



UNIVERSITÀ
DEGLI STUDI
DI PADOVA

Head Office: Università degli Studi di Padova

Department of Geosciences

Ph.D. COURSE IN: EARTH SCIENCES

SERIES XXXII

The Cenomanian-Turonian ichthyofaunas from the Scaglia-type succession of northeastern Italy

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Abstract

The Cretaceous period was affected by global perturbations (e.g., the Cenomanian-Turonian Oceanic Anoxic Event), which led to widespread changes in the ocean-climate system. Primary trophic levels (e.g., calcareous and other mineralized plankton) experienced accelerated rates of speciation and extinction at or near these events. Investigating the composition of fossil ichthyofaunas is crucial to reconstruct the changes induced by these disruptions in the higher trophic levels (e.g., fish communities), whose interpretation remains elusive. The broad ecological range occupied by actinopterygians today was probably quite similar in the Cretaceous because no other vertebrate groups competed with actinopterygians in their niches at that time. Considering the range of ecosystems occupied today by actinopterygians as being representative of the paleoecology of ray-finned fishes in the Cretaceous, they form a good proxy to study how vertebrates responded to global changes during the last half of the Mesozoic. In northeastern Italy, the upper Cenomanian Bonarelli Level and the Turonian-Coniacian “lastame” (Scaglia Rossa Formation) yielded diversified and well-preserved ichthyofaunas that recorded the fish assemblage composition in the Cenomanian-Turonian interval. The aim of this thesis is the study of the composition of these poorly known Tethyan assemblages, evidencing their diversity and ecological structure and comparing them to coeval assemblages. This study will hopefully provide significant data for adding new tiles for the reconstruction of the effects of the Cretaceous climatic disruptions on the higher trophic levels in the Tethyan domain.

How to consult the dissertation

This PhD dissertation, concerning the Cenomanian-Turonian ichthyofaunas from two selected *Fossil-Lagerstätten* of northeastern Italy, consist of four chapters. Each chapter includes sections. Each section follows the related published article or submitted manuscript outline. At the beginning of every chapters there is the title for each section, with the reference to the published articles. The appendices of each section are placed at the end of the dissertation.

The first chapter introduces aim and issues related to the research topic, with an overview on the climatic, paleogeographic and evolutionary settings.

The second chapter is focused on the Bonarelli Level ichthyofaunas.

The section 2.1. deals with fossils coming from both assemblages, but was placed in this section for author's choice, being introductive for the geological setting of the Bonarelli Level of northeastern Italy.

The third chapter deals with the 'lastame' assemblage.

The fourth chapter presents only some concluding remarks about the topic of the whole dissertation.

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Chapter 1.

Introduction

1.1. Why studying the fossil ichthyofaunas of northeastern Italy?

1.2. The Cenomanian-Turonian transition: climatic and geographical setting

1.3. General evolutionary dynamics inside the Tethyan ichthyofaunas during the Cenomanian-Turonian interval

1.1.

Why studying Cretaceous ichthyofaunas of northeastern Italy?

The Cretaceous period was affected by global perturbations (e.g., the Cenomanian-Turonian Oceanic Anoxic Event), which led to widespread changes in the ocean-climate system. Primary trophic levels (e.g., calcareous and other mineralized plankton; Leckie et al., 2002; Keller et al., 2008) experienced accelerated rates of speciation and extinction at or near these events. Investigating the composition of fossil ichthyofaunas is crucial to reconstruct the changes induced by these disruptions in the higher trophic levels (e.g., fish communities), whose interpretation remains elusive. Fishes are a particularly attractive system for exploring questions related to evolution and ecology over geological timescales (see Friedman and Sallan, 2012), because of the considerably body of work dissecting form-function relationship in living form generally, and teleosts specifically (e.g., Wainwright and Bellwood, 2002; Friedman, 2010). Additionally, the impact of fishes as predators, competitors and prey on the long-term macroevolution and macroecology of other clades (e.g., invertebrates and tetrapods) has likely been substantial (Friedman and Sallan, 2012). The broad ecological range occupied by actinopterygians today was probably quite similar in the Cretaceous because no other vertebrate groups competed with actinopterygians in their niches at that time (Cavin et al., 2007). Considering the range of ecosystems occupied today by actinopterygians as being representative of the paleoecology of ray-finned fishes in the Cretaceous, they form a good proxy to study how vertebrates responded to global changes during the last half of the Mesozoic (Cavin et al., 2007). Global disruption of geochemical cycles seemingly coincides with widespread events of exceptional preservation (see Retallack, 2011). In northeastern Italy, the upper Cenomanian Bonarelli Level and the Turonian-Coniacian “lastame” (Scaglia Rossa Formation) yielded diversified and well-preserved ichthyofaunas that recorded the fish assemblage composition in the Cenomanian-Turonian interval. The upper Cenomanian Bonarelli Level ichthyofauna was studied by Sorbini (1976), focused on a single locality, Cinto Euganeo (Padova), and in the last forty years has never been revised or updated with new findings coming from some new localities of Veneto region (e.g., Gomez et al., 2002; Dalla Vecchia et al., 2005). The ‘lastame’ assemblage is known since the 1970s, but it has never been investigated in detail. Cigala Fulgosi et al. (1980) were the only authors that cursorily examined the fossil remains coming from this peculiar lithofacies of the Scaglia Rossa Formation. In this framework, the aim of this thesis is the study of the composition of these poorly known Tethyan assemblages, evidencing their diversity and ecological structure and comparing them to coeval

assemblages. This study will hopefully provide significant data for adding new tiles for the reconstruction of the effects of the Cretaceous climatic disruptions on the higher trophic levels in the Tethyan domain.

1.2.

The Cenomanian-Turonian transition: climatic and geographical setting

The mid-Cretaceous, between the Aptian and the earliest Turonian (125-93 Ma), was characterized by intense tectonic forcing: high rates of seafloor spreading and multiple pulses of extensive volcanic activity are registered from this time (Arthur et al., 1985b; Larson, 1991; McLeod et al., 2008; Seton et al., 2009; Du Vivier et al., 2014; Jenkins et al., 2017). Volcanic out-gassing led to high atmospheric CO₂ concentrations of up to 3-5 times preindustrial levels (e.g., Jarvis et al., 2011 and references therein). Climate proxy data indicate a period of climatic optimum, high sea surface temperatures (SST), and a much reduced equator-to-pole thermal gradient (Barron, 1983; Huber et al., 1995, 2002; Bice et al., 2006; Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; Kidder and Worsley, 2012). High pCO₂ (partial pressure CO₂) and warm climates increased terrestrial weathering and input of fluvial nutrient fluxes, and decreased the levels of oxygen in the atmosphere and oceans (Jarvis et al., 2011). These processes led to episodic widespread black shale depositions, which represent a characteristic feature of the mid-Cretaceous sedimentary record (Schlanger and Jenkyns, 1976; Arthur et al., 1987; Schlanger et al., 1987). These events are termed Oceanic Anoxic Events (OAEs) and the causes of such phenomena remain hotly debated. It is likely that increased nutrient availability and intensified upwelling, associated with restricted basin geometries, generally poor oceanic oxygenation, and weakened circulation and possible density stratification, made the mid-Cretaceous oceans predisposed to periods of bottom water anoxia and local euxinic (sulfidic) conditions, thus enhancing the preservation of organic matter (e.g., see discussion in Jenkyns, 2010). Euxinic condition also promoted phosphate release back to bottom waters from degrading organic matter, establishing a positive feedback loop that maintained productivity, euxinia and carbon burial until the original forcing was removed (Mort et al., 2007; Meyer and Kump, 2008; Tsandev and Slomp, 2009; Martin et al., 2012). Additionally, the release of trace-metal micronutrients (Snow et al., 2005) and sulfur associated with massive volcanism (McLeod et al., 2008; Turgeon and Creaser, 2008; Du Vivier et al., 2014; Jenkins et al., 2017) may have further enhanced these conditions and nutrient recycling, which increased the already high levels of global primary production (Adams et al., 2010; Jarvis et al., 2011; Du Vivier et al., 2014; Jenkins et al., 2017). In addition to black shale deposition, OAEs are marked by the global development of shortlived (<1 Myr) positive carbon stable-isotope ($\delta^{13}\text{C}$) excursions in marine carbonates, and both marine and nonmarine organic matter

(Scholle and Arthur, 1980; Schlanger et al., 1987; Arthur et al., 1988; Hasegawa, 1997; Tsikos et al., 2004; Jarvis et al., 2006; Jenkyns, 2010; Jarvis et al., 2011; Du Vivier et al., 2014; Jenkins et al., 2017), caused by the enhanced burial of ^{13}C -depleted organic matter. OAEs thus represent dramatic short-term perturbations of the global carbon cycle. The last major mid-Cretaceous anoxic event, the Oceanic Anoxic Event 2 (OAE2), one of few with a truly global distribution, occurred across the Cenomanian-Turonian boundary (CTB) at 93.6 Ma (Ogg et al., 2008), and lasted for approximately 500 kyr (e.g., Sageman et al., 2006; Voigt et al., 2008). Various authors argued that high burial rates of organic carbon during the CTB event were sufficient to drastically reduce atmospheric CO_2 and cause transient cooling of the global climate (Arthur et al., 1988; Freeman and Hayes, 1992; Kuypers et al., 1999). Therefore, pCO_2 and SST maxima occurred at the onset of black shale deposition, followed by falling pCO_2 and cooling due to carbon sequestration by marine organic productivity and preservation, and increased silicate weathering (Jarvis et al., 2011). A marked pCO_2 minimum ($\sim 25\%$ fall) occurred with a SST minimum (Plenus Cold Event) showing a drastic cooling ($>4^\circ\text{C}$) phase of the duration of ca. 40 kyr (Jarvis et al., 2011). This cooling deeply affected the water masses (see e.g., Zheng et al., 2013; 2016) and led to important biotic turnovers (see Pearson et al., 2009). Renewed increases in pCO_2 , SST, and $\delta^{13}\text{C}$ during latest Cenomanian black shale deposition suggest that a continuing volcanogenic CO_2 flux overrode further drawdown effects (Jarvis et al., 2011). Maximum pCO_2 and SST followed the end of OAE2, associated with a falling nutrient supply during the early Turonian eustatic highstand (Jarvis et al., 2011). The Turonian is characterized by the deposition of the so-called Cretaceous Oceanic Red Beds (CORBs). Red colored pelagic sediments of varying carbonate content are exposed in the entire Tethys area and in parts of the Atlantic and the Pacific (Neuhuber et al., 2007; for a summary see Wang and Hu, 2005). Such simultaneous onset of CORBs deposition in the Turonian are attributed by authors to a fundamental change in the oxidation state of the ocean, which reflects changes in the circulation and the carbon budget of the ocean (e.g., Wang et al., 2005) and followed the period of extensive mid-Cretaceous black shale deposition (Neuhuber et al., 2007). A gradual nutrient depletion (most likely phosphate depletion in the surface waters) during this time interval resulted in enhanced oligotrophy, which ultimately led to the formation of CORBs. An increase in bottom water oxygenation in basins with black shale deposits can be seen (Neuhuber et al., 2007). Overall, the depth of the oxygen minimum zone in adjacent basins (Atlantic or southern part of the Tethys ocean) increased during this time period (Neuhuber et al., 2007). Sea-surface temperatures were highest in the early to middle Turonian, coincident with high eustatic sea-levels (Jarvis et al., 2015). Medium-term to long-term trends in $\delta^{18}\text{O}_{\text{carb}}$ profiles indicate a Europe-wide trend of stepped cooling that accompanied long-term sea-level fall, beginning in the late-middle

Turonian and culminating in the mid-late Turonian - the “Late Turonian Cool Phase” (Wiese and Voigt, 2002; Jarvis et al., 2015).

Concerning the paleogeographic setting (Fig. 1), Decourt et al. (2000) reported that the Cretaceous interval in the Tethys is primarily characterized by the opening of the South Atlantic Ocean and the individualization of the Africa-Arabia plate with its counter-clockwise displacement. The palaeomagnetic data accuracy evidences, therefore, a strong northward displacement of the eastern part of the plate, and a slight one of the western. This displacement brings about: (1) an important accentuation of the pre-existing oceanic subduction under the East European platform during Maastrichtian and, later on, a shift south of the Cimmerian blocks (Iran); (2) an initiation of subduction inside the micro-plates constituting the Mediterranean Sea; (3) a progressive continent/continent collision generative of mountain ranges (Pyrenees, Alps, Carpathian, Dinarides, Balkan, Pontides, Taurides, Maghrebides, then Zagros) and a general inversion of pre-existing faults inside both Peri-Tethyan platforms, which gives an east-west prominent structure (basins and heights) and inside the Northern platform, instead of the previously diverse directions (Decourt et al., 2000). In the northern Neo-Tethys, the mid-oceanic ridge ceased to be active in some places. At that time, plankton-bearing chinks covered some of the ophiolitic mélanges that formed previously in deep basins (Philip and Floquet, 2000). Similar kinds of pelagic limestone deposited more or less in all the Southern European Tethys domain (see individual geological setting paragraphs in next chapters for further details). Carbonate platforms existed at the same time producing detritals, which were resedimented as debris flows in surrounding basins. Some continental rises were eroded, and flysch-like deposits invaded other small basins (Philip and Floquet, 2000).

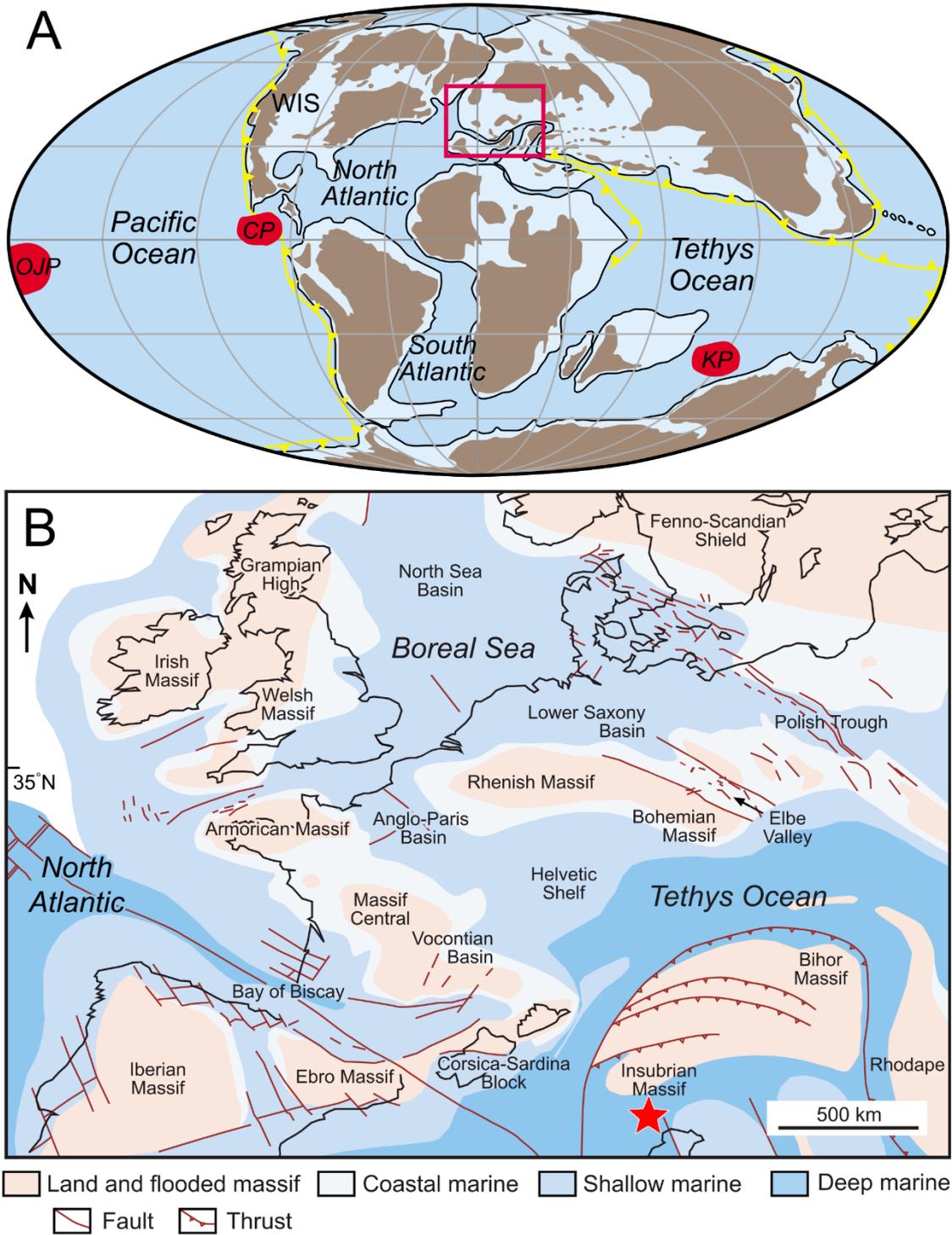


Fig. 1. Late Cenomanian paleogeography and location of sites. **A.** Global paleogeography at ca. 90 Ma showing position of Cretaceous subduction zones (yellow) and large igneous provinces or LIPs (red). Abbreviations **CP**: Caribbean Plateau; **KP**: Kerguelen Plateau; **OJP**: Ontong-Java Plateau; **WIS**: Western Interior Seaway. **B.** Cenomanian paleogeography of Northern Tethys showing location of the area of interest (red star). Image modified after Jarvis et al. (2011).

1.3.

General evolutionary dynamics inside the Tethyan ichthyofaunas during the Cenomanian-Turonian

The mid-Cretaceous was a time of rapid radiation and turnover in the marine plankton, benthic foraminifera and mollusks (Leckie et al., 2002; Keller et al., 2008). Among these groups, the plankton constitutes the base of the trophic pelagic chain on which depend so many marine fishes. Major changes in the abundance and composition of the plankton certainly affected the evolutionary dynamic of the fishes occupying the higher levels of the food chain (Cavin et al., 2007). A dramatic diversification event marks the global Late Cretaceous ichthyodiversity (Guinot and Cavin, 2016). Guinot and Cavin (2016) analyzed elasmobranch data sets evidencing a moderate magnitude diversification (see also Kriwet and Benton, 2004), while, on the other hand, the actinopterygian data were strikingly affected at both genus and family level, and equally in freshwater, marine and mixed-environments. The elasmobranchs are characterized by high-diversity faunas dominated by lamniforms (mackerel sharks), small carcharhiniforms (ground sharks), orectolobiforms (carpet sharks), diverse sclerorhynchoids (sawfishes), rhinobatoids (guitarfishes), stem dasyatoid and early miliobatoids (stingrays), and frequent squaliform sharks (dogfish sharks and others) (Guinot and Cavin, 2016). Among batoids, sclerorhynchoids diversify from the Cenomanian onwards and become major component of Late Cretaceous marine batoid assemblage (Guinot and Cavin, 2016). Rhinobatoids also show increasing diversity (Guinot and Cavin, 2016). Another radiating group is the Lamniformes and particularly the extinct predators family Cretoxyrhinidae ('ginsu' sharks) and Anacoracidae ('crow' sharks) (Guinot and Cavin, 2016). The latter become extremely diverse throughout this time interval and may be the major component of some fossil assemblage in terms of fossil remains (Guinot and Cavin, 2016). As regards ground and carpet sharks, these groups show increasing diversity during the Late Cretaceous and are apparently well-represented within warm epicontinental seas (Guinot and Cavin, 2016).

Considering Guinot and Cavin (2016) data about actinopterygians, the diversification of the Euteleostei (the second-largest jawed vertebrate diversification) occurred in the Cenomanian. This major evolutionary event was already identified by previous studies (for some groups see Alfaro et al., 2009; for global ichthyodiversity see Cavin and Forey, 2007; Cavin et al., 2007; Friedman and Sallan, 2012; Guinot and Cavin, 2015). The signal indicates that radiations affected only specific

clades, and not the whole range of teleosteans (Guinot and Cavin, 2016). These radiations concern the Stomiati, basal Ctenosquamata, Percopsiformes and, among euacanthomorphs the polyimixids and beryciforms and a clade of stem tetraodontiforms (Guinot and Cavin, 2016). Environmental factors have been proposed for explain this striking fish diversity burst (Cavin et al., 2007; Friedman and Sallan, 2012; Guinot and Cavin, 2015). Investigating marine fish genera as a whole, ichthyodectiforms, elopomorphs, tselfatiiforms, clupeomorphs, pachyrhizodontoids+protobramoids, salmoniforms, aulopiforms and basal acanthomorphs show significant positive correlations with sea temperature with a genuine radiation pattern peaking in the Cenomanian (Cavin et al., 2007; Friedman and Sallan, 2012) (Fig. 2). The mid-Cretaceous was characterized by major global changes in the Earth system (see paragraph above). The main factors affecting the marine fish environments are a sea level rise and a rise in sea temperature, both reaching their maxima in the Cenomanian (Cavin et al., 2007; see Gale, 2000 for an overview). Studies on modern marine, freshwater and land biological groups suggest correlations between geographic diversity distribution and temperature (see Guinot and Cavin, 2016 and literature therein). The effects observed include shorter generation times, faster mutation rates and faster selection. In addition, high seawater temperatures negatively affect both planktonic larval duration and planktonic egg duration time in marine organisms (see Hirst and Lopez-Urrutia, 2006; Duarte, 2007; O'Connor et al., 2007). Shorter planktonic larval and egg phases imply decreasing dispersion possibility and therefore increased speciation (Guinot and Cavin, 2016). The more marked diversification rates in actinopterygians (with larval and egg free egg phases) than in elasmobranchs (no larval or free egg phases) may indicate that this parameter had a strong influence on ray-finned fish paleodiversity (Guinot and Cavin, 2016). Developing Late Cretaceous reefs may have positively affected marine actinopterygian diversity (as in the Cenozoic) but these were mostly low reef-buildings being composed by rudist bivalves and thus this was probably not a major driver of Late Cretaceous fish diversifications (Guinot and Cavin, 2016). Another parameter possibly affecting the ichthyofaunas is eustasy. The rise in oceanic crust production, together with the rise in sea temperature and sea level, begins in the Aptian, which marks the starting point for the rise in marine fish diversity (Cavin et al., 2007). The sea level reaches its all-Phanerozoic highstand in the early Turonian, promoting the development of widespread epicontinental seas (Seaton et al., 2009) which are known to favor high diversity (Tittensor et al., 2010). The number of cladogenetic events expressed by the sea temperature indicator in the analysis by Cavin et al. (2007) starts to rise in the Barremian and a maximum stand in the Albian corresponding to the maximum Cenomanian diversity stand. At that time sea temperature is still positively correlated with the diversity of some of the old

Jurassic groups (ichthyodectiforms, elopomorphs and salmoniforms), but is especially correlated with several new groups, such as the tselfatiiforms, aulopiforms and the basal acanthomorphs (Fig. 2).

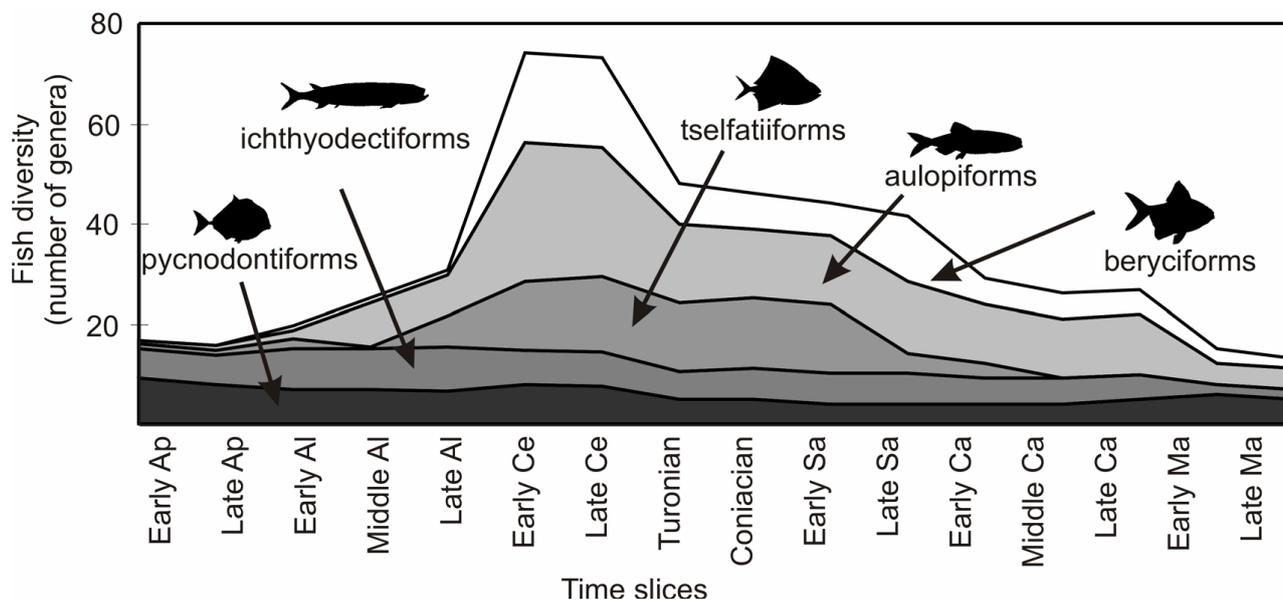


Fig. 2. Chart of the cumulative total numbers of genera (observed, Lazarus and ghost) from five Cretaceous actinopterygian orders. Note the almost constant numbers of genera of pycnodontiforms and ichthyodectiforms, while the tselfatiiforms, aulopiforms and beryciforms thrived in the Late Albian-Cenomanian (from Cavin and Forey, 2007, ESM).

All of the Cenomanian Tethyan fish assemblages share a large part of their taxa compared as distinct from the more endemic boreal Chalk fish fauna (Forey et al., 2003), as well as sharing numerous new taxa appearing for the first time in the fossil record and exceptionally preserved in the Tethyan localities (especially in the three Lebanese localities, Hakel, Hajula and Namoura, but also in Israel, Adriatic region and Morocco; Forey et al., 2003, Cavin, 2007; Friedman and Sallan, 2012). The Tethys probably represented a Cretaceous center of origin for fishes (Cavin et al., 2005; Cavin et al., 2007), just as the Indo-West Pacific is thought to be a center of origin (Mora et al., 2003; Briggs, 2003; Renema et al., 2008) for modern fishes. As regards other general trends, numerous vicariance and dispersal events are observed during the Cenomanian-Turonian interval (Gallo et al., 2007; Cavin, 2008; Silva and Gallo, 2016). These events are related to the paleoceanographic changes taking place during this time (see paragraph above). Most of the observed patterns concerned east-west events (both vicariance and dispersal) rather than north-south events (Cavin, 2008). This is probably because the separation between Laurasia and Gondwana is already underway in the Late Jurassic and affects only weakly the Cretaceous faunas (Cavin, 2008). The east-west pattern concerns mainly taxa from Africa versus South America and central versus western Tethys in the mid-Cretaceous, and Europe versus North America in the Late Cretaceous (Gallo et al., 2007; Cavin, 2008;

Silva and Gallo, 2016). These results are in accordance with the time of the opening of the Atlantic Ocean starting in the South and then extending northwards (Cavin, 2008).

As far as the post-Cenomanian interval is concerned, some authors evidenced a crisis immediately after the OAE2 in some groups (e.g., neoselachians, Kriwet and Benton, 2004) with a gradual recovery during the Turonian-Coniacian. However, these authors hypothesized that this signal might be artefact of a major marine transgression at that time. Another reason provided by Kriwet and Benton (2004) for the post-Cenomanian decline in neoselachian diversity might be that the Cenomanian has been studied more intensely by bulk sampling than the Turonian and Coniacian. There seems to be no decline when taxa with larger teeth that are more easily collected are considered (Kriwet and Benton, 2004), therefore it might represent a sampling bias. However, Guinot and Cavin (2016) recently evidenced that the exceptional fish Cenomanian diversification is followed by rather high extinction rates in the actinopterygian record, at both genus and family levels. This is particularly marked for the marine and mixed-environment data sets, whereas freshwater and elasmobranch taxa appear little affected (Guinot and Cavin, 2016). The Cenomanian-Turonian oceanic perturbations (i.e., OAE2) have been addressed as possible cause of the increase in extinction rates, but this event is more likely, also in this case, the result of sampling bias, here related to changes in representation of paleoenvironments in the sedimentary record between the Cenomanian (high-diversity onshore facies) and Turonian (offshore facies) stages linked to sea-level variations (Guinot and Cavin, 2016).

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Chapter 2.

The Bonarelli Level (OAE2) ichthyofauna from northeastern Italy

2.1. A reappraisal of the Italian record of the Cretaceous pachycormid fish *Protosphyraena* Leidy, 1857

Amalfitano et al., 2017. Rivista Italiana di Paleontologia e Stratigrafia, 123, 3, 475-485

2.2. The long-snouted bony fish ‘*Protosphyraena*’ *stebbingi* Woodward, 1909 from the Upper Cretaceous of northeastern Italy

Amalfitano et al., 2019. Cretaceous Research, 100, 51-60

2.3. Revision of the Bonarelli Level (OAE2) fish assemblage (upper Cenomanian, Upper Cretaceous) from northeastern Italy

Amalfitano et al., to be submitted to The Journal of Systematic Palaeontology

2.1.

A reappraisal of the Italian record of the Cretaceous pachycormid fish *Protosphyraena* Leidy, 1857

Jacopo Amalfitano, Luca Giusberti, Eliana Fornaciari and Giorgio Carnevale

Abstract

The genus *Protosphyraena* is known mainly from partial remains, consisting of isolated blade-like teeth, conical rostra and scythe-like pectoral fins. This paper provides a new insight into partial specimens of the genus *Protosphyraena* from the Cretaceous of NE Italy, housed in historical collections from local paleontological museums and previously poorly known to the international scientific community. The specimens are referred to the species *Protosphyraena ferox*, based on the morphology of the pectoral fin. This attribution is consistent with the paleobiogeographic distribution and stratigraphic range of this taxon. The Italian material provides new information about the distribution in time and space of *Protosphyraena*, which is relatively poorly known despite being an iconic taxon. The Italian remains, although fragmentary, contribute to fill a gap in the central Tethys record of the genus, whose range probably extended worldwide, considering also the genus *Australopachycormus* and its profound (possibly congeneric) similarities.

Introduction

Protosphyraena is an iconic Cretaceous fish belonging to the family Pachycormidae. This family includes several large sized pelagic fish taxa, some of which have been recently restudied in detail (e.g., Friedman et al. 2010, 2013; Liston et al. 2013; Schumacher et al. 2016). Among these fishes, *Protosphyraena* had a swordfish-like body form and was probably a fast swimming pelagic predator (Liston and Maltese, 2016). The first skeletal remain belonging to this fish was a fragment of the pectoral fin from the English Chalk reported by Mantell (1822), although it also seems to have featured in material collected from Grevesend and present in William Hunter's collection some years beforehand (Liston, 2015: fig. 12.4). About 35 years later, Leidy (1857) created the name *Protosphyraena* to also include the English specimens (see Everhart 2005). The genus had a worldwide distribution, from Europe to America, with the most important and complete specimens collected in the U.K. (English Chalk) and the U.S.A. (Niobrara Chalk) (e.g., Agassiz 1835; Everhart 2005; Shimada and Fielitz 2006; Woodward 1908). *Protosphyraena* remains are primarily represented by fragments of scythe-like pectoral fins (but see Maltese and Liston 2014), as well as by isolated blade-like teeth and almost conical rostra. In NE Italy some fragmentary specimens were found in peculiar intervals of the Cretaceous hemipelagic Scaglia-type succession of northeastern Italy (black shales of Mollàro, Bonarelli Level and the Scaglia Rossa Formation). The Italian material, although sparse and fragmentary, provides additional information about the stratigraphic and paleogeographic range of the genus *Protosphyraena*. The taxonomy of this genus is badly in need of a comprehensive revision (Stewart 1988; Friedman 2012), which is far beyond the scope of this paper, which is aimed at documenting the morphology and affinities of the neglected Italian specimens.

Historical background

The first report of *Protosphyraena* from Italy dates back to Bassani (1886), who described and figured an incomplete tooth from the 'Senonian' limestone of Castellavazzo (Longarone, Belluno), erroneously referred to *Saurocephalus lanciformis* (Fig. 1A). This tooth was later reassigned by D'Erasmus (1922) to *Protosphyraena ferox* Leidy, although its illustrated conical form is very different to the compressed blade-like form typical of the genus *Protosphyraena*. The specimen, housed in the collections of the Geological Museum of Pavia (*vide* D'Erasmus, 1922), together with other fish teeth from Castellavazzo (*Cretoxyrina mantelli*, *Ptychodus* spp., '*Lepidotus*' sp.; Bassani 1886), is

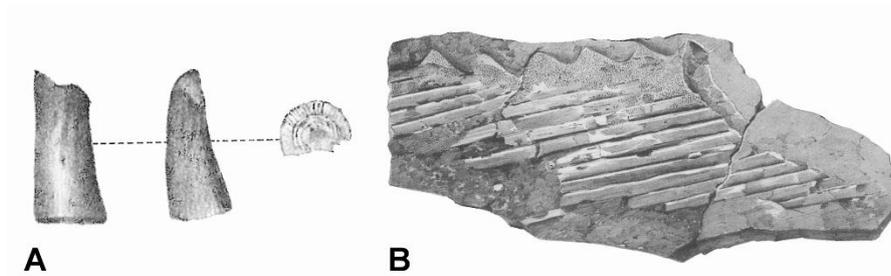


Fig. 1. The original illustrations of *Protosphyraena* remains from the Scaglia Rossa Formation of northeastern Italy. **A)** Tooth from Castellavazzo (from Bassani 1886) and **B)** the fin fragment from Novale (from D'Erasmus 1922). The images do not reflect the original size.

currently considered lost (Paolo Guaschi, pers. comm.). Dal Lago (1903) reported the first finding of pectoral fin fragments of *Protosphyraena* from the 'Senonian' Scaglia Rossa Formation outcropping near Novale

(Vicenza). This material was subsequently described by D'Erasmus (1922) and assigned to *Protosphyraena* sp. (Fig. 1B). Fabiani (1923) reported another partial pectoral fin from the black shales of Mollàro (Trento), which was tentatively assigned to *Protosphyraena*. This specimen was subsequently mentioned by D'Erasmus (1927) in a paper dealing with the fossil fishes housed in the Museum of Natural History of Trento. More recently, Sorbini (1976) described a pectoral fin with the associated girdle of *Protosphyraena* from the black shales of the Bonarelli Level of Cinto Euganeo (Padova) that he referred to *P. ferox*.

Stratigraphic and paleoenvironmental context

All the specimens described herein come from specific intervals of the basinal Scaglia-type succession of northeastern Italy and, more particularly, from the Lower Cretaceous black shales of Mollàro, the Upper Cenomanian Bonarelli Level, and the Upper Cretaceous Scaglia Rossa Formation (Fig.2).

