Morphology and paleobiology of the Late Cretaceous large-sized shark *Cretodus crassidens* (Dixon, 1850) (Neoselachii; Lamniformes)

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Abstract.—The definition of the Cretaceous shark genus *Cretodus* Sokolov, 1965 is primarily based on isolated teeth. This genus includes five species. Among these, *Cretodus houghtonorum* Shimada and Everhart, 2019 is the only species based on a partially preserved skeleton. Here, the taxonomic attribution of a virtually complete skeleton of *Cretodus* from the Turonian of northeastern Italy is discussed, together with a few specimens from the Turonian of England. One of the latter is investigated through micropaleontological analysis to determine its stratigraphic position. The material is referred to *Cretodus crassidens* (Dixon, 1850), the diagnosis of which is emended herein. The dentition is tentatively reconstructed, exhibiting strong similarities with congenerspecies, although it differs in having strong vertical folds on the main cusp labial face, a mesiodistally broad tooth aspect, weak and well-spaced ‘costulae’ at crown base, and a different dental formula in the number of parasymphyseal and lateral rows. Some tooth malformations are interpreted as feeding-related or senile characters. The Italian specimen suggests that *Cretodus crassidens* had a wide and laterally expanded mouth and head, a stout body, and attained a gigantic size. *Cretodus crassidens* was a moderate-speed swimming shark ecologically like the extant tiger shark *Galeocerdo cuvier* (Péron and Lesueur in Lesueur, 1822). The age estimate from vertebral-band counting suggests that the Italian individual was at least 23 years old and the growth model indicates a longevity of 64 years and a maximum attainable total length of 9–11 m. *Cretodus crassidens* occurs both in Boreal and Tethyan domains, implying a broad paleobiogeographic distribution and a preference toward offshore settings.

Introduction

The extinct shark *Cretodus* Sokolov, 1965, like many other extinct chondrichthians, was defined based on isolated teeth collected from Upper Cretaceous (Cenomanian–Turonian) marine deposits from all over the world (Cappetta, 2012). However, this large lamniform is also represented by associated skeletal remains recently reported from the middle-upper Turonian Scaglia Rossa of Veneto, northeastern Italy (Amalfitano et al., 2017a) and from the middle Turonian Blue Hill Shale Member of the Carlile Shale of Kansas, USA (Shimada and Everhart, 2019). The partial skeleton from Kansas was assigned to a new species, *Cretodus houghtonorum* Shimada and Everhart, 2019, whereas the Italian specimen has been regarded since its discovery as close to *Cretodus crassidens* (Dixon, 1850). Amalfitano et al. (2017a) prudently referred the Italian specimen to *Cretodus* sp. in a study focused on a pellet-like accumulation of turtle bones alongside the vertebral column of the shark, which was interpreted as its gastric content. Based on dental characters, Shimada and Everhart (2019) considered the specimen discussed by Amalfitano et al. (2017a) to be conspecific with, or closely allied to, *Cretodus crassidens*. The attribution to *Cretodus crassidens* is confirmed herein based on a detailed analysis of the Italian specimen and further supported by additional information and comparison with other material, including the holotype, from the English Chalk Group of southern England, UK. A tentative reconstruction of the dentition of this species is also provided here, together with a discussion on several paleobiological traits of the species.

Geological setting

The geological setting of the ‘Lastame’ lithofacies of the Scaglia Rossa of the Lessini Mountains (~30 km N of Verona, Veneto, Italy; Fig. 1), which yielded the *Cretodus* remains, has been thoroughly described in a series of papers dealing with the remarkable vertebrate assemblage of this Cretaceous Lagerstätte...
The 7 m thick nodular/subnodular interval of whitish and pinkish-reddish limestones of the Scaglia Rossa extensively quarried in Verona Province is characterized by abundant echinoids, inoceramids, ammonoids, and rudists, but also by vertebrate remains, e.g., lamniform sharks, sclerorhynchiforms, bony fishes, marine turtles, and mosasaurs. The Lastame spans from Turonian p.p. to Coniacian p.p. (e.g., Cigala-Fulgosi et al., 1980; Trevisani and Cestari, 2007; Walliser and Schöne, 2020), but most of the vertebrate skeletons and partial remains so far investigated come from the middle-upper Turonian interval (e.g., Amalfitano et al., 2017a, b, 2019; Amadori et al., 2020a, b; Palci et al., 2013). The 7 m thick nodular/subnodular interval of whitish and pinkish-reddish limestones of the Scaglia Rossa extensively quarried in Verona Province is characterized by abundant echinoids, inoceramids, ammonoids, and rudists, but also by vertebrate remains, e.g., lamniform sharks, sclerorhynchiforms, bony fishes, marine turtles, and mosasaurs. The Lastame spans from Turonian p.p. to Coniacian p.p. (e.g., Cigala-Fulgosi et al., 1980; Trevisani and Cestari, 2007; Walliser and Schöne, 2020), but most of the vertebrate skeletons and partial remains so far investigated comes from the middle-upper Turonian interval (e.g., Amalfitano et al., 2017a, b, 2019; Amadori et al., 2020a, b).

The Cretodus remains from southern England (UK) examined herein come from the Upper Cretaceous Chalk of Kent (especially near the town of Lewes; Fig. 2.1) and surrounding counties. The associated remains are referred to the classic ‘Middle Chalk Group’ of southern England (Hopson, 2005). This unit is part of the Chalk Group, specifically the White Chalk Subgroup, deposited in the northwestern part of the Anglo-Paris Basin and equivalent to the lowest part of the Lewes Nodular Chalk Formation, the New Pit Chalk Formation, and the Holywell Nodular Chalk Formation (with the exclusion of the Plenus Marl Member) in the Southern Province (Hopson, 2005; Wilkinson, 2011; Gale, 2019; Fig. 2.2). The ‘Middle Chalk’ spans from the upper Cenomanian (only the Plenus Marl Member) to the middle Turonian (Wilkinson, 2011) and yielded remains of numerous fossil fish taxa, although the number of vertebrates per volume of rock is very low (Mantell, 1822; Woodward, 1902, 1903, 1907, 1908, 1909, 1911, 1912; Kriwet, 2002; Friedman et al., 2016); the ichthyofauna therein includes a large variety of bony fishes (e.g., Dixon, 1850; Woodward, 1902, 1903, 1907, 1908, 1909, 1911, 1912; Kriwet, 2002) and several cartilaginous fishes (e.g., Cretoxyrhina and Ptychodus; Dixon, 1850; Woodward, 1902, 1903, 1907, 1908, 1909, 1911, 1912; Longbottom and Patterson, 2002).

**Materials and methods**

The material studied herein consists of a partial articulated skeleton (101 teeth, two segments of 86 disconnected and co-instacked vertebral centra and fragments of cranial mineralized cartilage) from the Scaglia Rossa exhibited at the Paleontological and Prehistorical Museum ‘Don Alberto Benedetti’ (Museo Paleontologico e Preistorico) of Sant’Anna d’Alfaedo, Verona Province, Italy (MPPSA IGVR 91032) and some
specimens from the Chalk Group of southern England (UK). The English material includes a disturbed tooth set with a single vertebral centrum housed at the Booth Museum of Natural History of Brighton, England, UK (BMB 007312), and a disarticulated tooth set (NHMUK PV OR 25786) and several isolated teeth that belong to the collections of The Natural History Museum of London (NHMUK PV OR 25823 [holotype of Cretodus crassidens], 41704, 44951, 44623, and NHMUK PV P 4577, 5402, 11144, 12368, 12860, 12870).

The specimens were photographed using a Nikon D810 camera with a 60–90 mm lens and a Canon PowerShot SX720 HS. Measurements were retrieved through the image analysis software ImageJ (https://imagej.nih.gov/ij/, v. 1.6; Schneider et al., 2012). Images and interpretative drawings of the specimens were produced using the free software packages GIMP (GNU Image Manipulation Program, https://www.gimp.org/, v. 2.10.6) and Inkscape (https://inkscape.org/, v. 0.92). The synonymy list follows the standards proposed by Matthews (1973) and include selected synonyms directly referring to the material described herein. The growth model was reconstructed using the software package Past 3.26 (https://past.en.lo4d.com/windows; Hammer et al., 2001) and plotted with the Desmos graphing software (https://www.desmos.com/).

The reconstruction of the dentition of Cretodus crassidens provided herein is based on the disarticulated dentition of the Italian specimen MPPSA IGVR 91032, therefore might be subject to biases such as taphonomic or preparation loss and interpretation bias. Specimen MPPSA IGVR 91032, in fact, was discovered between 1996 and 1997 by quarry owners Giovanni and Gianfranco Benedetti and was prepared by Giovanni Benedetti in 2003 (Amalfitano et al., 2017a). According to the preparator, the two slabs come from the same layer and were separated by a karst fissure; thus, the skeletal remains in the two slabs should belong to the same individual. Nevertheless, the two slabs differ slightly in color and the different sizes between the last vertebral centrum on the main slab and the first centrum on the second slab suggest that several vertebræ are missing between the two segments (Amalfitano et al., 2017a). Furthermore, the vertebræ on the second slab are all glued. Most of the teeth (~70%) detached from slabs A when it was exposed by quarry works or remained attached to the counterslab (now missing); they were glued onto the slab later and mostly not in their exact original position (some might be lost). However, the glued teeth undoubtedly belong to this specimen because their morphological characters are identical to the in-situ teeth (Amalfitano et al., 2017a). The teeth are figured only on the labial side or the lingual side because most of them are still embedded in the sedimentary matrix or were glued after detaching and are exposed mainly on one side. Chemical or physical preparation to separate the teeth from the matrix (e.g., Siversson et al., 2007), as well as sectioning the vertebral centra (e.g., Newbrey et al., 2015; Shimada and Everhart, 2019), was not possible because the specimen is subject to Italian cultural heritage care laws and cannot be altered without special permission. Ammonium chloride coating of the teeth (e.g., Siversson et al., 2007; Amadori et al., 2019) was also not performed because of technical issues related to the position and size of the specimen in the Museum exhibition. Teeth in the reconstruction are illustrated from the left side of the jaws and missing elements were filled with mirrored images of teeth from the right side. Tooth numbering of MPPSA IGVR 91032 in the text, figures, and tables is consistent with that of Amalfitano et al. (2017a, fig. 6). Some correction of the tooth measurements of MPPSA IGVR 91032 and new tooth measurements of BMB 007312 are provided in Appendices 1 and 2.

