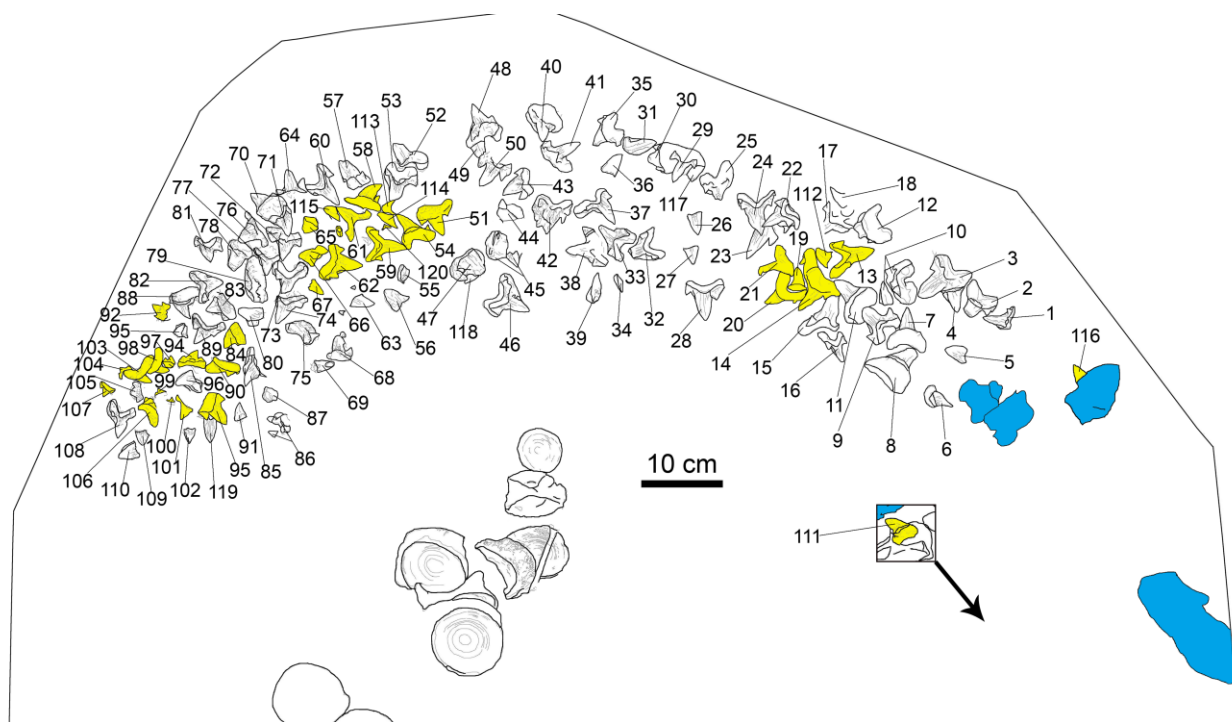


Figure 6