The 'bituminous-uraniferous black shales' Auctorum of Mollàro (Val di Non, Trento) are lensoid deposits within the Scaglia Variegata Alpina Formation, with a thickness ranging from 30 to 150 cm (Avanzini et al. 2012). The Mollàro horizon dates back to the Albian, based on planktic foraminiferal content (Fuganti 1964; Bosellini et al. 1978; Avanzini et al. 2012), and extends from Mollàro towards Tres and Vervò. This horizon, exploited in the XIX-XX centuries for the extraction of 'petroleum and bitumen' in the San Romedio Mine has provided a rather diverse fossil assemblage with fish remains, ammonites and belemnites, associated with plant remains (Fabiani 1923; Fuganti 1964). The fish remains from Mollàro consist of isolated, fragmentary and poorly preserved skeletal remains, including a single opercle, some cycloid scales and a caudal fin with some vertebrae assigned by D'Erasmus (1927: p. 10) to an indeterminate "isospondylous" fish.

The Bonarelli Level is an organic-rich marker bed accumulated during the late Cenomanian Oceanic Anoxic Event 2 (OEA2) (e.g., Coccioni and Luciani 2005; Gomez et al 2002, 2015). This level is discontinuously present, ranging from 30 to 300 cm in thickness, and drapes the Scaglia Variegata Alpina Formation in different sites of the Veneto and Trentino regions, which yielded several fossil fishes and plants (e.g., Bassani 1880, 1882; Dalla Vecchia et al. 2005; Gomez et al. 2002, 2015; Sorbini 1976). The ichthyofauna of the Bonarelli Level, currently under review, is quite diverse and includes bony fishes and less

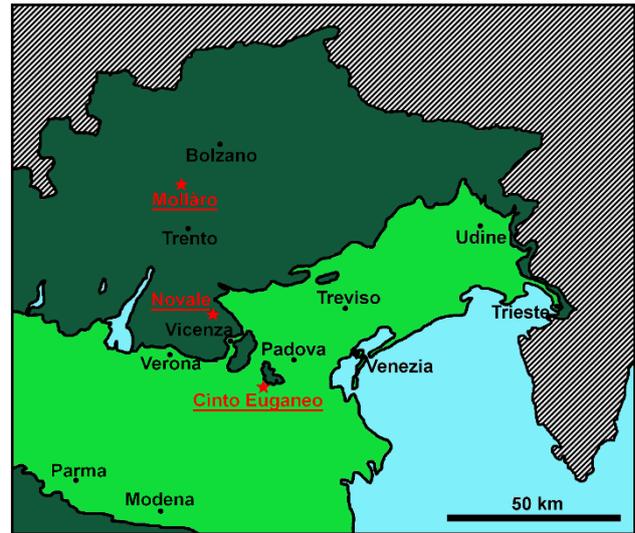


Fig. 2. Location map of the sites in northeastern Italy that yielded remains of the pachycormid fish *Protosphyraena* described in this paper. The stars indicate the fossiliferous sites.

common sharks, the latter solely represented by isolated teeth of lamniforms and ptychodontids. The bony fish assemblage includes aulopiforms, crossognathiforms, elopiforms, pachycormiforms, polymixiiforms, pycnodontiforms, stomiiforms, and tselfatiiforms (Amalfitano et al. 2017a).

The Scaglia Rossa Formation is a lithostratigraphic unit consisting of pink to reddish cherty limestones, marly limestones and marls rich in planktonic foraminifera that were originally deposited in a hemipelagic setting (e.g., Amalfitano et al. 2017b, c; Massari et al. 1983). It extends from the Upper Cretaceous to the lower Paleogene (i.e. lower Turonian-Eocene p.p.; Agnini et al. 2011; Cestari et al. 2013; Giusberti et al. 2016). The main source of the Cretaceous vertebrate remains from Scaglia Rossa is a condensed lithofacies called ‘lastame’, cropping out in the Lessini Mountains and consisting mainly of nodular limestones and marly limestones. This unit dates back to early Turonian-early Santonian and was deposited on a pelagic structural high (‘Trento Plateau’) (Lozar and Grosso 1997; Palci et al. 2013). The ‘lastame’ is known for large-sized vertebrates, including sharks (lamniforms and ptychodontids), marine turtles and rare mosasaurids, as well as for scattered fragmentary remains of bony fishes (e.g., Amalfitano et al. 2017b, c; Capellini 1884; Dalla Vecchia et al. 2005; Palci et al. 2013, 2014). Vertebrate remains (e.g., Bassani 1886, 1888) also come from the ‘Pietra di Castellavazzo’ lithofacies, another condensed interval equivalent to the ‘lastame’ and cropping out in the surroundings of Longarone (Belluno).

Materials and methods

The fossils described and figured herein consist of five specimens deposited in different small local museums:

- Civic Museum 'D. Dal Lago', Valdagno (Vicenza province): CDL (Collezione 'Dal Lago') 782, 2580, 2581 (Fig. 3-4);
- Geo-paleontological Museum of Cava Bomba, Cinto Euganeo (Padova Province): IG (Inventario Generale) 37527 (Fig. 5);
- MUSE, Trento: MUSE 6682 (ex 4176, erroneously reported by D'Erasmus 1927 as 4175) (Fig. 6).

The specimens were photographed and measured with image analysis software Image J (v. 1.47) using a Canon PowerShot SX720 HS, Fuji XE1 mounting 18-55 mm lens. The specimen MUSE 6822 was coated with ammonium chloride in order to enhance some morphological features. Images and illustrative drawings of the specimens were prepared using the softwares GIMP (v. 2.8.16) and ImageJ. The matrix of specimen CDL 782 was sampled with a millimetric tungsten carbide spherical drill bit mounted on an electric drill. The powder obtained was then utilized for a preparation of a smear slide for calcareous nannofossil analysis.

Open nomenclature follows the standard proposed by Bengston (1988).

Results

Systematic paleontology

Order Pachycormiformes Berg 1940
Family Pachycormidae Woodward 1895b
Genus *Protosphyraena* Leidy 1857

Type species: P. ferox Leidy 1857 from the White Chalk of Sussex, U.K.

Diagnosis. See Woodward (1908) and Mainwaring (1978).

Protosphyraena ferox Leidy 1857

Figs. 3-6

1822 "Undetermined" - Mantell, p. 228; pl. 33, fig. 7-9.

1837 *Saurocephalus lanciformis* Harlan - Agassiz, atlas vol. 5, pl. 25c, figs. 21-29.

1839 *Saurocephalus lanceolatus* [sic] Harl.- Agassiz, vol. 5, p. 8.

1844 *Saurocephalus lanciformis* Harl. - Agassiz, vol. 5, p. 102.

1850 *Saurocephalus lanciformis* - Dixon, p. 374, pl. 30, fig. 21, pl. 31, fig. 12, pl. 32, fig. 1, pl. 34, fig. 11.

- †1857 *Protosphyraena ferox* Leidy, p. 95 (cum syn.).
 1857 *Xiphias Dixoni* Leidy, p. 95.
 1877 *Erisichthe Dixoni* Leidy - Cope, p. 823.
 1878 *Erisichthe Dixoni*, Cope - Davies, p. 260, pl. 8, fig. 3.
 1878 *Protosphyraena ferox* Leidy, 1856 - Newton, p. 789.
 1886 *Saurocephalus lanciformis* Harl. - Bassani, p. 143; pl. 9, fig. 12.
 1888 *Saurocephalus lanciformis* Harl. - Bassani, p. 5.
 1888 *Protosphyraena ferox*, Leidy - Woodward, p. 321.
 1895 a*Protosphyraena ferox*, Leidy - Woodward, p. 211, woodcuts fig. 3.
 1895b *Protosphyraena ferox*, Leidy - Woodward, p. 400, text-fig. 41, no. 3.
 1903 *Protosphyraena* sp. - Dal Lago, p. 74.
 1908 *Protosphyraena ferox*, Leidy - Woodward, p. 147, text-fig. 45, pl. 31-32.
 1922 *Protosphyraena* sp. - D'Erasmus, p. 62; pl. 6, fig. 17.
 1976 *Protosphyraena ferox* Leidy 1856 - Sorbini, p. 485, pl. 9.
 1978 *Protosphyraena ferox* Leidy 1857 - Mainwaring, p. 105.
 1980 *Protosphyraena ferox* - Sorbini, p. 119, text-fig without number p. 121.
 1994 *Protosphyraena* sp. - Sirna et al., p. 271.
 2012 *Protosphyraena ferox* Leidy 1857 - Friedman, p. 120, fig. 3D.
 2016 *Protosphyraena ferox* Leidy 1857 - Friedman et al., table 1.

Holotype. PV OR 4135, teeth (Natural History Museum, U.K.) from the Chalk Group of Lewes, Sussex, U.K.

Diagnosis. See Woodward (1908).

Referred material. CDL 782, 2580, 2581; IG 37527.

Locality and horizon. The specimens CDL 782 and 2580, 2581 come from the ‘Senonian’ Scaglia Rossa Formation outcropping near Novale (Lessini Mountains, Vicenza), which is about 3 km north of Valdagno (Vicenza). The study of the calcareous nannofossil assemblage recovered from the rocky matrix of specimen CDL 782 allowed us to better constrain the age of the specimen. Specifically, the presence of *Lithastrinus septenarius* (= *L. moratus* of Varol 1992) allows to ascribe the fossil to the UC9-UC11 Zones of Burnett (1999), indicating a late Turonian-Coniacian age (see also Appendix A.1). IG 37527 comes from the excavations undertaken between 1974 and 1975 of the Bonarelli Level of Cava Bomba (Euganei Hills, Cinto Euganeo, Padova), upper Cenomanian.

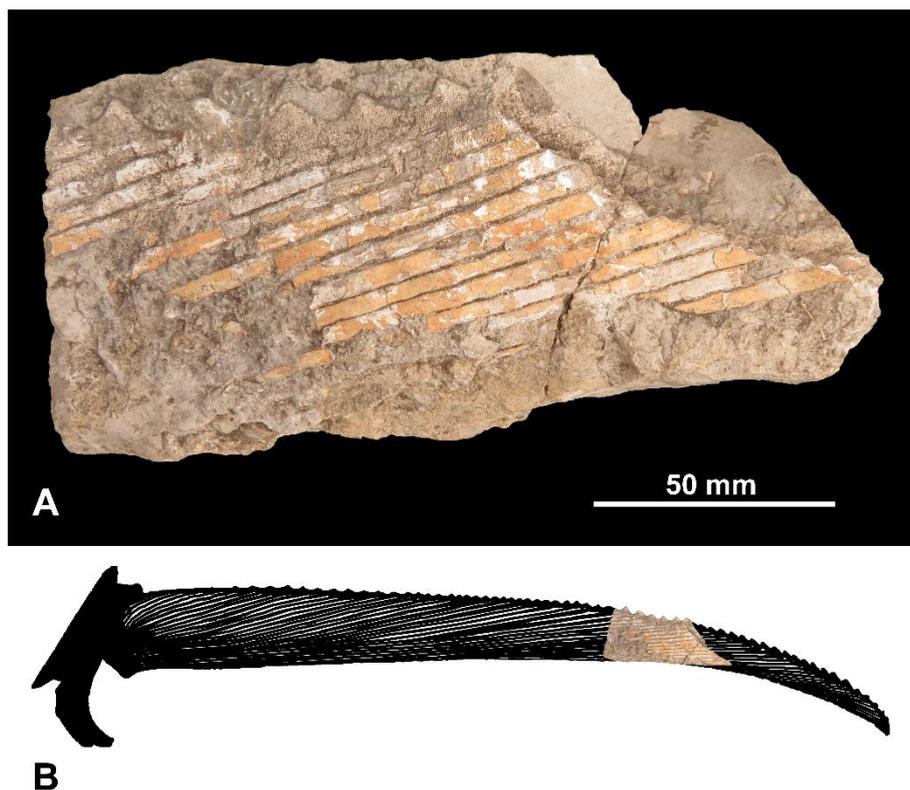


Fig. 3. *Protosphyraena ferox* from the upper Turonian-Coniacian Scaglia Rossa Formation of Novale (VI), CDL 782. **A)** Photo of the specimen. Scale bar: 50 mm. **B)** Interpretative reconstruction of the original position of CDL 782 based on a complete pectoral fin of *Protosphyraena* figured by Woodward (1908: fig. 43, p. 146).

Description. The specimen CDL 782 (Fig. 3) consists of a pectoral-fin fragment, characterized by a quadrangular outline, which comprises 16 partially preserved rays and the serrated leading edge showing six regularly spaced triangular tubercles emerging along its outer margin. The rays are solid and unsegmented or without traces of bifurcations. Their surface is generally smooth, except in relation to the leading edge in the first ray where the texture becomes finely rugose. Each ray has a rectangular outline in cross section. The fin has a high aspect ratio (Liston and Maltese 2016); the fragment has a length of 175 mm and a maximum width of 76 mm. The size and thickness of the partially preserved rays are consistent throughout their length; they are about 6 mm wide and 4 mm thick in cross section. The triangular tubercular serrations are 8 mm high from the apex to the base. The fragment CDL 782 was possibly located at mid-length of the original fin pertaining to a relatively large individual (Fig. 3B), roughly comparing the Italian fragment with the complete fin of *Protosphyraena* figured in Woodward (1908: fig. 43, p. 146).

Two additional small fragments (Fig. 4A-B) possibly associated in origin, CDL 2580 (52 x 16 cm) and CDL 2581 (48 x 27 mm) comprise, 12 and four ray fragments, respectively; the rays are similar in morphology and size to those of CDL 782.

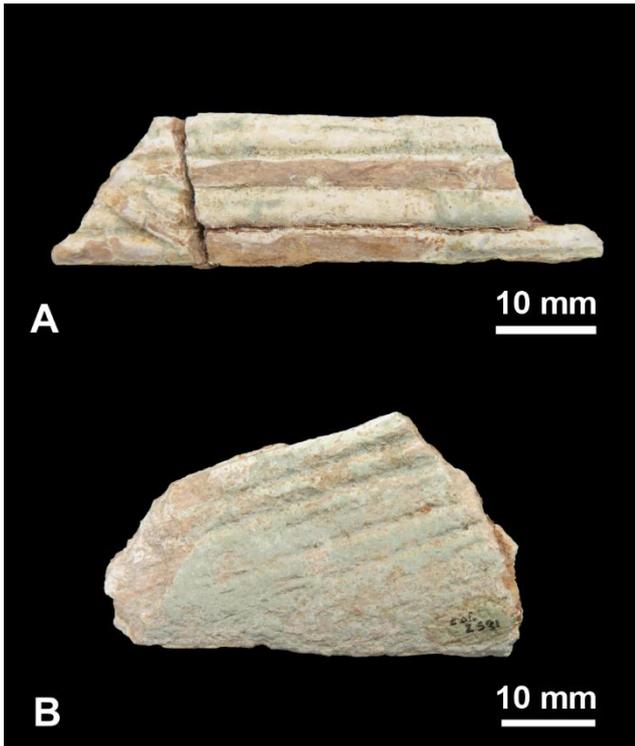


Fig. 4. Fragments of a fin of *Protosphyraena ferox* from the Scaglia Rossa Formation of Novale (VI), CDL 2580-2581. **A)** Photo of specimen CDL 2580. **B)** Photo of specimen CDL 2581. Scale bars: 10 mm.

The specimen IG 37527 (Fig. 5) includes parts of the pectoral girdle, the pectoral-fin radials, and 15 partially preserved pectoral-fin rays. The fin lacks its distal portion and has a narrow scythe-like overall appearance (but see Maltese and Liston 2014, Liston and Maltese 2016 for flaws in the use of this terminology), its preserved portion being about 238 mm long and ca. 50 mm wide. Only the proximal part of the rays and a fragment of the distal part are preserved. Part of the fin is preserved as impression only, including the serrated leading edge. This impression exhibits a serration pattern with granulate texture almost identical to that of specimen CDL 782.

The rays expand in thickness distally. The first ray has a thickness of 5 to 10 mm, while the subsequent rays have a similar thickness ranging 1 to 3 mm. The pectoral girdle includes part of the cleithrum, scapula and coracoid. Moreover, there are fragments of seven pectoral-fin radials, not clearly distinguishable from each other. The cleithrum is flat and crescent-shaped with broad extremities. The scapula and coracoid appear to be consistent with those described and figured by Woodward (1908).

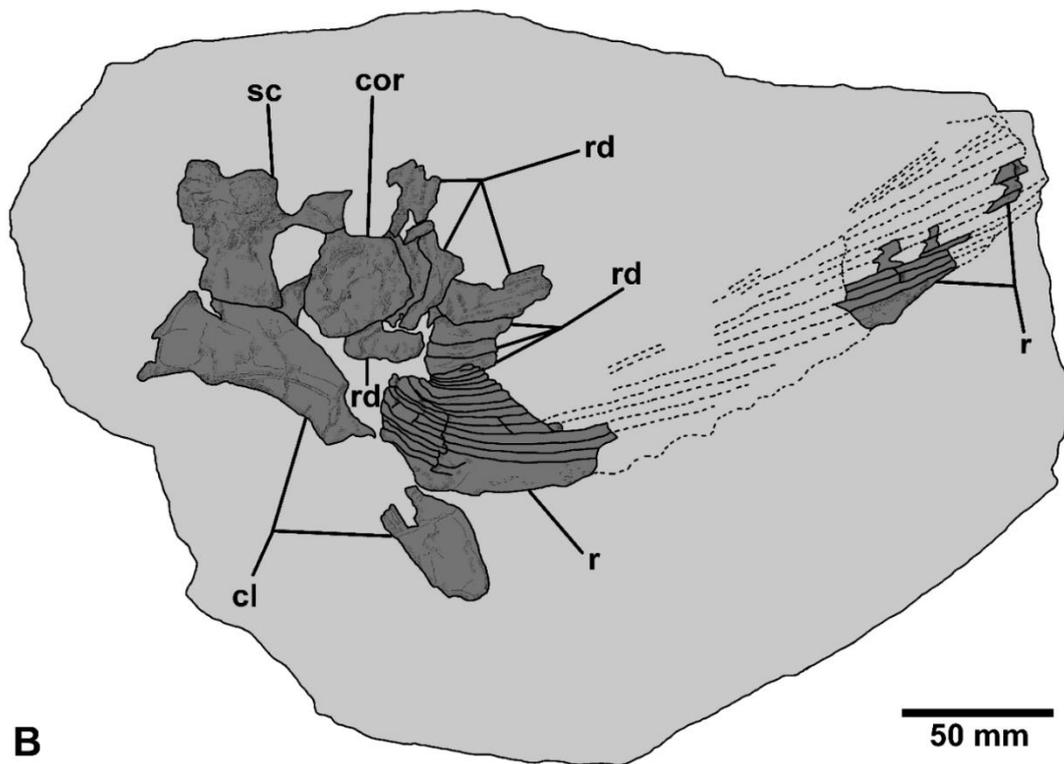


Fig. 5. *Protosphyraena ferox* from the Bonarelli Level of Cinto Euganeo (PD), IG 37527. **A)** Photo of the specimen. **B)** Interpretative drawing of the specimen in A. The bones are colored in dark grey, the matrix in light grey. The dashed line indicates the impression in the matrix. Scale bars: 50 mm. Abbreviations: cl, cleithrum; sc, scapula; cor, coracoid; rd, pectoral-fin radials; r, pectoral-fin ray fragments. Photo made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism. All rights reserved.

Taxonomic discussion. The genus *Protosphyraena* is known mainly from parts of the cranial skeleton (especially teeth and rostra), as well as fragments of the pectoral girdles and fins. Some caudal fins have also been recovered (McClung 1908). The specimens described herein exhibit the diagnostic features of the pectoral fins of this genus, in particular the high aspect ratio and scythe-like morphology (Liston and Maltese 2016), and the closely-spaced fin rays. These features are shared with another pachycormid genus, *Bonnerichthys*, which differs from *Protosphyraena* in the morphology of the leading edge of the fin (Friedman et al. 2010), with the exception of *P. nitida*. The well-defined serration along the leading edge is regarded as diagnostic of the species *Protosphyraena ferox* (Friedman 2012; Woodward 1908), but also present in two other congeners, *P. perniciosa* and *P. tenuis*. *Protosphyraena nitida*, on the contrary, is characterized by a smooth leading edge like *Bonnerichthys* (Everhart, 2012), but can be distinguished from the latter on the basis of the pectoral fin aspect ratio (see Liston and Maltese, 2016). The fin characters of *Protosphyraena tenuis* are not easily distinguishable from those of *P. perniciosa*, so that some authors (e.g., Everhart 2012) consider them as conspecific. The pectoral fin serrations of *Protosphyraena perniciosa* and its general aspect are very closely to those of the *P. ferox* fin and for this reason Woodward (1908: p. 150) considered these two taxa as possible conspecifics. Other authors (e.g., Everhart 2005; Shimada et al. 2006; Shimada and Fielitz 2006) still consider the two species to be distinct, especially because of their different rostral morphology.

We refer the Italian specimens to *Protosphyraena ferox* based on the pectoral-fin characters as defined by Woodward (1908), especially because of the serration pattern of the leading edge. Moreover, the Italian fossils are consistent with the paleogeographic range of *Protosphyraena ferox*, which was originally reported from the English Chalk (Woodward 1895a, b, 1908), and subsequently from other parts of Europe (e.g., Friedman, 2012), while the three other congeners primarily inhabited the American Western Interior Seaway (Everhart 2005; Loomis 1900; Shimada and Fielitz 2006). The genus *Protosphyraena* had a worldwide distribution, and was reported from Belgium (Friedman 2012), Canada (Manitoba, Bardack 1968; Saskatchewan, Cumbaa 1997), France (Vullo et al. 2003), Germany (e.g., Diedrich 2001), Jordan (Avnimelech 1949), Saudi Arabia (Kear et al. 2009), Spain (Vullo et al. 2009), Sweden (Bazzi et al. 2016), U.K. (e.g., Woodward 1908) and U.S.A. (e.g., Alabama, Applegate 1970 and Zangerl 1953; Colorado, Nagrodski et al. 2012, Shimada et al. 2006; Kansas, Everhart 2005; South Dakota, Schumacher 2007; Texas, Hill 1901). The fossils from NE Italy documented herein increase our knowledge of the paleobiogeography of this poorly known large pelagic predator, whose range probably extended worldwide during most of the Cretaceous, considering also the morphological similarity of the genus *Australopachycormus* (Kear 2007), strictly

related (possibly congeneric) to *Protosphyraena*. As far the stratigraphic range of the genus *Protosphyraena* is concerned, it extends from the Albian (Dineley and Metcalf 1999) to the Maastrichtian (Friedman 2012). Therefore, the stratigraphic positions of the Italian specimens described herein, dating back to the upper Cenomanian and to the Turonian-Coniacian interval, is in agreement with the known stratigraphic range of the genus.

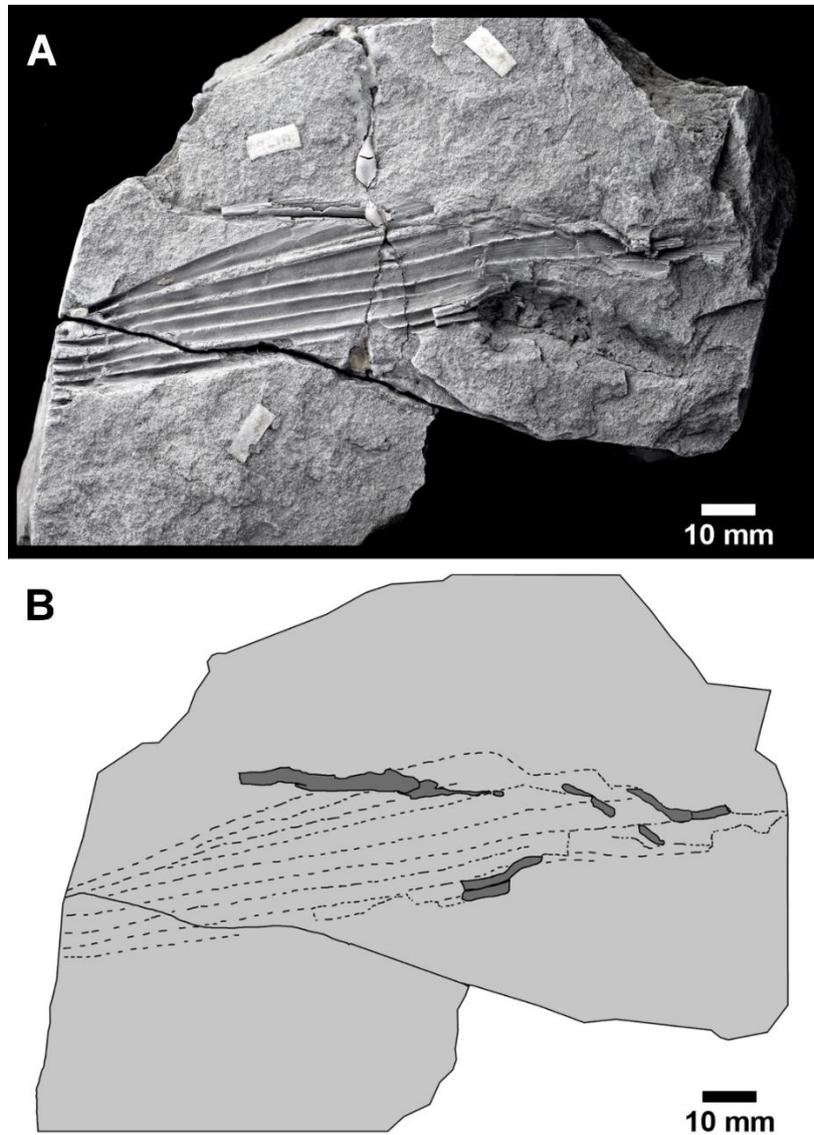


Fig. 6. Actinopterygii indet. from the black-shales of Mollàro (TN), MUSE 6822, originally ascribed by D'Erasmus (1927) to *Protosphyraena*. **A)** Photo of the specimen coated with ammonium chloride. **B)** Interpretative drawing of the specimen. The bones are colored in dark grey, the matrix in light grey. The dashed line indicates the impression in the matrix. Scale bars: 10 mm.

Actinopterygii indet.

Fig. 6

- 1923 *Protosphyraena* sp. - Fabiani, p. 39.
1927 *Protosphyraena* sp. - D'Erasmus, p. 10.
1994 *Protosphyraena* sp. - Sirna et al., p. 269.

Referred material. MUSE 6682.

Locality and horizon. The specimen MUSE 6682 comes from the bituminous-uraniferous black shales of Mollàro (Val di Non, Trento). The Mollàro horizon dates back to the Albian, based on planktic foraminiferal content (for references see “Stratigraphic and paleoenvironmental context” section).

Description. The specimen MUSE 6822 (Fig. 6) is figured herein for the first time and consists of the impression of what appears to be a partial fin. The fin consists of the impression of seven rays plus three additional ray fragments. The impression of the fin is ca. 126 mm long. The impression of the fin rays ranges from one to three millimeters in thickness; they are not segmented nor bifurcated, and characterized by a superficial fibrous aspect of the lepidotrichia.

Taxonomic discussion. The Mollàro specimen was assigned to *Protosphyraena* by D'Erasmus in Fabiani (1923) and its taxonomic status was subsequently confirmed by D'Erasmus (1927). We consider the attribution provided by D'Erasmus as dubious because of the inadequate state of preservation and the fibrous superficial aspect of the rays; the latter appears to be very similar to the peculiar pattern - characteristic, but not unique - of caudal fin rays of ichthyodectiforms, as documented by Cavin et al. (2013: p. 21).

Other dubious findings assigned to *Protosphyraena*

Another Italian finding doubtfully referred to *Protosphyraena* (*Protosphyraena?* sp.; Sirna et al. 1994, p. 270) is a flat and elongate rostrum (ca. 40 cm long) recovered from the Scaglia succession outcropping at Crespadoro (Vicenza Province). The fossil, never published, was originally cited by De Zigno (1883: p. 8) as rostrum of "*Xiphias*" and probably comes from the Bonarelli Level. The specimen, still housed in the collections of the Museum of Geology and Paleontology of Padova University (MGPPD 6716-Z), is consistent to certain flat rostra recovered in the English Chalk and traditionally attributed to *Protosphyraena stebbingi* Woodward 1909 (Amalfitano et al. in prep.).

According to Friedman et al. (2016), however, such rostra are in some ways related to tselatiiform fishes and do not correspond to the median rostrodermethmoid that contributes to the snout of *Protosphyraena* and other pachycormids. The Italian specimen is currently under study and represents a significant report of a poorly known species.

Conclusions

The revision of the rare Italian records of the pachycormid fish genus *Protosphyraena* seems to indicate that the examined material pertains to the species *P. ferox*, previously reported from the English Chalk. The Italian specimens, though being sparse and fragmentary, are important because they are part of historical collections and add new data about the paleobiogeographic and stratigraphic range of a poorly known taxon. The genus *Protosphyraena* had a worldwide distribution, with partial remains known from all over the Tethyan realm. The Italian specimens contribute to fill the gap in the central Tethyan record of the genus.

Acknowledgements

The authors deeply thank Bernardetta Palozzi (Museo Civico "Dal Lago" di Valdagno, Vicenza), Massimo Bernardi (MUSE, Science Museum of Trento), Mariagabriella Fornasiero (Museum of Geology and Paleontology of Padova University) and Franco Colombara and the Province of Padova for permissions to examine the specimens in the collections. We would also acknowledge Stefano Castelli (Department of Geosciences of University of Padova) for his valuable help with photographs and figures preparation. The photograph of IG 37527 is made available under permission of Ministero dei Beni e delle Attività Culturali e del Turismo (prot. no. 3418 07/09/2017-PD-Re). ©All rights reserved. We are grateful to the reviewers (L. Cavin and J. Kriwet) and to the Editor for their constructive comments that greatly improved the manuscript. Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled 'Reappraisal of two key *Fossil-Lagerstätten* in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach', assigned to Eliana Fornaciari).

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2.2.

The long-snouted bony fish ‘*Protosphyraena*’ *stebbingi* Woodward, 1909 from the Upper Cretaceous of northeastern Italy

Jacopo Amalfitano, Luca Giusberti, Eliana Fornaciari and Giorgio Carnevale

Abstract

In this paper we report for the first time remains of the long-snouted bony fish ‘*Protosphyraena*’ *stebbingi* Woodward, 1909 from the Upper Cretaceous of northeastern Italy. The material described herein consists of two rostra, one of which is nearly complete and the other only partially preserved, collected from Crespadoro (Monti Lessini) and Villa di Teolo (Colli Euganei), respectively. The overall morphology and internal structure of the rostrum of ‘*P.*’ *stebbingi* differ from those of the rostra characteristic of the genus *Protosphyraena* but exhibits a certain degree of similarity to those of some Cretaceous teleostiforms. Like in other long-snouted bony fishes, the rostrum of ‘*P.*’ *stebbingi* was probably used for prey capture and defense. The age of the Italian specimens is consistent with that of the English Chalk (Lower Chalk) where the type material of ‘*Protosphyraena*’ *stebbingi* was collected, especially the specimen from Colli Euganei, which comes from the upper Cenomanian Bonarelli Level. Taphonomic features of the specimens are also discussed, especially those of the rostrum from Crespadoro, which exhibits encrusting calcareous tubes, probably pertaining to deep-sea serpulids.

Introduction

'Protosphyraena' stebbingi is an enigmatic and poorly known taxon of long-snouted bony fishes from the Upper Cretaceous pelagic limestone of the English Chalk. The holotype was collected by W.P.D. Stebbing at the beginning of the 19th century and was named after him by the eminent British

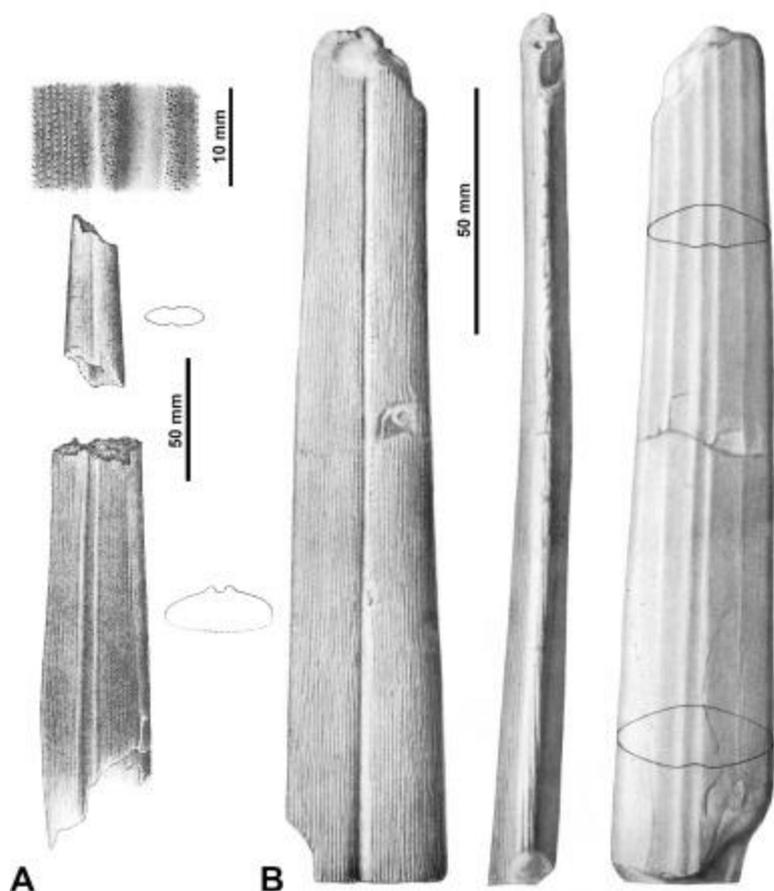


Fig. 1. *'Protosphyraena' stebbingi* Woodward (1909). A. Excerpts from the plates of Woodward (1909) figuring the holotype NHMUK P 11216 from the Lower Chalk of Betchworth, Surrey, UK and close-up. Scale bars equal respectively 50 mm and 10 mm. B. Excerpt from the plate of Woodward, 1912a, Woodward, 1912b figuring the specimen from South Ferriby, Lincolnshire (UK). Scale bar equals 50 mm.

paleontologist A.S. Woodward in his monograph “Fossil Fishes of the English Chalk” (Woodward, 1908, Woodward, 1912a, Woodward, 1912b, Friedman et al., 2016, Fig. 1A). The holotype consists of the basal portion plus a distal fragment of a rostrum, recovered from the Lower Chalk (Zone of *Holaster subglobosus*) at Betchworth, Surrey (UK) (Woodward, 1912b, Woodward, 1912a). A second specimen (Fig. 1B) was subsequently found at South Ferriby, Lincolnshire (UK) (Woodward, 1912a, Woodward, 1912b). Since the original description of the British material by Woodward, 1908, Woodward, 1912a, Woodward,

1912b), this taxon has been neglected for more than a century and has been reconsidered only recently by Friedman et al. (2016) in a paper

summarizing the knowledge about the fossil ichthyofauna of the English Chalk. However, a partially complete flattened rostrum very similar to those of the English Chalk was recovered in the second half of the 19th century near Crespadoro, northeastern Italy (De Zigno, 1883). Moreover, another partially complete rostrum was found in the upper Cenomanian Bonarelli Level cropping out near Teolo, northeastern Italy. In this paper we provide a complete description of these two Italian specimens for the first time and compare them with the British material of *'Protosphyraena' stebbingi*

to discuss their affinities. This work is part of a comprehensive ongoing revision of the fish fauna from the Bonarelli Level of northeastern Italy.