Except for the uninformative calcified cartilage fragments, the morphology of each anatomical element is described and figured in detail herein. Terminology and abbreviations follow usual standards for shark teeth, placoid scales, and vertebral centra (e.g., Ridewood, 1921; Shimada, 1997a, b, c; Siversson, 1999; Cappetta, 2012; Newbrey et al., 2015; Shimada and Everhart, 2019). Nevertheless, the symphyseal teeth sensu Shimada and Everhart (2019) are referred herein as parasymphyseal teeth, and the intermediate teeth from the same paper as third anterior teeth following Siversson’s (1999) terminology. In the literature of fossil lamniforms, teeth near the symphysis have been consistently addressed as symphyseal teeth (e.g., Siversson, 1999; Shimada, 2002). However, Lamniformes all lack symphyseal teeth (Smith et al., 2013), therefore the erroneous use in dental nomenclature of symphyseal teeth in Lamniformes should be replaced by the term parasymphyseal teeth, already used in other papers (e.g., Cook et al., 2011; Siversson et al., 2013). The intermediate position sensu Applegate (1967) refers to teeth arising from the area (intermediate bar) between the holows (bullae) where the other teeth accommodate in the odontaspidid dentition, but the majority of lamniforms do not exhibit this condition, having two separate holows in the upper jaw without teeth on the intermediate bar and a single hollow in the lower jaw (e.g., Siversson, 1999).

A least square linear regression method was applied to the vertebral centrum length data to estimate the original vertebral count of the shark and to provide a length estimate of MPPSA IGVR 91032 (modelled in Past 3.26, Supplemental Data 1; data from Amalfitano et al., 2017a, appendix B). Tooth size is usually employed as a parameter to infer total length of a fossil or extant shark, considering both crown or tooth height (e.g., Gottfried et al., 1996; Shimada, 2003, 2019) and tooth width. Tooth width exhibits less variability than crown height (Bass et al., 1975) and thus has been considered more reliable by several authors (e.g., Newbrey et al., 2015; Perez et al., 2021). In this paper, we considered both methods, despite that the total jaw width method is not directly applicable because of poor preservation of most of the tooth roots in the sample considered herein. Length estimates are provided using the equation by Shimada and Everhart (2019) that exploits the theoretical linear relationship of crown height (CH) and total length (TL) for Cretoxyrhina mantelli (see Shimada, 2008, fig. 5):

\[ TL(\text{cm}) = 12.5 \times CH(\text{mm}) \]  
(1)

However, Shimada et al. (2020) provided a more conservative estimate based on the linear function:

\[ TL(\text{cm}) = 11.784 \times CH(\text{mm}) - 0.331 \]  
(2)

with CH of any anterior tooth in any given non-Alopias macrophagous lamniform taxon, although this possibly underestimates the body total length.
Using the definition of bite circumference sensu Lowry et al. (2009) to bypass the lack of a reliable total jaw width and applying the reverse of their formula:

$$\log(\text{bite ‘circumference’}[\text{mm}]) = 1.007 \times \log(\text{TL}[\text{mm}]) - 0.8$$  \hspace{1cm} (3)

for the great white shark *Carcharodon carcharias* (Linnaeus, 1758), it is possible to have a TL estimate of *Cretodus crassidens* also from the arch-like arrangement of teeth in specimen MPPSA IGVR 91032 (geometrical approximation in Supplemental Data 2).

An attempt to assess the growth pattern of the fossil shark using the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938) is proposed below. The VBGF has been widely used to describe the growth of fish (Haddon, 2001). This function was specifically used as a quantitative method to describe the growth of extant elasmobranchs based on growth bands on calcified structures such as vertebral centra (e.g., Cailliet and Goldman, 2004; Goldman, 2004). The method has also been applied to some extinct sharks (e.g., Shimada, 2008; Cook et al., 2011; Newbrey et al., 2015; Shimada and Everhart, 2019; Jambura and Kriwet, 2020; Shimada et al., 2021). The VBGF method applied here exploits original and derived measurements (Table 1) from a single but best-preserved specimen, that would be considered dependent measurements. This exploratory method has been recently applied in other papers (e.g., Shimada and Everhart, 2019; Shimada et al., 2021) and has proven to be a viable approach to attempt to explore the growth pattern of extinct elasmobranchs, although with the obvious limits dependent from the restricted sample. Parameters obtained from the VBGF and other derived measurements are applied with equations from Natanson et al. (2006) for longevity to discuss and compare the results of the analyses.

Specimen BMB 007312 is still embedded in Chalk soft matrix. The matrix was hence collected as powdered residual fallen from the specimen after simple handling. The sample was prepared as unprocessed material on a smear slide and examined under a light microscope at 1250X magnification to establish the stratigraphic position of the specimen. The calcareous nannofossil content of the samples was analyzed with semiquantitative methods (three vertical traverses corresponding to 6–7 mm$^2$) following Gardin and Monchi (1998).

Repositories and institutional abbreviations.—Types, figured, and other specimens examined in this study are deposited in the following institutions: Booth Museum of Natural History of Brighton, UK (BMB); Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA (FHSM); Museo Paleontologico e Preistorico di Sant’Anna d’Alfaedo, Verona, Italy (MPPSA IGVR); and The Natural History Museum, London, UK (NHMUK).

### Systematic paleontology

#### Class Chondrichthyes Huxley, 1880

*Subclass* Elasmobranchii Bonaparte, 1838

*Cohort* Euselachii Hay, 1902

*Order* Lamniformes Berg, 1958

*Family* Pseudoscapanorhynchidae Herman, 1979 (sensu Sokolov, 1965; Cappetta, 1987)

*Genus* *Cretodus* Sokolov, 1965 (sensu Shimada and Everhart, 2019)

**Type species.**—*Otodus sulcatus* Geinitz, 1843; †unterer Pläner (plenus-marl), upper part of upper Cenomanian, Plauen, Saxony, Germany.

*Cretodus crassidens* (Dixon, 1850)

**Figures 3–10**

Selected synonymy:

†1850 *Oxyrhina crassidens* Dixon, p. 367, pl. 31, figs. 13, 13A.

1889 *Oxyrhina crassidens*; Woodward, p. 382.

1911 *Oxyrhina crassidens*; Woodward, p. 205, pl. 44, figs. 1, 2.

1987 *Cretodus crassidens*; Cappetta, p. 98.

2012 *Cretodus crassidens*, Cappetta, p. 255.

2017a *Cretodus* sp.; Amalfitano et al., p. 109, figs. 2, 4, 6–9, 15.

2019 *Cretodus crassidens*; Shimada and Everhart, p. 4, fig. 9A–P.

**Holotype.**—NHMUK PV OR 25823 (isolated tooth).

**Diagnosis (emended).**—A *Cretodus* species that differs from all other species of the genus by teeth with mesiodistally broad

### Table 1

| BN | CR (mm) | pCR (%) | TL$_1$ (cm) | TL$_2$ (cm) | CH (mm) |
|----|---------|---------|-------------|-------------|---------|
| 0  | 10.7    | 21.5    | 141.9       | 167.7       | 12.0    |
| 1  | 14.1    | 28.5    | 187.8       | 221.9       | 15.9    |
| 2  | 16.9    | 34.0    | 224.3       | 265.1       | 19.0    |
| 3  | 19.4    | 39.1    | 258.1       | 305.0       | 21.9    |
| 4  | 21.4    | 43.2    | 285.1       | 336.9       | 24.2    |
| 5  | 23.5    | 47.3    | 312.1       | 368.9       | 26.5    |
| 6  | 25.5    | 51.4    | 339.1       | 400.8       | 28.8    |
| 7  | 27.3    | 55.0    | 362.8       | 428.7       | 30.8    |
| 8  | 29.1    | 58.6    | 387.1       | 457.5       | 32.8    |
| 9  | 30.8    | 62.1    | 410.0       | 484.6       | 34.8    |
| 10 | 32.7    | 65.8    | 434.4       | 513.4       | 36.9    |
| 11 | 34.5    | 69.5    | 458.7       | 542.1       | 38.9    |
| 12 | 36.5    | 73.6    | 485.7       | 574.0       | 41.2    |
| 13 | 38.0    | 76.5    | 504.6       | 596.4       | 42.8    |
| 14 | 39.2    | 78.9    | 520.8       | 615.5       | 44.2    |
| 15 | 40.7    | 82.0    | 541.1       | 639.5       | 45.9    |
| 16 | 42.4    | 85.5    | 564.1       | 666.6       | 47.9    |
| 17 | 44.4    | 89.4    | 589.8       | 697.0       | 50.0    |
| 18 | 45.3    | 91.2    | 601.9       | 711.3       | 51.1    |
| 19 | 46.3    | 93.2    | 615.4       | 727.3       | 52.2    |
| 20 | 47.2    | 95.1    | 627.6       | 741.7       | 53.2    |
| 21 | 48.0    | 96.7    | 638.4       | 754.5       | 54.2    |
| 22 | 48.7    | 98.2    | 647.8       | 765.6       | 55.0    |
| 23 | 49.6    | 100.0   | 660.0       | 780.0       | 56.0    |
Figure 3. Partial articulated skeleton of *Cretodus crassidens* (Dixon, 1850) from the middle Turonian of the Scaglia Rossa Veneta of northeastern Italy. MPPSA IGVR 91032: (1) Orthophoto of the specimen. The slab embedding the tooth accumulation, the tessellated cartilage elements, the anterior portion of the vertebral column, and the turtle remains is Slab A. The one embedding the caudalmost vertebral centra is Slab B. (2) Interpretative drawing of (1). (3) Interpretative drawing of the tooth accumulation. Teeth in situ are indicated (yellow in electronic version), with tessellated cartilage elements (dark gray) and anteriormost vertebral centra (light gray). Scale bars = 1 m (1, 2), 20 cm (3).
aspect (crown width to 82% of crown height even in a2), slightly ogival to triangular main cusp, with vertical strong folds and deep grooves on the labial main cusp, weak and well-spaced basalmassive, and almost straight, with convex labial and lingual faces; root concavity are deeply sinusoid (especially in anterior teeth). Main cusp is massive, slightly ogival to triangular, with strong vertical folds and two to five deep grooves on labial face. Lateral teeth have triangular main cusp. Lateral cusplets are well separated from main cusp but connected on labial side with basally extended crown base on both root lobes. Numerous, regularly and well-spaced, well-marked, and very short vertical grooves and ridges (‘costulae’ or ‘striae’) are present at crown base on both labial and lingual sides, more marked on labial side. Cutting edges are usually continuous and sharp, connecting main cusp and cusplets. Mesial root lobe is usually slightly pointed, whereas distal lobe is more expanded and rounded. Labial face of root is flat or slightly recessed at crown base. Lingual face of root is overall swollen and bulgy, with lingual protuberance (more evident and protruding in parasymphyses, anteriors, and medialmost laterals). Lateral teeth exhibit more splayed root lobes than parasymphyses and anteriors.