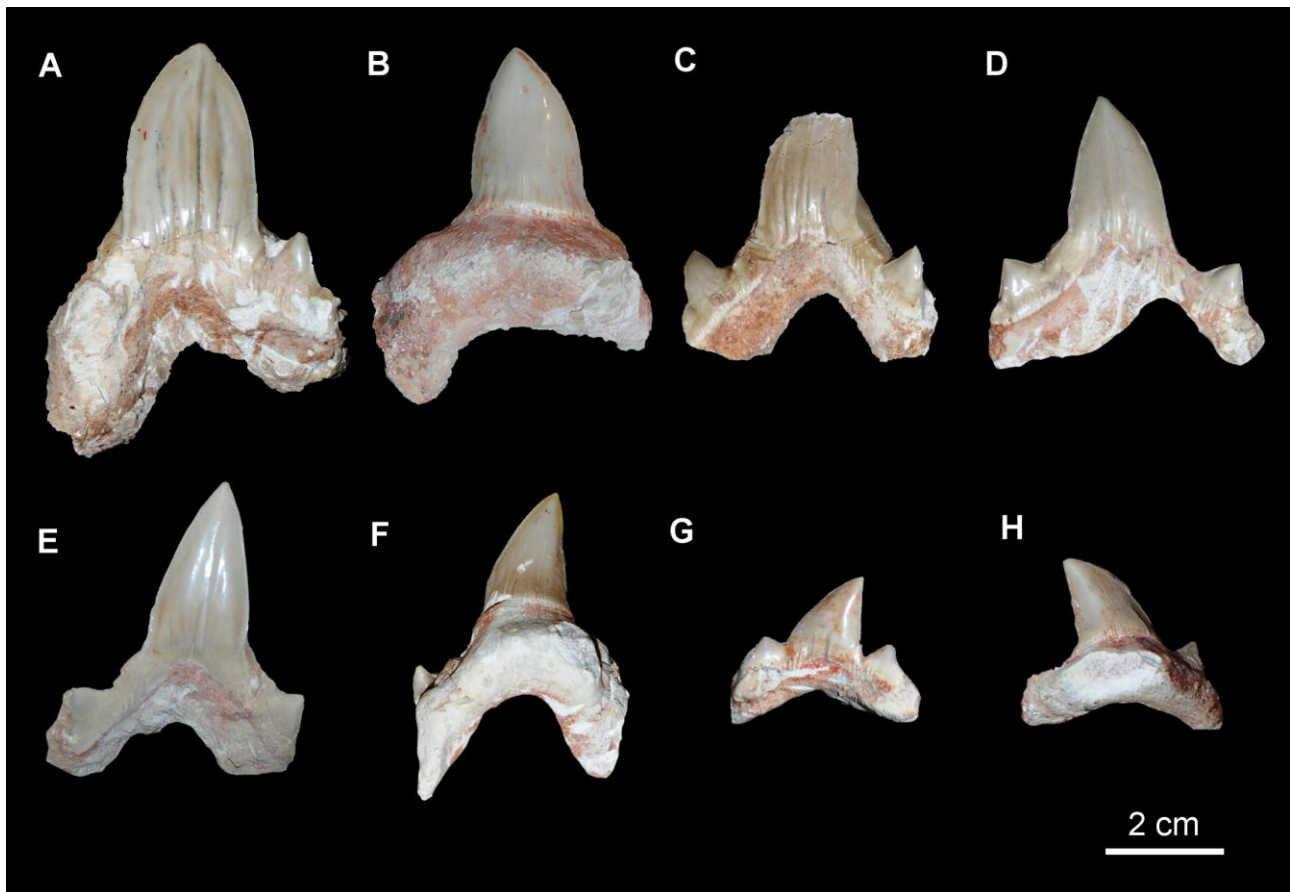


Figure 7