Geological and historical background

The specimens described herein come from two localities in the Veneto region, Crespadoro, Monti Lessini (Lessini Mountains, Vicenza Province), and Villa di Teolo, Colli Euganei (Euganei Hills, Padova Province) (Fig. 2). The specimen from Villa di Teolo was found in the Bonarelli Level cropping out in the Sinigaglia quarry. The Bonarelli Level is a peculiar black shales marker bed, deposited during the late Cenomanian Oceanic Anoxic Event 2 (OAE2). This horizon is discontinuous in the Southern Alpine domain and drapes the Scaglia Variegata Alpina Formation, with a thickness that varies from 0.3 to over 3 m (Gomez et al., 2002, Gomez et al., 2015, Coccioni and Luciani, 2005). The Bonarelli Level of northeastern Italy is well known for its paleontological content, including remains of plants, fishes and marine turtles (Sorbini, 1976, Gomez et al., 2002, Gomez et al., 2015, Dalla Vecchia et al., 2005). The first report of fossil discoveries from the



Fig. 2. Location map of the sites in northeastern Italy that yielded remains of *Protosphyraena stebbingi* described in this paper. The blue stars indicate the fossiliferous sites. Scale bar equals 100 km. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Bonarelli Level of northeastern Italy dates back to Massalongo (1857), who described the plants and fish remains from the Monte Colle site, not far from the famous ‘Pesciara’ Konservat-Lagerstätte of Bolca (Verona Province; Massalongo, 1857, Gomez et al., 2014, Gomez et al., 2015). Subsequently, Bassani, 1880, Bassani, 1882) reported some fragmentary fish remains coming from the black shales of the Bonarelli Level cropping out in the surroundings of the village of Crespadoro del Grappa (Treviso Province), at the top of the Scaglia Variegata Formation. De Zigno (1883) in his review of the Mesozoic

vertebrates from the Venetian Alps reported the finding of a rostrum attributed to the genus *Xiphias* coming from “bituminous limestones” cropping out at Crespadoro (Vicenza Province), which he correlated with the fish-bearing black shales of Crespano del Grappa (= Bonarelli Level) previously reported by Bassani (1880). The presence of vertebrate remains from the Bonarelli Level of the Colli Euganei (Padova Province) was firstly reported by Squinabol (1904) who described and figured an isolated tooth of *Ptychodus* ‘*latissimus*’ and mentioned some fragmentary remains of bony fishes (*Thrissops* sp.; see also D’Erasmus, 1922). Fish remains from Villa di Teolo were reported by Sorbini (1974) for the first time. The Bonarelli Level ichthyofauna from Bomba quarry, near the village of Cinto Euganeo (Colli Euganei) was subsequently studied and described by Sorbini, 1974, Sorbini, 1976, Sorbini, 1980 and Astolfi and Colombara (2003).

De Zigno's “Fossiles de la Vénétie” and the rostrum from Crespadoro

Baron Achille De Zigno (1813-1892) was a renowned Italian paleobotanist who also worked on fossil vertebrates, particularly on Triassic and Paleogene fishes (Pearson, 2005, Bizzarini, 2013). Many of the original manuscripts by De Zigno are currently housed in the Library of the Department of Geosciences of the University of Padova, including several unpublished papers. Among the latter there is a voluminous monograph entitled “*Fossiles de la Vénétie* (or *Atlas paleontologique de la Vénétie*)” (Fig. 3A), aimed at illustrating fossil plants, vertebrates and invertebrates from northeastern Italy. The manuscript includes two volumes of drafts of color plates and various handwritten drafts of published and unpublished papers, possibly gathered together by the author to create the text of the monograph. The stack of papers includes a manuscript of ten pages titled “*Nuovo genere di pesce xifioide scoperto nel terreno cretaceo del Vicentino*” (translation: A new genus of xiphioid fish from the Cretaceous of the Vicenza province; Fig. 3B) probably originally conceived as a stand-alone paper that, for unknown reasons, was never published. Based on a letter received from the curator of the Laboratoire d’herpetologie et d’ichthyologie of the Muséum national d’Histoire naturelle, Paris, included in the manuscript and dated 1889, we only know that De Zigno was still working on this fossil three years before his death. In the manuscript, De Zigno proposed the creation of a new genus and new species based on the rostrum from Crespadoro, *Homalorhynchus xiphioides* (*nomen in litteris*), providing the following diagnosis: “This genus is distinguished from all the known [members] of this family by having a remarkably flat rostrum with smooth lower surface and upper surface marked by longitudinal parallel and anastomosing ridges creating a narrow and extended meshed pattern, as well as by an obtuse and rounded tip with the extremity bordered by a marginal edge” (our translation of the Italian description). In the first volume of the plates of De Zigno's

“*Fossiles de la Vénétie*” there is a color plate illustrating in great detail the Crespadoro's rostrum (Fig. 4), associated with teeth of fishes (*Ptychodus*, *Lepidotes*) and mosasaurs. The name ‘*Homalorhynchus xiphioides*’ proposed in the unpublished manuscript is also reported as *nomen in schedis* in the original label of the fossil, handwritten by De Zigno himself (Fig. 5).

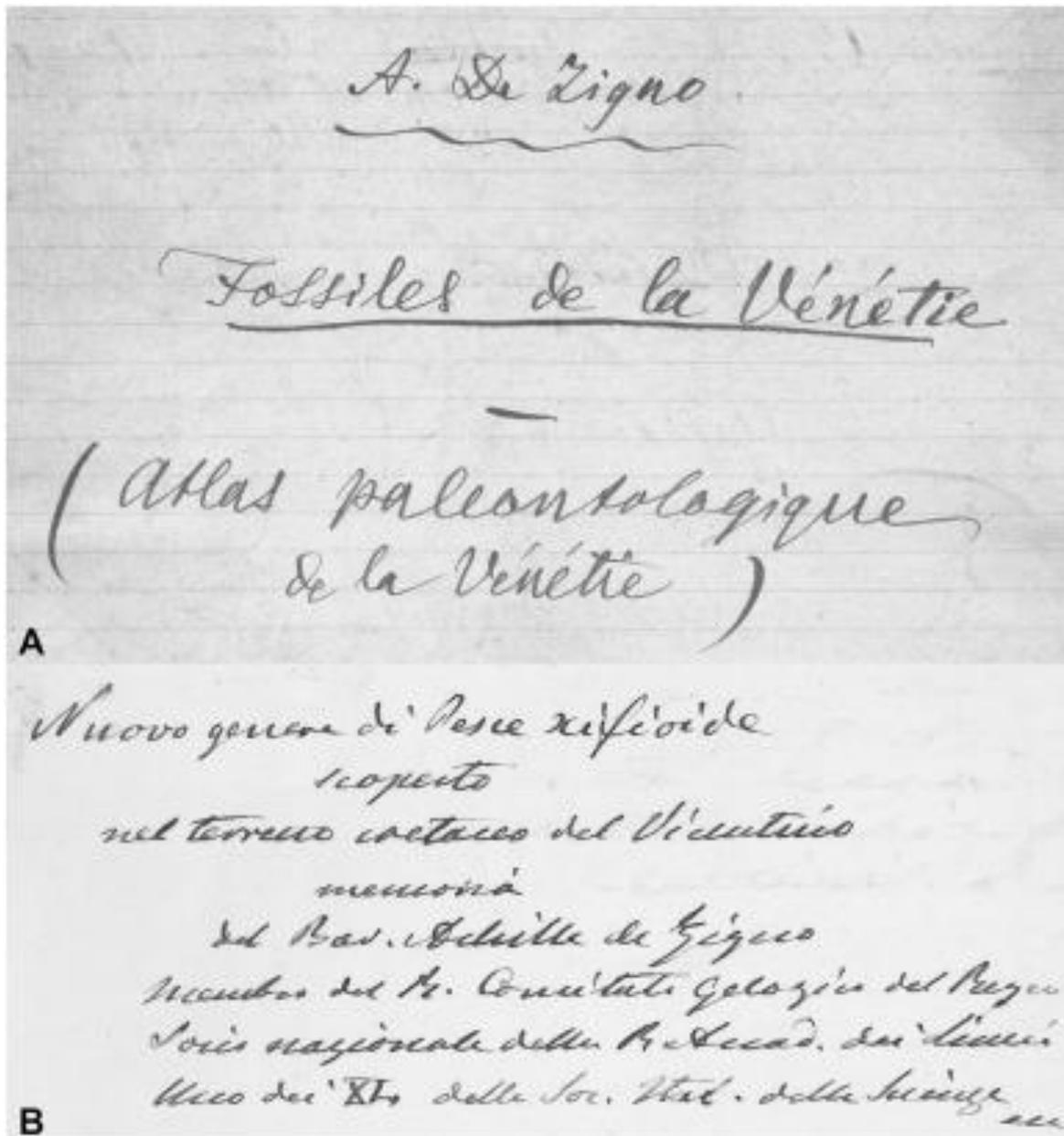


Fig. 3. The handwritten unpublished manuscript by Baron Achille De Zigno. **A.** Heading of the complete oeuvre “*Fossiles de la Vénétie* (or *Atlas paléontologique de la Vénétie*)”. **B.** Heading of the manuscript “*Nuovo genere di pesce xifioide scoperto nel terreno cretaceo del Vicentino*” (“A new genus of xiphioid fish from the Cretaceous of the Vicenza province”) that was included in the stack of papers of the unpublished monograph.



Fig. 4. ‘*Protosphyraena*’ *stebbingi* Woodward (1909). **A.** De Zigno’s “*Fossil de la Vénétie*” unpublished plate. Excerpt figuring “*Homalorhynchus xiphoides*” (= ‘*Protosphyraena*’ *stebbingi*) from Crespadoro (Vicenza Province, northeastern Italy). **B.** The specimen MGP-PD 6716Z from Crespadoro. The photo is in true colors and shows the two sides of the rostrum and a detail of the lateral edge. Scale bar equals 50 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



Fig. 5. Handwritten label of MGP-PD 6716Z by Baron Achille De Zigno. Text as follows: “*Homalorhynchus xiphioides* Zigno. Scaglia bituminosa di Crespadoro. Orizzonte del Calcare nero bituminoso subordinato ai Calcari del P.° Turoniano. Vicentino [?]”. Translation: “*Homalorhynchus xiphioides* Zigno. Bituminous Scaglia [rocks] from Crespadoro. Black bituminous limestone horizon below the Turonian limestone. Vicenza area [?]”.

Material and methods

Institutional abbreviations

NHMUK: Natural History Museum, London, UK; **MCSNV:** Museo Civico di Storia Naturale (Civic Museum of Natural History), Verona, Italy; **MGCB-VT:** Museo Geopaleontologico (Geopaleontological Museum), Cava Bomba di Cinto Euganeo - material from Villa di Teolo, Padova, Italy; **MGP-PD:** Museo di Geologia e Paleontologia (Museum of Geology and Paleontology), University of Padova, Padova, Italy (**Z** = De Zigno's collection).

Material

The material described herein includes two rostra housed in the collections of two paleontological museums of the Veneto Region (Italy). MGP-PD 6716Z is part of the historical De Zigno collection of the Museum of Geology and Paleontology of the University of Padova. The specimen MGCB-VT 001 is housed in the Geopaleontological Museum of Cava Bomba of Cinto Euganeo (Padova Province). The type material of ‘*Protosphyraena*’ *stebbingi* housed in the NHMUK, London (NHMUK PV P 11216) was analyzed for comparative purposes. The specimen described in Woodward, 1912a, Woodward, 1912b belonged to the collection of the Hull Municipal Museum

(England, UK), but the building housing the rostrum was destroyed by an incendiary bomb in 1943 (Friedman et al., 2016). Therefore, the specimen is now lost.

Methods

The specimens were measured with a Vernier caliper (brand Mauser). Photographs were taken using a Nikon D810 camera with a 60-90 mm lens and a Canon PowerShot SX720 HS camera. Specimen MGP-PD 6716Z was coated with ammonium chloride in order to enhance some morphological features. Illustrative drawings and images of the specimens were prepared using the software GIMP (v. 2.10.6) and ImageJ. The matrix of specimen MGP-PD 6716Z was sampled with a millimetric tungsten carbide spherical drill bit mounted on an electric drill. The powder obtained was then utilized for preparing a smear slide for calcareous nannoplankton analysis. We follow Matthews, 1973, Bengtson, 1988 and Sigovini et al. (2016) for synonymy list rules.

Results

Systematic paleontology

Order Tselfatiiformes? Nelson, 1994

'Protosphyraena' stebbingi Woodward (1909)

Fig. 1, 4, 6-11

v1883 *Xiphias* - De Zigno, p. 8.

v†1909 *Protosphyraena stebbingi* sp. nov. - Woodward, p. 153, pl. 33, figs. 1-2.

1912a *Protosphyraena stebbingi* A. S. Woodward - Woodward, p. 251.

1912b *Protosphyraena stebbingi* - Woodward, p. 329, pl. 19.

v1994 *Protosphyraena?* sp. - Sirna et al., p. 270.

v2016 *Protosphyraena stebbingi*. Woodward (1909). Type - Bernard and Smith, p. 120, text-fig. p. 120.

2016 *'Protosphyraena' stebbingi* Woodward (1909) - Friedman et al., p. 182, tab. 1, fig. 4b

Type material. Two fragments of a single rostrum (NHMUK PV P 11216) from the Lower Chalk (zone of *Holaster subglobosus*) of Betchworth, Surrey, England, UK.

Emended diagnosis. Long-snouted bony fish characterized by the following combination of rostral characters: rostrum dorsoventrally flattened, with rounded lateral edges; tip rounded and blunt; width

decreasing distally; surface raising to the midline, traversed by a longitudinal groove; one side of the rostrum ornamented mainly with thin and low parallel longitudinal and anastomosing ridges, also exhibiting a knobby and rope-like pattern due the presence of rounded or pitted tubercles; medial groove on this side wide in the proximal portion of the rostrum; groove shrinking and shallowing distally along the rostrum, where it begins to be ornamented by parallel or anastomosing ridges; medial groove bordered by sharply-raised edges, with thickness gradually decreasing distally; opposite side of the rostrum with smooth surface; medial longitudinal groove less deep than that on the ornamented side and delimiting raised edges less marked; lateral edges of the rostrum ornamented with stronger ridges, partly longitudinal, partly oblique; cross section of the rostrum flattened ellipsoidal proximally and bulkier; ornamented side more convex than smooth side; a pair of medial large and flattened subquadrangular nutrient canals, shrinking and gradually separating distally along the rostrum; walls of the medial canals progressively becoming thicker distally along the rostrum.

Examined material. MGP-PD 6716Z, MGCB-VT 001, NHMUK PV P 11216.

Locality and horizon. MGP-PD 6716Z was collected from the “bituminous black limestones” of Crespadoro (Monti Lessini), correlated by De Zigno (1883: p. 8) with the bituminous shales of the Bonarelli Level cropping out near Crespano del Grappa (Vicenza province). The lithology of the rock inside the medial groove and partly encrusting the rostrum, however, is a grayish marl rich in spumellarid and nassellarid radiolarians. This lithology is more consistent with the limestones and marls of the upper part of Scaglia Variegata Alpina Formation (lower Aptian-Cenomanian; Roghi and Romano, 2009) rather than with the typical carbonate-free black shales of the Bonarelli Level. A smear slide prepared for calcareous nannofossil analysis from the matrix of the specimen under study unfortunately yielded only few and badly preserved not biostratigraphically significant taxa. However, it should be noticed that in the De Zigno's original label associated with the specimen, the

stratigraphic position of the fossiliferous bed is indicated to underly the Turonian limestone (possibly the Scaglia Rossa Formation). The late Cenomanian age of the specimen from Villa di Teolo (MGCB-VT 001) is confirmed by its occurrence in the black shales of the Bonarelli Level (e.g., Coccioni and Luciani, 2005).

Stratigraphic range. Cenomanian (100,5-93,9 Ma; Ogg et al., 2016).

Description. The specimen MGP-PD 6716Z (Fig. 6, Fig. 7, Fig. 8) is a partial rostrum, consisting of two main portions that are splitted into ten and seven fragments, respectively. The two portions represent the distal part of the rostrum, including the anterior tip (186 mm long, but originally 191 mm long because of a fragment slightly offset for taphonomic deformation), and a more proximal part originally placed close to the base of the rostrum (217 mm long). We estimated that the rostrum could be at least 434 mm long (for this rough estimate see Appendix A.1). The rostrum is dorsoventrally flattened, with rounded lateral edges. The tip is rounded and blunt. The width of the

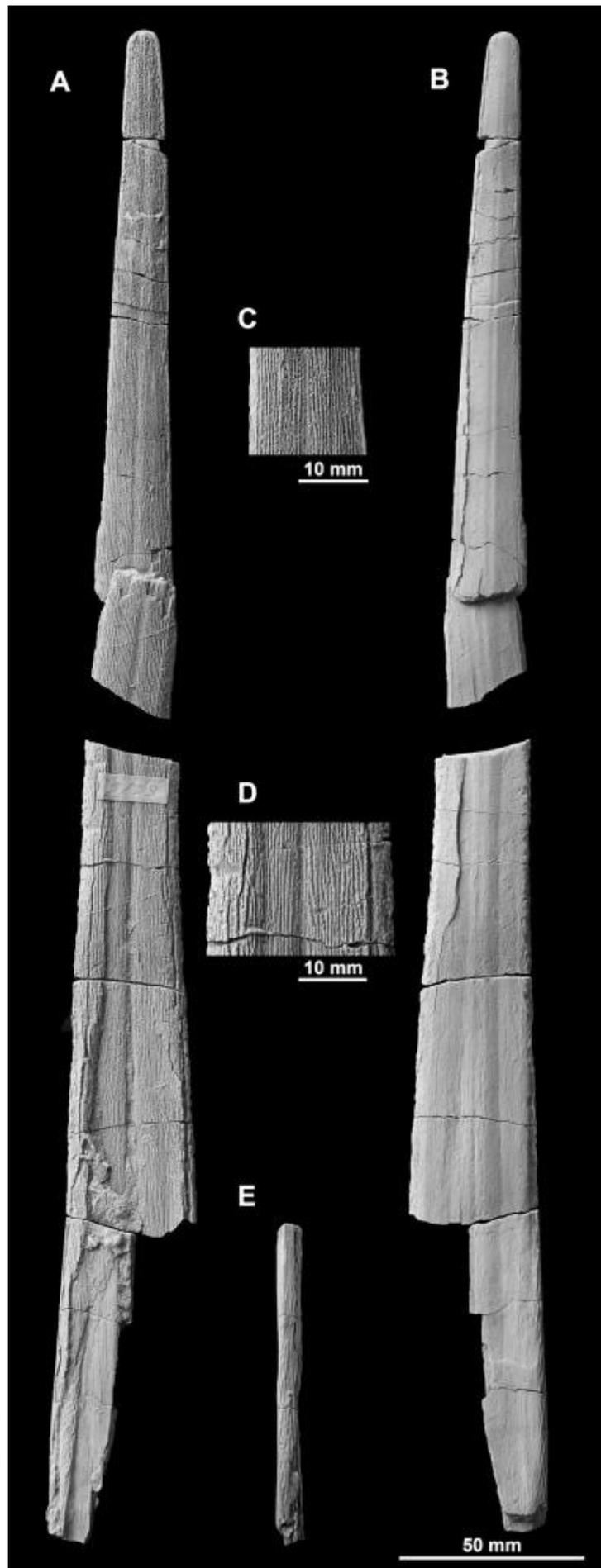


Fig. 6. '*Protosphyraena*' *stebbingi* Woodward (1909). MGP-PD 6716Z. Specimen coated with sublimed ammonium chloride. **A.** Ornamented face. **B.** Smooth face. **C.** Close-up of the ornamentation toward the distal extremity. **D.** Close-up of the ornamentation toward the proximal extremity. **E.** Close-up of the lateral edge. Scale bar in A-B, E equals 50 mm. Scale bars in C-D equal 10 mm.

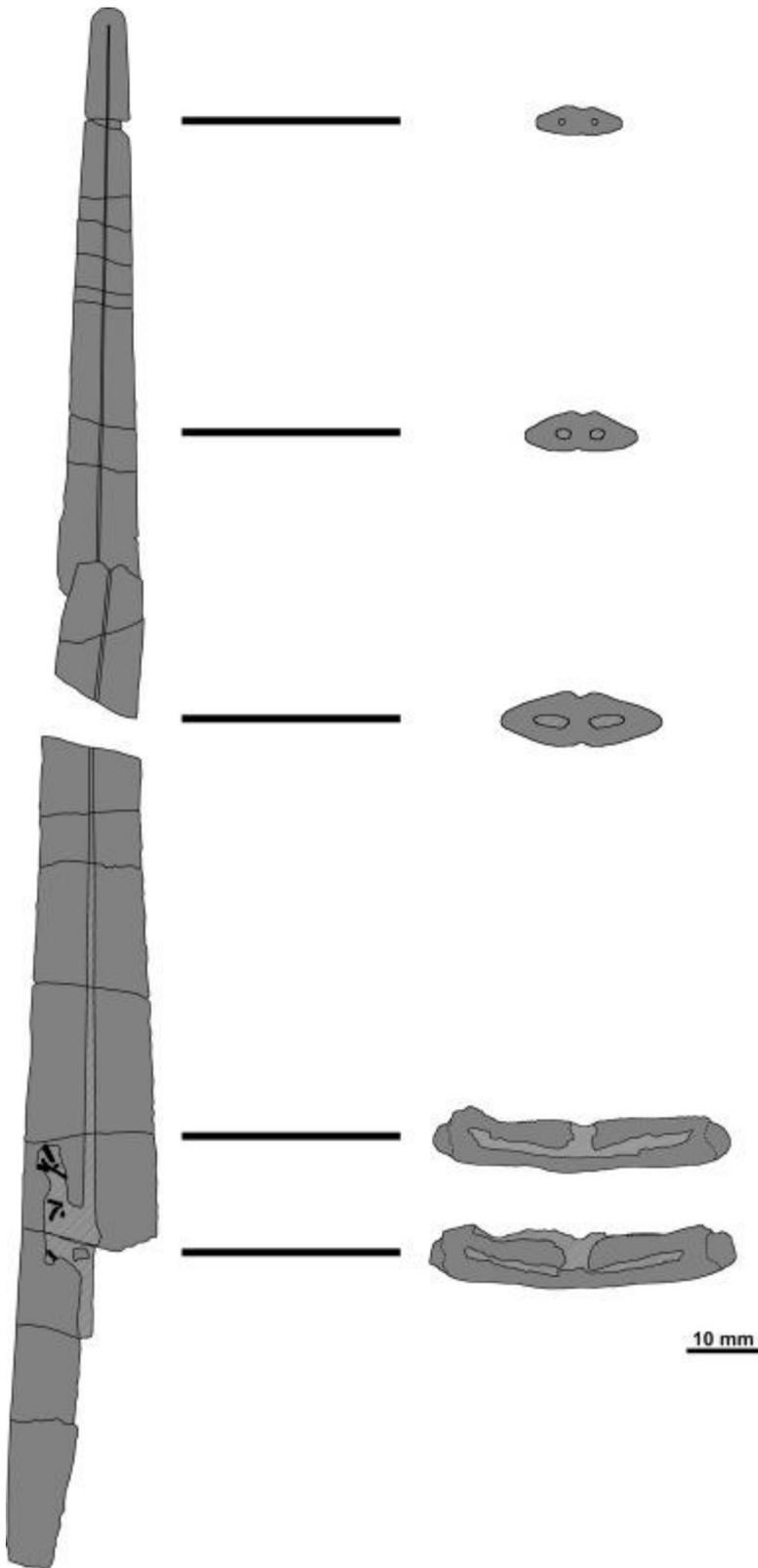


Fig. 7. '*Protosphyraena*' *stebbingi* Woodward (1909). **A.** Detail of the section of the rostrum, located basally to the proximal portion of the rostrum. **B.** Detail of the section of the rostrum, located slightly distally to the section in Fig. 8A. Scale bars equals 10 mm.

rostrum decreases distally, from a maximum of ca. 36 mm near the base to a minimum of ca. 9 mm at the tip. The rostrum surface raises to the mid line, where it is traversed by a longitudinal groove, that shrinks toward the tip. The maximum width of the groove is ca. 3 mm, decreasing to a minimum of ca. 1 mm toward the tip. One side of the rostrum (Fig. 6A) is ornamented mainly with thin and low parallel longitudinal and anastomosing ridges, also exhibiting a knobby and rope-like pattern due the presence of

rounded or pitted tubercles (Fig. 6C-D). The medial groove on this side is wide toward the base and partially filled by the marly sedimentary matrix. The groove shallows distally, where it is ornamented by parallel or anastomosing ridges that cover the whole surface of this side of the rostrum (see Fig. 6C-D). The groove is bordered by sharply-raised edges, which gradually decrease in thickness distally along the rostrum.

The opposite side of the rostrum has a smooth surface (Fig. 6B). The medial longitudinal groove is less deep than that on the ornamented side and the delimiting raised edges are less marked. The lateral edges of the rostrum are ornamented with stronger ridges, which are partly longitudinal, partly oblique (Fig. 6E). The shape of the cross section of the rostrum varies antero-posteriorly (Fig. 7, Fig. 8). In the proximal sector of the most basal portion of the rostrum, the cross section is subrectangular and flattened except for the medial groove raised edges and the lateral edges, that exhibit a slightly bulgy aspect (Fig. 7). The cross section becomes bulkier and ellipsoidal along the rostrum distally, slightly increasing in thickness along the proximal portion and decreasing again from the base of the distal portion toward the tip of the rostrum (Fig. 8). While the lateral edges become gradually flattened anteriorly, the ornamented side becomes more convex, and the smooth side more flattened. In cross section it is possible to observe a pair of medial large and flattened subrectangular nutrient canals that seem to reach the distal end of the rostrum. The canals progressively decrease in width and become more separated from each other distally along the rostrum. The walls of the medial canals progressively become thicker distally along the rostrum and the canals appear to be collapsed



proximally (see below the taphonomic remarks concerning the change of the section shape along the total length of the rostrum and the collapsed medial canals).

Specimen MGCB-VT 001 (Fig. 9) represents part of a rostrum ca. 240 mm long with broken tip. The width ranges from 30 mm at the base, to ca. 11 mm at the distal extremity. The rostrum is still embedded in the rock and exhibits only the smooth side. The morphology corresponds well with that of specimen MGP-PD 6716Z, especially in the morphology of the medial groove, which is bordered by slightly raised edges, and bulgy lateral edges at the base that flatten distally along the rostrum. The lateral edges also exhibit the same oblique and longitudinal strong ridges (see close-up in Fig. 9).

Fig. 8. '*Protosphyraena*' *stebbingi* Woodward (1909). Line drawing of the ornamented side of MGP-PD 6176Z. Grey color indicates bone tissue, barred areas indicate encrusting matrix, black color indicates serpulid-like calcareous tubes encrusting the rostrum. Scale bar, valid for the sections, equals 10 mm.



Fig. 9. ‘*Protosphyraena*’ *stebbingi* Woodward (1909). The specimen MGCB-VT 001 from Villa di Teolo. The close-up on the top left shows the oblique and longitudinal strong ridges on the lateral edge, indicated by white arrows. Scale bars equal respectively 50 mm and 10 mm.

Discussion

Taxonomic remarks

The characters described above are fully consistent with those indicated by Woodward (1909) in the diagnosis of ‘*Protosphyraena*’ *stebbingi* (see Fig. 10, Fig. 11, Fig. 12 for comparison), as well as with those exhibited by the second specimen reported by Woodward, 1912a, Woodward, 1912b. As already evidenced in Friedman et al., 2016, Amalfitano et al., 2017 advocated a tselfatiiform interpretation for this taxon. The rostra are certainly different from those of the genus *Protosphyraena* due to the presence of midline grooves and paired nutrient canals, indicating that they probably consisted of paired bones rather than the medial rostrodermethmoid that forms the rostrum of *Protosphyraena* and other pachycormids (Friedman et al., 2016). Elongate and dorsoventrally flattened rostra formed by paired premaxillae very similar to those of ‘*P.*’ *stebbingi* are known in some tselfatiiforms (see Friedman et al., 2016), including the Coniacian

Martinichthys (McClung, 1926, Taverne, 2000), and an undescribed Cenomanian taxon from

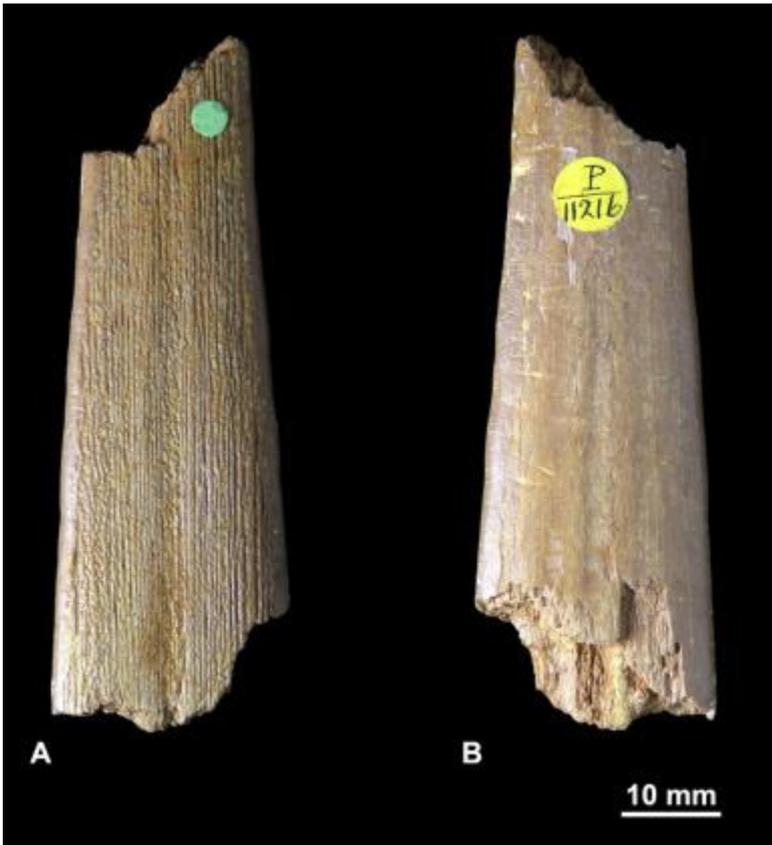


Fig. 10. ‘*Protosphyraena*’ *stebbingi* Woodward (1909). NHMUK P 11216 (holotype) from Betchworth, Surrey (UK). Distal fragment of the rostrum. **A.** Ornamented side. **B.** Smooth side. Scale bar equals 10 mm.

Lebanon (see Gayet et al., 2012: p. 168). Due to the fragmentary nature of the rostra we prefer to avoid the creation of a new genus; therefore, we provide a revised diagnosis of the species, until additional more complete material will be available.

Several long-snouted bony fishes are known from the Mesozoic and Cenozoic records (e.g., *Protosphyraena*, *Cylindracanthus*, blochiids, hemingwayids and palaeorhynchids; Fierstine, 2006, Gottfried et al., 2012, Santini and Sorenson, 2013, Amalfitano et al., 2017), which exhibit a morphology in

many ways convergent with that of extant billfishes (swordfishes,

sailfishes, spearfishes and marlins; Fierstine, 2006). ‘*P.*’ *stebbingi* and the other long-snouted tselfatiiformes can be added to the group of bony fishes exhibiting a convergent long-snouted morphology with the billfishes. The so-called billfishes include all the percomorph fishes plus other *incertae sedis* taxa with elongated premaxillae forming a (non-protrusible or mobile) rostrum or bill that is fused distally (Fierstine, 2006). The function of the elongated pointed rostrum in billfishes was extensively investigated in several papers, which evidenced that it is primarily used for food capture and defense (see, e.g., Frazier et al., 1994, Domenici et al., 2014). The rostrum of ‘*Protosphyraena*’ *stebbingi*, as well as that of the long-snouted tselfatiiforms (and also that of pachycormids of the genus *Protosphyraena*), could be interpreted as a convergent trait related to their feeding behavior, probably very similar to that of extant billfishes. Recently, Habbeger et al. (2019) observed that the more flattened rostrum of the swordfish is apparently specialized for lateral swiping during prey



Fig. 11. '*Protosphyraena*' *stebbingi* Woodward (1909). NHMUK P 11216 (holotype) from Betchworth, Surrey (U.K.). Basal portion of the rostrum. Scale bar equals 50 mm.

capture. The flattened rostrum of '*Protosphyraena*' *stebbingi* is very similar to the rostrum of a swordfish, thereby suggesting a similar use during prey capture.

The stratigraphic distribution of '*Protosphyraena*' *stebbingi* is poorly defined. The previous records of this species are from the English Chalk (Woodward, 1909, Woodward, 1912a, Woodward, 1912b) and the Italian specimens described herein represent the only report of this taxon outside the UK known to date. The two British specimens reported by Woodward, 1912a, Woodward, 1912b come from the Zone of *Holaster subglobosus* (see Woodward, 1909), which corresponds to the upper part of the Lower Chalk of the Southern Province (the Grey Chalk), dating back to the upper Cenomanian (Dibley, 1900, Jukes-Browne and Hill, 1903, Jukes-Browne and Hill, 1904; see; Hopson, 2005).

Therefore, the age of the Italian specimens described herein is consistent with that of the British findings.