Upper dentition.—Upper teeth are labiolingually thick, massive, and almost straight, with convex labial and lingual faces and tip slightly turned outward in certain specimens. Cutting edges are straight and continuous. Crown base and basal root concavity are deeply sinusoid (especially in anterior teeth). Root-lobes angle is acute in parasymphyses, anteriors, and medialmost laterals. Lateral teeth exhibit more splayed root lobes than parasymphyses and anteriors.

Upper parasympathetic tooth (P): Main cusp is rather slender (PCH-PCW ratio 1.4–1.5). P1 exhibits a mesial curved main cusp. P2 almost straight and is the smallest among these teeth. The height of the lateral cusplet represents 32% of crown height.
Figure 4. Selection of representative teeth of *Cretodus crassidens* (Dixon, 1850) from the middle Turonian of the Scaglia Rossa Veneta of northeastern Italy, MPPSA IGVR 91032: (1) first upper parasympyseal tooth (no. 16), labial view; (2) first lower parasympyseal tooth (no. 22), labial view; (3) first upper anterior tooth (no. 37), labial view; (4) second lower anterior tooth (no. 3), labial view; (5) second lower anterior tooth (no. 11), lingual view; (6) second upper anterior tooth (no. 13), labial view; (7) third upper anterior tooth (no. 53), labial view; (8) third lower anterior tooth (no. 24), labial view; (9) first lower lateral tooth (no. 62), labial view; (10) third lower lateral tooth (no. 59), labial view; (11) sixth upper lateral tooth (no. 20), lingual view; (12) fourth upper lateral tooth (no. 61), labial view; (13) seventh lower lateral tooth (no. 103), lingual view; (14) eighth lower lateral tooth (no. 94), labial view; (15) ninth lower lateral tooth (no. 92), lingual view; (16) commissural upper lateral tooth (no. 104), labial view. Numbers match those used by Amalfitano et al. (2017a, fig. 6). Scale bar = 20 mm.
Figure 5. Associated remains of *Cretodus crassidens* (Dixon, 1850) from the lower Turonian of the Chalk Group of England, BMB 007312: (1, 2) blocks with embedded teeth; (3, 4) complete vertebral centrum in frontal and dorsal views; (5) two fragments of a partial vertebral centrum in frontal view; (6) isolated teeth from the same tooth set (second one from left in labial view, all others in lingual view). Scale bars = 50 mm.
(2) Upper anterior teeth (A): A1 is reduced (maximum observed height 51 mm) and strongly oblique distally (21° referring to the vertical axis). A2 and A3 have almost upright and apparently symmetrical main cusps; A2 is imperceptibly slanted mesially, and A3 distally. These teeth are rather large (A2 is 61 mm total height, the largest one of upper anteriors) and slender (TH-TW ratio 1.3–1.4). The root lobes of A1 are less splayed with respect to those of the adjacent teeth and U-shaped. The height of the lateral cusplet is ~28–33% of crown height.

(3) Upper lateral teeth (L): Main cusp slightly to strongly distally oblique. Their maximum height ranges from 48 to 16 mm. L1-L3 teeth have an almost upright main cusp, from L4 onward the inclination becomes more evident. L11?-L12? possibly represent the commissural teeth. Teeth are generally larger than high except for the first three, with L2 representing the highest tooth (like in many other lamniforms; Shimada, 2002); lateral cusplet height is 35–54% of crown height, with the ratio increasing toward the commissural rows. Root lobes become generally more divergent distally.

Lower dentition.—Lower teeth have a sigmoid profile (labiolingual direction), nearly flat labial face, and convex lingual face; the tip has a reversed curvature, so that although most of the crown is curved inward toward the mouth cavity, the tip is turned outward (as also observed in other sharks; Frazzetta, 1988), which confers a more labiolingually compressed and curved aspect with respect to the upper teeth. Main cusp of lower teeth is generally mesiodistally broader than those of upper teeth. Crown base and root concavity are shallow and more parabolic than those of upper teeth. Cutting edges are sigmoid in profile. Crown base slightly overhangs the upper portion of the root, creating a shallow recess and conferring a slightly inflated aspect. Root-lobes angle is almost right in parasympphyseals and anteriors, obtuse in laterals. Root-lobes apices slightly diverge. Lower dentition includes a single parasympphyseal row, three anterior rows, and at least eight lateral rows, with a gap in the posteriormost positions, including commissural teeth. Distinctive characters of tooth rows are:

(1) Lower parasympphyseal teeth (p): These two teeth have a rather symmetric outline and slender main cusp (PCH-PCW ratio 1.3). Lateral cusplets are strongly divergent. The lateral cusplet height is ~21–26% of crown height.

(2) Lower anterior teeth (a): These are the largest teeth in the dentition (a1 is 67 mm high, whereas a2 is 69 mm high, although incompletely mineralized; in this case it could be higher; 56 mm high in crown height). Tooth a1 is more symmetrical than a2, which is slightly slanted in distal direction. Main cusp of a2 bears four deep enameloid folds on the labial face extending for almost its entire height. Tooth a2 enlarged (crown width to 82% of crown height). Lateral cusplets height is 25–31% of crown height (similar to upper anterior ratio). Tooth a3 is rather large (60 mm TH in functional row), with main cusp slightly bent distally and divergent cusplets. Tooth as high as wide (TH-TW ratio 1.18–1.02). Lateral cusplet height is ~29% of crown height.

(3) Lower lateral teeth (l): Main cusp is almost upright to slightly oblique. The inclination of the cusp increases distally. Total height ranges 32–53 mm, but this range does not include the distalmost rows (which comprises teeth with crown height measuring 22 mm, l7, and 17 mm, l8). Teeth l1–l4 are almost as large as high, with almost upright cusps. Observing the size of l8 compared with those of the corresponding upper laterals, it is possible to suggest that there are at least four missing rows in the commissural part of the lower dentition. Lateral cusplet height represents

Figure 6. Second lower anterior tooth of Cretodus crassidens (Dixon, 1850), BMB 007312: (1) labial view; (2) mesial view; (3) distal view; (4) lingual view. Arrow indicates a dental malformation (crenulation on the cutting edge between the distal cusplet and the main cusp). Scale bar = 50 mm.
Figure 7. Interpretation of the dentition pattern in *Cretodus crassidens* (Dixon, 1850), based on specimen MPPSA IGVR 91032. Numbers in gray match those used by Amalfitano et al. (2017a, fig. 6). * = mirrored right teeth; dotted lines = reconstructed portions of the teeth based on other teeth in the sample; ? possibly missing tooth rows; // = gaps in the reconstruction. Scale bar = 50 mm.

Figure 8. Vertebral centra of *Cretodus crassidens* (Dixon, 1850), MPPSA IGVR 91032: (1) interpretive drawing of slabs, with glued vertebral centra in dark gray; (2) exposed articular surface of corpus calcareum; (3) exposed intermedialia showing pattern of calcification of the vertebral centrum, showing radial and concentric lamellae patterns; (4) lateral side of vertebral centra exhibiting septae. Black and white scale bars in centimeters.
prominent concentric rings that are interpreted to be annual growth bands. These bands are not easily discernable on the vertebral centra of BMB 007312, probably due to erosion. In MPPSA IGVR 91032, a vertebral centrum deprived of the articular surface of the corpus calcareum due to biostratinomic processes (Fig. 8.3) presents concentric lamellae in the intermedialia and radial lamellae that are moderately thick (~1 mm). The radial lamellae tend to branch near the half of the radius length, enlarging and merging into composite and thick longitudinal septae toward the centrum periphery. The longitudinal septae, visible in lateral view in both MPPSA IGVR 91032 and BMB 007312 (Figs. 5.4, 8.4), are well-spaced with low density along the lateral surface of the centrum, separated by large fossae (~20 mm wide), except for the dorsal and ventral sides of the centrum, which exhibit a higher density of septae (three or four in an interval of ~20 mm). Diagonal or transverse septae are absent. Articular foramina are visible on some centra from MPPSA IGVR 91032 but are better visible on the complete vertebral centrum of BMB 007312, being more oval and larger than adjacent fossae (Figs. 5.4, 8.4).

**Vertebral column.**—MPPSA IGVR 91032 comprises only 86 vertebral centra, 51 on slab A and 35 on slab B. Measurements were provided by Amalfitano et al. (2017a, appendix B). Centra on slab A are partially articulated and represent the anterior part of the vertebral column (Figs. 3.1–3.2, 8.1). Centra on slab B are artificially aligned and decrease in size posteriorly (Figs. 3.1–3.2, 8.1). Vertebral centra are round, with height equal to width (Fig. 8.2). The sizes of the last centrum on slab A and the first centrum on slab B differ by ~20 mm, suggesting that a portion of the vertebral column between the two segments is missing (Amalfitano et al., 2017a). This is also indicated by the low vertebral count (86). The diameter of the centra on slab A ranges from 115 mm (vertebra 16) to 53 mm (vertebra 1); that on slab B ranges from 79 mm (first centrum of the slab) to 28 mm (last three centra) (Amalfitano et al., 2017a, appendix B). The mean length of the vertebral centra is ~32.5 ± 6.22 mm (Amalfitano et al., 2017a, appendix B). The centra are well-calcified and structurally match the definition of ‘lamnoid vertebrae’ (sensu Applegate, 1967, p. 62; Fig. 8.2–8.4). Many centra of MPPSA IGVR 91032 suffer slight taphonomic distortion and some are incomplete, whereas a single one of BMB 007312 is nearly intact. The articular surface of the corpus calcareum is devoid of any kind of ornamentation and generally exhibits ~20 prominent concentric rings that are interpreted to be annual growth bands.