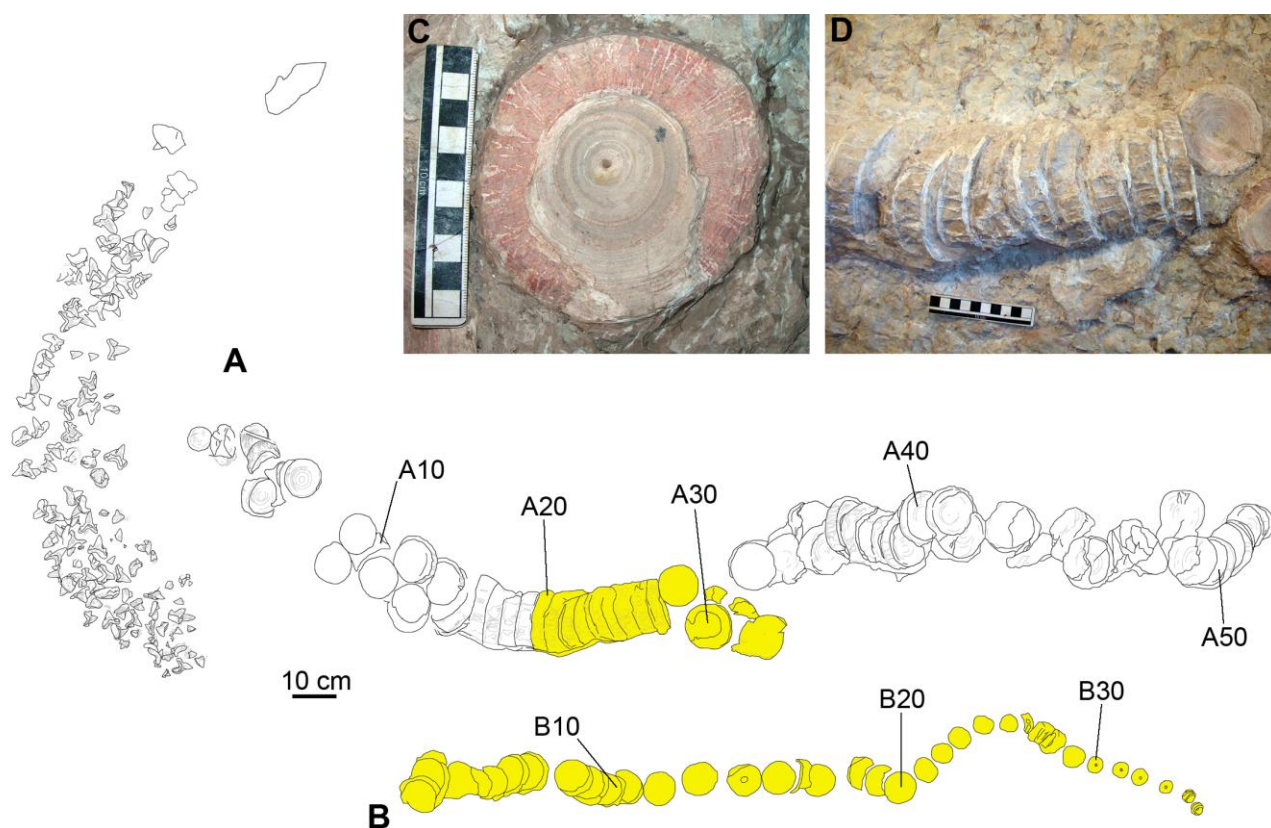


Figure 8