Taphonomic notes

As far as the fragmentary nature of the fossils discussed herein is concerned, it is worth to mention that the findings of isolated rostra of long-snouted bony fishes generally are relatively common (e.g., *Aglyptorhynchus*, *Cylindracanthus*, *Makaira*, *Protosphyraena*; see Woodward, 1908, Fierstine, 2006, Grandstaff et al., 2017). The thickness of the bony walls and the diameter of the nutrient canals of hollow rostra change along their length (see Grandstaff et al., 2017). The rostrum of '*Protosphyraena*'

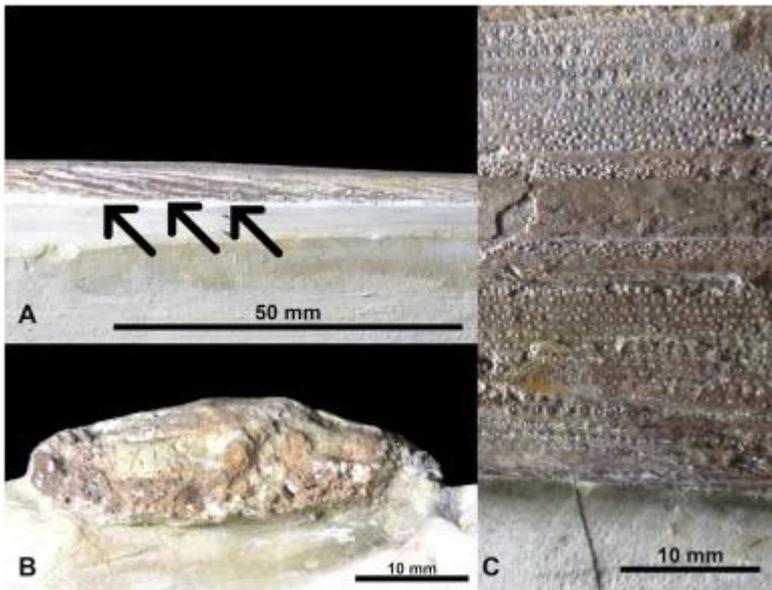


Fig. 12. ‘*Protosphyraena*’ *stebbingi* Woodward (1909). NHMUK P 11216 (holotype). Close-ups of the basal portion of the rostrum. **A.** Lateral view of the oblique and longitudinal strong ridges on the lateral edge, indicated by black arrows. Scale bar equals 50 mm. **B.** Transverse view of the basal portion of the rostrum, revealing the medial canals. Scale bar equals 10 mm. **C.** Ornamentation of the rostrum. Scale bar equals 10 mm.

stebbingi exhibits the same condition, with thin bony walls and wide medial nutrient canals at the base of the rostrum, and thickening of the walls and decreasing width of the canals distally. In this context, the thin proximal walls of the rostrum could have represented a zone of structural weakness that could explain the presence of isolated rostra in the record, without any associated cranial elements (Grandstaff et al., 2017). If compared with the type material, which exhibits an ellipsoidal section in its proximal portion (Fig. 12B), the

proximal portion of the rostrum MGP-PD 6716Z is affected by taphonomic deformations. These include the collapsed medial nutrient canals, a subrectangular section and the fractures on the ornamented side (Fig. 6, Fig. 7, Fig. 8), probably due to compression induced by compaction of overlying sediment after burial.

The ornamented side of the rostrum MGP-PD 6716Z bears encrusting serpulid-like calcareous tubes proximally (Fig. 7, Fig. 13). The slightly curved tubes are poorly preserved within the marly embedding matrix. The presence of serpulids indicates a prolonged exposure on an oxygenated seafloor before final burial of the rostrum (see Grange and Benton, 1996, Giannetti et al., 2014). However, the area encrusted by the calcareous tubes is very limited and this could be due to intermittent phases of oxic and anoxic conditions in the depositional environment (see Grange

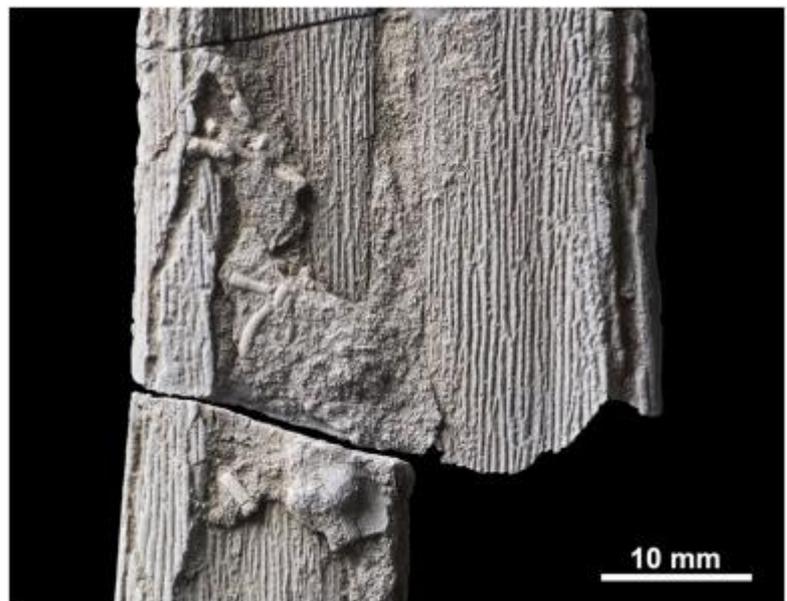


Fig. 13. Serpulid-like calcareous tubes encrusting the rostrum MGP-PD 6716Z. Close-up of the proximal fragment of the rostrum. Scale bar equals 10 mm.

and Benton, 1996). In any case, totally anoxic or disoxic conditions of the depositional environment can be ruled out representing an argument against the possible provenance of the rostrum from the anoxic black shales of the Bonarelli Level. Deep-sea serpulids are known in the fossil record since the Mesozoic (e.g., Di Geronimo et al., 2001, Kupriyanova and Ippolitov, 2015) and the lithology of the embedding matrix is consistent with a deep-sea depositional setting. Serpulids encrusting vertebrate skeletons have been reported in several studies so far, focusing on both fossil and extant taxa (e.g., Allison et al., 1991; Grange and Benton, 1996), although rarely on fossil fish remains; therefore, that described herein could represent one of the few evidences of serpulids encrusting fish remains reported up to date.

Concluding remarks

The rostra described herein from the Upper Cretaceous rocks of northeastern Italy are assigned to '*Protosphyraena*' *stebbingi* Woodward (1909). Despite their incompleteness, the rostra exhibit distinct diagnostic traits that allow to exclude any possible assignment to the genus *Protosphyraena*. '*Protosphyraena*' *stebbingi* is tentatively referred to the Tselfatiiformes although its affinities remain elusive, and only complete specimens will help to clarify its overall morphology and phylogenetic relationships within bony fishes, pending further studies of complete remains of Cenomanian long-snouted fishes from Lebanon (e.g., Gayet et al., 2012: p. 168) or other localities. However, the Italian specimens represent some remarkable findings, particularly the rostrum MGP-PD 6716Z from Crespadoro probably represents the best-preserved specimen referred to '*Protosphyraena*' *stebbingi* known to date. This fossil also contributes to better define the stratigraphic record of the taxon, which probably roamed in the Tethys Ocean at least up to the late Cenomanian. The fragmentary preservation of the Italian specimens is consistent with the relatively high frequency of findings of isolated bony fish rostra (see Grandstaff et al., 2017). Furthermore, the occurrence of a limited patch of serpulid-like tubes encrusting the ornamented side of the rostrum from Crespadoro suggests that the specimen was deposited in possibly oxic or intermittently anoxic conditions. The lithology of the rock encrusting the rostrum also provide evidence that it was deposited in deep-sea setting, thereby suggesting that the calcareous tubes could be referred to as deep-sea serpulids. In summary, the analysis of the Italian specimens has provided new information about the composition of the ichthyofauna from the Upper Cretaceous of Northeastern Italy that exhibits some similarities with that of the English Chalk (see Sorbini, 1976, Friedman et al., 2016; Amalfitano J., pers. obs.).

Acknowledgements

The authors warmly thank Mariagabriella Fornasiero (MGP-PD) and Franco Colombara and the Province of Padova for permissions to examine the specimens in the collections. We thank Emma Bernard (NHMUK) for access to the specimen NHMUK PV P 11216 and to the information about the collections. We would also acknowledge Stefano Castelli (Department of Geosciences of University of Padova) for his valuable help with photographs and figures preparation and Letizia Del Favero (MGP-PD) for the restoration of the rostrum MGP-PD 6716Z. We are very grateful to the Editors (Eduardo Koutsoukos and John Jagt), an anonymous reviewer and Jürgen Kriwet for their constructive and valuable comments and suggestions. The Department of Geosciences of the University of Padova is deeply acknowledged for kind permission to reproduce the excerpt of an unpublished plate of the oeuvre “*Fossiles de la Vénétie*” by Achille De Zigno, housed at the Library of the Department of Geosciences of Padova University. The copyright of the NHMUK photos is reserved to the NHMUK (“NHM”). Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled ‘Reappraisal of two key *Fossil-Lagerstätten* in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach’, assigned to Eliana Fornaciari).

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2.3.

Upper Cenomanian fish assemblage from the Bonarelli Level (OAE2) of northeastern Italy

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Abstract

The Bonarelli Level (BL) is an important radiolarian-ichthyolithic, organic-rich marker bed that was deposited close to the Cenomanian/Turonian boundary (CTB) representing the sedimentary expression of the global Oceanic Anoxic Event 2 (OAE2). In northeastern Italy this horizon yielded fossil remains of a diversified ichthyofauna. The assemblage was studied by Sorbini in 1976, but this study was based on a single locality. Subsequently, other localities yielding fish remains were found. Our revision comprises the findings coming from three new fish-bearing localities: Carcoselle Quarry, Valdagno-Schio tunnel and Quero. At least 28 taxa were recognized, including six new additions (*Scapanorhynchus raphiodon*, *Cretalamna appendiculata*, *Archaeolamna kopingensis*, ‘*Nursallia*’ *tethysensis*, at least two species of *Belonostomus*, *Dixonanogmius dalmatius*, ‘*Protosphyraena*’ *stebbingi* and *Hoplopteryx* sp.). The overall assemblage mostly consist of crossognathiforms, tselfatiiforms and aulopiforms. A brief comparison with coeval assemblages evidences a general similarity with nearby western Tethyan fish assemblages and especially with the Jebel Tselfat and German ichthyofaunas, but additional information would be necessary to more properly define the main global ichthyogeographic patterns during the Cenomanian.

Introduction

The Bonarelli Level (BL) is an important radiolarian-ichthyolithic, organic-rich marker bed that was deposited close to the Cenomanian/Turonian boundary (CTB) and represents the sedimentary expression of the global Oceanic Anoxic Event 2 (OAE2) (e.g., Gomez et al., 2002; Coccioni and Luciani, 2005). The sediments accumulated during this event received considerable attention in Italy during the 1990s and early 2000s with a number of geochemical, sedimentological and micropalaeontological studies (e.g., Bellanca et al., 1996; Salvini and Marcucci Passerini, 1998; Luciani and Cobianchi, 1999; Premoli Silva et al., 1999; Coccioni and Luciani, 2004, 2005), as well as of a series of studies on plants remains (e.g., Gomez et al., 2002; 2015). Moreover, in northeastern Italy, the Bonarelli Level yielded one of the better-known Cenomanian ichthyofauna (see Patterson, 1993). The rich fish assemblage of the BL from the locality of Bomba Quarry near Cinto Euganeo has been largely examined and discussed by several authors (Sorbini, 1976, 1980; Astolfi and Colombara, 1990, 2003; Bizzarini and Coccioni, 1990; Avanzini and Luciani, 2002, Dalla Vecchia et al., 2005). However, recent findings from other localities and a need of revision of the material originally described by Sorbini (1976) have renewed the interest towards this remarkable ichthyofauna. Within the framework of a wider project aimed at revising the most important vertebrate *Fossil-Lagerstätten* of the mid-Cretaceous of northeastern Italy, we started a revision of this fossil ichthyofauna integrating the data from new localities, and updating and/or revising the interpretations of the systematic analysis realized by Sorbini (1976). This project started in 2016, exactly 40 years after the publication of the first work on the BL fish assemblage by Sorbini (1976). A potentially new and informative framework emerges from this analysis, including that provides some paleobiogeographic implications in the dynamics of the late Cenomanian Tethyan ichthyofaunas related to the environmental perturbations induced by the OAE2.



Fig. 1. Location of the four main Bonerelli Level outcrops that yielded fish remain. The black stars indicate the localities. Scale bar equals 50 km.

Geological context

The Southern Alpine domain during the Cretaceous was characterized by three different depositional environments derived from the palaeogeographic setting, with a horst and graben trend inherited from the rifting associated with the opening of the central North Atlantic (Winterer and Bosellini, 1981) (Fig. 1). An external carbonate platform, the Friuli Platform, bordered eastwards a continental margin basin, the Belluno Basin, that was separated westwards from another basin (the Lombardian Basin) by a structural high, the Trento Plateau (Channel et al., 1992; Gomez et al., 2002, 2015). Reef limestones characterized the margin of the Friuli Platform, and limestones composed of re-sedimented shallow-water debris with pelagic material were deposited in the eastern part of the Belluno Basin (Winterer and Bosellini, 1981). The western part was characterized by pelagic limestones that form the Maiolica Formation. At the beginning of the Aptian, these limestones were succeeded everywhere by repeated alternations of limestones, varicolored marlstones and organic, carbon-rich shales known in the literature as the Scaglia Variegata Alpina Formation (Gomez et al., 2002; Roghi and Romano, 2009). The Trento Plateau (Trento-Vicenza-Verona-Padova provinces) is characterized by thinner successions, compared with the adjacent basins, of pelagic deposits, comprising calcareous pelagic and hemipelagic oozes mostly consisting of calcareous nanofossils, alternated with varicoloured marlstones of the Scaglia Variegata Alpina Formation and pinkish micrites and marlstones of the Scaglia Rossa (Coccioni and Luciani, 2005). The black shales of the

Bonarelli Level (close to the Cenomanian/Turonian boundary) represent the top of the Scaglia Variegata Alpina Formation and grade upward into the typical red-pinkish cherty limestones of the Scaglia Rossa Formation (Upper Cretaceous-lower Eocene) (Gomez et al., 2002). This level is discontinuously present, ranging from 30 to 300 cm in thickness (Gomez et al., 2015; Amalfitano et al., 2017). It also varies in its lithological composition depending on the locality. We studied the ichthyofaunas from four main localities: Bomba Quarry near Cinto Euganeo (Euganei Hills, Padova), Carcoselle Quarry near Possagno (Venetian Prealps, Treviso), Schievenin Valley near Quero (Belluno), Schio-Valdagno tunnel (Vicenza). There are also minor outcrops that yielded fish remains near Crespano del Grappa (Treviso), and in Sinigaglia Quarry near Villa di Teolo (Euganei Hills, Padova). Bassani (1880, 1882) reported probably the first findings from the Bonarelli Level of northeastern Italy, coming from Crespano del Grappa. The BL of Bomba Quarry, at the foot of Mt. Cinto in Cinto Euganeo (ca. 30 km south-west of Padova), was discovered and excavated between 1974 and 1975 (Sorbini, 1976) and subsequently in 1988 and 1990 (Astolfi and Colombara, 1990). There, the BL consisted of a lensoid body of alternating grey to black bituminous shales and bituminous marls. The excavation reports clearly indicate that the fish assemblage mainly derived from the lower laminated bituminous shales. The BL of Carcoselle Quarry was well exposed in the active front. This quarry is located near the village of Possagno, between Bassano (del Grappa) to the west and the Piave river to the east, and some 50 km north of Padova. The lithology of the BL is very similar to that of Bomba Quarry. As regards the Schio-Valdagno tunnel, the excavations took place in the mounts between the villages of Valdagno and Schio (ca. 20 km north-west of Vicenza) in the early 2000s and intercepted the BL, which mainly consists of greenish-grey to black mudstones and shales, alternated with radiolarian-rich layers (Coccioni and Luciani, 2005) and, remarkably, contains an appreciable amount of CaCO₃. In Schievenin Valley, near the village of Quero (ca. 30 km south-west of Belluno) the BL consists of yellowish-brown laminites, alternating with olive-grey, silty shales and olive-green, radiolarian-rich, silty-sandy layers (Gomez et al., 2002). Limonite nodules, representing the alteration of original Fe-sulphide nodules (e.g., pyrite), are also present. The fossil remains are mainly concentrated in the laminites of the lower-middle part of the level and were mostly collected from exposure B of Gomez et al. (2002).

Material and methods

The material comes from the collection of five museum of northeastern Italy. It consists of mainly fragmentary fish debris embedded in blocks of rock coming from the BL of the localities mentioned above. Some of the specimen may be composed by part and counterpart and the two portions may be divided and hosted in different museum collections. Synonymy lists in the systematic analysis includes only papers and works that directly figured and/or described material from northeastern Italy, in order to review the historical record of the studies of the Bonarelli Level ichthyofaunas from this area. The specimens were documented with different photographic techniques depending on the size of the slabs (e.g., the photogrammetric technique to obtain an orthophoto) using digital cameras (Canon PowerShot SX720 HS, Fuji X-E1 mounting 18-55 mm lens, Nikon D810 mounting 60-90 mm lens). Images and interpretative drawings of the specimens were produced using the freewares GIMP (v. 2.10.6). The synonymy list and open nomenclature follow the standards proposed by Matthews (1973), Bengston (1988) and Sigovini et al. (2016). We follow Forey et al. (2003: fig. 2) for morphological measurements and meristic data and their abbreviations.

PCA and neighbor joining analyses were performed on a selected list of Cenomanian/Turonian localities using the software Past 3.26 (Hammer et al., 2001) to compare the BL assemblage to other coeval marine assemblages. The data set is presented in Tab. A.1 (Appendices S.2.3). The references used for the data set compilation are listed in Tab. A.2. Parameters of the PCA analyses are provided in Tab. A.3.

Institutional abbreviations

MCSNVR: Museo Civico di Storia Naturale di Verona (Civic Museum of Natural History of Verona); **MCSNVE:** Museo Civico di Storia Naturale di Venezia (Civic Museum of Natural History of Venice); **MCV:** Museo Civico di Valdagno (Civic Museum of Valdagno); **MGCB:** Museo Geopaleontologico di Cava Bomba di Cinto Euganeo (Geopaleontological Museum of Bomba Quarry of Cinto Euganeo); **MGPPD:** Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (Museum of Geology and Paleontology of the University of Padua).

Results

Systematic analysis

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Order Lamniformes Berg, 1958

Family Mitsukurinidae Jordan, 1898

Genus *Scapanorhynchus* Woodward, 1889

Scapanorhynchus raphiodon (Agassiz, 1835)

Fig. 2A-C

1922 *Scapanorhynchus* sp. - D'Erasmus, p. 28, pl. 3, fig. 18-20.

1994 *Scapanorhynchus* sp. - Sirna et al., p. 272.

Referred material. MGCB IG220945.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The mitsukurinid shark *Scapanorhynchus raphiodon* is represented by an isolated anterior tooth (Fig. 2A-C), with a crown height of about 8 mm. The crown is characterized by a slender straight cusp with convex lingual face bearing numerous weak striations parallel near the base and more flexuous towards the top, extending nearly to its apex. The labial face is smooth. The cutting edge lacks serrations. The root is poorly preserved, especially the lobes. However, the lingual protuberance is very prominent and bears a short but deep nutritive groove. These characters support the assignement to the genus *Scapanorhynchus* (see Hamm and Shimada, 2002; Cappetta 2012). The species *S. raphiodon* is "the most frequently cited species" (Cappetta, 1987: p. 93; Cappetta, 2012: p. 187), but its morphological characterization is still uncertain (see Cappetta and Case, 1975; Hamm and Shimada, 2002; Welton and Farish, 1993). However, the weak striations, the size and the stratigraphic position of the specimen are consistent with those of *S. raphiodon* (Hamm and Shimada, 2002). *Scapanorhynchus raphiodon* is reported from the upper Cenomanian to the Santonian in pelagic sediments from several parts of the world (Hamm and Shimada, 2002 and references therein). This is the first report of the genus and the species from the Bonarelli Level in Italy. *Scapanorhynchus* was already reported in the Scaglia Rossa Formation of northeastern Italy by D'Erasmus (1922) and Sirna et al. (1994).

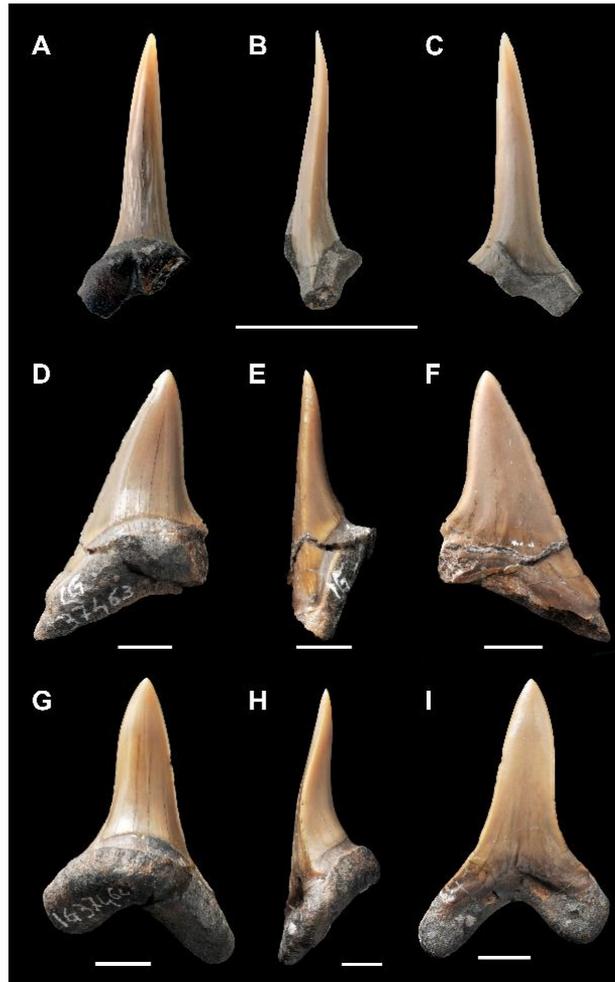


Fig. 2. Lamniformes teeth. **A-C.** *Scapanorhynchus raphiodonon*, MGCB IG220945 (lingual, lateral, labial view). **D-I.** *Cretoxyrhina mantelli*. 2 teeth: MGCB IG37463 (D-F), 37465 (G-I) (lingual, lateral, labial view). Scale bars equal 5 mm.

Family Cretoxyrhinidae Glickman, 1958

Genus *Cretoxyrhina* Glickman, 1958

Cretoxyrhina mantelli (Agassiz, 1835)

Fig. 2D-I

1922 *Oxyrhina Mantelli* Ag. - D'Erasmus, p.36, pl. 3, fig. 1-3.

1976 *Isurus mantelli* (Agassiz) 1843 - Sorbini, p. 481, pl. 1.

p. 1976 *Lamna serrata* (Agassiz) 1838-1843 - Sorbini, p. 481, pl. 2 (IG 37465).

1980 *Isurus mantelli* - Sorbini, p. 119.

1990 *Isurus mantelli* (Agassiz) - Astolfi and Colombara, p. 144, fig. 205.

1994 *Cretoxyrhina mantelli* (Agassiz, 1833-43) - Sirna et al., p. 271.

2005 *Cretoxyrhina mantelli* - Dalla Vecchia et al., p. 106, p. 108, fig. 81.

Referred material. MGCB IG37463-37465, IG220953; MCV IG362609.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Schio-Valdagno Tunnel (Vicenza).

Description and remarks. Five isolated teeth can be assigned to *Cretoxyrhina mantelli* (Fig. 2D-I). The triangular crown is slender and asymmetrical in anterior teeth with the cusp located above the mesial branch of the root (IG 37463, 37464, 362609). The enameloid is smooth and the cutting edges are continuous. The root lobes have rounded extremities. The lateral teeth have well-marked heels (IG 220953) or vestigial cusplets (IG 37465). The distal root lobe in IG 37463 and the mesial root lobe in IG 220953 are broken. The teeth have different sizes: IG 37463 is 26 mm high and 18 mm wide, IG 37464 is 27 mm high and 18 mm wide, IG 37465 is 14 mm high and 15 mm wide, IG 220953 is 12 mm high and 11 mm wide, and IG 362609 is 23 mm high and 15 mm wide. The morphology of the reported specimens is fully consistent with those of *Cretoxyrhina mantelli* reported by various authors (e.g., Shimada, 1997; Cappetta, 2012; Amalfitano et al., 2019). *Cretoxyrhina* is so far the most common lamniform shark in Cretaceous rocks in Italy (Amalfitano et al., 2019).

Genus *Cretalamna* Glickman, 1958

Cretalamna appendiculata (Agassiz, 1835)

Fig. 3A-C

1922 *Lamna appendiculata* (Ag.) - D'Erasmus, p. 38, pl. 4, fig. 8.
p. 1976 *Lamna serrata* (Agassiz) 1838-1843 - Sorbini, p. 481, pl. 3 (IG 37467).
1994 "*Lamna*" *serrata* (Agassiz, 1833-1843) - Sirna et al., p. 271.

Referred material. MCSNVR IG37467.

Description and remarks. The available material consists of a single isolated tooth (a lateral one, 9 mm high and 8 mm wide; Fig. 3A-C), characterized by a triangular and rather thick principal cusp (5 mm high and 7 mm wide) with a rather broad base and smooth enameloid, and a pair of well developed, not divergent lateral cusplets. The cutting edge is smooth and continuous. The principal cusp is slightly inclined. The root has short well-developed lobes forming a broad concavity and a slightly prominent lingual protuberance.

The described characters fit well with the diagnosis of *Cretalamna appendiculata* (Shimada, 2007; Cappetta, 2012). The taxon is rather common in Cretaceous pelagic deposits worldwide from the Albian to the Ypresian (Cappetta, 1987, 2012; Shimada, 2007). In Italy *C. appendiculata* was reported by D'Erasmus (1922) from the 'Senonian' red-purple chalk (Scaglia Rossa Veneta) of Feltre (Belluno).

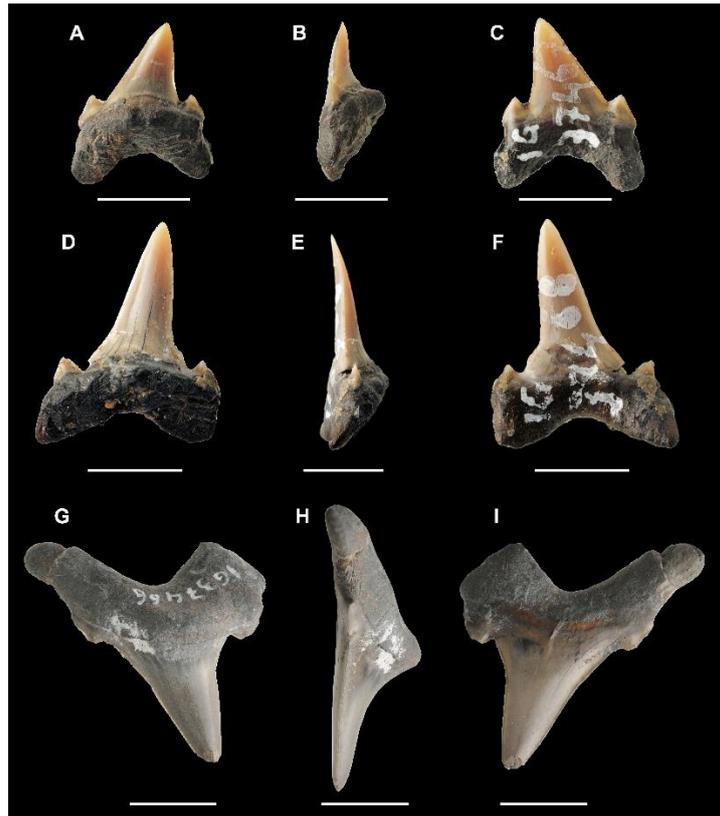


Fig. 3. Lamniformes teeth. **A-C.** *Cretalamna appendiculata*, MCSNVR IG37467 (lingual, lateral, labial view). **D-H.** *Archaeolamna kopingensis*. 2 teeth: MGCB IG37466; MCSNVR IG37468 (lingual, lateral, labial views). Scale bars equal 5 mm.

Family Archaeolamnidae Underwood and Cumbaa, 2010

Genus *Archaeolamna* Siversson, 1992

Archaeolamna kopingensis (Davis, 1890)

Fig. 3D-I

p. 1976 *Lamna serrata* (Agassiz) 1838-1843 - Sorbini, p. 481, pl. 2 (IG 37466), pl. 3 (IG 37468).
 1994 "*Lamna*" *serrata* (Agassiz, 1833-1843) - Sirna et al., p. 271.

Referred material. MGCB IG37466; MCSNVR IG37468.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. There are two antero-lateral isolated teeth (IG37466: 13 mm high, 14 mm wide; IG37468: 12 mm high, 10 mm wide; Fig. 3D-I), which have a broad-based cusp drastically tapering at one third of its height, and divergent lateral cusplets. The surface of the crown is smooth with the exception of a superficial hollow at the base of the labial face. The crown is slightly bent

towards the distal side. The cutting edge is smooth and continuous. The lingual protuberance is slightly prominent, and the root lobes are slender and rounded.

The overall morphology of these two teeth is consistent with that of *Archaeolamna kopingensis* (see Siverson, 1996; Cook et al., 2011). This is the first record of this taxon from Italy.

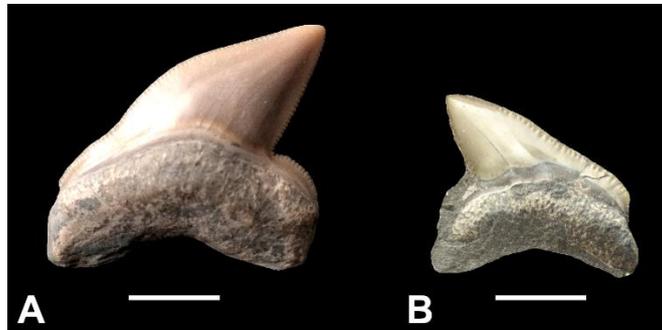


Fig. 4. *Squalicorax falcatus*. **A.** MGCB U3S1/3. **B.** MSNVE 12430. Scale bars equal 5 mm.

Family Anacoracidae Casier, 1947

Genus *Squalicorax* Whitley, 1939

Squalicorax falcatus (Agassiz, 1843)

Fig. 4

- 1976 *Corax* cfr. *falcatus* Agassiz 1843 - Sorbini, p. 482, plate 4.
- 1994 *Squalicorax* cf. *falcatus* (Agassiz 1833-1843) - Sirna et al., p. 271.
- 1994 *Squalicorax falcatus* (Agassiz 1833-1843) - Sirna et al., p. 273.
- 2003 *Squalicorax* sp. - Dalla Vecchia, p. 23, fig. 1.
- 2005 *Squalicorax* - Dalla Vecchia et al., p. 105.
- 2005 *Squalicorax falcatus* - Dalla Vecchia et al., p. 106.
- 2008 *Squalicorax* - Dalla Vecchia, p. 222, fig. 215.

Referred material. MGCB IG 37469; MGCB U3S1/3; MSNVE 12430.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Carcoselle Quarry (Possagno, Treviso).

Description and remarks. All the three examined teeth have a triangular crown with lateral serrations (see Fig. 4). These teeth are wider than high (MGCB IG37469: 7 mm [only the cusp] wide, 7 mm high; MGCB U3S1/3: 15 mm wide, 13 mm high; MSNVE 12430: 11 mm wide, 9 mm high). The crown exhibits two rounded heels. One of the teeth (MGCB IG37469) has a nearly erect cusp (probably an antero-lateral tooth), while the others (MGCB U3S1/3 and MSNVE 12430) have an inclined cusp and possibly represent two lateral elements. The mesial cutting edge is longer than the distal one and has a gibbosity at its midlength, more evident in MGCB U3S1/3 and in MSNVE 12430.

The mesial extremity in MGCB IG373469 is broken. The other two teeth are complete and still embedded within the matrix, solely exposing the lingual face.

The described characters can fit the definition of *Squalicorax falcatus* provided by Cappetta (2012). The taxon occurs from the Cenomanian to the Santonian (Cappetta, 2012; Shimada and Cicimurri, 2005). Sorbini (1976) tentatively referred a single tooth (MGCB IG 37469) to *Corax* (= *Squalicorax*) cf. *falcatus* due to the inadequate preservation of the specimen. The only other occurrence of the genus *Squalicorax* from NE Italy was reported by Dalla Vecchia (2003), based on a single tooth coming from the Vernasso quarry (Udine). It was identified as *Squalicorax* sp., although it shows clear affinities with *S. kaupi* (Dalla Vecchia, 2003).

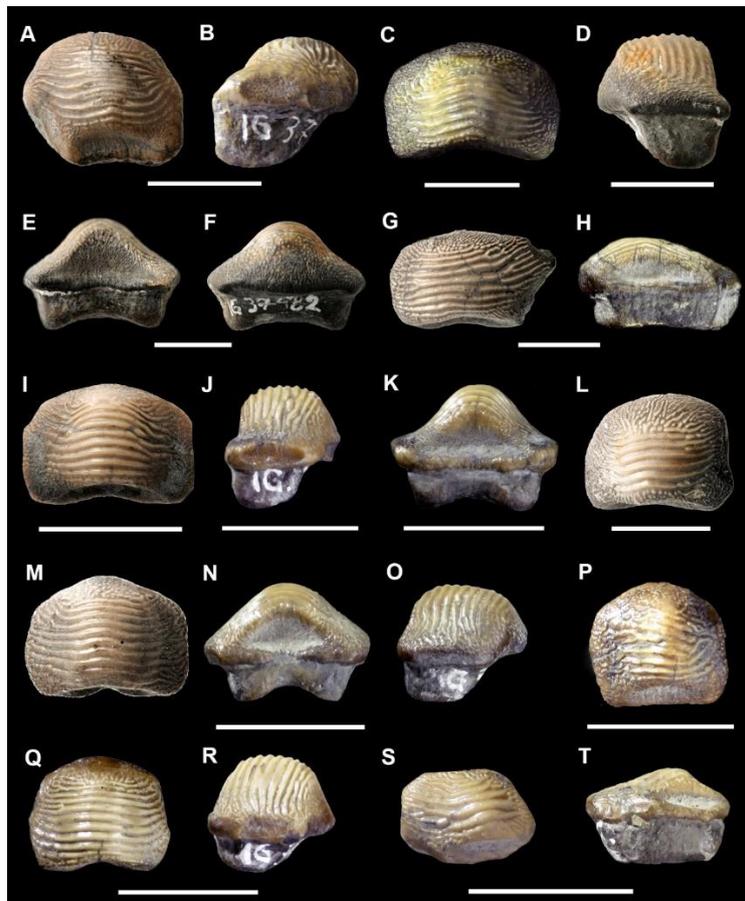


Fig. 5. *Ptychodus decurrens*. **A-B.** MGCB IG37483 (occlusal and lateral view). **C-F.** MGCB IG 37482 (occlusal, lateral, posterior and anterior view). **G-H.** MGCB IG37481 (occlusal and posterior view). **I-K.** MGCB IG37479 (occlusal, lateral, posterior). **L.** MGCB 446 (occlusal view). **M-O.** MGCB IG37478 (occlusal, posterior, lateral view). **P.** MGCB IG37477 (occlusal view). **Q-R.** MGCB IG37476 (occlusal and lateral view). **S-T.** MGCB IG37475 (occlusal and posterior view). Scale bars equal 5 mm.

Order *incertae sedis*

Family Ptychodontidae Jaekel, 1898

Genus *Ptychodus* Agassiz, 1934a

Ptychodus decurrens Agassiz, 1838

Fig. 5

- 1904 *Ptychodus latissimus* Ag. - Squinabol: p. 8; pl. 1, fig. 1.
1921 *P. decurrens* - Fossa-Mancini: p. 194.
1922 *Ptychodus decurrens* Ag. - D'Erasmus: p. 17; pl. 2, fig. 7, 8.
1976 *Ptychodus decurrens* Agassiz 1839 - Sorbini: p. 482; pl. 5 (IG 37471-IG 37482).
1976 *Ptychodus polygyrus* Agassiz 1839 - Sorbini: p. 483; pl. 4, lower fig. (IG 37483).
1980 *Ptychodus decurrens* - Sorbini: p. 119.
1990 *Ptychodus decurrens* Agassiz - Astolfi and Colombara, p. 145, fig. 206.
1990 *Ptychodus polygyrus* Agassiz - Astolfi and Colombara, p. 146.
1994 *Ptychodus decurrens* Agassiz - Sirna et al., p. 271, 273.
1994 *Ptychodus polygyrus* Agassiz - Sirna et al., p. 271.
1994 *Ptychodus mediterraneus* Agassiz - Sirna et al., p. 273.
2005 *Ptychodus* - Dalla Vecchia et al., fig. 79.