~25–53% of crown height, with the ratio increasing toward the distalmost rows.

**Placoid scales.**—Placoid scales (or dermal denticles) that covered the body of *Cretodus crassidens* are common in the reddish calcareous marly limestone embedding MPPSA IGVR 91032. They appear as whitish submillimetric prisms in the reddish rock. They are usually composed of a base, with a nutrient foramen at the bottom, and a crown (Fig. 9). The base is often missing because it is delicate and is easily damaged by the action of the acid used to dissolve the limestone to isolate them (Amalfitano et al., 2017a). Placoid scale height ranges 1–0.3 mm and width 0.6–0.3 mm. It was not possible to determine how the placoid scales were originally distributed. All scales are ornamented with strong parallel basoapical ridges and plications on the convex anterior face of their crown; ridges and plications do not extend posteriorly and have different sizes (from broad to slender) and general shapes (e.g., rhomboid, Fig. 9.1, 9.2; rounded or drop-like, Fig. 9.3). Except for some tricuspid scales (Fig. 9.1), the cusp is usually single, varying usually from pointed to rounded in shape (Fig. 9.2, 9.3).
Figure 10. Variability in cusplet number and tooth malformations within the dentition of Cretodus crassidens (Dixon, 1850), MPPSA IGVR 91032: (1) tooth no. 10: the right shoulder of the central cusp has a crenulated cutting edge, whereas the other (arrows in detail view) bears a cusplet with two additional cuspules (a tricuspid cusplet); (2) tooth no. 24: the cutting edge between the main cusp and the cusplet has an accessory papilla (arrow in detail view); (3) tooth no. 33: cutting edge between the main cusp and the left cusplet has an accessory papilla (arrow in detail view); (4) tooth no. 35: smaller accessory cusplet occurs mesial to the mesial cusplet (arrow in detail view); (5) tooth no. 7: smaller accessory cusplet occurs mesial to the mesial cusplet (arrow in detail view); (6) tooth no. 32: left cusplet (arrow in detail view) is much smaller than the right cusplet; (7) tooth no. 10: right shoulder of the main cusp has an irregularly crenulated heel (the cusplet is absent; arrows in detail view), whereas the left shoulder has a cusplet with two additional cuspules (tricuspid cusplet); (8) tooth no. 47: the main cusp is bent lingually and the right cusplet is enlarged, bulky, and recurved lingually (arrow in main view; detail view is from the side); (9) tooth no. 58: right distal cusplet is enlarged and high; a distal slice of the main cusp grew independently and has its own apex (arrow in detail view); (10, 11) tooth no. 66 in labial and lateral view: the main cusp is partially twisted; its upper part is blunt and bears a diminutive and demarcated apex (arrow). Numbers matching those used by Amalftano et al. (2017a, fig. 6). Scale bars = 10 mm.
Discussion

Taxonomy.—Genus-level taxonomy was recently commented upon by Siversson and Machalski (2017, p. 453, 454) and Shimada and Everhart (2019). The types of the first two described species of Cretodus—Cretodus semiplicatus (Münster in Agassiz, 1843) from the Turonian of Germany and Cretodus crassidens from the Turonian of the UK—are each based on isolated and poorly preserved teeth (Shimada and Everhart, 2019). The syntypes of Cretodus semiplicatus are considered marginally diagnostic for their poor preservation state and position (lateroposterior tooth, generally conservative in morphology among lamniforms and thus less taxonomically informative; Siversson and Machalski, 2017; Shimada and Everhart, 2019). Furthermore, being almost coeval, they could be conspecific with the type specimen of Cretodus crassidens (see Siversson and Machalski, 2017). Differences in morphology are addressed as dependent on different tooth position (syntype of Cretodus semiplicatus interpreted as a lower lateroposterior tooth, thus a more posterior position) and ontogenetic stage (Siversson and Machalski, 2017). The type specimen of Cretodus crassidens, a large, robust tooth with crenulated heels and lateral cusplet loss, might indicate a senile, female morphotype (Siversson and Machalski, 2017).

Shimada and Everhart (2019) clearly distinguished five species of the genus—Cretodus crassidens, Cretodus giganteus (Case, 2001), Cretodus houghtonorum, Cretodus longiplicatus Werner, 1989, and Cretodus semiplicatus—and proposed a phylogenetic hypothesis recognizing three categories based on similarities between the species (‘longiplicatus/semiplicatus-grade,’ ‘giganteus/houghtonorum-grade,’ and ‘crassidens-grade’). Based on the original illustration of the holotype of Cretodus sulcatus (Geinitz, 1843), it is possible that Cretodus longiplicatus is a junior synonym of Cretodus sulcatus (see Siversson and Machalski, 2017). Cretodus crassidens is easily distinguished from its congenerics by its mesiodistally broad teeth with large main cusp, robust lateral cusplets, and long vertical folds (to two-thirds of CH) and grooves on the labial face, especially in anteriormost rows. A rather large main cusp is also present in Cretodus giganteus, but this species seems to be more related to Cretodus houghtonorum for other characters and displays a thinner mesiodistal aspect (Shimada and Everhart, 2019). Basal crown ‘costulae’ (or ‘striae’; Shimada and Everhart, 2019) are stronger and wider spaced than those of the ‘giganteus/houghtonorum-grade’ (sensu Shimada and Everhart, 2019) but weaker and less dense than those of the ‘semiplicatus/longiplicatus-grade’ (sensu Shimada and Everhart, 2019) and less evident in large teeth, but the difference is well recognizable in lateral teeth. Lateral cusplets of Cretodus crassidens also...

Figure 11. Estimated total length range for Cretodus crassidens (Dixon, 1850), MPPSA IGVR 91032. Gray silhouette indicates the lower limit (660 cm); black silhouette indicates the upper limit (780 cm). Silhouette modified after illustration by O.E. Demuth figured by Cooper et al. (2020, fig. 2D).
differ from those of *Cretodus giganteus* by having a more robust aspect and divergent mesial and convergent distal cusplets, whereas both the cusplets of *Cretodus giganteus* are divergent (Shimada and Everhart, 2019).

The reconstruction of the dentition of *Cretodus crassidens* differs from that of the congeneric *Cretodus houghtonorum* in its mesiodistally broad morphology and strong vertical enameloid folds; the number of parasymphyseal teeth (‘symphyseal’ of Shimada and Everhart, 2019), three in the upper dentition and one in the lower one in *Cretodus houghtonorum*, two in both dentitions in *Cretodus crassidens*; and the presence of a reduced first upper anterior in *Cretodus crassidens*, although Shimada and Everhart (2019) interpreted it as an upper ‘intermediate’ (third upper anterior) tooth. The lateral teeth have similarly upright cusp, becoming more oblique distally, in both *Cretodus crassidens* and *Cretodus houghtonorum*. The number of lateral tooth rows is different: *Cretodus crassidens* has at least 10 upper laterals and eight lower laterals, whereas *Cretodus houghtonorum* has 11 upper laterals and eight lower laterals. Therefore, *Cretodus crassidens* has the following dental formula:

\[
\begin{array}{c}
2P3A10(+2?)L \\
2p3a8(+4?)L
\end{array}
\]

It must be noted that ontogenetic variation could strongly affect the taxonomy of *Cretodus*. Tooth size has been variously addressed as dependent on ontogenetic stage and dietary shifts during ontogeny, and care must be taken when using it as taxonomic character (Adnet, 2006; Purdy and Francis, 2007; Belben et al., 2017; Marramà and Kriwet, 2017).

Comparing the dentition pattern presented herein with that of other Cretaceous lamniform sharks, the lack of specialized intermediate teeth combined with the presence of at least one upper parasymphyseal file is commonly found in Cretaceous taxa other than *Cretodus* (e.g., *Archaeolamna* Silversson, 1992, *Cardabiodon* Siversson, 1999, *Cretalamna* Glickman, 1958, *Cretoxyrhina* Glickman, 1958, *Haimrichia* Vullo, Gui- not, and Barbe, 2016; Shimada, 1997c, 2007; Siverson, 1999; Cook et al., 2011; Dickerson et al., 2013; Siverson et al., 2013, 2015; Vullo et al., 2016). The presence of a reduced first upper anterior has been reported in other Cretaceous and modern lamniforms (e.g., *Alopias* Rafinesque, 1810, *Carcharias* Rafinesque, 1810, *Cardabiodon*, *Haimrichia*, *Odontaspis* Agassiz, 1838; *Applegate*, 1965; Shimada, 2002; Siverson, 1999; Vullo et al., 2016).

Vertebral centra are considered poor in diagnostic characters in lamniforms, except for a few cases in which their morphology has been observed in detail (e.g., Newbrey et al., 2015). Comparing vertebral centrum morphology in *Cretodus* with that of other neoselachians (Newbrey et al., 2015), *Cretodus* is characterized by distinctive radial lamellae branching and organizing in composite and thick septae toward the periphery of the centrum, divided by large fossae. These structures are different from those observed in other extant and extinct lamniform sharks and could represent a genus- or family-level diagnostic character. However, a family-level taxonomic discussion is well beyond the scope of this paper and needs further evidence.
from additional complete or associated remains of closely related genera.