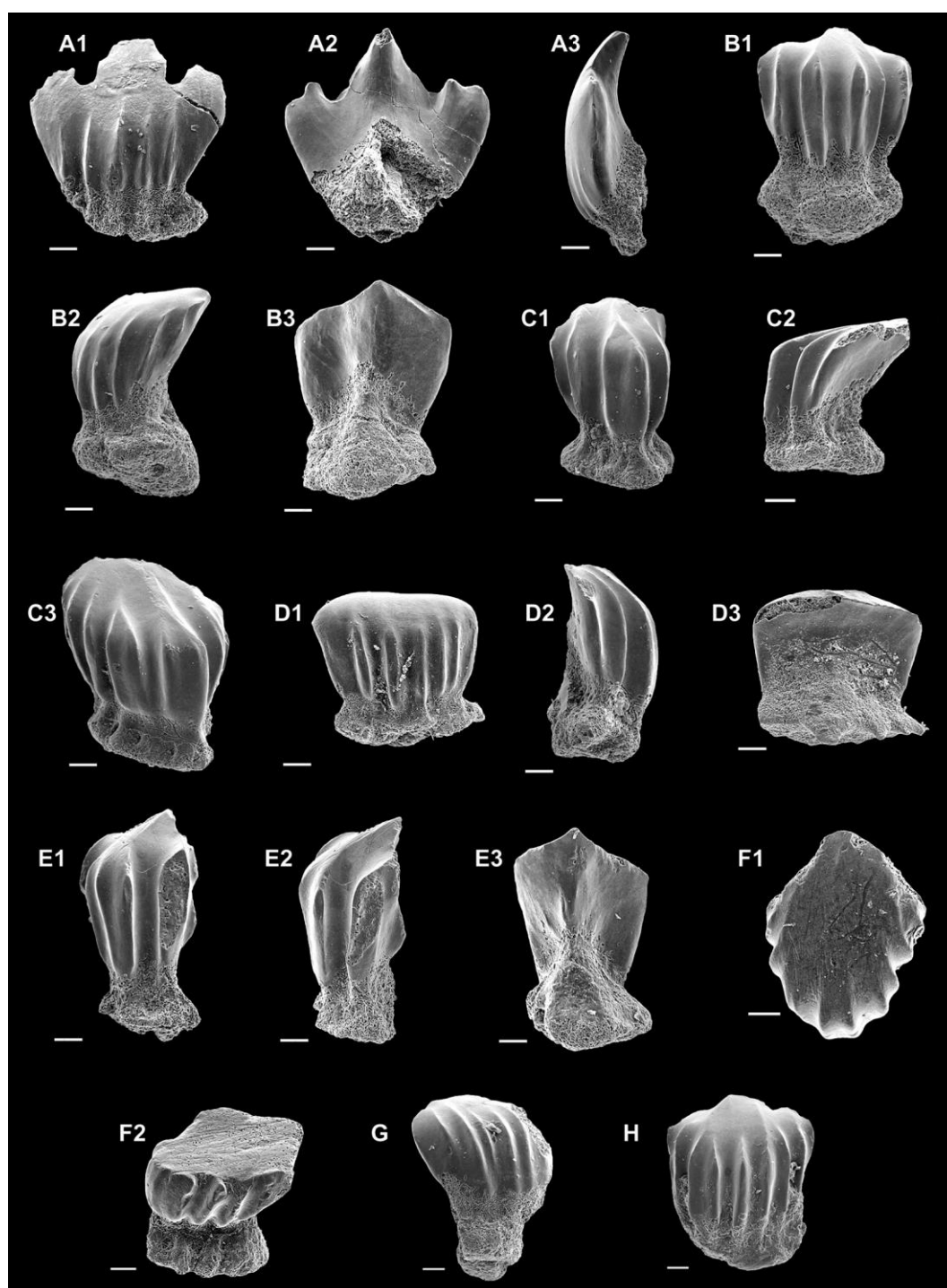


Figure 9

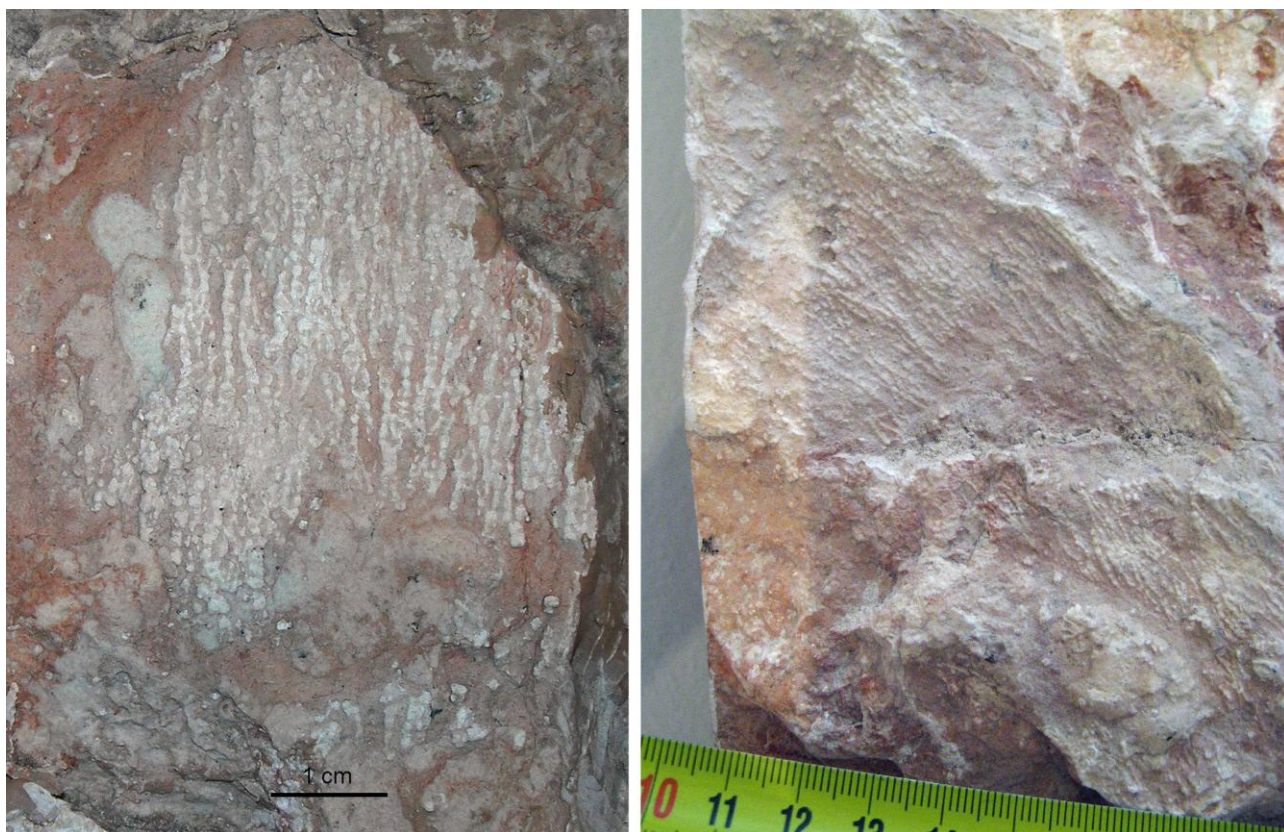