Referred material. MCSNVE 12431(36a-36b); MCV IG292956; MGCB 313, 446, IG37471-37483.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Carcoselle Quarry (Possagno, Treviso); Schio-Valdagno Tunnel (Vicenza).

Description and remarks. The available material consists of 17 isolated teeth (Fig. 5). They are wider than long on the occlusal plane. The size on the occlusal plane ranges from 4x3 mm to 18x12 mm. The teeth exhibit the following characters: generally low and rounded crown (more elevated in lower jaw teeth), anterior protuberance poorly developed and shallow posterior sulcus; numerous parallel transverse ridges along the occlusal plane, laterally extending and bifurcating onto the marginal area; fine and dense wrinkles perpendicular to the transverse ridges extending on anterior and posterior marginal area. The teeth are well-preserved and the root, largely overhanged by the crown, exhibits a deep longitudinal sulcus.

The overall morphology of the available teeth fits well with the definition of *P. decurrens* (see Woodward, 1912; Cappetta, 2012). This species was already reported from the Bonarelli Level of Colli Euganei by Squinabol (1904) and has been recently reported from the Cenomanian of Trentino-Alto Adige by Amadori et al. (2019). One of these teeth (MGCB IG37483) was erroneously referred to *Ptychodus polygyrus* by Sorbini (1976).

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887 (*sensu* Rosen et al., 1981)
Series Neopterygii Regan, 1923 (*sensu* Rosen et al., 1981)
Division Halecostomi Regan, 1923 (*sensu* Poyato-Ariza, 2015)
Superorder Pycnodontomorpha Nursall, 2010
Order Pycnodontiformes Berg, 1937 (*sensu* Nursall, 2010)

Remarks. The pycnodont fishes from the Bonarelli Level include only four specimens, coming from Bomba quarry (Cinto Euganeo) and from the Quero outcrop. As stated by Forey et al. (2003), alpha-level taxonomy of pycnodont fishes is quite confused and in need of a complete revision. Poyato-Ariza and Wenz (2002) realized a first attempt to improve the systematics of this group, although this and other similar papers were primarily devoted to understanding the higher-level phylogenetic relationships (see also subsequent papers, e.g., Kriwet, 2005; Nursall, 2010; Poyato-Ariza, 2015). Recently, a number of the exquisitely-preserved Cenomanian pycnodont taxa have been described from the Middle East (see e.g., Marramà et al., 2016, Cawley and Kriwet, 2019 and references therein), but taxa from other localities are badly in need of a revision (see, for instance, the recent revisions by Poyato-Ariza, 2010, Poyato-Ariza, 2013, and Vullo et al., 2018). The pycnodont material from the Bonarelli Level is poorly preserved. Currently, dental characters are useful and essential tools for identifying taxa in fossil assemblages with none or poorly preserved articulated remains (see Kriwet, 2005). The specimens from Bonarelli Level of Veneto exhibit few autapomorphic characters but preserve partial or complete dentitions, which are therefore very helpful for supporting identification.



Fig. 6. *Paranursallia gutturosa*. MGCB IG 37484. Scale bar equals 50 mm.

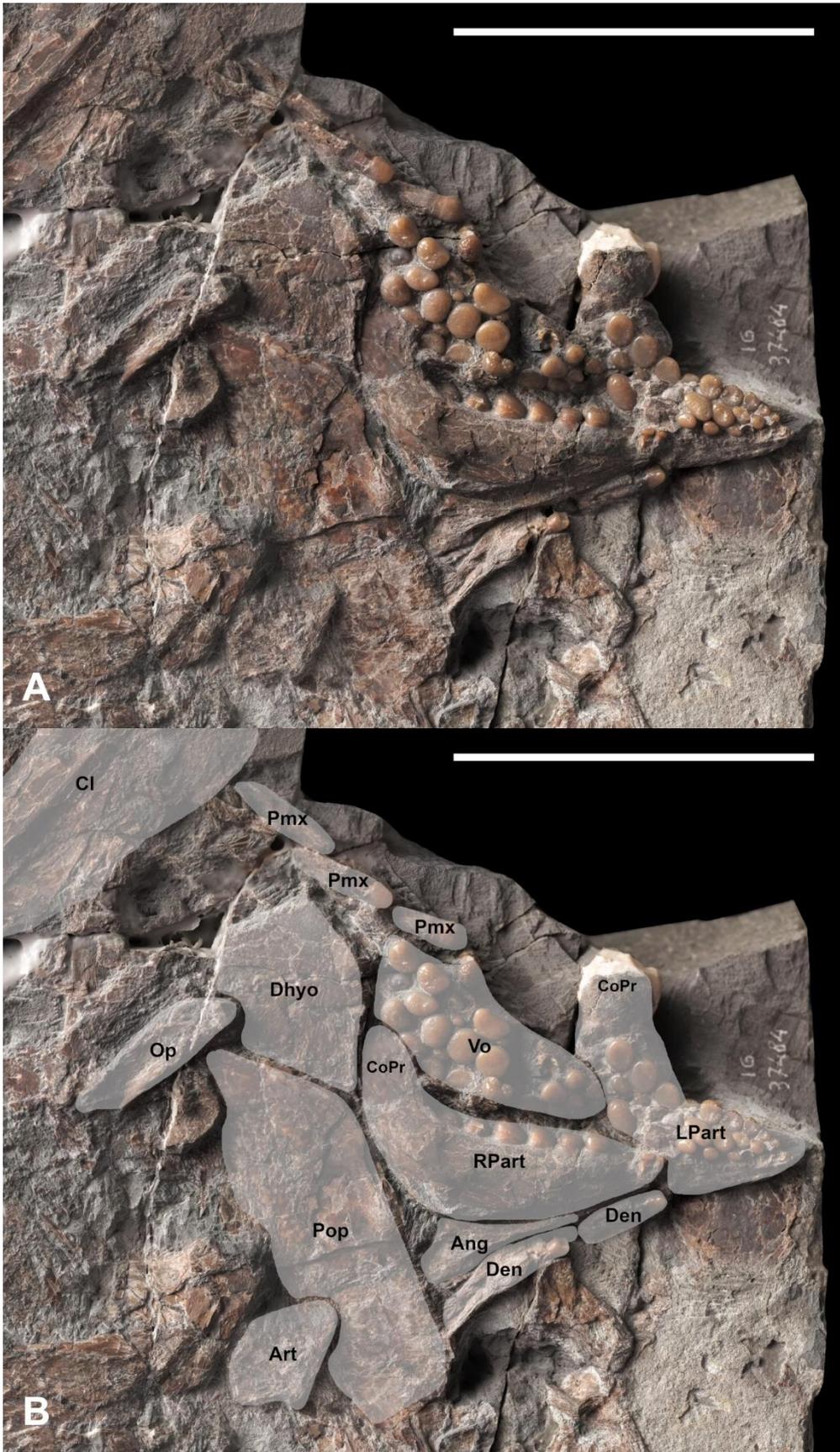


Fig. 7. *Paranursallia gutturosa*. MGCB IG37484. **A.** Detail of the oral region. **B.** Bones identification. Light grey areas represent identified bones. Abbreviations: **Ang**: angular; **Art**: articular; **Cl**: cleithrum; **CoPr**: coronoid process; **Den**:

dentary; **Dhyo**: dermohyomandibula; **Op**: opercle; **Pmx**: premaxilla; **RPart**: right prearticular; **LPart**: left prearticular; **Pop**: preopercle. Scale bars equal 50 mm.

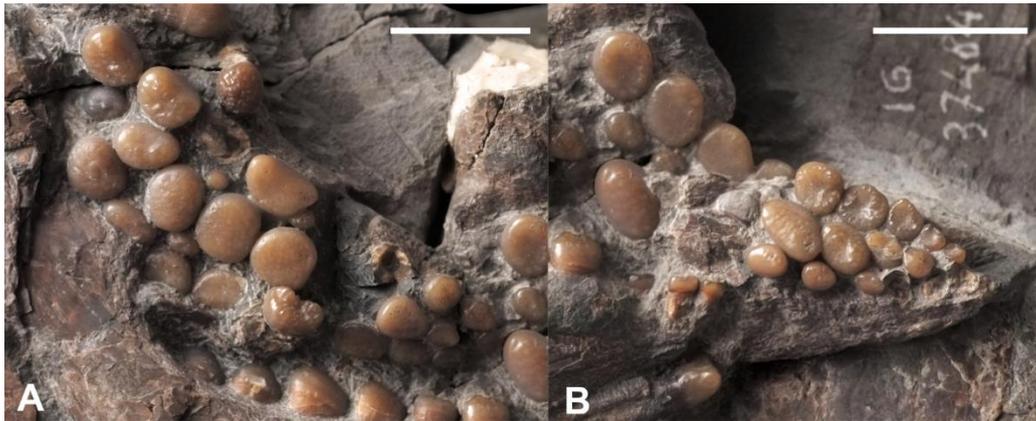


Fig. 8. *Paranursallia gutturosa*. MGCB IG37484. **A.** Detail of the vomerine dentition. **B.** Detail of the prearticular dentition. Scale bars equal 50 mm.

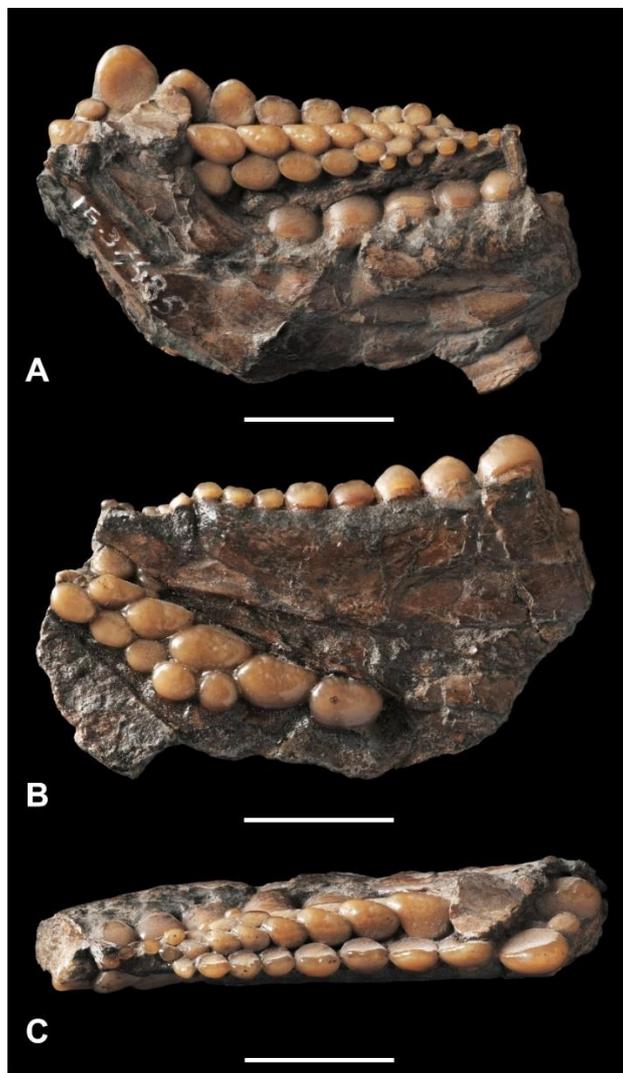


Fig. 9. *Paranursallia gutturosa*. MGCB IG37485. **A.** Right prearticular. **B.** Left prearticular. **C.** Occlusal view of left prearticular dentition. Scale bars equal 50 mm.

Family Pycnodontidae Agassiz, 1833 (*sensu* Nursall, 1996a)

Subfamily Nursalliinae Poyato-Ariza and Wenz, 2002

Genus *Paranursallia* Taverne et al., 2015

Paranursallia gutturossa (Arambourg, 1954)

Fig. 6-10

- 1976 *Paleobalistum* cfr. *gutturosum* Arambourg, 1954 - Sorbini, p. 484, pl. 7-8.
1980 *Paleobalistum* cfr. *gutturosum* - Sorbini, p. 119, text-fig. p. 119.
1987 *Nursallia gutturossum* - Blot, p. 200.
1990 *Paleobalistum* cfr. *gutturosum* Arambourg - Astolfi and Colombara, p. 146, fig. 209.
1990 *Paleobalistum* - Bizzarini and Coccioni, p. 79.
1994 *Paleobalistum* cf. *gutturosum* - Sirna et al., p. 271.
2005 *Nursallia?* *gutturosum* - Dalla Vecchia et al., p. 106.
2007 *Nursallia gutturossum* (Arambourg 1954) - Capasso, p. 190, fig., 2.
2010 *Nursallia gutturossum* - Khalloufi, p. 48.
2015 *Paranursallia gutturossa* - Taverne et al., p. 226.

Referred material. MGCB IG37484, MGCB IG37485; MCSNVE 24521, 24556.

Locality. Bomba Quarry (Cinto Euganeo, Euganei Hills, Padova).

Description and remarks. The specimen MGCB IG37484 (Fig. 6-8) consists of fragmentary remains of the head of a single adult individual. The oral region and dentitions are only partially articulated. Only a few elements are easily recognizable (see Fig. 7 for details). The recognizable bones include mostly elements of the right side of the head: a styliform (possibly right) premaxillary, a wide subtriangular right dermohyomandibular, an expanded subrectangular right preopercle, a reduced right opercle, the vomer, left and right prearticulars, the dentaries, the right articular, a fragmentary cleithrum (possibly the right one). Other remains include fragments of the scales and additional unidentifiable bones. The reduced opercle, vomerine teeth and prearticulars arranged in rows allow to refer the specimen to the Pycnodontiformes (see Poyato-Ariza and Wenz, 2002). The presence of a dermohyomandibular (hyomandibula *sensu* Kriwet, 2005) allow to include it in Pycnodontoidea (*sensu* Poyato-Ariza and Wenz, 2002). The combination of characters listed herein allows to refer the specimen to *Paranursallia gutturossa* (see Poyato-Ariza and Wenz, 2002), including: premaxillary and dentary teeth two for each bone, robust, barely incisiform, with a simple crown; vomerine teeth with a circular to subcircular contour and arranged in regular rows; five vomerine tooth rows; teeth of the main vomerine row form a series of regularly increasing size backward, with no alternation pattern; seven teeth in the principal vomerine tooth row; dentary small, posteriorly elongated and

simple; prearticular teeth with an oval contour and arranged in three regular rows, with regularly increasing size caudally; nine teeth on main prearticular tooth row; coronoid process of the prearticular with high and straight dorsal border.

The vomerine and prearticular teeth are slightly ornamented (Fig. 8). The occlusal surface of the outer vomerine and prearticular teeth is slightly concave with coarsely serrated edges; the central vomerine teeth show coarse granulations covering the occlusal surface as well as the serrated edges.

The specimen MGCB IG37485 (Fig. 9) comprises two prearticulars (left and right) of a single individual. The bones are slightly disarticulated. The prearticular dentition exhibits the same characters of the previous specimens (prearticular teeth with oval contour and arranged in three regular rows, with regularly increasing size caudally; nine teeth on main prearticular tooth row), allowing its assignment to the same species.

MCSNVE 24521 solely consists of scattered and fragmentary cranial remains and teeth with circular to subcircular contour arranged in two partial rows. This specimen is tentatively referred to *Paranursallia gutturosa* based on dental morphology.

MCSNVE 24556 (Fig. 10) represents only a portion of postcranial remains of a large pycnodontiform. The squamation is peltate (forming with the haemal spines the typical pycnodontiform crossed pattern). Neural and haemal arcocentra in the vertebral column contact each other surrounding the notochord such as in *Paranursallia gutturosa* and other Nursallinae (see Poyato-Ariza and Wenz, 2002: p. 179). Adjacent arcocentra have hyper-complex contact. This character is typical of *Nursallia* and *Paranursallia* (see Poyato-Ariza and Wenz, 2002; Capasso et al., 2009; Taverne et al., 2015). Anterior sagittal flanges are preserved on certain neural spines. There are also remains of pelvic fin rays and pterygiophores and probably of the supracleitrum. The specimen is so far the largest pycnodontiform taxon so far reported from Bonarelli Level of NE Italy.



Fig. 10. *Paranursallia gutturossa*. MCSNVE 24556. Scale bars equal 50 mm.

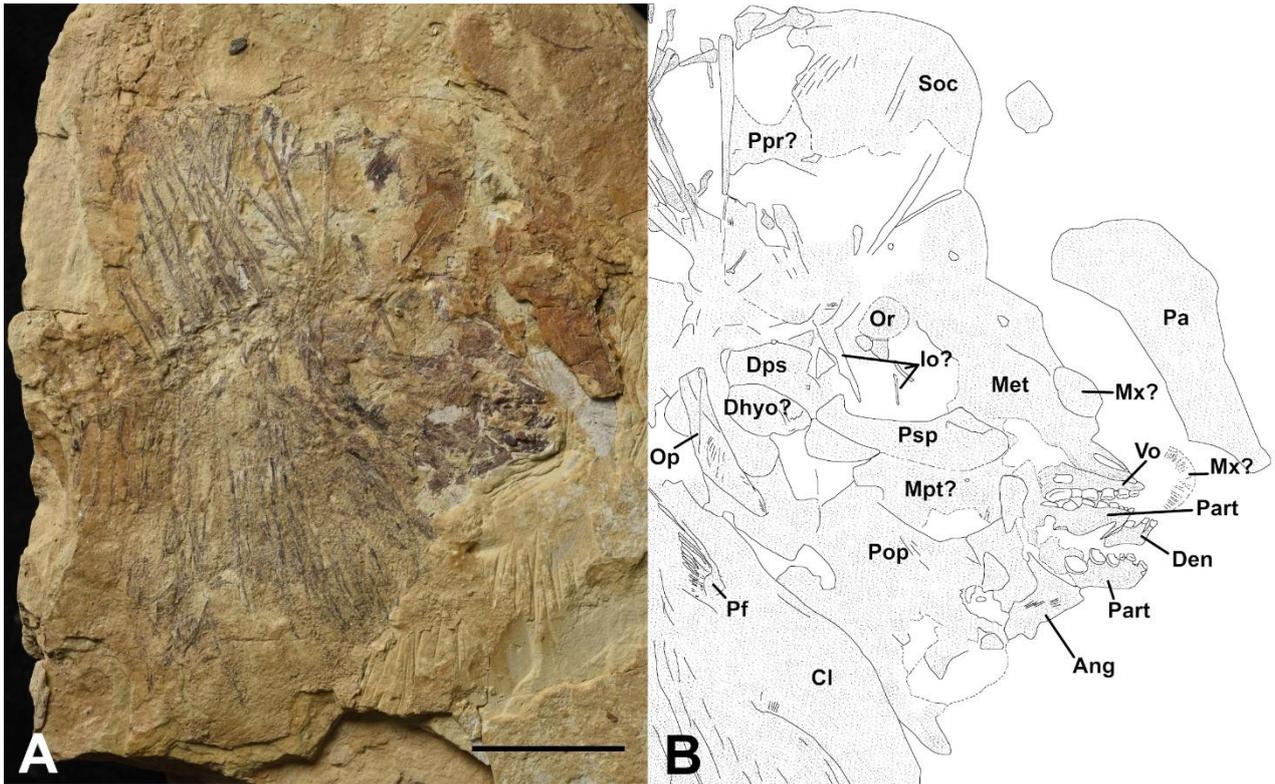


Fig. 11. *'Nursallia' tethysensis*. MGPPD 32093. **A.** The specimen. Scale bar equals 10 mm. **B.** Schematic drawing with bones identification. Dashed lines indicate lacking portions or undefined borders. Abbreviations: **Ang**: angular; **Cl**: cleithrum; **Den**: dentary; **Dhyo**: dermohyomandibula; **Dps**: dermosphenotic; **Io**: infraorbitals; **Met**: mesethmoid; **Mpt**: metapterigoid; **Mx**: maxilla; **Op**: opercle; **Or**: orbit; **Pa**: parietal (or frontal); **Part**: prearticular; **Pf**: pectoral fin; **Pop**: preopercle; **Ppr**: postparietal process; **Psp**: parasphenoid; **Soc**: dermal supraoccipital.

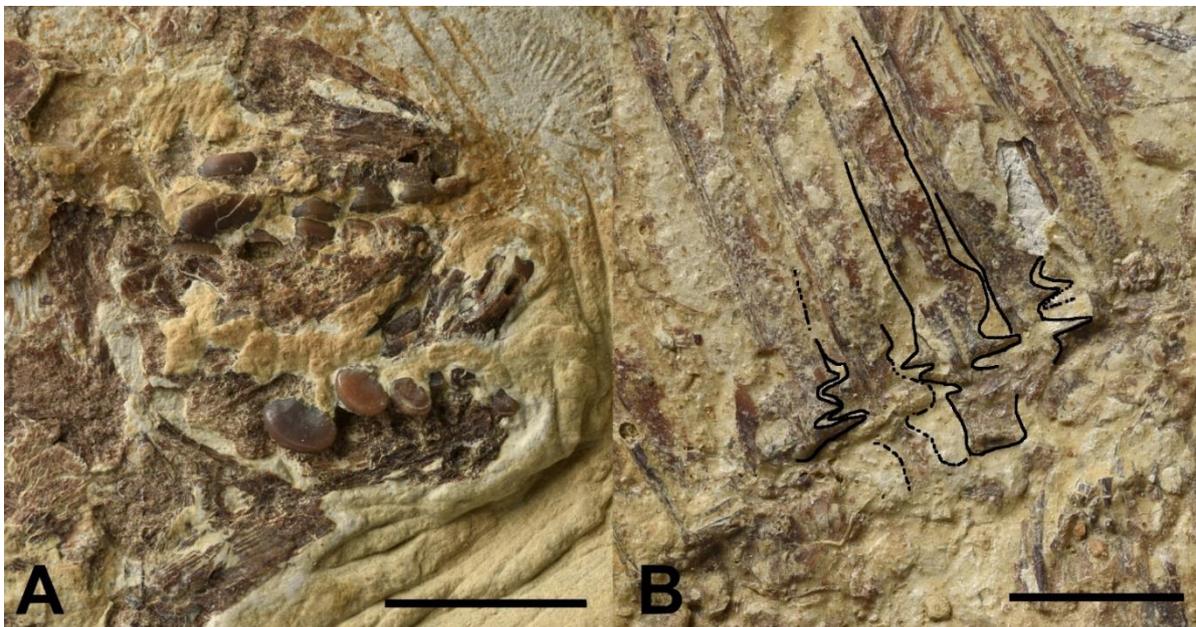


Fig. 12. *'Nursallia' tethysensis*. MGPPD 32093. **A.** detail of the dentition. **B.** detail of the vertebrae, the contour of the vertebral arcocentra and haemal spines are remarked in black to evidence the hyper-complex contact of adjacent arcocentra. Dashed lines indicate lacking portions or undefined borders. Scale bars equal 5 mm.

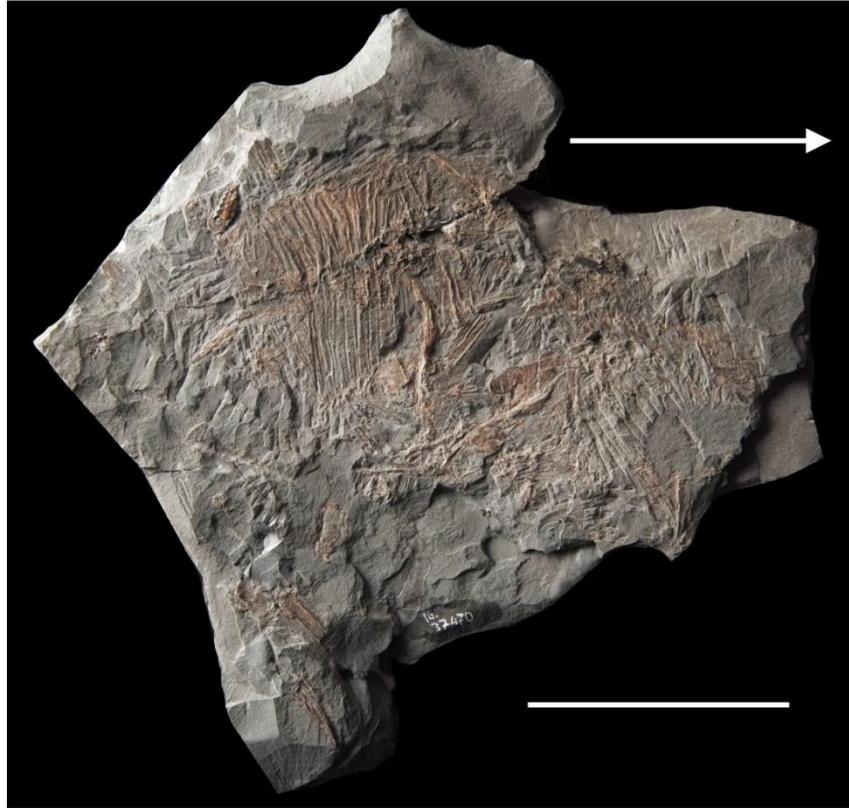


Fig. 13. '*Nursallia*' *tethysensis*. MGCB IG37470. The arrow indicates the alleged anterior part of the specimen. Scale bar equals 50 mm.

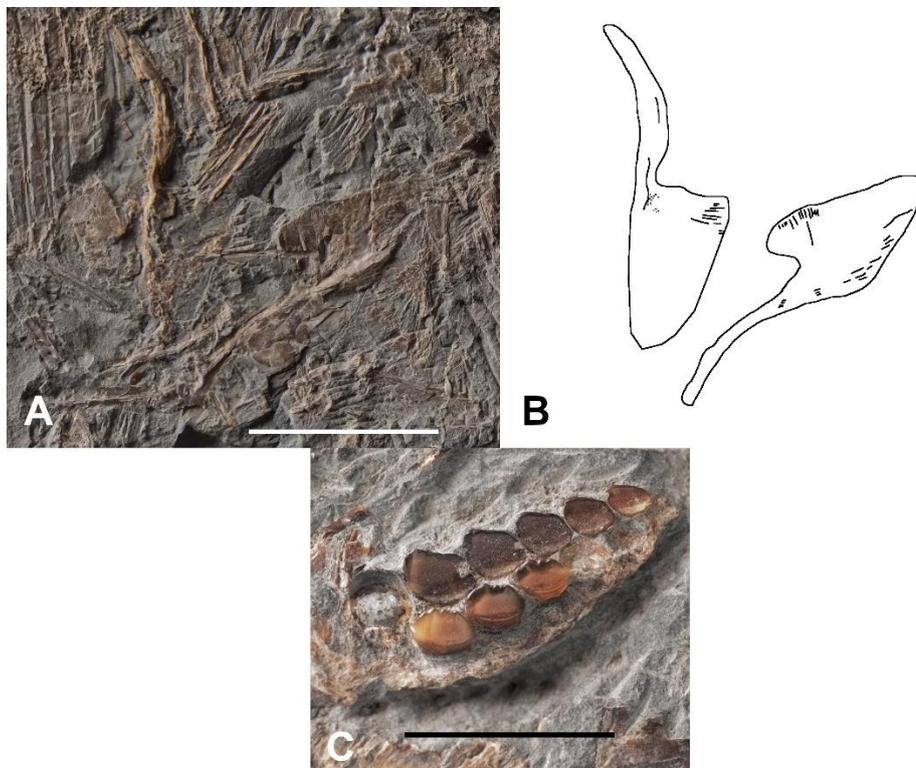


Fig. 14. '*Nursallia*' *tethysensis*. MGCB IG37470. **A.** Detail of the specimen with the cleithra. **B.** Line drawing to remark their contour and position. Scale bars equal 20 mm. **C.** Detail of the prearticular dentition. Scale bar equals 5 mm.

Genus *Nursallia* Blot, 1987

'Nursallia' tethysensis Capasso et al., 2009

Fig. 11-14

- 1976 *Coelodus* cfr. *saturnus* Heckel, 1856 - Sorbini, p. 483, pl. 6, 12.
1980 *Coelodus* cfr. *saturnus* - Sorbini, p. 119.
1990 *Coelodus* cfr. *saturnus* Heckel - Astolfi and Colombara, p. 146, fig. 208.
1994 *Coelodus* cf. *saturnus* - Sirna et al., p. 271.
2002 *Coelodus* - Gomez et al. 2002, p. 672.
2005 *Coelodus* cf. *C. saturnus* - Dalla Vecchia et al., p. 106.
2010 *Coelodus* cfr. *saturnus* - Khalloufi, p. 48.

Referred material. MGCB IG37470, MGPPD 32093.

Locality. Bomba Quarry (Cinto Euganeo, Euganei Hills, Padova), Schievenin Valley (Quero, Belluno).

Description and remarks. Two specimens are referred herein to *'Nursallia' tethysensis*. The specimen MGP-PD 32093 (Fig. 11-12) was collected from the Schievenin Valley (Quero) and is described herein for the first time. It consists of a nearly complete skeleton of a single individual, lacking the caudal portion of the body. The specimen is moderately well-preserved and a series of . characters are clearly recognizable (Fig. 11), including: peltate squamation; head relatively large, with a wide orbit and a short snout; frontal (parietal *sensu* Kriwet, 2005 and Cawley et al., 2018, labelled as Pa in Fig. 11) broad and curved, forming a round profile to the upper surface of the head; apparently not covering the mesethmoid (possible taphonomical biases); crescent-shaped maxilla preserved as impression in front of the vomer; mesethmoid large immediately anterior to the narrow and long parasphenoid. The vomer (Fig. 12) bears five molariform teeth, while the left prearticular bears six molariform teeth (like *'Nursallia' tethysensis*; Capasso et al., 2009). The right prearticular bears only five molariform teeth with a distinct crenulation on the margin of the occlusal surface, as in *'Nursallia' tethysensis* and *Paranursallia gutturosa*. All these teeth regularly increase in size posteriorly. The dentary is small, posteriorly elongate and bears three incisiform teeth with a short apical notch. The right prearticular is immediately anterior to the angular. The preopercle separates the lower jaw from the cleithrum on this specimen, not exhibiting a large V-shaped notch in the ventral profile between the head and the abdomen as in other specimens. This large V-shaped notch is reported in *'Nursallia' tethysensis*, *P. gutturosa* and *P. spinosa* (Capasso et al., 2009; Taverne et al., 2015) but may possibly result from taphonomic bias. The opercle is well-preserved and reduced, as typically found in Pycnodontiformes (Poyato-Ariza and Wenz, 2002). The neural and haemal

arcocentra contact each other surrounding the notochord such as in *Paranursallia gutturosa* and other Nursallinae (see Poyato-Ariza and Wenz, 2002: p. 179). Furthermore, adjacent arcocentra have hyper-complex contact (apparently with at least two prezygapophyses and postzygapophyses, see Fig. 12B). This character is typical of *Nursallia* and *Paranursallia* (see Poyato-Ariza and Wenz, 2002; Capasso et al., 2009; Taverne et al., 2015). Anterior sagittal flanges are preserved on some neural spines. All described characters allow to refer the specimen to '*Nursallia*' *tethysensis*.

The specimen MGCB IG37470 comes from Bomba Quarry (Cinto Euganeo) and includes mainly disarticulated or partially articulated and fragmentary cranial and postcranial elements of a single individual (see Fig. 13-14 for details). The squamation is peltate. A portion of prearticular with molariform teeth arranged in rows and remains of the axial skeleton (arcocentra with ribs, haemal and neural spines) are well recognizable. The portion of the prearticular dentition formed by crushing teeth arranged in rows and the reduced opercle allow to refer the specimen to the Pycnodontiformes (see Poyato-Ariza and Wenz, 2002 and Kriwet et al., 2018). The small portion of right prearticular dentition is in occlusal view and includes the main row and first lateral row, with six teeth and a in the inner main row and five teeth in the outer row (Fig. 14C). The teeth have a trapezoidal to subtriangular contour on occlusal surface in the main inner row and a subcircular contour in the first lateral row. The occlusal surface also exhibits intense wear, with a blunt ridge contouring the most anterior and external teeth becoming a coarse crenulation on the inner margin of the teeth of the first lateral row. The outer row exhibits teeth increasing in size posteriorly, while those of the inner row are similar in size. Furthermore, the posterior teeth of the outer row became larger than those of the inner row. Sorbini (1976) referred these remains coming from Bomba Quarry to *Coelodus* cfr. *saturnus* based on dental characters. However, *Coelodus* teeth are completely different, being extremely elongated in transversal sense (Poyato-Ariza, 2002: p. 175). The crenulations and morphology of teeth recall those of '*Nursallia*' *tethysensis* (Capasso et al., 2009). The number of teeth in the prearticular main row is six (or seven, see Fig. 14), similarly to '*N.*' *tethysensis* (six teeth) and *Paranursallia gutturosa* (seven teeth) (see Capasso et al., 2009; Poyato-Ariza and Wenz, 2002). We tentatively refer the specimen to '*N.*' *tethysensis* based on the extremely similar prearticular dentition. The taxon is currently known only from the Cenomanian of Lebanon (Capasso et al., 2009).



Fig. 15. *Protosphyraena ferox*. Specimen MGCB IG37527. Scale bar equals 50 mm.

Subdivision Teleostei Müller, 1846 (*sensu* Patterson and Rosen, 1977)

Order Pachycormiformes Berg, 1940

Family Pachycormidae Woodward, 1895

Genus *Protosphyraena* Leidy, 1857

Protosphyraena ferox Leidy, 1857

Fig. 15

1922 *Protosphyraena* sp. - D'Erasmus, p. 62; pl. 6, fig. 17.

1976 *Protosphyraena ferox* Leidy 1856 - Sorbini, p. 485, pl. 9.

1980 *Protosphyraena ferox* - Sorbini, p. 119, text-fig without number p. 121.

1994 *Protosphyraena ferox* - Sirna et al., p. 271.

2005 *Protosphyraena ferox* - Dalla Vecchia et al., p. 106.

2010 *Protosphyraena* - Khalloufi, p. 48.

2017 *Protosphyraena ferox* Leidy, 1857 - Amalfitano et al., p. 477 (*errata corrige*), fig. 3-6.

Referred material. MGCB IG37527.

Locality. Bomba Quarry (Cinto Euganeo, Euganei Hills, Padova).

Remarks. A single specimen was found and referred to this taxon (Fig. 15). It consists of the proximal portion of a pectoral fin associated to the bones of the pectoral girdle. The specimen was originally reported by Sorbini (1976) and recently redescribed by Amalfitano et al. (2017).