**Teratologic remarks.**—A certain variability in the morphological pattern of the cusplets that could be interpreted as malformations (Gudger, 1937; Becker et al., 2000) can be observed in MPPSA IGVR 91032 (Figs. 10, 11; Amalitano et al., 2017a, fig. 6). In tooth number 10, one of the shoulders of the central cusp bears a cusplet with two further cuspules, i.e., a tricuspid cusplet (Fig. 10.1). The other shoulder has a crenulated cutting edge (Fig. 10.1). In three teeth (nos. 22, 24, and 33), a papilla is present on the cutting edge between the central cusp and the normally developed cusplet. In two cases (nos. 24 and 33; Fig. 10.2, 10.3), this occurs in the mesial half of the crown. A small supplementary cusplet is found in three teeth (nos. 2, 7, and 35; Fig. 10.4, 10.5) mesial to the mesial cusplet. In another tooth (no. 9), it is unclear whether the small supplementary cusplet is mesial to the mesial cusplet or distal to the distal cusplet. In two cases (nos. 2 and 35), it is triangular in outline and pointed, whereas in others it is papilla-like. In one tooth (no. 32; Fig. 10.6), one cusplet (the distal one) is smaller than the other.

Besides those with additional or smaller cusplets, the sample also contains malformed teeth (Fig. 10.7–10.11). Tooth number 10 has a weakly and irregularly crenulated heel on the shoulder of the main cusp instead of a well-formed cusplet (Fig. 10.7). This kind of malformation also occurs in three other teeth (nos. 52, 81, and 96). The main cusp of tooth number 47 (Fig. 10.8) is bent lingually and one cusplet is overgrown, bulky, and also recurved lingually. Tooth number 58 (Fig. 10.9) has the central cusp divided into two parts by a deep notch; the distal slice grew independently with its own apex, like a shark tooth figured by Welton and Farish (1993, fig. 17K). Furthermore, the distal cusplet is overgrown and tall. Tooth number 66 (Fig. 10.10, 10.11) has a main cusp that is partially twisted, and its apical part is blunt with a demarcated, diminutive apex.

Malformed teeth also occur in other *Cretodus crassidens* specimens from the Chalk Group of England discussed herein. The most common malformation is the loss of lateral cusplet and replacement by a weakly, irregularly crenulated heel on the shoulder of the main cusp. This kind of malformed tooth is present in specimens with associated tooth sets, e.g., NHMUK PV OR 25786 and BMB 007312, but also in isolated teeth, namely the holotype NHMUK PV OR 25823, NHMUK PV OR 49951, and NHMUK PV P 12870.

Malformed teeth have been object of several studies and reports on both fossil and living sharks. Gudger (1937) provided the probably first methodic report of malformed teeth in extant sharks. Later, some authors focused on tooth pattern reversal (Compagno, 1967; Reif, 1980), which also contributed to the development of subsequent studies on pattern formation in development of chondrichthyan dentitions from an evolutionary perspective (Smith et al., 2013). Other studies focused on feeding-related malformations in early growth stages (Becker et al., 2000; Becker and Chamberlain, 2012). Tooth anomalies in fossil and extant sharks consist mainly of curved or twisted crowns, punctures or notches, deformed or missing cusps, fusion of teeth of the same tooth family, excessive growth of dentine, or abnormal root morphology (Becker et al., 2000; Witzmann et al., 2021). Because damaged shark teeth cannot heal, Johnson (1987) and Welton and Farish (1993) regarded all shark tooth deformities as developmental in origin, i.e., the result of mutation or damage at an early growth stage (Witzmann et al., 2021). Based on comparisons with extant sharks, Becker et al. (2000) noted that many of the observed tooth anomalies in extant and fossil sharks were likely from feeding-related injury to the dental lamina of the jaws, particularly by impaction of chondrichthyan and teleost fin and tail spines. Furthermore, these authors explicitly stated that at least some malformed teeth could be caused by disease or mutation. However, the original cause of any dental anomaly could be virtually impossible to determine in a fossil shark (Shimada, 1997c; Witzmann et al., 2021).

Teeth of the sample described above are affected by several malformations that do not differ from malformations listed above and reported in other sharks. Fifteen teeth out of 120 total (including those with atypical size or number of cusplets)
exhibit malformations. Despite the incompleteness of the sample, the incidence of malformations in only one specimen is rather high, if compared with other Cretaceous species numbers with larger datasets (e.g., from ∼0.015% in *Squalicorax kaupi* (Agassiz, 1843) to ∼0.36% in *Paranomotodon* sp.; Becker et al., 2000). This difference is certainly due to a sampling bias, but the high incidence could be due to the peculiar trophic preferences of *Cretodus crassidens*, as evidenced by the association with marine turtle remains, or to the ontogenetic stage of the individual. Thus, the dental malformations could be interpreted as feeding-related injuries to the dental lamina (e.g., Becker et al., 2000) or as senile characters (especially the lateral cusplet loss and replacement with crenulated heel; Siversson and Machalski, 2017).

**Body size and body form: paleoecological remarks.**—The Italian specimen MPPSA IGVR 91032 allows some suppositions on the overall morphology and size of *Cretodus crassidens*. The two segments preserved measure ∼244 cm and 182 cm (although the latter was completely reworked by the preparator). The sum is ∼426 cm, but many vertebral centra are missing and this could be an underestimation of the TL of the individual. Applying the least square linear regression method (Supplemental Data 1; $r^2 = 0.86115$), it is possible to estimate an original vertebral count of 169 vertebral centra, similar to the vertebral count of other extant and extinct large lamniform sharks (Springer and Garrick, 1964; Shimada et al., 2006; Natanson et al., 2018). The mean length of the vertebral centra is ∼32.5 ± 6.22 mm, therefore the estimated articulated vertebral column is ∼549 cm long. Considering the intervertebral disc length (+10%; Newbrey et al., 2015), taphonomic compression (+20%; Newbrey et al., 2015), and skull length (+50 cm; approximation based on the *Cretoxyrhina* skull length, 60 cm, from Shimada, 1997c and Newbrey et al., 2015, and presuming a shorter and more laterally expanded skull in *Cretodus*), the estimated total length of the Italian specimen is ∼764 cm. The body size estimates reported by Amalfitano et al. (2017a) suggested a TL ranging 661–776 cm based on the size of the vertebral centra. The new estimate, based on the vertebral centroid length and approximate vertebral count, falls within the previous estimated range. This estimate can be compared also to TL estimates based on tooth size. The largest CH measured in the Italian specimen is ∼56 mm (Appendix 1) and if the CH of 56 mm is applied to the equation used by Shimada (2008), the calculation provides a TL of 700 cm. On the other hand, the linear function from Shimada et al. (2020) provides an estimated TL of ∼659.6 cm, which, if applied to the largest teeth of the *Cretodus crassidens* dentition, is very close to the original value of 661 cm based on vertebral centra diameter.

Shimada and Everhart (2019) also suggested that *Cretodus* had a stouter body than *Cretoxyrhina*, observing the arrangement of the teeth in a 120 cm wide arch (assuming that they are not dislodged) and the 156 cm long, 108 cm wide elliptical accumulation of turtle bones interpreted as gastric content. These indicate a rather stout body, with an abdominal width of at least 108 cm, and a wide, gently curved, laterally expanded mouth aperture, almost semielliptical, more like *Galeocerdo* Müller and Henle, 1837 (Randall, 1992) or, compared to any other lamniform shark, *Squalicorax* Whitley, 1939 (Shimada and Cicimurri, 2005). Accordingly, the head would also be laterally expanded. The shape of vertebral centra, almost perfectly circular and rostrocaudally short, is like many other Cretaceous lamniform sharks (e.g., *Cretoxyrhina*, Shimada, 1997c; *Cardabidion*, Newbrey et al., 2015; *Squalicorax*, Shimada and Cicimurri, 2005). Thus, it could be inferred that this shark had a fusiform body with a circular girth at the trunk region, with a great vertebral column elasticity that allowed carangiform swimming behavior (Newbrey et al., 2015). The length of the entire semielliptical dental arch, calculated with a geometric approximation (Supplemental Data 2), is ∼137 cm. Using, then, this new value applied to the relation between ‘bite circumference’ and TL by Lowry et al. (2009), the estimated TL of the individual is ∼813 cm. All of these estimates are more or less consistent, and it is reasonable to define an estimated range of TL between ∼660 and ∼780 cm (Fig. 11), based on the vertebral centroid diameter, which is apparently the least biased proxy.