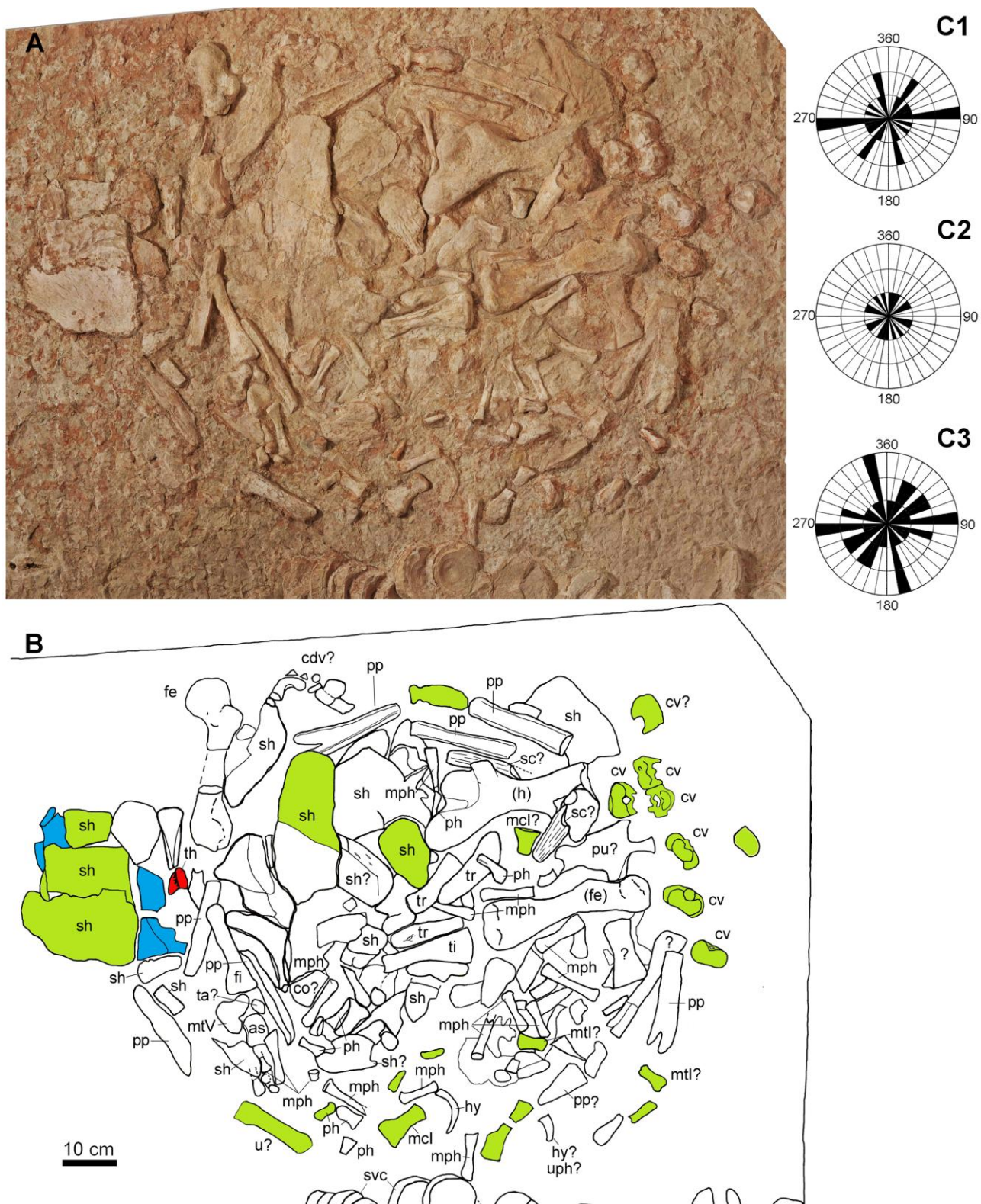