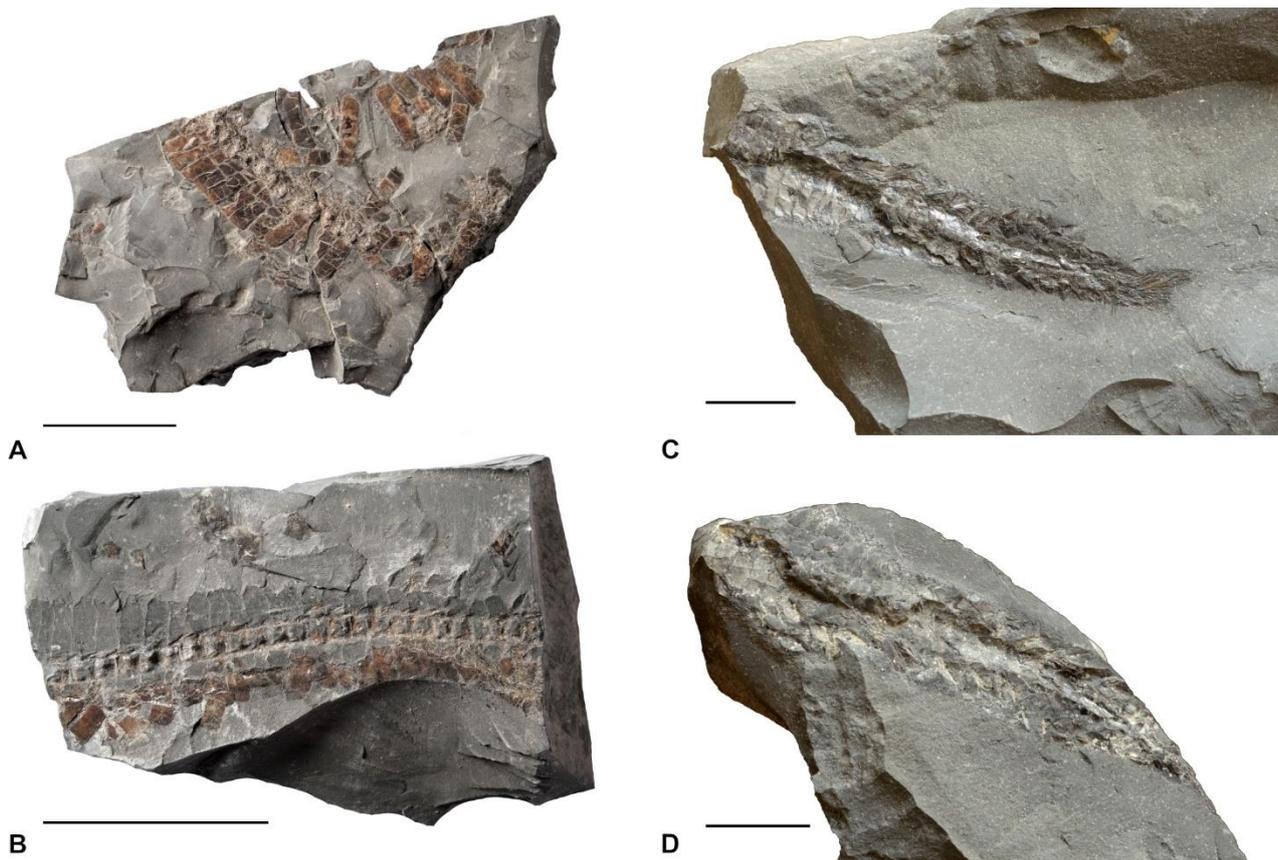


Fig. 16. *Belonostomus*. **A-B.** *Belonostomus* sp. (A) MCV 10/25; (B) MCV 10/26. Scale bars equal 50 mm. **C-D.** *Belonostomus* sp. 2 *sensu* Forey et al. (2003). Specimen MCSNVE V 25515: part (C) and counterpart (D). Scale bars equal 20 mm.

Subdivision Teleostei Müller, 1846 (*sensu* Patterson and Rosen, 1977)

Family Aspidorhynchidae Nicholson and Lydekker, 1889

Genus *Belonostomus* Agassiz, 1834b

Remarks. The greatly elongated and long-snouted fishes with very deep lateral-line scales unquestionably support the assignment of the aspidorhynchiforms of the Bonarelli Level to the genus *Belonostomus* (see Brito, 1997; Forey et al., 2003: tb. 2). Despite the specimens described herein consist of a few fragmentary remains, at least three species-level taxa can be recognized. Remains of the genus *Belonostomus* were reported from the Bonarelli Level by Bassani (1880, 1882), who described material collected from outcrops in the vicinity of the village of Crespano del Grappa (Treviso), very close (ca. 2,5 km) to Carcoselle Quarry.

***Belonostomus* sp.**

Fig. 16A-B

1880 *Belonostomus* Agassiz - Bassani, p. 153.
1882 *Belonostomus* cfr. *lesinensis* - Bassani, p. 72, pl. 11, fig. 1.
1922 *Belonostomus* sp. - D'Erasmus, p. 64.
1994 *Protosphyraena ferox* - Sirna et al., p. 273.

Referred material. MCV 10/25-10/26.

Locality. Schio-Valdagno Tunnel (Valdagno, Vicenza).

Description and remarks. The specimen is poorly preserved and largely incomplete consisting of part of the trunk. showing a portion of the vertebral column and the overlying squamation with the scales partially articulated or scattered or even preserved as impression only. The lateral-line scales are deeper than the adjacent scales thereby supporting the attribution to the genus *Belonostomus*.

***Belonostomus cinctus* Agassiz, 1837**

Fig. 17-18

Referred material. MCSNVE V 24519a-b.

Provenance locality. Carcoselle Quarry (Possagno, Treviso).

Description and remarks. The specimen, in part and counterpart (Fig. 16A-B), is largely incomplete and consists of the head and anterior portion of the trunk. The head lacks the distal portion of prementaries and premaxillae. The prementary has needle-like teeth marked by fine striations and fluted bases (Fig. 17A-B); prementary teeth are much longer than premaxillary teeth. The morphology of the prementary teeth support the alignment of the specimen described herein with the species *B. cinctus*, up to date known exclusively from the Turonian of England (see Forey et al., 2003).

***Belonostomus* sp.**

Fig. 16C-D, 19

Referred material. MCSNVE V 25515a-b.

Locality. Carcoselle Quarry (Possagno, Treviso).

Description and remarks. This largely incomplete specimen, in part and counterpart, consists of the caudal and posterior portion of the trunk. The caudal fin is poorly preserved, solely represented by its proximal part. The most relevant feature of this specimen is the curved prominent ridge, terminating into a spiny posterior process, of the dorsal scutes immediately anterior to the tail (see Fig. 18). This character is diagnostic of the species-level taxon *Belonostomus* sp. 2 described by Forey et al. (2003: p. 243, fig. 13-15) from Namoura (Lebanon). This shape of the dorsal scutes has also reported in a

single specimen from Komen (Slovenia) referred to *Belonostomus lesinaensis* by D'Erasmus (1946: fig. 9). *Belonostomus lesinaensis* has been considered as a junior synonym of *B. crassirostris* by Brito (1997) and Forey et al. (2003).



Fig. 17. *Belonostomus cinctus*. MCSNVE V 24519. Part (A) and counterpart (B). Scale bars equal 50 mm.

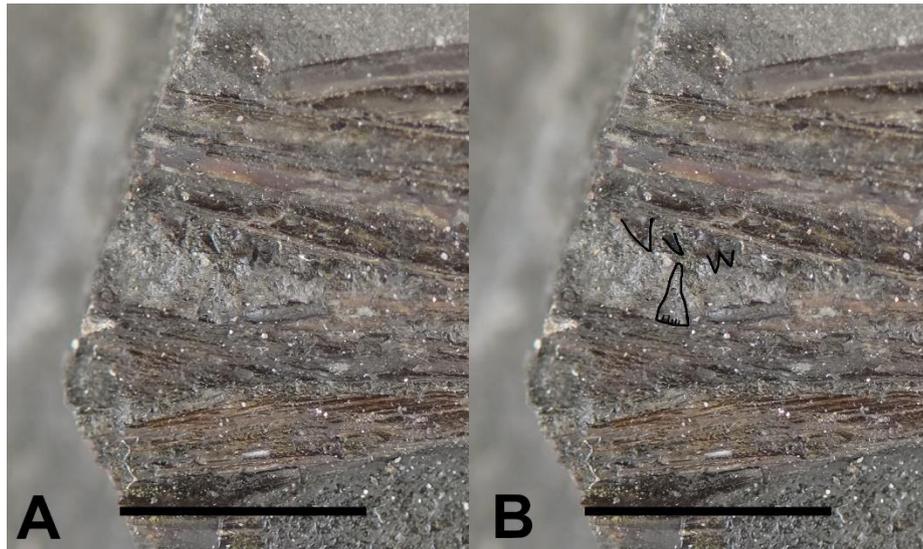


Fig. 18. *Belonostomus cinctus*. MCSNVE V 24519. **A.** Detail of the teeth. **B.** Detail with the contour remarked in black to evidence the different size of teeth and fluted base of the larger teeth. Scale bars equal 5 mm.

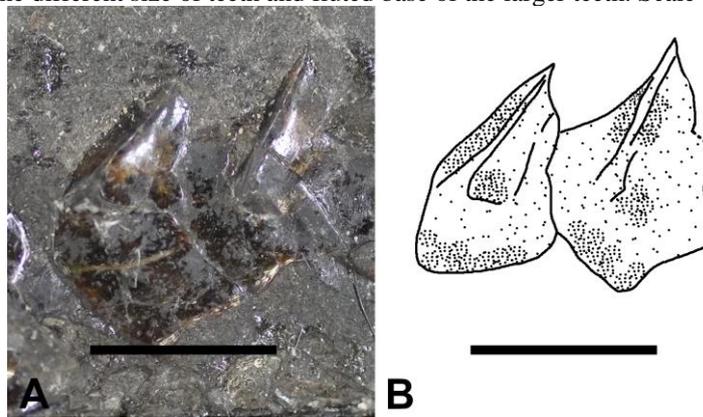


Fig. 19. *Belonostomus* sp. MCSNVE V 25515, detail of the scales (**A**) and line drawing (**B**). Dashed lines indicate lacking portions or undefined borders. Scale bars equal 20 mm.

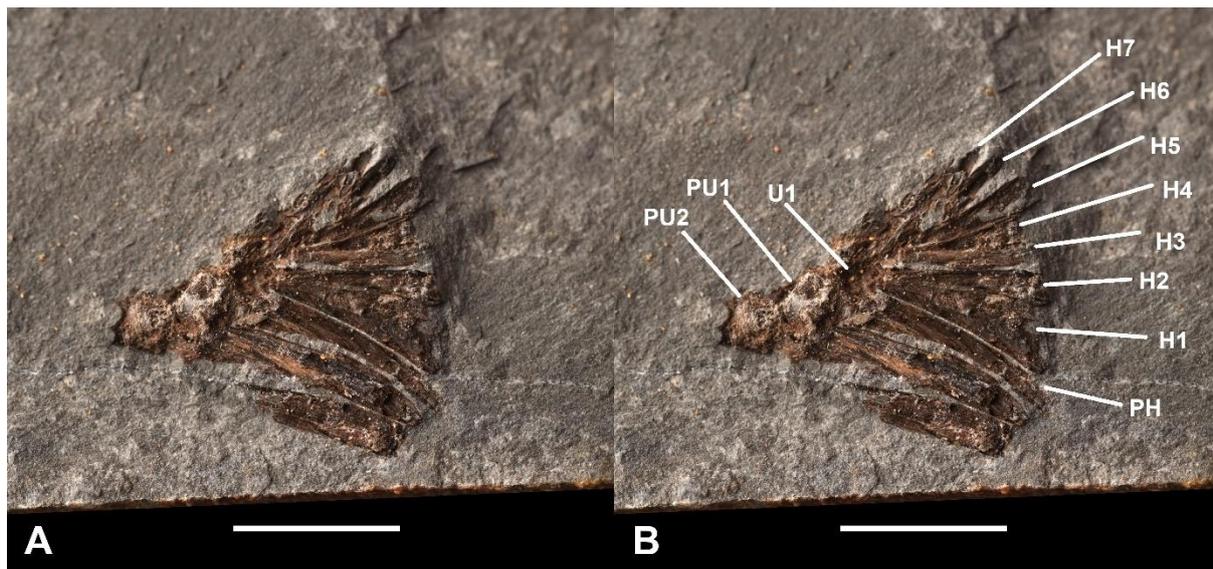


Fig. 20. Ichthyodectoidei indet. MGCB U3/5. **A.** Detail of the specimen. **B.** Bones identification. Abbreviations: **H**: hypural; **U**: ural vertebra; **PH**: parhypural; **PU**: preural vertebra. Scale bars equal 5 mm.

Order Ichthyodectiformes Bardack and Sprinkle, 1969

Suborder Ichthyodectoidei Romer, 1966

Ichthyodectoidei indet.

Fig. 20

Referred material. MGCB U3/5.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The specimen referred herein to an indeterminate ichthyodectoid is solely represented by an isolated caudal skeleton in part and counterpart (Fig. 20). The first hypural articulates with the ural centrum through a ball-and-socket joint (see Patterson and Rosen, 1977 and Cavin et al., 2013) and the second hypural is smaller compared to the first one. The ball-and-socket articulation between the first hypural and the ural centrum and the reduction of the second hypural compared to the first one are typical of the Cretaceous ichthyodectiforms (Cavin et al., 2013). The incompleteness and inadequate preservation of specimen does not allow a more detailed identification.

Family Ichthyodectidae Crook, 1892 (*sensu* Patterson and Rosen, 1977)

Genus *Heckelichthys* Taverne, 2008

***Heckelichthys vexillifer* (Heckel, 1856)**

Fig. 21-23

1976 *Thrissops microdon* (Heckel) 1850 - Sorbini, p. 486, fig. 1, pl. 5.

1980 *Thrissops microdon* - Sorbini, p. 119.

1990 *Thrissops microdon* (Heckel) - Astolfi and Colombara, p. 146.

1994 *Thrissops microdon* Heckel, 1849 - Sirna et al., p. 271, 273.

2005 *Thrissops microdon* - Dalla Vecchia et al., p. 106.

2008 *Ch. vexillifer* (erroneously *Ch. microdon*) - Taverne, p. 211.

2010 *Heckelichthys microdon* - Khalloufi, p. 48.

Referred material. MCSNVR IG37486-MGCB IG37487;MCSNVR 37488-37489, 37551.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

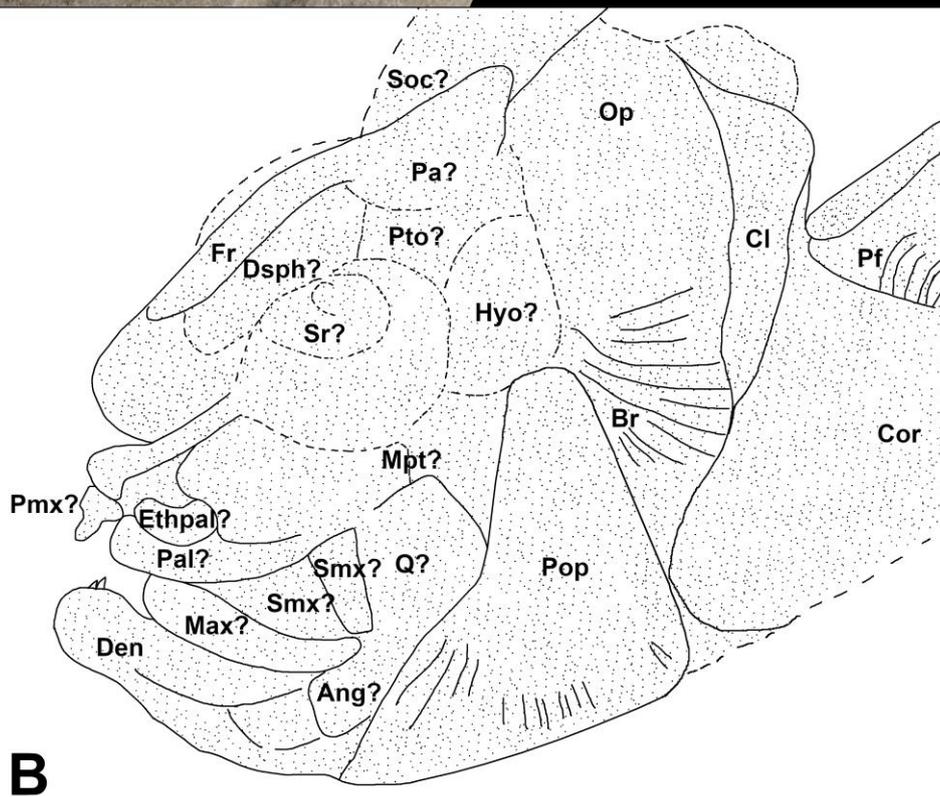


Fig. 21. *Heckelichthys vexillifer*. MCSNVR IG37486. **A.** Photo of the specimen. Scale bar equals 20 mm. **B.** Interpretative drawing with bones identification. Dashed lines indicate lacking portions or undefined borders. Abbreviations: **Ang**: angular; **Br**: branchiostegal rays; **Cl**: cleithrum; **Cor**: coracoid; **Den**: dentary; **Dsph**: dermosphenotic; **Ethpal**: ethmopalatine; **Fr**: frontal; **Hyo**: hyomandibula; **Max**: maxilla; **Op**: opercle; **Pa**: parietal; **Pal**: palatine bone; **Pf**: pectoral fin; **Pmx**: premaxilla; **Pop**: preopercle; **Pto**: pterotic; **Q**: **Smx**: supramaxilla.; **Soc**: supraoccipital.



Fig. 22. *Heckelichthys vexillifer*. MCSNVR IG37489. Scale bar equals 20 mm. Abbreviations: **Ang**: angular; **Br**: branchiostegal rays; **Cl**: cleithrum; **Cor**: coracoid; **Den**: dentary; **Dsph**: dermosphenotic; **Ethpal**: ethmopalatine; **Fr**: frontal; **Hyo**: hyomandibula; **Max**: maxilla; **Op**: operculum; **Pa**: parietal; **Pal**: palatine bone; **Pf**: pectoral fin; **Pmx**: premaxilla; **Pop**: preopercle; **Pto**: pterotic; **Q**: **Smx**: supramaxilla.; **Soc**: supraoccipital.

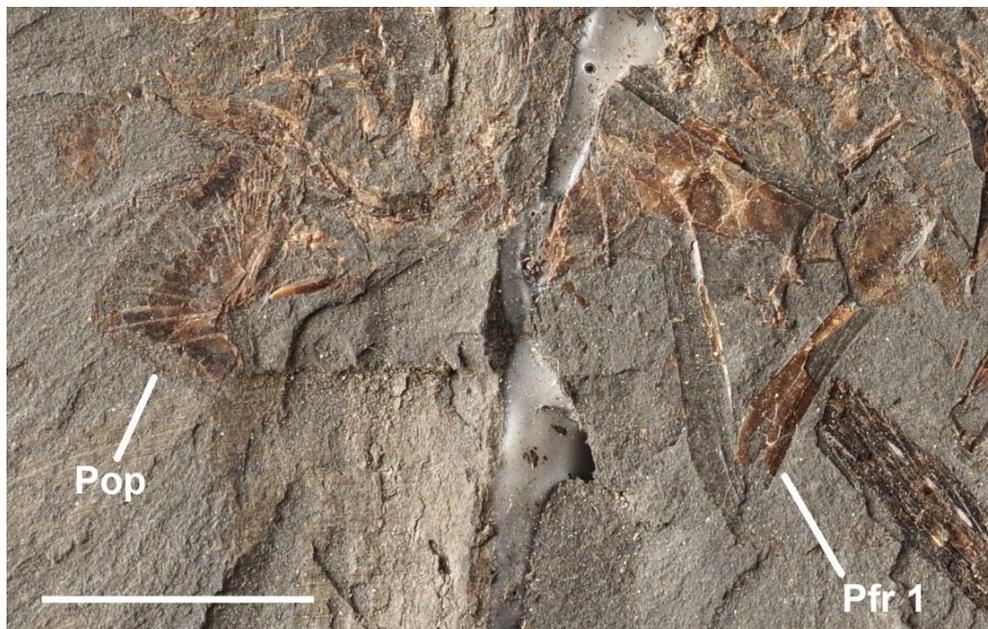


Fig. 23. *Heckelichthys vexillifer*. MCSNVR IG37489. Detail of the remains. Abbreviations: **Pfr 1**: First pectoral-fin ray; **Pop**: preopercle.

Description and remarks. The specimens were formerly described by Sorbini (1976, 1980) and referred to *Thrissops microdon* and subsequently assigned to the genus *Heckelichthys* by Taverne (2008). MCSNVR IGVR 37486-MGCB IG 37487 (Fig. 21) is represented by the head and pectoral girdle and fin of a single individual, in part and counterpart of the head (HL 39 mm; HD 30 mm). The ventrally expanded coracoid is diagnostic for the Ichthyodectiformes (Patterson and Rosen, 1977). The head is longer than deep, with a slightly concave anterior profile. The maxilla is slightly curved. The lower jaw is short, with a moderately deep symphyseal border. The lower jaw joint is located just before the posterior border of the orbit. The mandibular sensory canal is not located into a groove. Teeth are not recognizable. The horizontal arm of the preopercle is longer and larger than the vertical branch. The ventrally expanded coracoid is clearly indicative of the Ichthyodectiformes (Patterson and Rosen, 1977). There are 10 pectoral-fin rays and the first one is thicker and widens distally into a paddle-like expansion with a pointed distal extremity. The overall morphology of the head skeleton and the paddle-like expansion of the first pectoral-fin ray are consistent with those of *Heckelichthys vexillifer* (see Arambourg, 1954; Taverne, 2008; Cavin et al., 2013).

The specimen MCSNVR IG37488-37489, also in part and counterpart, is represented by scattered bones and scales (Fig. 22). The morphology of the preopercle (ventral and dorsal arms ratio) and the paddle-like first pectoral-fin ray (Fig. 23) concur to support its attribution to *Heckelichthys vexillifer*. The specimen IGVR 37551 represents an isolated preopercular that exhibit the same morphology of the specimen above mentioned, thus can be referred to the same taxon.

Superorder Elopomorpha Greenwood et al., 1966

Order Elopiformes Greenwood et al., 1966

?Elopiformes indet.

Fig. 24A

1976 *Protelops* sp. - Sorbini, p. 493, fig. 5, pl. 13.

1980 *Protelops* sp. - Sorbini, p. 119.

1990 *Protelops* sp. - Astolfi and Colombara, p. 147.

1994 *Protelops* sp. - Sirna et al., p. 271.

2005 *Protelops* sp. - Dalla Vecchia, p. 106.

2010 *Protelops* sp. - Khalloufi, p. 48.

Referred material. MCSNVR IG37502.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The specimen is represented by an isolated robust lower jaw with dentition restricted to its anterior portion (Fig. 24A). The teeth, preserved as impressions only, are thin and are densely packed, showing a pattern which is in some way reminiscent of the dentition of some elopiformes, to which the specimen is provisionally referred (see Forey, 1973).

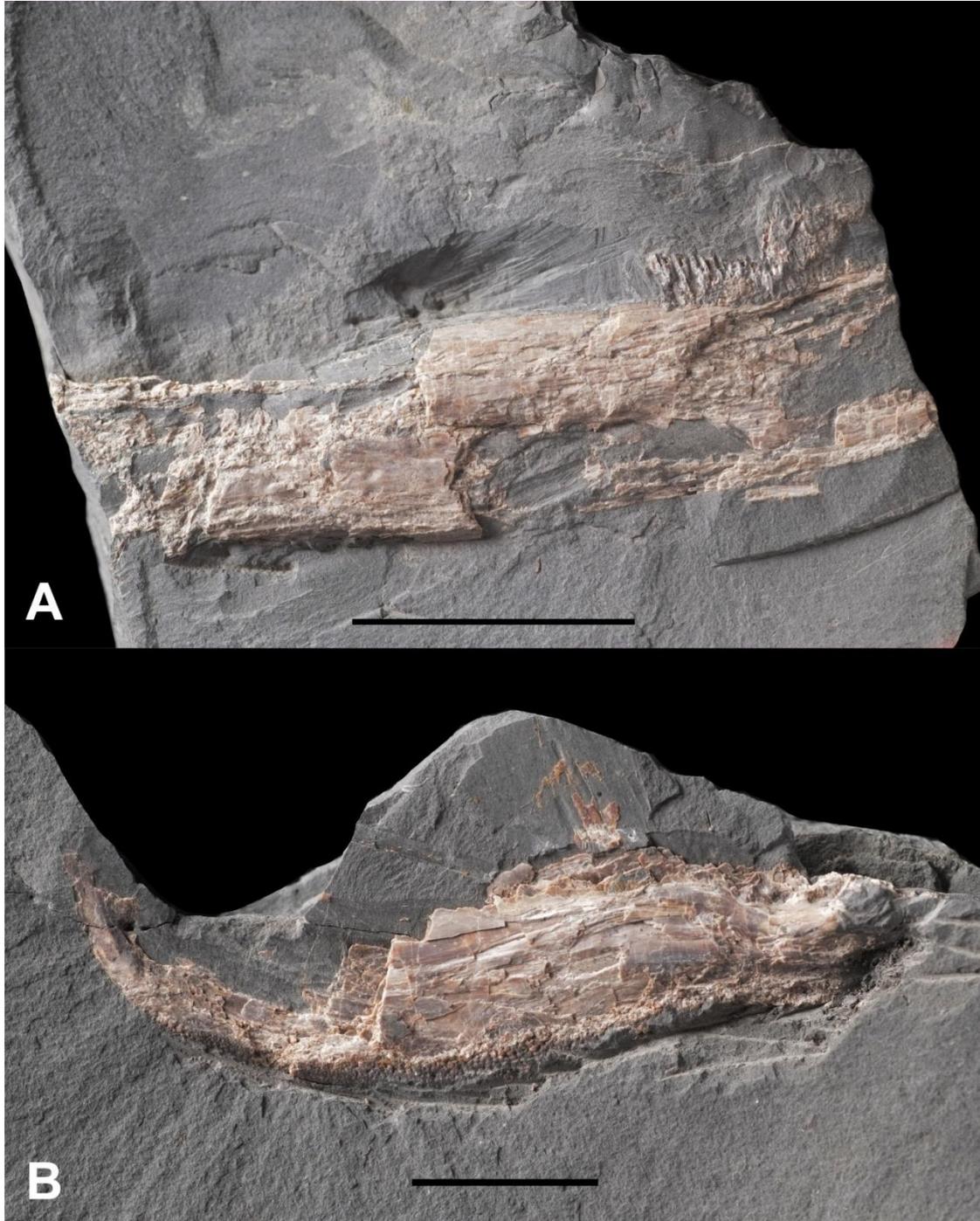


Fig. 24. Elopiformes. **A.** ?Elopiformes indet. MCSNVR IG37502. Scale bar equals 20 mm. **B.** *Davichthys lacostei*, MGCB IG37529. Scale bar equals 10 mm.

Genus *Davichthys* Forey, 1973

Davichthys lacostei (Arambourg, 1954)

Fig. 24B

- 1976 *Holcolepis* sp. - Sorbini, p. 502, fig. 11, pl. 19.
1980 *Holcolepis* sp. - Sorbini, p. 119.
1990 *Holcolepis* sp. - Astolfi and Colombara, p. 148.
1994 *Holcolepis* sp. - Sirna et al., p. 271.
2010 ?*Davichthys* sp. - Khalloufi, p. 48.

Referred material. MCSNVR IG37528-37529.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The single available specimen, in part and counterpart, consists of a partially preserved upper jaw (Fig. 24B). The maxilla has a distinctly convex ventral margin. The maxilla is also characterized by a band of tiny and pointed teeth arranged in rows or in a plate-like fashion. Both the supramaxillae are large and rounded in outline. The upper jaw bones are fully consistent with those of *Davichthys lacostei* (see Arambourg 1954; Forey 1973; Khalloufi, 2010). In his description of this specimen, Sorbini (1976) referred it to *Holcolepis* sp. due to its similarity to *H.* (= *Davichthys*) *lacostei* from Jebel Tselfat (Arambourg, 1954), although the species was assigned to the genus *Davichthys* by Forey (1973).

Order Crossognathiformes Taverne, 1989 (*sensu* Arratia, 2008)

Suborder Pachyrhizodontoidei Forey, 1977 (*sensu* Cavin, 2001)

Family Pachyrhizodontidae Cope, 1872 (*sensu* Cavin, 2001)

Taxonomic remarks. The extinct family Pachyrhizodontidae comprises twelve genera, including *Rhacolepis*, *Pachyrhizodus*, *Elopopsis*, *Greenwoodella*, *Platinx*, *Goulmimichthys*, *Tingitanichthys*, *Michin*, *Nardopiscis*, *Aquilopiscis*, *Apricenapiscis*, *Motlayoichthys* (see Arratia et al., 2018). A revision of the limits and composition of the group formed by the genera *Rhacolepis*, *Pachyrhizodus*, and *Goulmimichthys* is in need of a revision (see Cavin, 2008). Although relatively common in the mid-Cretaceous fossil record, pachyrhizodontid fishes appear to be absent from the very rich Lebanese assemblages (Cavin, 2008), but re-examination of private collections recently evidenced the presence of Lebanese pachyrhizodontid specimens (Gayet et al., 2012).

Genus *Pachyrhizodus* Dixon, 1850

***Pachyrhizodus* indet.**

Fig. 25-30

1976 Pachyrhizodontidae - Sorbini, p. 500, fig. 10, pl. 17-18.

1987 *Pachyrhizodus* sp. - Taverne, fig. 4-5.

1990 *Pachyrhizodus* - Bizzarini and Coccioni, p. 79.

1990 Pachyrhizodontidae - Astolfi and Colombara, fig. 212.

2005 *Pachyrhizodus* sp. - Dalla Vecchia et al., p. 106-107.

2007 *Pachyrhizodus* sp. - Capasso, p. 189.

Referred material. MCSNVR IG37530-37536; MGCB IG37545-37546, U3/1-U3/4; MCR 6136; MCV IG292958; MGPPD 32092; MCSNVE 24517, 24518, 24546, 24554, 24557, 24559, 24581, 24582, 24583.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

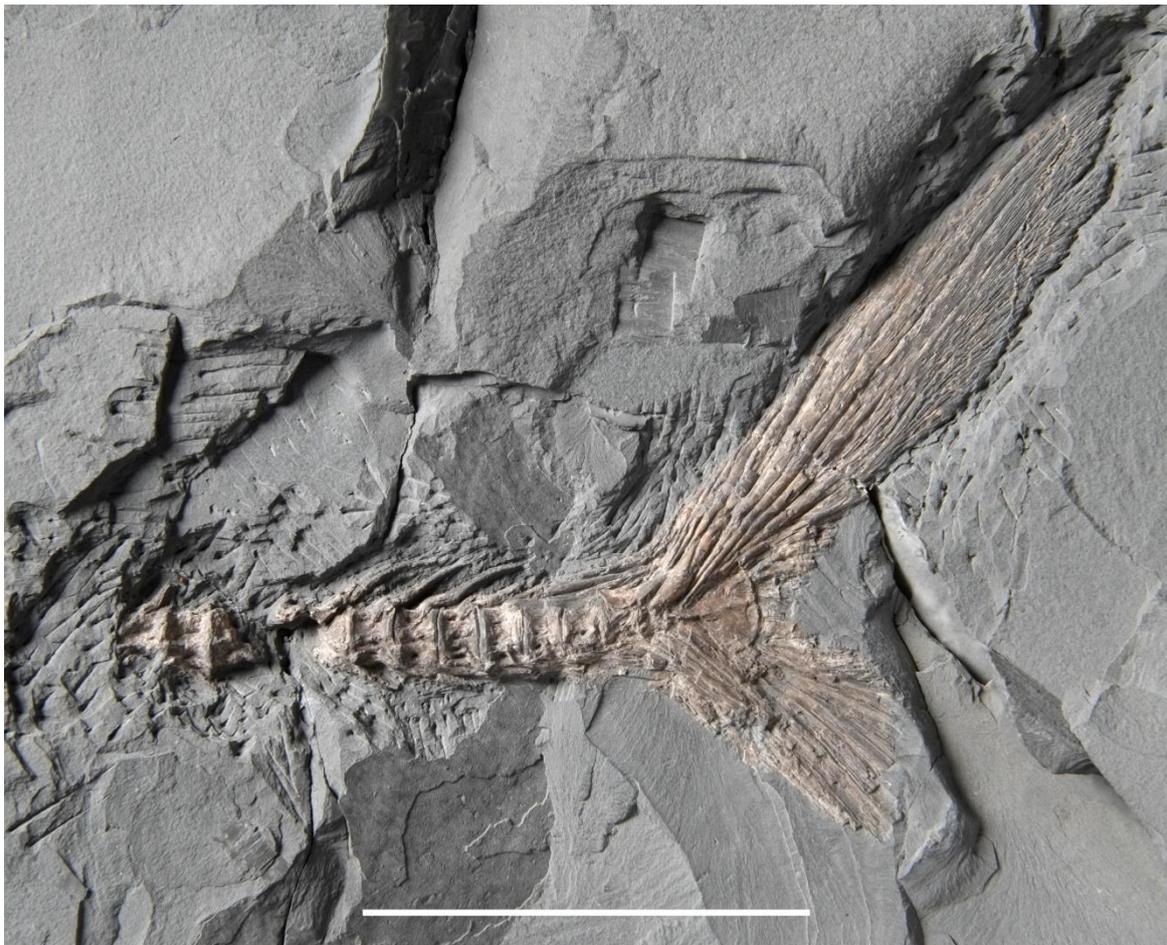


Fig. 25. *Pachyrhizodus* indet. MGCB IG37545. Scale bar equals 50 mm.

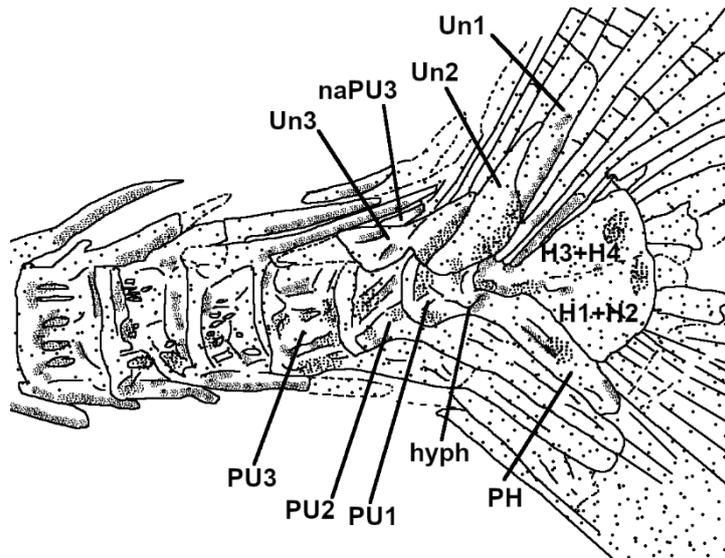


Fig. 26. *Pachyrhizodus* indet. MGCB IG37545. Schematic drawing with bones identification. Dashed lines indicate lacking portions or undefined borders. Abbreviations: **H**: hypural; **hyph**: hypuropahysis; **PH**: parhypural; **PU**: preural vertebra; **naPU**: neurapophysis of the preural vertebra; **Un**: uroneural.