Another parameter useful to infer body form and paleoecology of a shark is the morphology of the placoid scales (Reif, 1982, 1985; Reif and Dinkelacker, 1982), which are preserved in MPPSA IGVR 91032. Amalfitano et al. (2017a) and Shimada and Everhart (2019) discussed the morphology of the placoid scales to infer the swimming behavior of *Cretodus*. Shimada and Everhart (2019) observed, contra Amalfitano et al. (2017a), that the strong ridges and plications ornamenting the placoid scale crown do not extend posteriorly on the exterior crown face, unlike those of typical fast-swimming lamniforms, including fossil taxa interpreted as fast pelagic-hunting sharks, e.g., *Cretoxyrhina* (Shimada, 1997b, c; Shimada et al., 2006; Amalfitano et al., 2019) and *Cardabidion* (Dickerson et al., 2013; Newbrey et al., 2015). This morphological condition is also present in scales of the holotype of *Cretodus houghtonoun* (FHSM VP 17575; Shimada and Everhart, 2019). For this reason, the ridge spacing and the crown width from the original sample of Amalfitano et al. (2017a) were measured (Appendix 3). The mean scale crown width is 562 ± 103.31 μm, whereas the mean ridge spacing is 87.32 ± 30.65 μm. Plotting these values with those of extant sharks and *Cretoxyrhina mantelli* Agassiz, 1835 (data retrieved from Reif, 1985, Shimada, 1997a, and Amalfitano et al., 2019; Fig. 12), the *Cretodus crassidens* value falls close to the group of large nearshore predators and moderate-speed pelagic predators (sensu Reif, 1985). This confirms the assumption made by Shimada and Everhart (2019) that considers *Cretodus* a more sluggish swimmer with higher maneuverability (as also evidenced by vertebral centra morphology) than thunniform fast-cruising swimmers, e.g., *Cretoxyrhina*. This assumption is corroborated by association with the turtle remains, which suggests a trophic preference of *Cretodus crassidens* toward these reptiles, similar to that of the extant tiger shark, *Galeocerdo cuvier* (Péron and Lesueur in Lesueur, 1922), which displays very similar placoid scale ornamentation combined with the ecological niche of a large nearshore predator (Reif, 1985). Shimada and Everhart (2019), in their discussion of the ecology of the genus *Cretodus*, reported that during excavation of the holotype of *Cretodus houghtonoun* (FHSM VP 17575) that remains of two additional species of sharks were identified from the same stratigraphic
Figure 14. Suggested growth models of *Cretodus crassidens* (Dixon, 1850) based on MPPSA IGVR 91032 (see text; Table 1): (1) von Bertalanffy growth function fitted to data points that show the relationship of number of vertebral growth band pairs with estimated total body length of 660 cm (TL<sub>1</sub>); (2) von Bertalanffy growth function fitted to data points that show relationship of number of vertebral growth band pairs with estimated total body length of 780 cm (TL<sub>2</sub>). Gray silhouette indicates the lower limit (660 cm); black silhouette indicates the upper limit (780 cm). Silhouette modified after illustration by O.E. Demuth figured by Cooper et al. (2020, fig. 2D).
A relationship between teeth are more commonly found in nearshore deposits whereas those of indicates that they likely practiced resource partitioning within eously (Shimada, 2006), the distribution of the two taxa assumption is supported by the fact that although Cretodus at least sometimes, in shallow-nearshore environments. This fossil association is interpreted as another case of a ‘vertebrate three-level trophic chain’ (Kriwet et al., 2008, p. 183), but involving three species of sharks in this instance (Shimada and Everhart, 2019). The individual of Cretodus houghtonorum must have died shortly after ingesting the hybodont because of the absence of acid-etching alteration on the hybodont remains; the Cretodus houghtonorum carcass was scavenged by S. cf. S. falcatus before or during the decay, followed by disarticulation and scattering of the skeletal and dental elements of Cretodus houghtonorum due to the presence of weak currents on the seafloor (Shimada and Everhart, 2019). Hybodont remains are more common in shallow-nearshore environments, if not in fresh or brackish water environments (e.g., Underwood and Rees, 2002; Underwood, 2004; Sweetman and Underwood, 2006), and the presumed predator-prey relationship between Cretodus houghtonorum and the hybodont shark suggests that Cretodus houghtonorum dwelled, at least sometimes, in shallow-nearshore environments. This assumption is supported by the fact that although Cretodus houghtonorum and Cretoxyrhina mantelli lived contemporaneously (Shimada, 2006), the distribution of the two taxa indicates that they likely practiced resource partitioning within the North American Western Interior Sea, because Cretodus houghtonorum teeth are more commonly found in nearshore deposits whereas those of Cretoxyrhina mantelli are common in offshore deposits (Shimada and Everhart, 2019). The occurrence of Cretodus crassidens in the pelagic deposits of the Scaglia Rossa and Chalk Group, however, implies that this species preferentially dwelled in the offshore setting. It must be remarked, however, that Cretodus crassidens is represented by a single specimen in the Scaglia Rossa to date, whereas Cretoxyrhina mantelli and Ptychodus spp. remains are much more common (Amadori et al., 2019, 2020a, b; Amalfitano et al., 2019).

**Age estimate and growth model.**—One of the vertebral centra of MPPSA IGVR 91032 exhibits a total of 23 pairs of growth bands on the articular surface of the corpus calcareum (Fig. 13, Table 1). Each pair of growth bands is traditionally interpreted to have been deposited annually (Cailliet, 1990; Cailliet and Goldman, 2004), with the total band pair number (BN) indicating the age at death. Such growth band pairs do not necessarily record age or time but rather are related simply to growth or vertebral size (Harry, 2018; Natanson et al., 2018; Natanson and Deacy, 2019). Hence, the relationship of BN with time or age is loosely correlated (Natanson et al., 2018) and generally tends to retrieve an underestimation or an overestimation, because not all growth bands are necessarily consistent with aging for the entire lifespan (Passerotti et al., 2014; Harry, 2018, Natanson et al., 2018), especially in older individuals or when later growth bands are not annual. However, it is possible to hypothesize that the individual of Cretodus crassidens MPPSA IGVR 91032 was at least 23 years old at the time of its death if the deposition of each pair of growth bands is annual. The hypothetical von Bertalanffy growth function (VBGF) is here reconstructed based on the individual MPPSA IGVR 91032 and following the same estimates made by Shimada and Everhart (2019), with the aim to compare the ontogenetic growth of the two species Cretodus crassidens and Cretodus houghtonorum (Figs. 14, 15). The VBGF is applied to the size estimated above, namely ~660 cm and ~780 cm. The VBGF fitted to the BN-TL (660 cm) (Fig. 14.1) data gives the following growth parameter estimates: $L_\infty$ (maximum TL) = 955.22 cm; $L_0$ (total length at birth) = 141.9 cm; $k$ = 0.045 yr$^{-1}$; estimated longevity (after Natanson et al., 2006) = 64.429 yr. The BN-TL (780 cm) data (Fig. 14.2), on the other hand, retrieve the following parameters: $L_\infty$ = 1128.8 cm; $L_0$ = 167.7 cm. The longevity estimate of ~64 yr is consistent with those for extant large lamniform sharks (Camhi et al., 2008) and that of Cretodus houghtonorum (~55 years; Shimada and Everhart, 2019).

The percentage increment of the centrum radius of Cretodus crassidens and Cretodus houghtonorum was also considered to find any significant variation in growth rate and for further comparison (Fig. 15). The percentage increment of the two species is almost identical, except for two delayed peaks, which could correspond to the maturity onset at 12–17 years and 10–15 years, respectively. The maturity onset is consistent with those of other large macropredatory lamniform sharks (Camhi et al., 2008). The delayed growth peaks could alternatively be caused by sexual dimorphism, with females maturing later than males (Camhi et al., 2008). However, despite the strong similarities between the two species, there is no evidence to support Cretodus crassidens and Cretodus houghtonorum dentitions as gynandric heterodont variants, but rather they were vicariant species dwelling in different environments (Cretodus crassidens in offshore settings, Cretodus houghtonorum in nearshore settings) or geographically separated (Cretodus crassidens in the European Tethys and Boreal seas, Cretodus houghtonorum in the Western Interior Seaway; see also Guinot and Cavin, 2016 for vicariances related to the Cenomanian diversification event). After attaining maturity, the growth rate
The growth model provided herein allows calculation of the possible TL of other specimens. The growth bands are not well preserved on the two vertebral centra of BMB 007312. The specimen also includes the lower second anterior tooth, the CH of which measures 47 mm (Appendix B). If the linear functions CH-TL extrapolated from MPPSA IGVR 91032 is applied, i.e.,

\[ TL_1(\text{cm}) = 11.78 \times \text{CH(mm)} + 0.24 \]  \hspace{1cm} (4)

\[ TL_2(\text{cm}) = 13.92 \times \text{CH(mm)} + 0.29 \]  \hspace{1cm} (5)

the estimated TL of BMB 007312 results in a range between ~554 cm and ~654 cm (versus an estimated TL range of 546–573 cm when applying the equations used by Amalitano et al. [2017a] based on vertebral centrum diameter). The age at death was ~16–17 years if the CH is considered, comparing this specimen to MPPSA IGVR 91032 (Table 1).

Conclusions

The specimen MPPSA IGVR 91032 and others described herein provide new morphological and paleobiological information about the Late Cretaceous large-sized shark genus *Cretodus*. The specimen is assigned to *Cretodus crassidens* and reconstruction of its dentition based on the Italian specimen reveals the peculiarities of this species with respect to other species of the genus. *Cretodus crassidens* likely represents a separate lineage within *Cretodus* (see the phylogenetic hypothesis by Shimatada and Everhart, 2019). The body form and size estimates are indicative of a large-sized macropredatory shark, reaching a size over the limit that defines gigantic elasmobranch species (> 6 m; Pimiento et al., 2019). The maximum estimated total length (9–11 m) and length at birth are comparable to those of the giant Cenozoic genus *Otodus* Agassiz, 1838 (Shimatada et al., 2021). *Cretodus crassidens* was probably characterized by a moderate-speed swimming behavior, suggested by the morphology of the vertebral centra and the placoid scales. This shark was a large predator feeding on, among others, large protostegid turtles, as evidenced by the gastric content preserved within the individual from the basinal high settings of the large protostegid turtles, as evidenced by the gastric content preserved within the individual from the basinal high settings of the giant Cenozoic genus *Cretodus* crassidens Tethyan domains at the same interval, implying a broad paleo-

Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.31zcrjdnk.

References

Adnet, S., 2006, Biometric analysis of the teeth of fossil and Recent hexanchid sharks and its taxonomic implications: Acta Palaeontologica Polonica, v. 51, no. 3, p. 477–488.

Agassiz, L.J.R., 1835, Rapport sur les Poissons Fossiles Découverts Depuis la Publication de la Troisième Livraison, Feuillet Additionnel sur les Recherches sur les Poissons Fossiles, 4th Livraison: Neuchâtel, Switzerland, Petitpierre et Prince, p. 39–64.

Agassiz, L.J.R., 1838, Recherches sur les Poissons Fossiles, 11th Livraison: Neuchâtel, Switzerland, Petitpierre et Prince (text) and H. Nicolet (plates), v. 2, pls. 42, 43; v. 3, p. [73]–140, pls. 1a, 8a, 8b, 15, 17, 19, 20, 24, 25b, 30–35, 39, 40; v. 5, pl. 60; Feuillet Additionnel, p. 107–116.

Agassiz, L.J.R., 1843, Recherches sur les Poissons Fossiles, 15th and 16th Livraisons: Soleure, Switzerland, Jenet and Gassmann (text), and Neuchâtel, Switzerland, H. Nicolet (planches), v. 2, pt. 2, p. [1]–72, pls. B’’, B’, Ca, G, 23b, 25c, 31, 33a, 36–38, 42a, 44; v. 3, p. 157–390, 382–382**, 1–32, [33]–54, pls. 1, 18, 22, 22a, 22b, 26a, 38, 40h–40d, 45h, vol. 4, pl. 23b; vol. 5, pt. 2, p. 57–84, pls. B, C, E, H, J, K, 9, 10, 28, 29, 37b, 44–48; Feuillet Additionnel, p. 139–144.

Amadori, M., Amalitano, J., Giuberti, L., Fornaciari, E., Luciani, V., Carnevale, G., and Kirvet, J., 2019, First associated tooth set of a high-cusped *Psychodus* (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of northeastern Italy, and resurrection of *Psychodus altior* Agassiz, 1835: Cretaceous Research, v. 93, p. 330–345, https://doi.org/10.1016/j.cretres.2018.10.002.