Figure 10



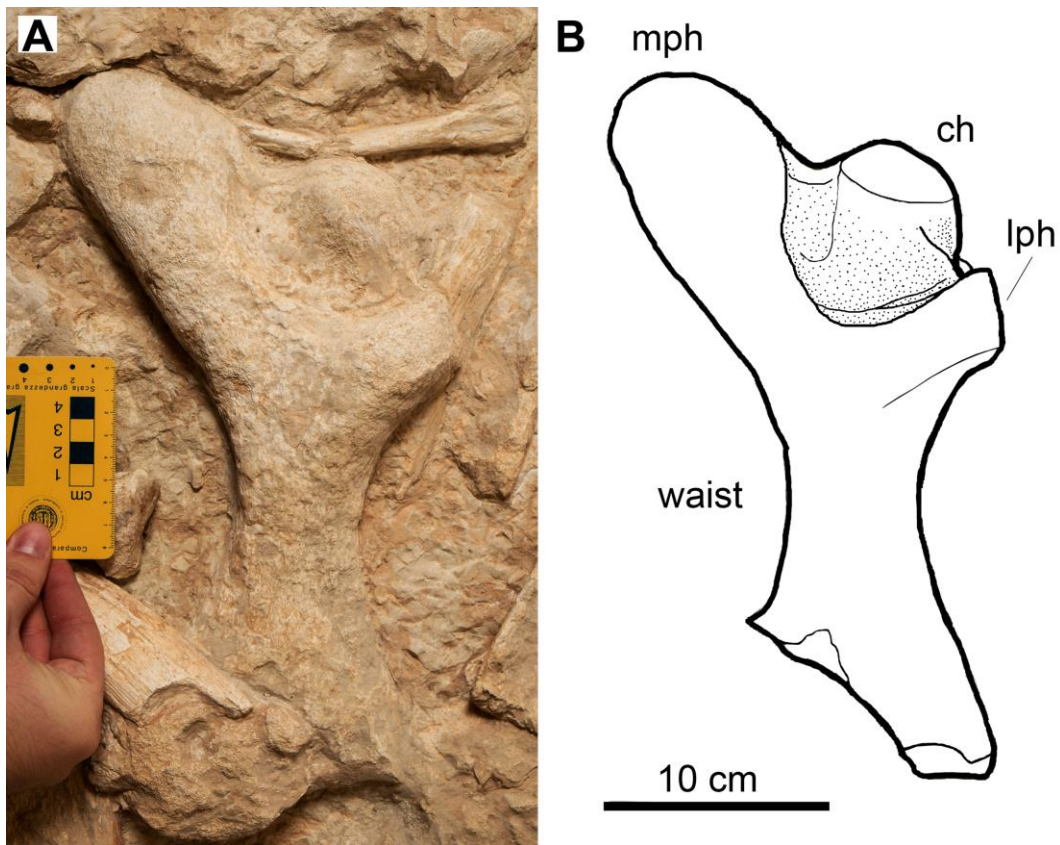


Figure 12

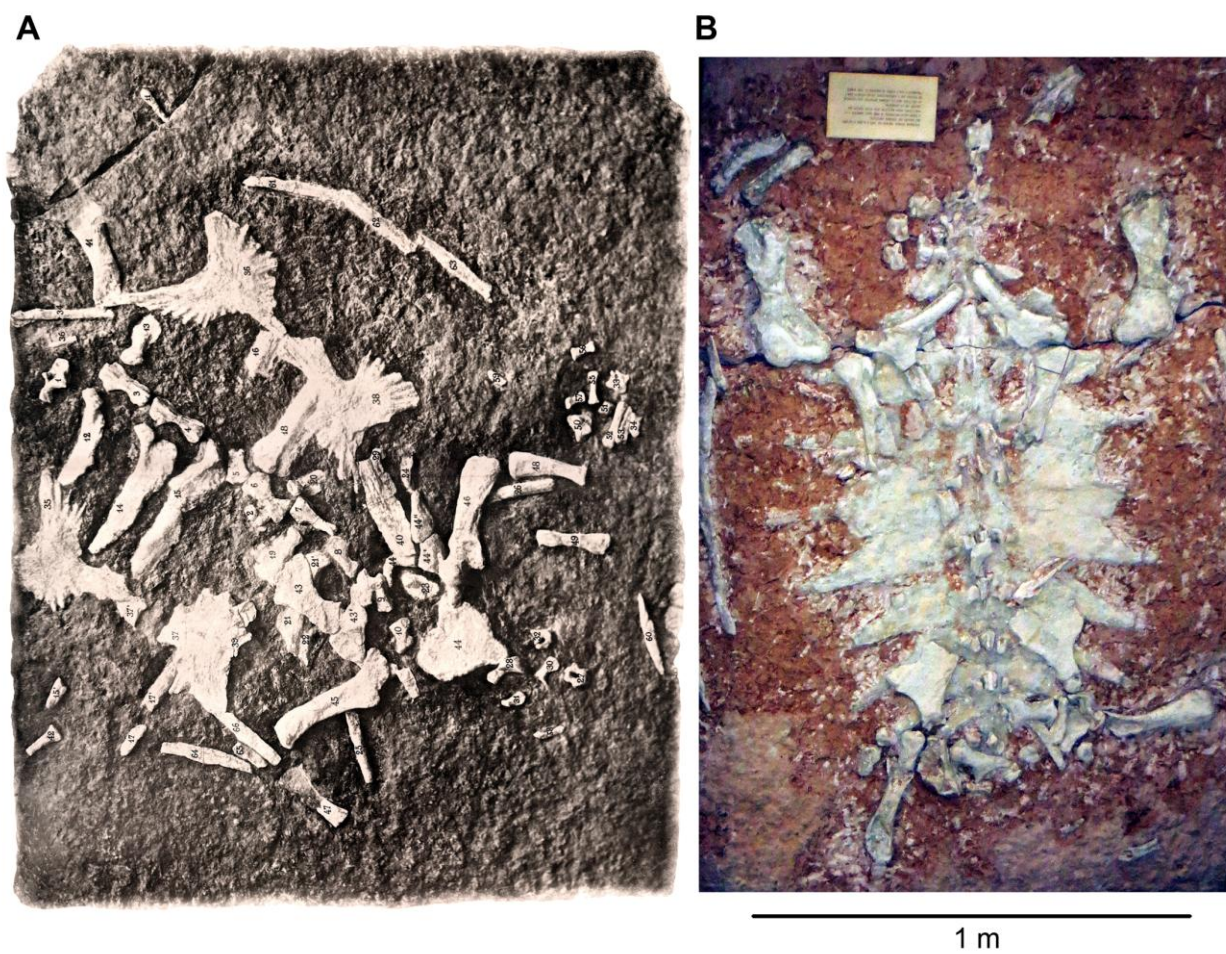


Figure 13

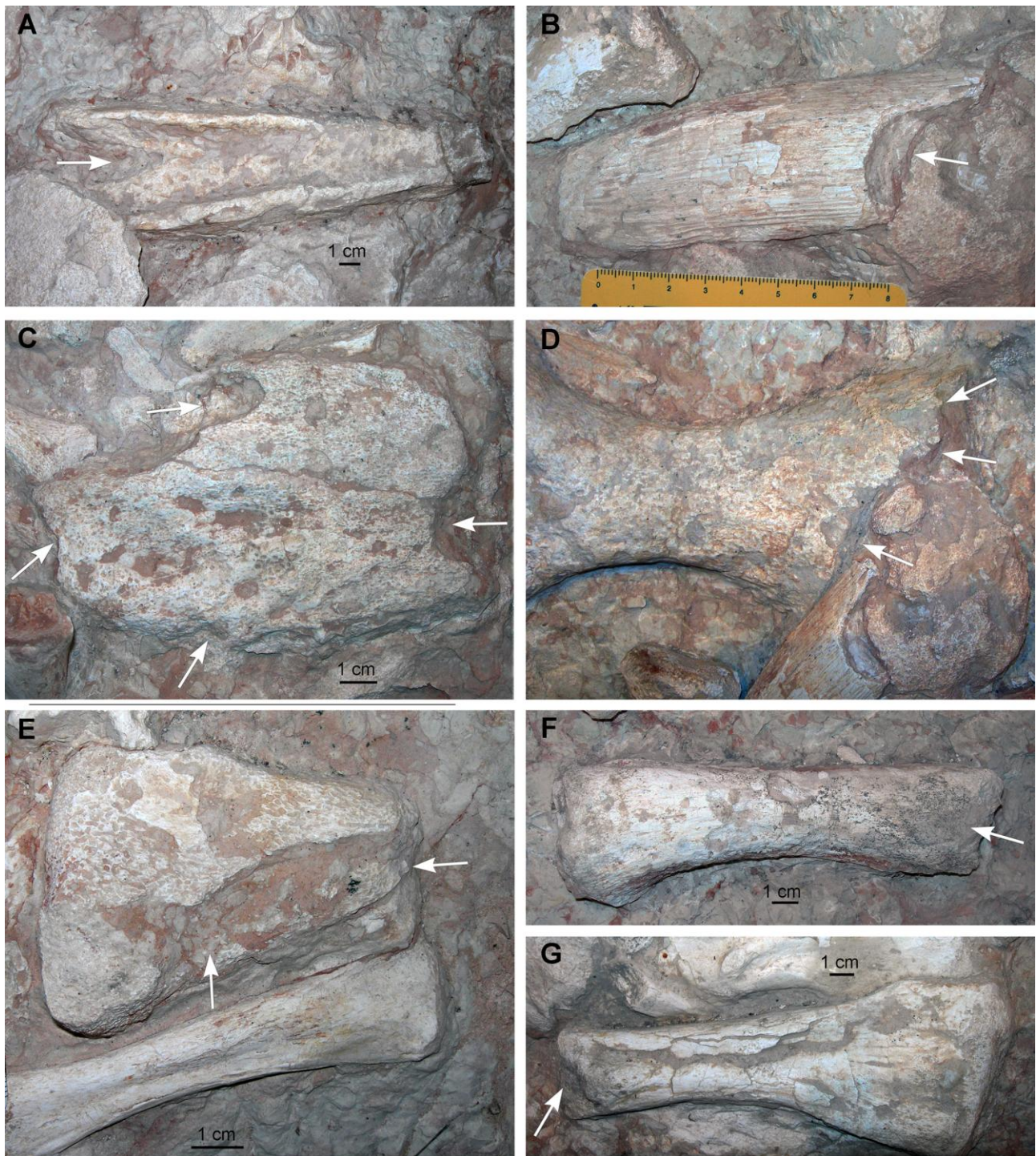


Figure 14

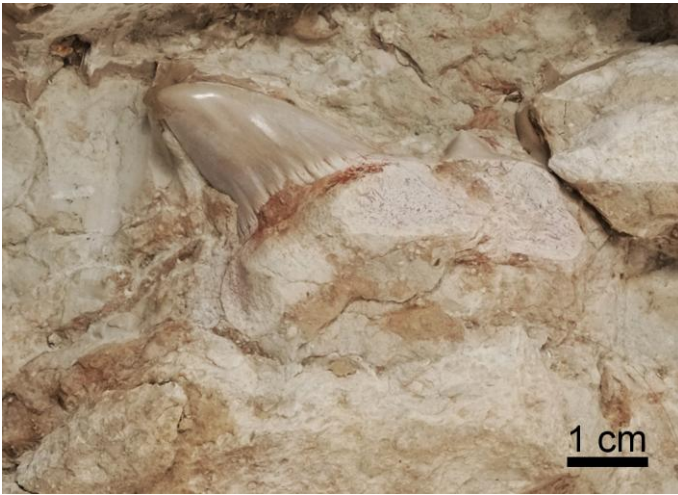


Figure 15

Highlights

- A specimen of the Upper Cretaceous shark *Cretodus* is described from northern Italy
- The fossil is the most complete specimen of *Cretodus* so far discovered
- The specimen is associated with a pellet-like accumulation of a marine turtle
- The turtle remains are interpreted as stomach content of the shark
- The fossil represents a direct evidence of possible dietary preferences of *Cretodus*