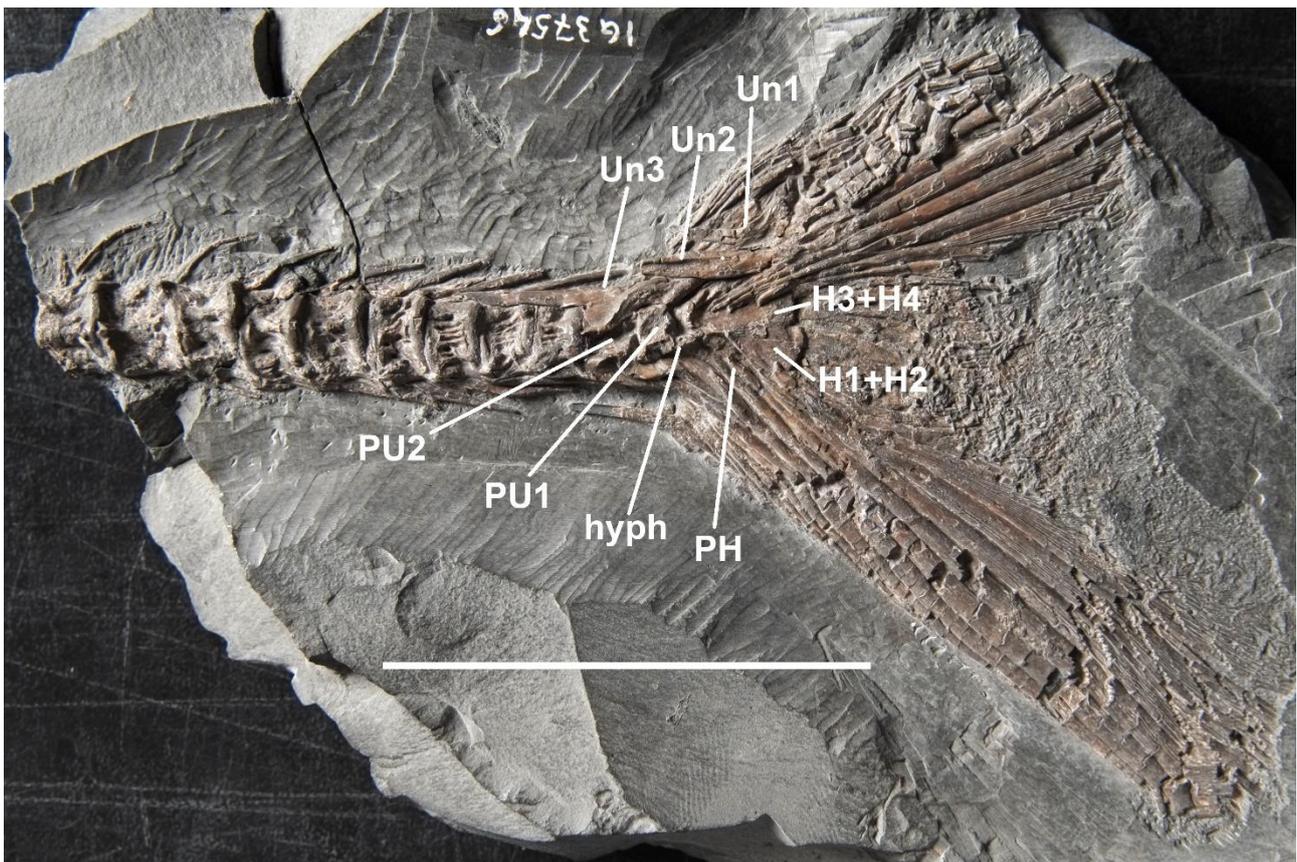


Fig. 27. *Pachyrhizodus* indet. MGCB IG37546. Photo of the specimen with bones identification. Abbreviations: **H**: hypural; **hyph**: hypuropahysis; **PH**: parhypural; **PU**: preural vertebra; **Un**: uroneural. Scale bar equals 50 mm.



Fig. 28. *Pachyrhizodus* indet. MCR 6136. Scale bar equals 50 mm.

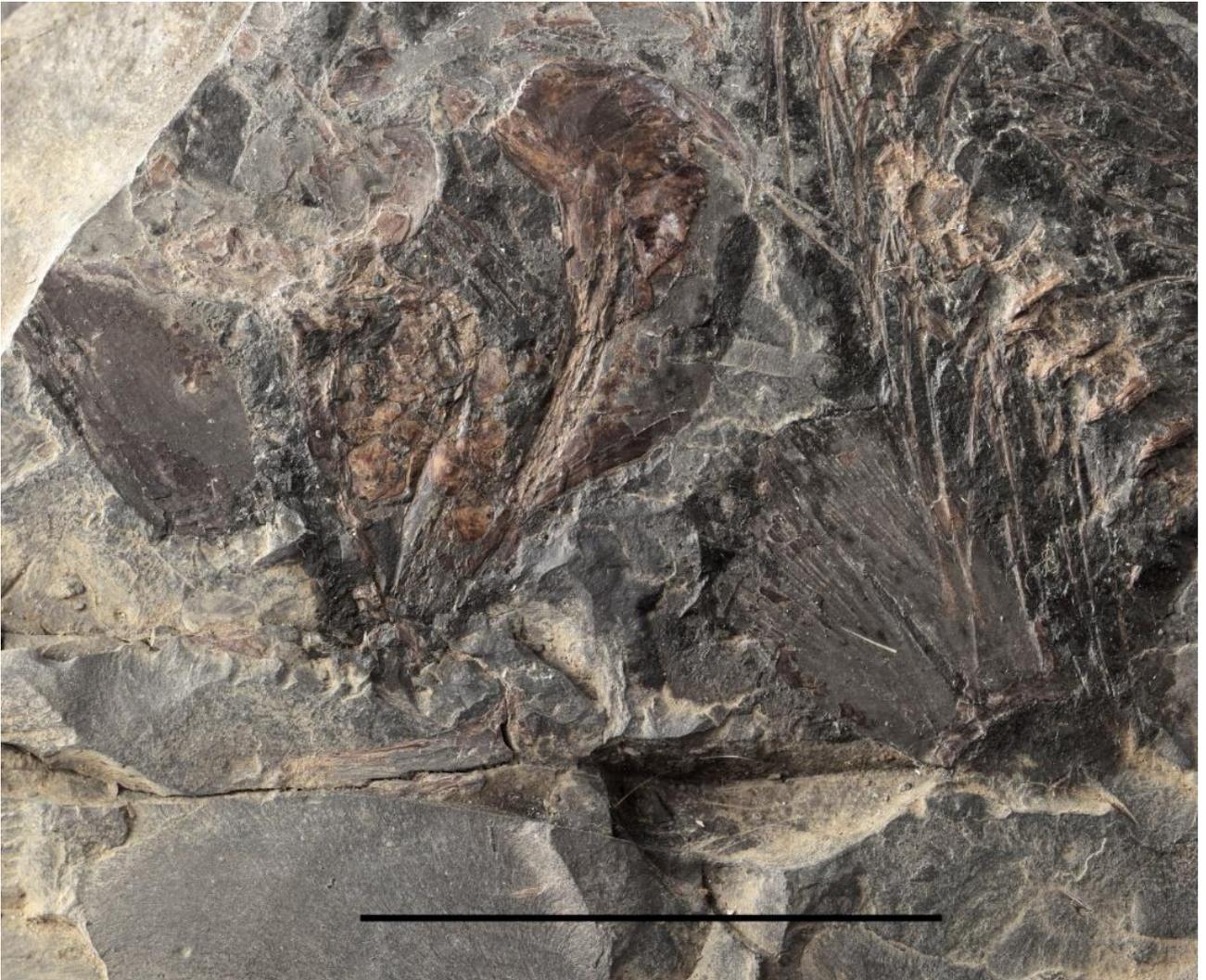


Fig. 29. *Pachyrhizodus* indet. MCR 6136. Detail of the cranial remains. Scale bar equals 50 mm.



Fig. 30. *Pachyrrhizodus* indet. MCV IG292958. Scale bar equals 50 mm.

Description and remarks. The examined material includes several articulated caudal fins and their endoskeletal supports, associated in some cases to the caudal vertebrae (Fig. 25-27). The deeply forked caudal fins exhibit a high degree of hypurostegy and the first uroneural extends forwards to the second preural vertebra (see Fig. 26-27), revealing their affinity to the Pachyrrhizodontoidei (*sensu* Cavin, 2001). The presence of hypurapophysis and the forked anterior extremity of the anteriormost uroneural support their assignment to the family Pachyrrhizodontidae (Cavin, 2001). Within the Pachyrrhizodontidae (*sensu* Cavin, 2001) the closely related genera *Rhacolepis*, *Goulmimichthys* and *Pachyrrhizodus* possess two hypural plates. In the specimens examined herein the hypurals 1 and 2 are fused together for more than half of their length and the dorsal hypurals are fused into a consolidated plated. In addition, the bases of the dorsalmost principal rays of the caudal fin may cross obliquely over the entire upper hypural series or, alternatively, may be aligned with hypurals so that no fin-ray base overlies more than one hypural. The second condition is present in both *Rhacolepis* and *Pachyrrhizodus* (Cavin, 2001), but *Pachyrrhizodus* may also exhibit the first condition (Forey,

1977; Taverne, 1987; Cavin, 2001). The neural spine of the second preural centrum is also shortened as in *Pachyrhizodus* (Taverne, 1987; Khalloufi, 2010).

Only three specimens (MCSNVE 24518; MCR 6136, MCV IG292958) include some cranial and anterior postcranial remains. The specimen MCSNVE 24518 exhibits some large scattered subquadrangular bones tentatively interpreted as infraorbitals.

MCR 6136 shows traces of the dorsal and pelvic fins and also some cranial elements including the expanded infraorbitals (Fig. 28-29).

Finally, the specimen MCV IG292958 (Fig. 30) includes a large portion of the vertebral column, the dorsal fin containing 22 rays, two broad infraorbitals, and other poorly preserved cranial bones and some scales.

***Pachyrhizodus subulidens* (Owen, 1840)**

Fig. 31-36

- 1976 *Thrissopater magnus* Woodward - Sorbini, p. 491, fig. 4, pl. 12.
1976 *Pachyrhizodus subulidens* (Owen) 1842 - Sorbini, p. 494, fig. 6, pl. 14-16.
1976 *Pachyrhizodus intermedius* Sorbini 1976 - Sorbini, p. 497, fig. 7-9.
1980 *Thrissopater magnus* - Sorbini, p. 119.
1980 *Pachyrhizodus subulidens* - Sorbini, p. 119, text-fig. p. 120.
1980 *Pachyrhizodus intermedius* - Sorbini, p. 119.
1987 *Pachyrhizodus magnus* (Woodward, 1901) - Taverne, p. 136.
1987 *Pachyrhizodus subulidens* (Owen, 1840) - Taverne, p. 136, fig. 1-3.
1987 *Pachyrhizodus intermedius* n. sp. - Taverne, p. 136.
1990 *Pachyrhizodus* - Bizzarini and Coccioni, p. 79.
1990 *Thrissopater magnus* Woodward - Astolfi and Colombara, p. 147.
1990 *Pachyrhizodus subulidens* (Owen) - Astolfi and Colombara, p. 147.
1990 *Pachyrhizodus intermedius* Sorbini - Astolfi and Colombara, p. 148, fig. 210-211.
1994 *Thrissopater magnus* (Woodward, 1899) - Sorbini, p. 271.
1994 *Pachyrhizodus subulidens* (Owen, 1840) - Sirna et al., p. 271.
1994 *Pachyrhizodus intermedius* (Sorbini, 1976) - Sirna et al., p. 271.
2005 *Thrissopater* (= *Pachyrhizodus*) *magnus* - Dalla Vecchia et al., p. 106.
2005 *Pachyrhizodus subulidens* - Dalla Vecchia et al., p. 106.
2005 *Pachyrhizodus intermedius* - Dalla Vecchia et al., p. 106.
2007 *Pachyrhizodus* sp. - Capasso, p. 189.
2010 *Pachyrhizodus subulidens* - Khalloufi, p. 48.
2010 *Pachyrhizodus intermedius* - Khalloufi, p. 48.

Referred material. MCSNVE 24526, 24544, 24553; MCSNVR IG37492-37493, IG37495, IG37497; MCR 3749, MCV 157, 158, 311, 312, 313, 314; MGCB IG37491, 37494, 37496; MGPPD 32091.

Locality. Bomba Quarry (Cinto Euganeo, Padova), Carcoselle Quarry (Possagno, Treviso), Valdagno-Schio tunnel (Vicenza).



Fig. 31. *Pachyrhizodus subulidens*. MGCB IG37491. Scale bar equals 50 mm.

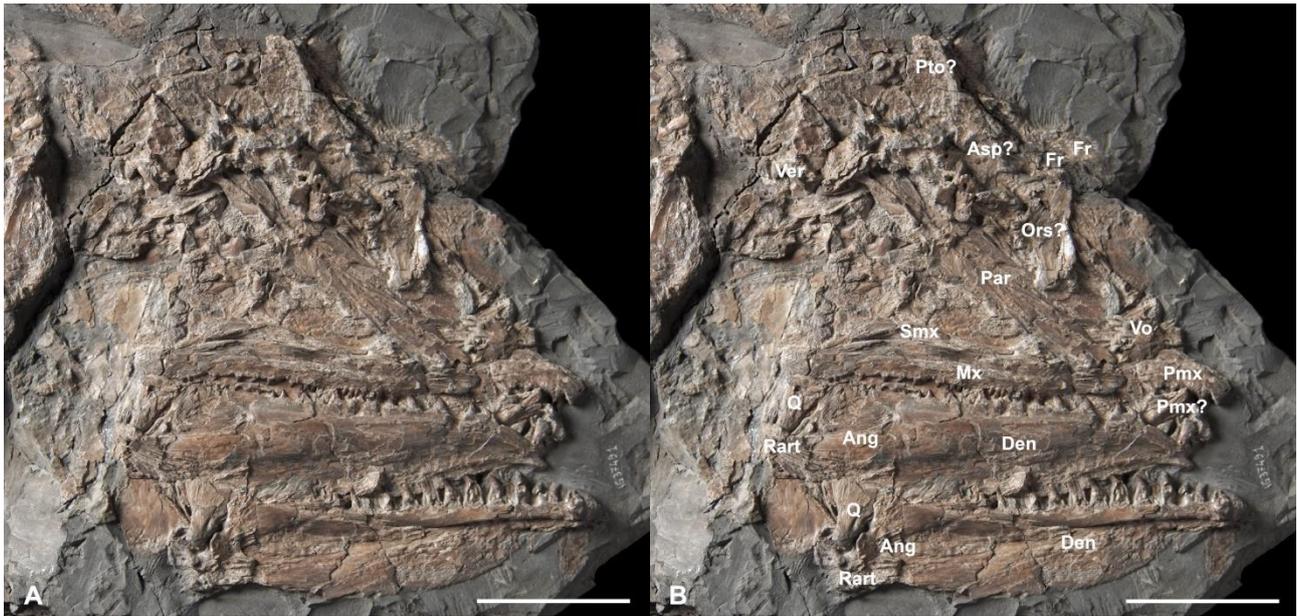


Fig. 32. *Pachyrhizodus subulidens*. MGCB IG37491. **A.** Detail of cranial region. **B.** Detail of cranial region with bones identification. Scale bars equal 50 mm. Abbreviations: **Ang**: angular; **Asp**: autosphenotic; **Den**: dentary; **Fr**: frontal; **Mx**: maxilla; **Ors**: orbitosphenotic; **Par**: parasphenoid; **Pmx**: premaxilla; **Pto**: pterotic; **Q**: quadrate; **Rart**: retroarticular; **Vert**: vertebra.

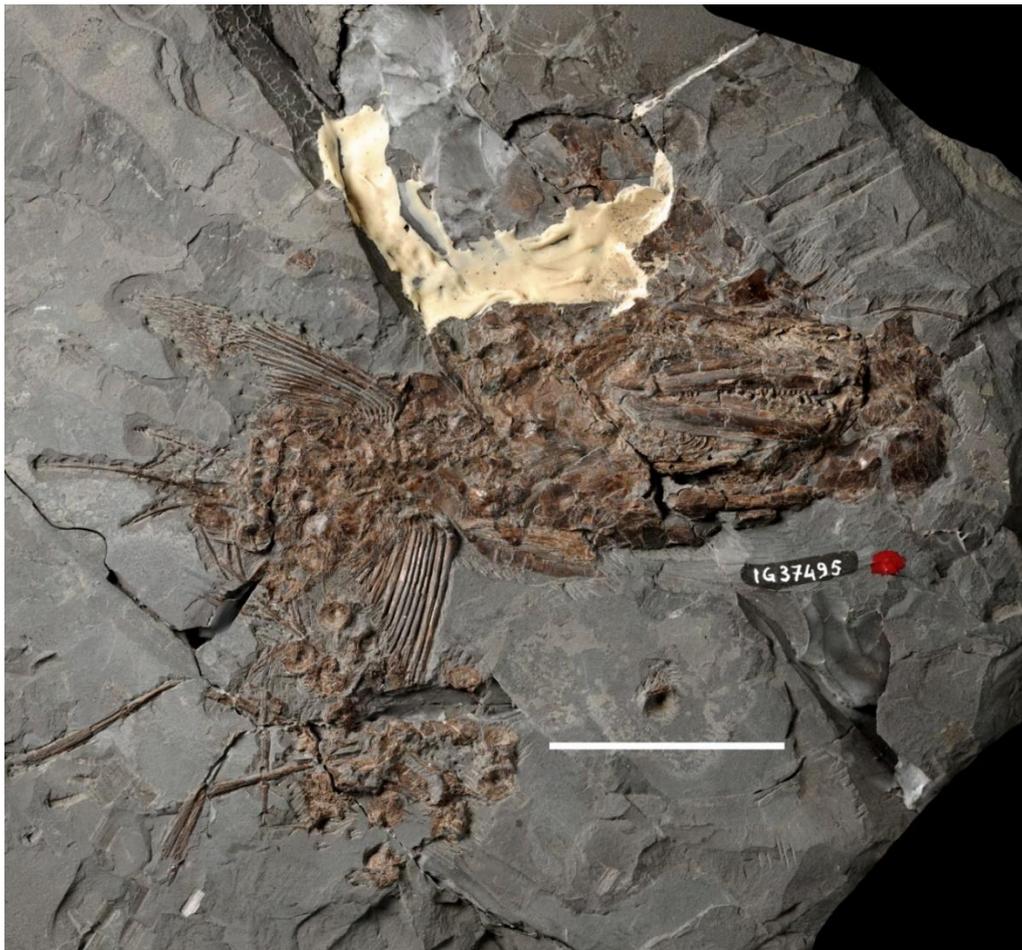


Fig. 33. *Pachyrhizodus subulidens*. MCSNVR IG37495. Scale bar equals 50 mm.

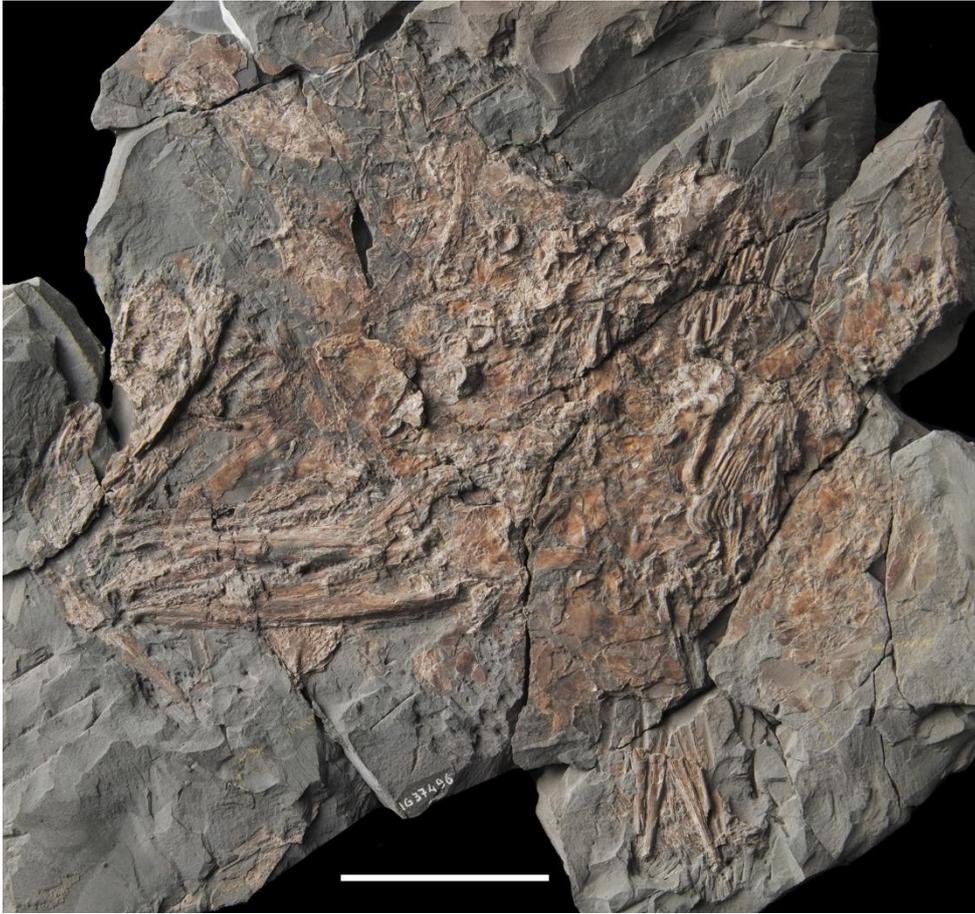


Fig. 34. *Pachyrhizodus subulidens*. MGCB IG37496. Scale bar equals 50 mm.



Fig. 35. *Pachyrhizodus subulidens*. MCSNVE 24553. Scale bar equals 50 mm.



Fig. 36. *Pachyrhizodus subulidens*. MCSNVE 24553. Counterpart of the head. Scale bar equals 50 mm.

Description and remarks. Several moderately preserved specimens are referred herein to the species *Pachyrhizodus subulidens* (Fig. 31-36). All of these specimens exhibit a combination of features that support the assignment to the species *Pachyrhizodus subulidens* (see Forey, 1977). The skull roof is characterized by a marked frontal depression. The bones of the infraorbital series are quadrangular in outline and considerably expanded. The marginal premaxillary and maxillary teeth are similar in size usually reaching a height of 3 or 4 mm. The lower jaw teeth are larger than those of the upper jaw, reaching a height of 6 or 7 mm. The teeth of both the upper and lower jaws are recurved. The premaxilla bears 10-13 marginal teeth plus a single inner tooth slightly larger than the marginal teeth. The maxilla shows at least 33 sockets and the dentary has not less than 30 sockets. The ventral margin of the dentary is inflected, and the overall width of the bone does not exceed its depth. The pectoral fins contain more than 16 closely associated rays, of which the first one is enlarged (see Forey, 1977). The specimen MCSNVR IG37495 (Fig. 33) was considered by Sorbini (1976) as the holotype of *Pachyrhizodus intermedius*, although there are no substantial differences allowing a separation from *P. subulidens*. Based on the revision of the morphological characters of the holotype, *P. intermedius* is considered herein as junior synonym of *P. subulidens*.

The specimens MGCB IG37496 (Fig. 34) and MCSNVR IG37497 were assigned by Sorbini (1976) to *Thrissopater* (= *Pachyrhizodus*) *magnus*. However, they exhibit recurved teeth of different size in the upper and lower jaws identical to those *P. subulidens*. The upper and lower jaw teeth of *P. magnus* are nearly equal in size (see Forey, 1977).

Order Tselfatiiformes Nelson, 1994

Family Plethodidae Loomis, 1900

Genus *Tselfatia* Arambourg, 1943

Tselfatia formosa Arambourg, 1943

Fig. 37-43

- 1976 *Tselfatia formosa* Arambourg 1943 - Sorbini, p. 518, fig. 20-22, pl. 27-30.
- 1980 *Tselfatia formosa* - Sorbini, p. 119.
- 1980 *Tselfatia formosa* Arambourg, 1943 - Bardack and Teller-Marshall, p. 1075, text-fig. 1-3.
- 1983 *Tselfatia formosa* Arambourg, C., 1943 - Taverne, p. 165.
- 1990 *Tselfatia formosa* Arambourg - Astolfi and Colombara, p. 150, fig. 215.
- 1994 *Tselfatia formosa*, Arambourg, 1943 - Sirna et al., p. 271, 273.
- 2000a *Tselfatia formosa* - Taverne, p. 9, fig. 1, 3-7.
- 2000b *Tselfatia formosa* - Taverne, p. 98, fig. 6D.
- 2000 *Tselfatia formosa*, Arambourg, 1943- Maisch and Lehmann, p. 500.
- 2001 *Tselfatia formosa* - Avanzini and Luciani, p.
- 2005 *Tselfatia formosa* - Dalla Vecchia et al., p. 106, fig. 80.
- 2005 *Tselfatia formosa* Arambourg, 1943 - Taverne and Gayet, p. 67, fig. 2.
- 2010 *Tselfatia formosa* - Khalloufi, p. 48.

Referred material. MGCB IG37537 and MCSNVR IG37538; MCSNVR IG37539-37544; MGCB IG295829; MGPPD 32090; MCSNVE 24522, 24545, 24547, 24548, 24549, 24564, 24565, 24567, 24570, 24571, 24574, 24592, 24702.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Carcoselle Quarry (Possagno, Treviso); Valdagno-Schio Tunnel (Vicenza); Schievenin Valley (Quero, Belluno).

Description and remarks. Numerous specimens from four localities have been referred to *Tselfatia formosa*. Among the available material, there are only three large and relatively well-preserved specimens (MGCB IG37537 and MCSNVR IG37538, MCSNVR IG37539). The other specimens are represented only by some fragmentary postcranial remains with portions of the vertebral column, and median and paired fins with enlarged fin rays.

MGCB IG37537 and MCSNVR IG37538 are part and counterpart of a single large specimen exposed in lateral view (SL 220 mm; HL 56 mm; PD 52 mm; PA 132 mm; TD 95 mm; Fig. 37-39). The skeleton is almost complete and, in large part articulated. The body is deep and laterally compressed,

oval in outline. The head has an obtuse antero-dorsal profile being particularly high at the occiput. The vertebral column contains about 71 vertebrae. The dorsal and anal fins are very long, reaching the caudal peduncle. The specimen also shows a series of characters that allow to refer it to the family Plethodidae (Taverne and Gayet, 2005), including ural centra greatly reduced and fused into a small terminal compound centrum; first four hypurals consolidated into a large hypural and notched plate joined to the terminal vertebra and characterized with deep horizontal groove separating the plate into a dorsal and a ventral parts; jaws, palate and lingual plates covered with patches of small teeth; toothed bones pierced by numerous small pits; cleithrum with very long and obliquely oriented ventral arm. The opercle exhibits a ventral arm notably shorter than the dorsal one like in more advanced plethodids (Taverne and Gayet, 2005). The specimen can be referred to the species *Tselfatia formosa* based on the following characters: skull particularly high at the occiput; first large dorsal- and anal-fin rays (the fifth and third one, respectively) segmented and bearing a row of pseudo-fulcra all along their anterior border (Fig. 39); neural and haemal arches partially or totally fused with the corresponding centra; tips of the dorsal- and anal-fin pterygiophores expanded in large semi-circular plates; pectoral fin inserting just above the vertebral column; scales with pectinated posterior border (Bardack and Teller-Marshall, 1980; Taverne and Gayet, 2005). The first three of these characters are shared with *Dixonanogmius*, while the others are autapomorphic of *Tselfatia* (Taverne and Gayet, 2005). *Dixonanogmius dalmatius* differs from *Tselfatia formosa* especially for the pectoral fin inserting just above the vertebral column (Bardack and Teller-Marshall, 1980).

MCSNVR IG37539 (Fig. 40-43) is probably one of the largest individuals ever reported (HL ca. 160 mm, TD ca. 320 mm). It consists of the cranial and anterior post-cranial region exposed in lateral view. It shows several of the diagnostic features listed above, including the pitted dental plates (Fig. 43) and the anterior portion of the dorsal fin with four short and spiny rays (Fig. 41).

The other referred specimens mostly consist fragmentary remains of the vertebral column and of the dorsal, pectoral and caudal fins. The specimen MGPPD 32090 is represented by a large caudal fin collected from the Schievenin Valley.

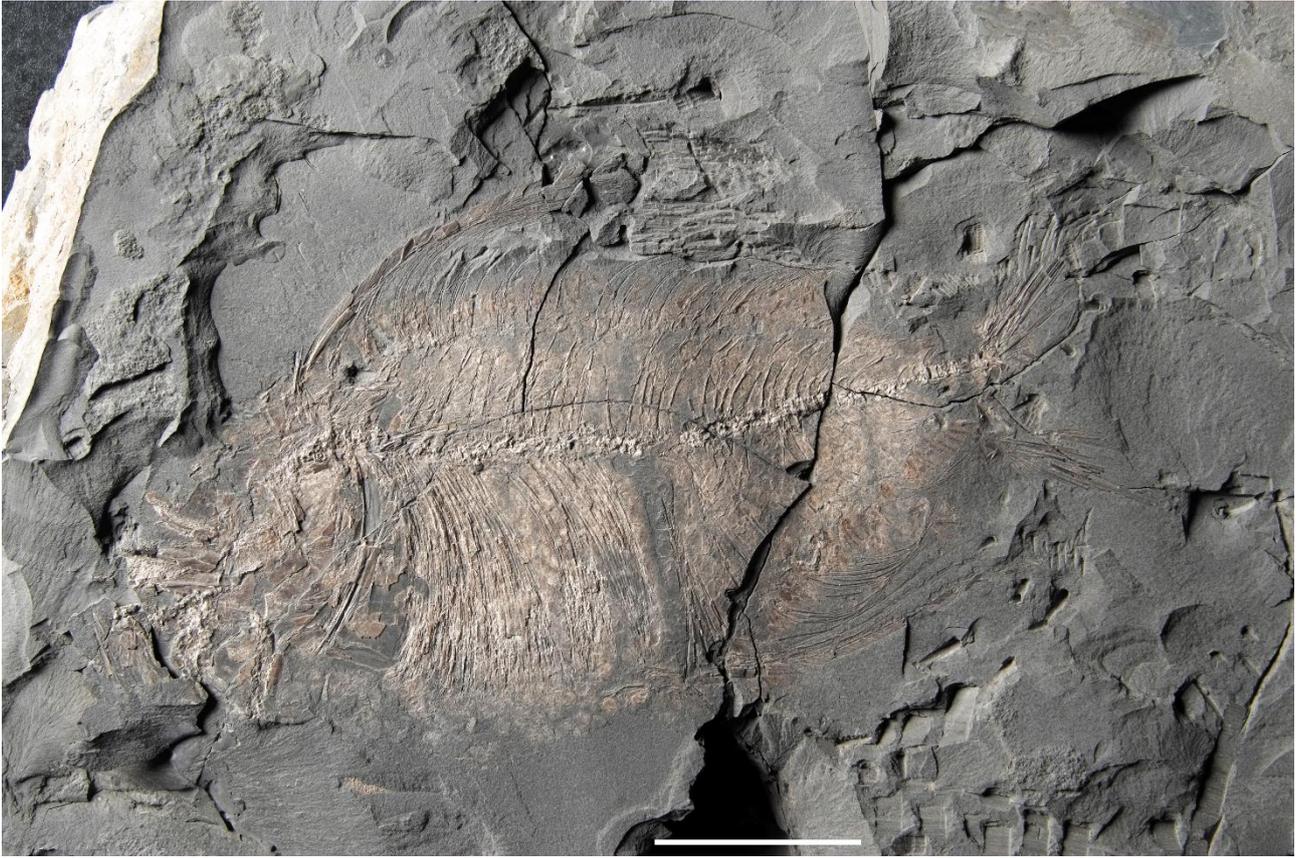


Fig. 37. *Tselfatia formosa*. MGCB IG37537. Scale bar equals 50 mm.



Fig. 38. *Tselfatia formosa*. MCSNVR IG37538. Scale bar equals 50 mm.



Fig. 39. *Tselfatia formosa*. MCSNVR IG37538. Detail of the first large dorsal fin rays. Scale bar equals 50 mm.



Fig. 40. *Tselfatia formosa*. MCSNVR IG37539. Scale bar equals 50 mm.



Fig. 41. *Tselfatia formosa*. MCSNVR IG37539. Detail of the first large dorsal fin rays. Scale bar equals 20 mm.



Fig. 42. *Tselfatia formosa*. MCSNVR IG37539. Detail of the head. Scale bar equals 50 mm.

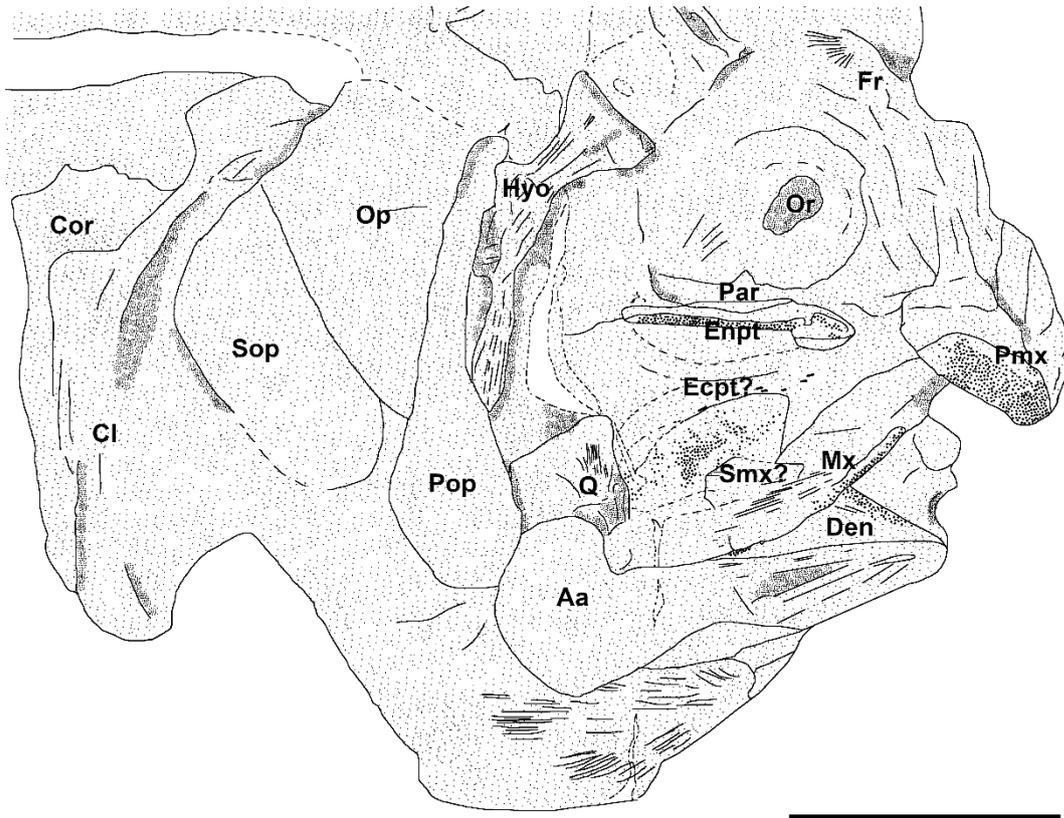


Fig. 43. *Tselfatia formosa*. MCSNVR IG37539. Line drawing of the head with bones identification. Dashed lines indicate lacking portions or undefined borders. Abbreviations: **Aa**: angulo-articular; **Cl**: cleithrum; **Cor**: coracoid; **Ecpt**: ectopterygoid; **Enpt**: entopterygoid; **Den**: dentary; **Fr**: frontal; **Hyo**: hyomandibula; **Mx**: maxilla; **Op**: opercle; **Or**: orbit; **Par**: parasphenoid; **Pmx**: premaxilla; **Pop**: preopercle; **Q**: quadrate; **Smx**: supramaxilla; **Sop**: subopercle.