Amadori, M., Amalitano, J., Giuberti, L., Fornaciari, E., Carnevale, G., and Kirvet, J. 2020a, The Italian record of the Cretaceous shark, *Psyrhus latissimus* Agassiz, 1835 (Chondrichthyes; Elasmobranchii) from the Upper Cretaceous of northeastern Italy, and resurrection of *Psychodus altior* Agassiz, 1835: Cretaceous Research, v. 110, p. 104386, https://doi.org/10.1016/j.cretres.2020.104386.

Amalitano, J., Dalla Vecchia, F.M., Giuberti, L., Fornaciari, E., Luciani, V., and Roghi, G., 2017a, Direct evidence of trophic interaction between a large lamniform shark, *Cretodus sp.*, and a marine turtle from the Cretaceous of northeastern Italy: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 469, p. 104–121, https://doi.org/10.1016/j.palaeo.2016.12.044.

Amalitano, J., Giuberti, L., Dalla Vecchia, F.M., and Kirvet, J., 2017b, First skeletal remains of the giant sawfish *Onchodon* (Neoselachii,
Spain provide insights into gigantism, growth rate and life history of psychodontid sharks: PLoS One, v. 15, no. 4, p. e203544, https://doi.org/10.1371/journal.pone.0203544.

Johnson, G.D., 1987, Described xenacanthidid shark teeth from the Permian of Texas: Dakotaol, v. 3, p. 22–27.

Kriwet, J., 2002, Anomoedossus pauciserrale n. sp. (Neopterygii, Pycnodontiformes) from the White Chalk Formation (Upper Cretaceous) of Sussex, south England: Palaeontologische Zeitschrift, v. 76, p. 117–123, https://doi.org/10.1515/posc.2002.39988.190.

Kriwet, J., Witzmann, F., Klug, S., and Heidtke, U.H., 2008, First direct evidence of a vertebrate three–level trophic chain in the fossil record: Proceedings of Royal Society B, Biological Sciences, v. 275, no. 1631, p. 181–186, https://doi.org/10.1098/rspb.2007.1170.

Lesueur, G.A., 1822, Description of a Squalus, of a very large size, which was taken on the coast of New Jersey: Journal of the Academy of Natural Sciences of Philadelphia, v. 2 (ser. 1), p. 343–352.

Linnaeus, C., 1758, Systema Naturae per Regna Tria Naturae (tenth edition), v. 1, pars 12. London, 1049 p., 300 maps.

Longbottom, A.E., and Patterson, C., 2002, Fishes; PLoS One, v. 12, no. 11, p. e0188806, https://doi.org/10.1371/journal.pone.0188806.

Lowry, D., de Castro, A.L.F., Mara, K., Whitenack, L.B., Delius, B., Burgess, D.J., eds., Fossils of the Chalk (second edition): Field Guides to Fossils of the Chalk Number 2: London, Paleontological Association, p. 296.

Müller, J., and Henle, F.G.J., 1837, Gattungen der Hai: Einige von ihm mit Hrn. Henle unternommen gemeinschaftlichen Arbeit, zur Bekanntm. und geeigneten Verhandlungen der Königlichen Preussische Akademie van Wetenschappen, ser. B, v. 80, no. 3, p. 169–181.

Mantell, G., 1822, The Fossils of the South Downs, or Illustrations of the Geology of the Sussex Coast: London, Lipton Relle, 328 p.

Munivit, H., Perch-Nielsen, K., Prins, B., and Verbeek, W., 1977, Mid Cretaceous calcareous nannofossil biostratigraphy: Proceedings of the Koninklijne Nederlands Seminarie van Wetenschappen, v. 71, no. 3, p. 588–617.

Natanson, L.J., and Deacy, B.M., 2019, Using oxytetracycline validation for determining lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans: Marine and Freshwater Research, v. 65, no. 8, p. 674–687, https://doi.org/10.1071/MF171479.

Parsons, R.T., England, P.K., McDougall, I., and Berggren, W.A., 1976, The Triassic–Jurassic absolute time scale: Geology, v. 4, no. 6, p. 211–215, https://doi.org/10.1130/0091-7613(1976)4[211:TTATS]2.0.CO;2.

Purdy, R.W., and Francis, M.P., 2007, Ontogenetic development of teeth in Lamna nasus (Bonamarte, 1758) (Chondrichthyes: Lamnidae) and its implications for the study of fossil shark teeth: Journal of Vertebrate Paleontology, v. 27, no. 4, p. 790–791, https://doi.org/10.1671/0272-4634(2007)27[790:DODOTL]2.0.CO;2.

Quoy, J.R.C., and Gaimard, J.P., 1824, Description des Poissons, in de Freycinet, L., ed., Voyage Autour du Monde, Entrepris par Ordre du Roi, Exécuté sur les Corvettes de S.M. l’Uranie et la Physicienne, Pendant les Annees 1816, 1817, 1819 et 1820, Zoologie: Paris, Chez Pillet Aîné, p. 192–401, Atlas pls. 43–65.

Reif, W.E., 1980, A mechanism for tooth pattern reversal in sharks: The polarity switch model: Wilhelm Roux’s Archives of Developmental Biology, v. 188, no. 2, p. 113–122.

Reif, W.E., 1982, Morphogenesis and function of the squamation in sharks: Neues Jahrbuch für Geologie und Paleontologie, Abhandlungen, v. 164, no. 1/2, p. 172–183.

Reif, W.E., 1985, Squamation and ecology of sharks: Courier Forschungsinstitut Senckenberg, v. 78, p. 1–255.

Reif, W.E., and Dinkelaeker, G., 1982, Hydrodynamics of the squamation in fast swimming sharks: Neues Jahrbuch für Geologie und Paleontologie, Abhandlungen, v. 164, no. 1/2, p. 184–187.

Reinhardt, P., 1986, Zur Taxionomie und Biostratigraphie des fossilen Nannoplanktons aus dem Malm, der Kreide und dem Alitherme Mitteleuropas: Freiherr Burger Forschungshefte, C 196 Paleontologie, p. 5–109, pls. 1–23.

Ridewood, W.G., 1921, On the calcification of the vertebral centra in sharks and rays: Philosophical Transactions of the Royal Society of London B, Containing Papers of a Biological Character, v. 210, nos. 372–381, p. 311–407.

Schneider, C.A., R ashand, W.S., and Eliceiri, K.W., 2012, NIH Image to Ima gia: 25 years of image analysis: Nature Methods, v. 9, no. 7, p. 671–675, https://doi.org/10.1038/nmeth.2089.

Shimada, K., 1997a, Dentition of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli from the Niobrara Chalk of Kansas: Journal of Vertebrate Paleontology, v. 17, no. 2, p. 268–279.

Shimada, K., 1997b, Paleontological relationships of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli (Agassiz): Journal of Paleontology, v. 71, no. 5, p. 926–933.

Shimada, K., 1997c, Skeletal anatomy of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli, from the Niobrara Chalk in Kansas: Journal of Vertebrate Paleontology, v. 17, no. 4, p. 642–652.

Shimada, K., 2002, Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii): Journal of Morphology, v. 251, p. 38–72, https://doi.org/10.1002/mor.1073.

Shimada, K., 2003, The relationship between the tooth size and total body length in the white shark, Carcharodon carcharias (Lamniformes: Lamnidae): Journal of fossil Research, v. 35, p. 28–33.

Shimada, K., 2005, Types of tooth sets in the fossil record of sharks, and comments on reconstructing dentitions of extinct sharks: Journal of Fossil Research, v. 38, p. 141–145.

Shimada, K., 2006, Marine vertebrates from the Blue Hill Shale Member of the Carlile Shale (Upper Cretaceous: Middle Turonian) in Kansas: Bulletin of New Mexico Museum of Natural History, v. 35, p. 165–175.

Shimada, K., 2007, Skeletal and dental anatomy of lamniform shark, Cretoxyrhina mantelli, from western New Mexico: Journal of Vertebrate Paleontology, v. 27, p. 584–602, https://doi.org/10.1671/0272-4634(2007)27[584:SADALM]2.0.CO;2.

Shimada, K., 2008, Ontogenetic parameters and life history strategies of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli, based on vertebral growth increments: Journal of Vertebrate Paleontology, v. 28, no. 1, p. 21–33. https://doi.org/10.1671/0272-4634(2008)28[21:OPALHS]2.0.CO;2.

Shimada, K., 2019, The size of the megatooth shark, Otodus megalodon (Lamniformes: Otodontidae) revisited: Historical Biology, v. 33, no. 7, p. 904–911, https://doi.org/10.1080/08912963.2019.1666840.

Shimada, K., and Cicimurri, D.J., 2005, Skeletal anatomy of the Late Cretaceous shark, Squillarchius (Neoselachii: Anacoraciidae): Palaeontologische Zeitschrift, v. 79, no. 2, p. 241–261, https://doi.org/10.1007/BF02990187.

Shimada, K., and Everhart, M.J., 2019, A new large Late Cretaceous lamniform shark from North America, with comments on the taxonomy, paleoecology, and evolution of the genus Cretodus: Journal of Vertebrate Paleontology, v. 39, no. 4, p. e1673399, https://doi.org/10.1080/02724634.2019.1673399.
Shimada, K., Cumbaa, S.L., and van Rooyen, D., 2006, Caudal fin skeleton of the Late Cretaceous shark, *Cretotaxyrhina mantelli* (Lamniformes: Cretotaxyrhiniidae) from the Niobrara Chalk of Kansas: Bulletin of New Mexico Museum of Natural History, v. 35, p. 185–192.

Shimada, K., Becker, M.A., and Griffiths, M.L., 2020, Body, jaw, and dentition lengths of macropagous lamniform sharks, and body size evolution in Lamniformes with special reference to ‘off-the-scale’ gigantism of the megatooth shark, *Ododus megalodon*: Historical Biology, v. 33, no. 11, p. 2543–2559, https://doi.org/10.1080/08912963.2020.1812598.

Shimada, K., Bonnan, M.F., Becker, M.A., and Griffiths, M.L., 2021, Ontogenetic growth pattern of the extinct megatooth shark *Ododus megalodon*: Implications for its reproductive biology, development, and life expectancy: Historical Biology, v. 33, no. 12, p. 3254–3259, https://doi.org/10.1080/08912963.2020.1861608.

Siversson, M., and Machalski, M., 2017, Late Late Albian (Early Cretaceous) shark teeth from the uppermost Gerele Silstone (Cenomanian, Late Cretaceous) of Western Australia: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 90, no. 1, p. 49–66.

Siversson, M., and Machalski, M., 2017, Late late Albian (Early Cretaceous) shark teeth from Annopol, Poland: Alcheringa: An Australasian Journal of Palaeontology, v. 41, no. 4, p. 453–463, https://doi.org/10.1080/03115518.2017.1282981.

Siversson, M., Lindgren, J., and Kelley, L.S., 2007, Anacoracid sharks from the Albian (Lower Cretaceous) Pawpaw Shale of Texas: Palaeontology, v. 50, no. 4, p. 939–950, https://doi.org/10.1111/j.1475-4983.2007.00691.x.

Siversson, M., Ward, D.J., Lindgren, J., and Kelley, L.S., 2013, Mid-Cretaceous *Cretotaxyrhina* (Euselachii) from Mangyshlak, Kazakhstan and Texas, USA: Alcheringa: An Australasian Journal of Palaeontology, v. 37, no. 1, p. 87–104, https://doi.org/10.1080/03115518.2012.709440.

Siversson, M., Lindgren, J., Newbury, M.G., Cederström, P., and Cook, T.D., 2015, Cenomanian–Campanian (Late Cretaceous) mid-paleolatitude sharks of *Cretalasma annuliculata* type: Acta Palaeontologica Polonica, v. 60, p. 339–384, https://doi.org/10.4202/app.2012.0137.

Smith, M.M., Johansen, Z., Underwood, C., and Dickwisch, T.G., 2013, Pattern formation in development of chondrichthyan dentitions: A review of an evolutionary model: Historical Biology, v. 25, no. 2, p. 127–142, https://doi.org/10.1080/08912963.2012.662228.

Snodgrass, R.E., and Heller, E., 1905, Papers from the Hopkins-Stanford Galapagos Expedition, 1898–1899, 17, Shore fishes of the Revillagigedo, Clipperon, Coco, and Galapagos islands: Proceedings of the Washington Academy of Sciences, v. 6, p. 333–427.

Springer, V.G., and Garrick, J.A.F., 1964, A survey of vertebral numbers in sharks: United States National Museum Proceedings, v. 116, p. 73–96.

Sokolov, M.I., 1965, Evolutsiya zubov nekotorykh rodov melovykh akul i rekonstruktziya ikh ozublenniya [Teeth evolution of some genera of Cretaceous sharks and reconstruction of their dentition]: Byulleten’ Moskovskogo Obschestva Ispytateley Prirody, n.s., v. 70, Otdel Geologicheskii, v. 40, no. 4, p. 133–134, [in Russian]

Sweatman, S.C., and Underwood, C.J., 2006, A neoselachian shark from the non-marine Wessex Formation (Wealden Group: Early Cretaceous, Barremian) of the Isle of Wight, southern England: Palaeontology, v. 49, no. 2, p. 457–465, https://doi.org/10.1111/j.1475-4983.2006.00549.x.

Trevisani, E., and Cestari, R., 2007, Upper Cretaceous bivalves from basinal highs (Venetian Prealps, northern Italy): in Scott, R.W., ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback: SEPM Special Publications, v. 87, p. 71–80.

Underwood, C.J., 2004, Environmental controls on the distribution of neoselachian sharks and rays within the British Bathonian (Middle Jurassic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, no. 1/2, p. 107–126, https://doi.org/10.1016/S0031-0182(03)00663-1.

Underwood, C.J. and Rees, J., 2002, Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England: Special Papers in Palaeontology, v. 68, p. 83–101.

Valenciennes, A., 1822, Sur le sous-genre Marteau, *Zygaena*: Mémoires du Muséum d’Histoire Naturelle, v. 9, p. 222–228, pl. 1, 2 von Bertalanffy, L., 1938, A quantitative theory of organic growth (inquiries on growth laws 2): Human Biology, v. 10, p. 181–213.

Vullo, R., Guinot, G., and Barbe, G., 2016, The first articulated specimen of the Cretaceous mackerel shark *Haimeirichia amonensis* gen. nov. (Haimeirichidae fam. nov.) reveals a novel ecomorphological adaptation within the Lamniformes (Elasmobranchii). Journal of Systematic Palaeontology, v. 14, no. 12, p. 1003–1024, https://doi.org/10.1080/14772019.2015.1137983.

Walliser, E.O., and Schöne, B.R., 2020, Paleoceanography of the Late Cretaceous northwestern Tethys Ocean: Seasonal upwelling or steady thermocline?: PloS One, v. 15, no. 8, p. e0238040, https://doi.org/10.1371/journal.pone.0238040.

Welton, B.J., and Farish, R.F., 1993, The Collector’s Guide to Fossil Sharks and Rays from the Cretaceous of Texas: Lewisville, Texas, Before Time, 204 p.

Werner, C., 1989, Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Oberenemnon) der Oase Bahariya, Agypten: Palaeo Ichthyologica, v. 5, p. 1–112.

Whitley, G.P., 1939, Taxonomic notes on sharks and rays: Australian Zoologist, v. 9, p. 227–262.

Wilkinson, I.P., 2011, Foraminiferal biozones and their relationship to the lithostratigraphy of the Chalk Group of southern England: Proceedings of the Geologists’ Association, v. 122, no. 5, p. 842–849, https://doi.org/10.1016/j.peola.2011.10.002.

Witzmann, F., Hartiy, Y., Hilger, A., Manke, I., and Asbach, P., 2021, Rarity of congenital malformation and deformity in the fossil record of vertebrates—A non-human perspective: International Journal of Paleopathology, v. 33, p. 30–42, https://doi.org/10.1016/j.ijppa.2020.12.002.

Woodward, A.S., 1889, Catalogue of the Fossil Fishes in the British Museum, Part 1 Containing the Elasmobranchi: London, British Museum (Natural History), 474 p.

Woodward, A.S., 1902, The fossil fishes of the English Chalk, part 1: Monographs of the Palaeontographical Society, London, v. 56, p. 1–56.

Woodward, A.S., 1903, The fossil fishes of the English Chalk, part 2: Monographs of the Palaeontographical Society, London, v. 57, p. 57–96.

Woodward, A.S., 1907, The fossil fishes of the English Chalk, part 3: Monographs of the Palaeontographical Society, London, v. 61, p. 97–128.

Woodward, A.S., 1908, The fossil fishes of the English Chalk, part 4: Monographs of the Palaeontographical Society, London, v. 62, p. 129–152.

Woodward, A.S., 1909, The fossil fishes of the English Chalk, part 5: Monographs of the Palaeontographical Society, London, v. 63, no. 308, p. 153–184.

Woodward, A.S., 1911, The fossil fishes of the English Chalk, part 6: Monographs of the Palaeontographical Society, London, v. 64, p. 185–224.

Woodward, A.S., 1912, The fossil fishes of the English Chalk, part 7: Monographs of the Palaeontographical Society, London, v. 65, no. 320, p. 225–264.

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Appendix 1. Corrections to tooth measurements of MPPSA IGVR 91032 (in mm). The numbers of teeth are those reported by Amalitano et al. (2017a, fig. 6). CH = crown height; CT = crown thickness (labiolingual); CW = crown width; DCL = distal cutting-edge length; LCH = cusplet height; MCL = mesial cutting-edge length; PCH = central cusp height; PCW = central cusp width; TH = tooth height; TT = tooth thickness (labiolingual); TW = tooth width. Gray-shaded cells are those corrected.

| Tooth | TH | TW | TT | CH | CW | CT | LCH | PCH | PCW | MCL | DCL |
|-------|----|----|----|----|----|----|-----|-----|-----|-----|-----|
| 3     | 69 | 52 | 22 | 46 | 16 | 16 | 39  | 27  | 42  | 41  |     |
| 6     | 41 |   | 21 | 33 | 10 | 10 | 24  | 17  |     |     |     |
| 16    | 48 | 36 | 10 | 34 | 25 | 11 | 22  | 14  | 26  | 24  |     |

Appendix 2. Tooth measurements of BMB 007312 (in mm). The table includes measurements of some of the best-preserved teeth. CH = crown height; CT = crown thickness (labiolingual); CW = crown width; DCL = distal cutting-edge length; LCH = cusplet height; MCL = mesial cutting-edge length; PCH = central cusp height; PCW = central cusp width; TH = tooth height; TT = tooth thickness (labiolingual); TW = tooth width; * = tooth isolated from the matrix.

| Tooth | TH | TW | TT | CH | CW | CT | LCH | PCH | PCW | MCL | DCL |
|-------|----|----|----|----|----|----|-----|-----|-----|-----|-----|
| a2    | 51 | 36 | 20 | 47 | 33 | 11 | 8   | 38  | 22  | 50  | 49  |
| l2*   | -  | -  | -  | -  | -  | 12 | -   | 29  | 19  | -   | -   |
| a1    | -  | -  | -  | -  | -  | -  | -   | 38  | 22  | -   | -   |
| L1?   | -  | -  | -  | 26 | 19+| 6  | 4   | 18  | 14  | -   | 25  |
| L8?   | 19?| -  | -  | 16 | 20?| -  | -   | 4   | 13  | 10  | 16  |

Appendix 3. Placoid scale measurements of Cretodus crassidens (Dixon, 1850).

| Sample | Scale location | Ridge spacing (μm) | Scale width (μm) |
|--------|----------------|--------------------|------------------|
| IGVR 91032 unknown | 88-123-162 | 433 | 99-113-92 | 711 |
|          | 78-83-93-58-60-89 | 548 | 82-138-105-137-86-76 | 694 |
|          | 49-50-46-76-116-88-49-74-65-25 | 497 | 115-115-81-59 | 600 |
|          | 69-130 | 451 |

mean (n = 7) 87.32 ± 30.65 562 ± 103.31