Genus *Dixonanogmius* Taverne, 2000b

Dixonanogmius dalmatius (Bardack and Teller-Marshall, 1980)

Fig. 44-47

Referred material. MCV IG292955.

Locality. Valdagno-Schio Tunnel (Vicenza).

Description and remarks. MCV IG292955 consists of a partially complete skeleton of a large individual lacking most of the head and the caudal fin (Fig. 44). Of the head, only part of the hyomandibula and the bones of the opercular series are preserved (Fig. 45). Apparently, the fossil resembles *T. formosa* in the overall aspect and possession of a very large dorsal-fin ray (Fig. 46). However, it can be referred to *Dixonanogmius dalmatius* because of its deeper body aspect and the

pectoral-fin insertion that is placed just above the vertebral column (see Bardack and Teller-Marshall, 1980; Taverne and Gayet, 2005; Fig. 47). This is the first report of this taxon from the Bonarelli Level of Italy.



Fig. 44. *Dixonanogmius dalmatius*. MCV IG292955. Scale bar equals 50 mm.



Fig. 45. *Dixonanogmius dalmatius*. MCV IG292955. Detail of the cranial portion. Scale bar equals 50 mm.



Fig. 46. *Dixonanogmius dalmatius*. MCV IG292955. Detail of the first large dorsal fin rays. Scale bar equals 50 mm.



Fig. 47. *Dixonanogmius dalmatius*. MCV IG292955. Detail of the pectoral fin inserting above the axis of the vertebral column. Scale bar equals 50 mm.

Order Tselfatiiformes? Nelson, 1994

“Protosphyraena” stebbingi Woodward, 1909

Fig. 48

1994 *Protosphyraena?* sp. - Sirna et al., p. 270

2019 *“Protosphyraena” stebbingi*, Woodward, 1909 - Amalfitano et al., p. 53, figs. 1, 4, 6-11.

Referred material. MGCB VT 001.

Locality. Sinigaglia quarry (Teolo, Padova).



Fig. 48. *‘Protosphyraena’ stebbingi*. MCV IG292955. Isolated rostrum. Scale bar equals 50 mm.

Description and remarks. The material is represented by a single isolated rostrum (Fig. 48) from the Sinigaglia quarry near Villa di Teolo (Colli Euganei, Padova). The flattened aspect, blunt tip, lateral furrows and smooth surface are distinctive characters of *‘Protosphyraena’ stebbingi* rostrum. This taxon was reported before only from the English Chalk and the specimen described herein constitutes the only evidence of the presence of this taxon outside the U.K. A detailed analysis of this specimen has been recently realized by Amalfitano et al. (2019) who also reported an additional more complete isolated rostrum found near Crespadoro (Lessini Mountains, Vicenza) and possibly coming from the Scaglia Variegata Alpina Formation (lower Aptian-Cenomanian; see Amalfitano et al., 2019).

Family Protostomiidae Arambourg, 1943

Remarks. The family includes *Protostomias* and the very similar-looking *Pronotacanthus* (Arambourg, 1943). The position of the family is still debated. Some authors relate it to the Stomiiformes (e.g., Arambourg, 1954; Taverne, 1991; Fink and Weitzman, 1982). Recently, Prokofiev (2005) excluded any relation with the Stomiiformes. Khalloufi (2010) evidenced the existence of a number of similarities between *Protostomias* and *Pronotacanthus* and two other taxa from the Santonian of Lebanon, *Spaniodon* and *Thrissopteroides*.

Genus *Protostomias* Arambourg, 1943

Protostomias maroccanus Arambourg, 1943

Fig. 49-54

- 1976 *Protostomias maroccanus* Arambourg 1943 - p- 505, fig.13, pl. 22.
- 1976 *Paravinciguerrria praecursor* Arambourg 1954 - Sorbini, p. 503, fig. 12, pl. 20-21.
- 1980 *Protostomias maroccanus* - Sorbini, p. 119.
- 1980 *Paravinciguerrria praecursor* - Sorbini, p. 119.
- 1990 *Paravinciguerrria praecursor* Arambourg - Astolfi and Colombara, p. 148.
- 1991 *Protostomias maroccanus* Arambourg 1943 - Taverne, p. 57.
- 1994 *Paravinciguerrria praecursor* Arambourg, 1954 - Sirna et al., p. 271.
- 2005 *Protostomias maroccanus* - Dalla Vecchia et al., p. 106.
- 2010 *Protostomias maroccanus* - Khalloufi, p. 48.
- 2010 *Paravinciguerrria praecursor* - Khalloufi, p. 48.

Referred material. MCSNVR IG37507, 37508, 37510-37511, 37549; MGCB IG37509; MGCB IG37548, 37550, 37551.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The specimens are partial and fragmentary (Fig. 49-53). The specimen MCSNVR IG37510-37511 (Fig. 49-50) is the only one with a nearly complete head skeleton (HL ca. 48 mm), showing several characters that unambiguously justify the assignment to *Protostomias maroccanus*, including: head enlarged with a deep mouth gape, bordered by a large arcuated maxilla; dentary with narrow symphysis oriented upward and bearing at the symphysis level large conical, posteriorly recurved teeth, and a broad coronoid process with parallel striations on its outer side; opercular series well-developed with large opercle (see Arambourg, 1943, 1954).

The specimen MGCB IG37550 (was previously referred by Sorbini (1976) to *Paravinciguerrria praecursor*, probably due to the recurved maxilla (Fig. 52). However, the dentary clearly shows the parallel striations on the coronoid process, which are not present in *Paravinciguerrria praecursor*. The

other specimens solely consist of fragmentary and scattered remains, which can be referred to *Protostomias* because of the peculiar morphology of the dentary. Also, the specimens MGCB IG37548, 37551 and MCSNVR IG37549 previously referred by Sorbini (1976) to *Paravinciguerria praecursor* are here referred to *Protostomias maroccanus*. MGCB IG 37548 (Fig. 53), the best preserved one among these specimens, was already referred by Khalloufi (2010: p. 245), together with the specimen MCSNVR IG 37507 (Fig. 54), to *Protostomias maroccanus* for the ectopterygoid extending beyond the dorsal edge of the quadrate and along the parasphenoid. Furthermore, the shape of the quadrate, characterized by an isosceles triangular outline with a short dorsal edge and by the condylum antero-ventrally located, supports the attribution to *Protostomias*. The quadrate in *Paravinciguerria* has a more equilateral triangular outline, with a long dorsal edge, and the condylum is located medio-ventrally.

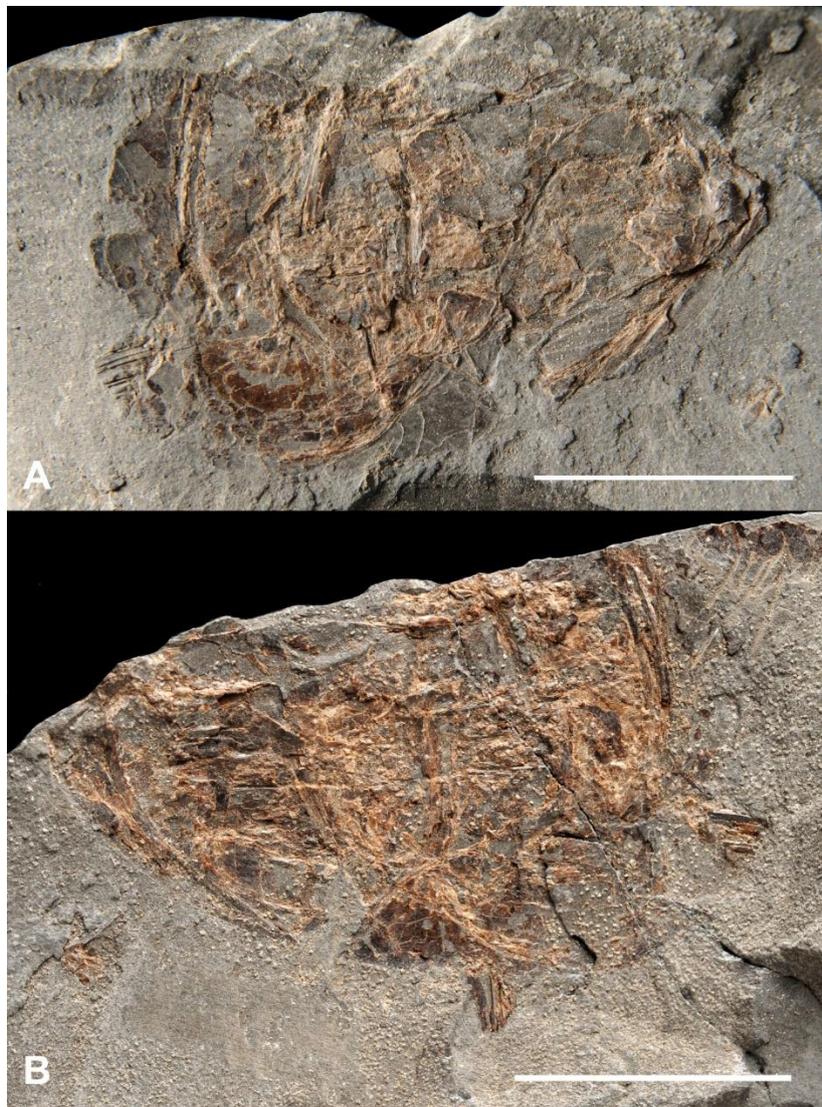


Fig. 49. *Protostomias maroccanus*. MCSNVR IG37510-37511. Part and counterpart (A-B). Scale bars equal 20 mm.

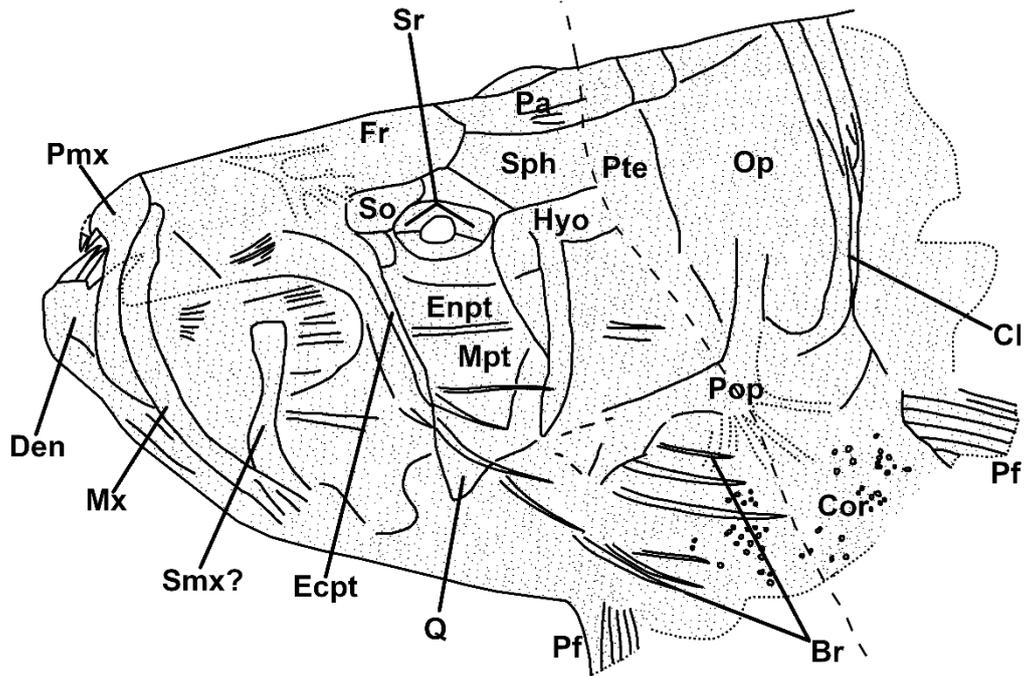


Fig. 50. *Protostomias maroccanus*. MCSNVR IG37510-37511. Interpretative drawing of the head with bones identification. Abbreviations: **Br**: branchiostegal rays; **Cl**: cleithrum; **Cor**: coracoid; **Den**: dentary; **Ecpt**: ectopterygoid; **Enpt**: entopterygoid; **Fr**: frontal; **Hyo**: hyomandibula; **Mpt**: metapterygoid; **Op**: opercle; **Pa**: parietal; **Pf**: pectoral fin; **Pmx**: premaxilla; **Pop**: preopercle; **Pte**: pterotic; **Q**: quadrate; **Smx?**: supramaxilla; **So**: supraorbital; **Sop**: subopercle; **Sph**: sphenotic.



Fig. 51. *Protostomias maroccanus*. MCSNVR IG37509. Scale bar equals 10 mm.

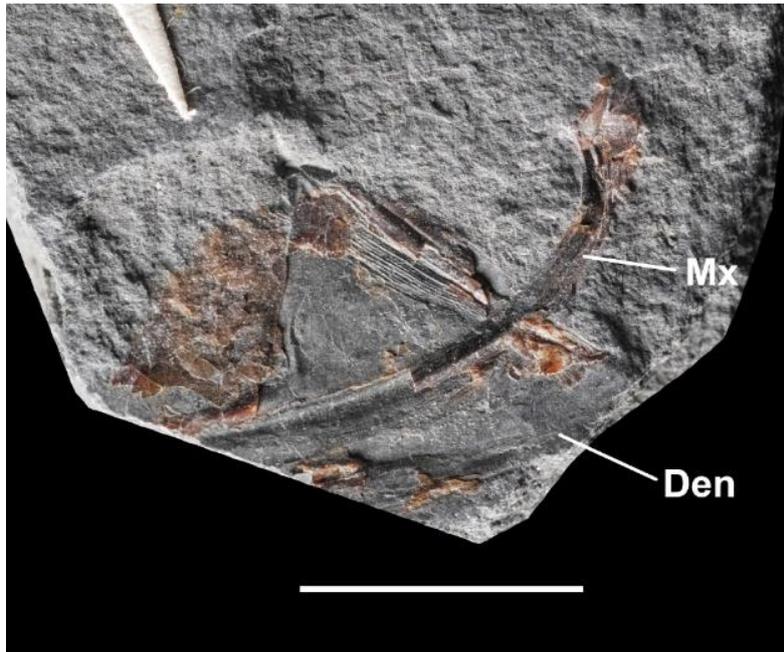


Fig. 52. *Protostomias maroccanus*. MCSNVR IG37550. Scale bar equals 10 mm. Abbreviations: **Den**: dentary; **Mx**: maxilla.

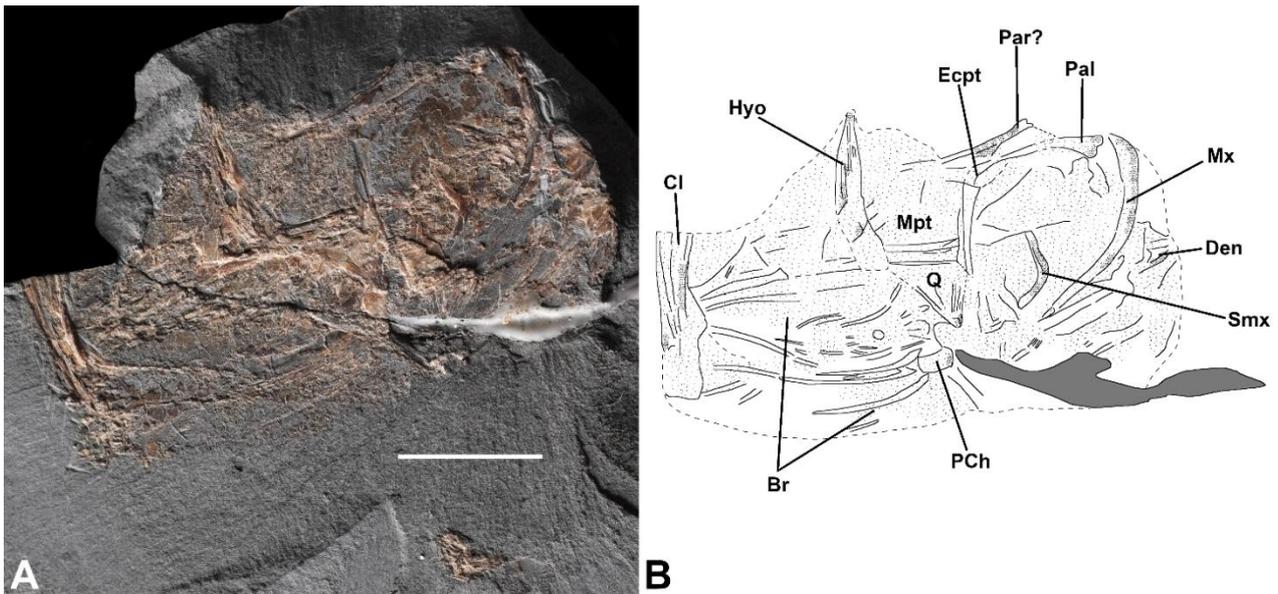


Fig. 53. *Protostomias maroccanus*. MCSNVR IG37548. **A.** Detail of the specimen. Scale bar equals 10 mm. **B.** Interpretative drawing. Dashed lines indicate lacking portions or undefined borders. Gray areas indicate glue patches. Abbreviations: **Br**: branchiostegal rays; **Cl**: cleithrum; **Den**: dentary; **Ecpt**: ectopterygoid; **Hyo**: hyomandibula; **Mpt**: metapterygoid; **Mx**: maxilla; **Pal**: palatine; **PCh**: posterior ceratohyal; **Par**: parasphenoid; **Q**: quadrate; **Smx**: supramaxilla.

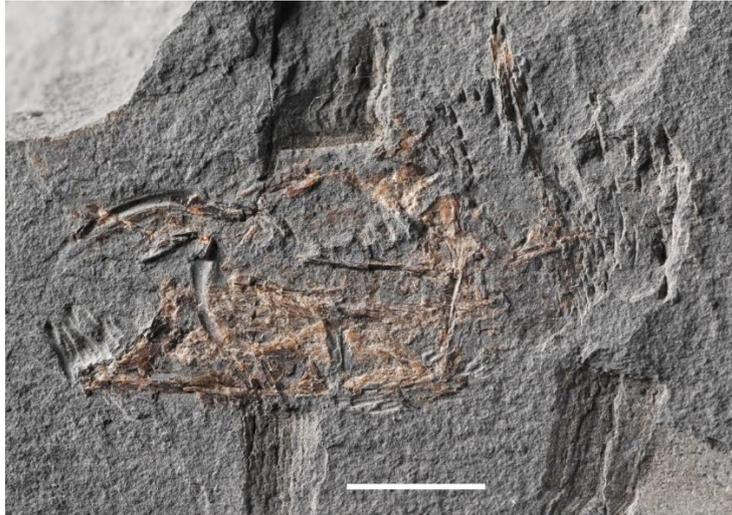


Fig. 54. *Protostomias maroccanus*. MCSNVR IG37507. Scale bar equals 5 mm.



Fig. 55. *Ichthyotringa africana*. MCSNVR IG37520. Scale bar equals 10 mm.

Order Aulopiformes Rosen, 1973 (*sensu* Nelson, 1994)

Suborder Ichthyotringoidei Goody, 1969

Family Ichthyotringidae Jordan, 1905

Genus *Ichthyotringa* Cope, 1878

Ichthyotringa africana (Arambourg, 1954)

Fig. 55-57

- 1976 *Rhinellus* sp. - Sorbini, p. 507, fig. 14, pl. 23.
1976 *Clupavus* cfr. *maroccanus* Arambourg 1968 - Sorbini, p. 489, fig. 2, pl. 11.
1980 *Rhinellus* sp. - Sorbini, p. 119.
1980 *Clupavus* cfr. *maroccanus* - Sorbini, p. 119.
1990 *Rhinellus* sp. - Astolfi and Colombara, p. 149, fig. 213.
1994 *Clupavus* cfr. *maroccanus* Arambourg, 1954 - Sirna et al., p. 271.
1994 *Clupavus* cfr. *maroccanus* Arambourg, 1954 - Sirna et al., p. 271.
2006 *Ichthyotringa africana* Arambourg, 1954 - Taverne, p.32, fig. 1-7.
2010 *Ichthyotringa africana* - Khalloufi, p. 48.

Referred material. MCSNVR IG37504 and MGCB IG37526; MCSNVR IG37517-37518, 37515-37516, 37519, 37520-37521; MGCB IG37547, U4S1/1, U3/6; MCSNVE 24520, 24604, 24605.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Carcoselle Quarry (Possagno, Treviso).

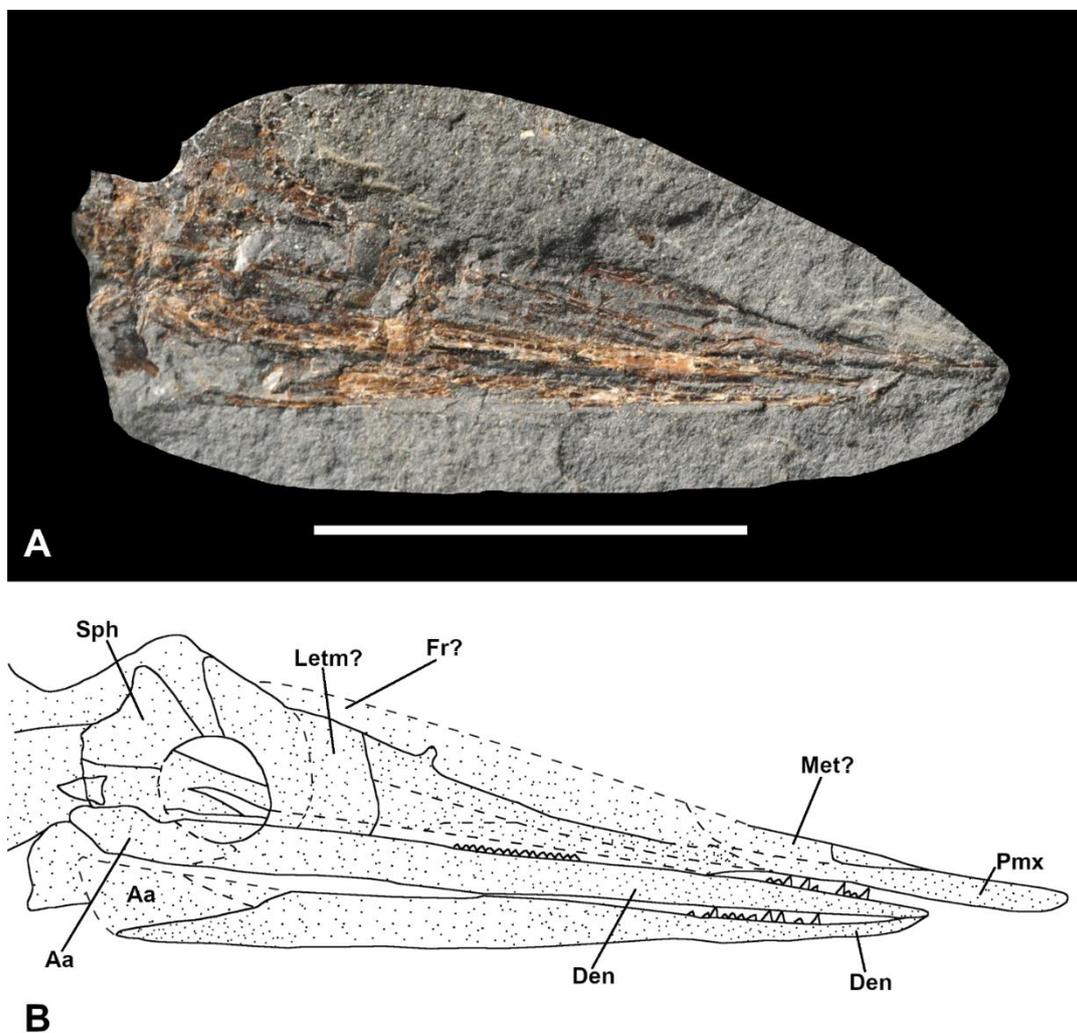


Fig. 56. *Ichthyotringa africana*. MCSNVR IG37515. **A.** Detail of the specimen. Scale bar equals 10 mm. **B.** Interpretative drawing. Abbreviations: **Aa**: angulo-articular; **Den**: dentary; **Fr**: frontal; **Letm**: lateral ethmoid; **Met**: mesethmoid; **Pmx**: premaxilla; **Q**: quadrate; **Sph**: sphenotic.



Fig. 57. *Ichthyotringa africana*. MCSNVR IG37517. Scale bar equals 10 mm.

Description and remarks. The specimens are mainly represented by isolated jaw elements. There are also partially complete isolated head skeletons (e.g., MCSNVR IG37520; Fig. 55) and few postcranial remains (e.g., MCSNVR IG 37517; Fig. 57). The specimens can be referred to the genus *Ichthyotringa* for the following combination of characters: head very shallow and elongated anteriorly into a prominent rostrum, dermal bones of the head smooth and unornamented, teeth present on premaxilla, palatine, endopterygoid, ectopterygoid and dentary, jaw suspension almost vertical or slightly inclined forward, vertebral centra longer than deep, (Goody, 1969). Sorbini (1976) referred these specimens to “*Rhinellus*” (= *Ichthyotringa*) sp. whereas, more recently Taverne (2006) assigned them to *Ichthyotringa africana*.

The specimens MCSNVR IG37504 and MGCB IG37526 (Sorbini, 1976: pl. 21) represent part and counterpart of the cranial remains of a single individual. These remains are represented by the neurocranium in dorsal view. The surface of the bones of the skull roof is smooth and unornamented. The frontals are long and slender and are crossed by the supraorbital sensory canal, which than branches toward the sphenotic forming an obtuse angle. The parietals contact each other along the midline. There is an oval structure between the frontal and the parietals on the counterpart (MCSNVR IG 37504), which could be interpreted as a frontoparietal depression or fontanelle. These neurocranial remains were referred by Sorbini (1976) to *Clupavus* cf. *maroccanus*, although the pattern of branching of the suborbital sensory canal at the level of the osphenotic in the latter taxon is completely different since it diverges into three separate elements (Taverne, 2006; Khalloufi, 2010).

Family Dercetidae Pictet, 1850
Genus *Rhynchodercetis* Arambourg, 1943

***Rhynchodercetis* indet.**

Fig. 58

- 1976 *Rhynchodercetis* sp. - Sorbini, p. 507, fig. 14, pl. 23.
1980 *Rhynchodercetis* sp. - Sorbini, p. 119.
1990 *Rhynchodercetis* sp. - Astolfi and Colombara, p. 149.
1994 *Rhynchodercetis* sp. - Sirna et al., p. 271, 273.
2005 *Rhynchodercetis* sp. - Dalla Vecchia et al., p. 106.
2010 *Rhynchodercetis* sp. - Khalloufi, p. 48.
2011 *Rhynchodercetis* sp. - Silva and Gallo, tab. 2.

Referred material. MGCB IG37514.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. The only available specimen consists of the anterior portion of a single individual (Fig. 58). The fossil is poorly preserved. The head is elongate and shallow. The jaw bones bear small, conical and posteriorly recurved teeth. The anterior vertebral centra are slender and elongate, with well-developed transverse process. All of these features fit well with the definition of the family Dercetidae provided by Chalifa (1989). The cranium is elongated into a rostrum, that extends beyond the mandibular symphysis, and therefore the dentary does not reach the tip of the snout. This condition supports the attribution to the genus *Rhynchodercetis* (see Chalifa, 1989 and Blanco and Alvarado-Ortega, 2006). However, due to the incompleteness of the specimen it is not possible to provide a more detailed taxonomic interpretation. The presence of *Rhynchodercetis* in the Cenomanian of northeastern Italy was also reported by Sirna et al. (1994).

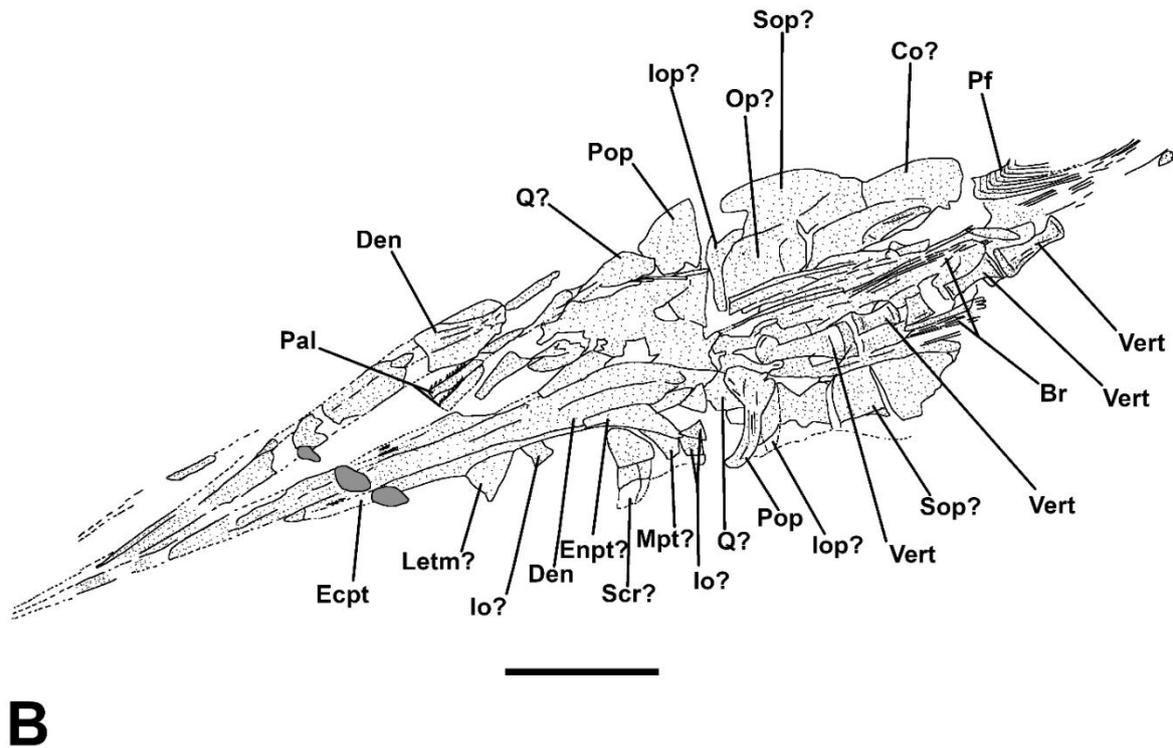


Fig. 58. *Rhynchodercetis* indet. MGCB IG37514. Scale bars equal 10 mm. **A.** Detail of the specimen. **B.** Interpretative drawing. Dashed lines indicate lacking portions or undefined borders. Gray areas indicate glue patches. Abbreviations: **Br:** branchiostegal rays; **Co:** coracoid; **Den:** dentary; **Ecpt:** ectopterygoid; **Enpt:** entopterygoid; **Io:** infraorbital; **Iop:** interopercle; **Letm:** lateral ethmoid; **Mpt:** metapterygoid; **Op:** opercle; **Pal:** palatine; **Pf:** pectoral fin; **Pop:** preopercle; **Q:** quadrate; **Scr:** sclerotic ring; **Sop:** subopercle; **Vert:** vertebra.

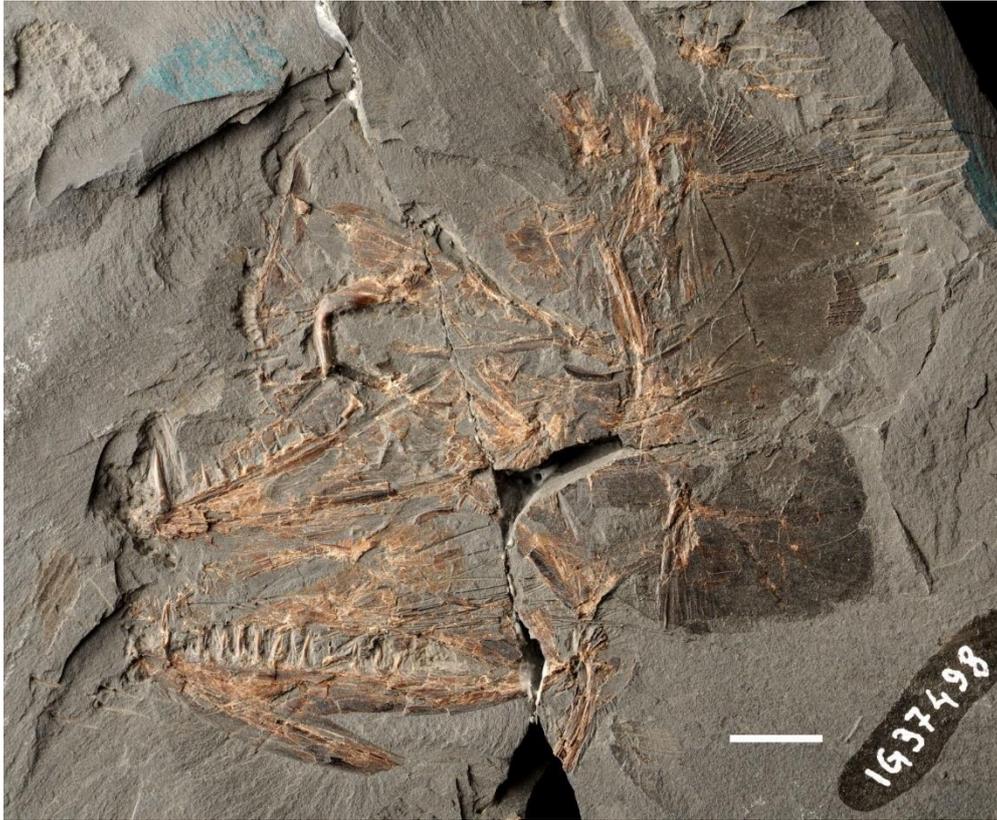


Fig. 59. *Enchodus venator*. MCSNVR IG37498 and MGCB IG37499 (part and counterpart). Detail of MCSNVR IG37498. Scale bar equals 10 mm.

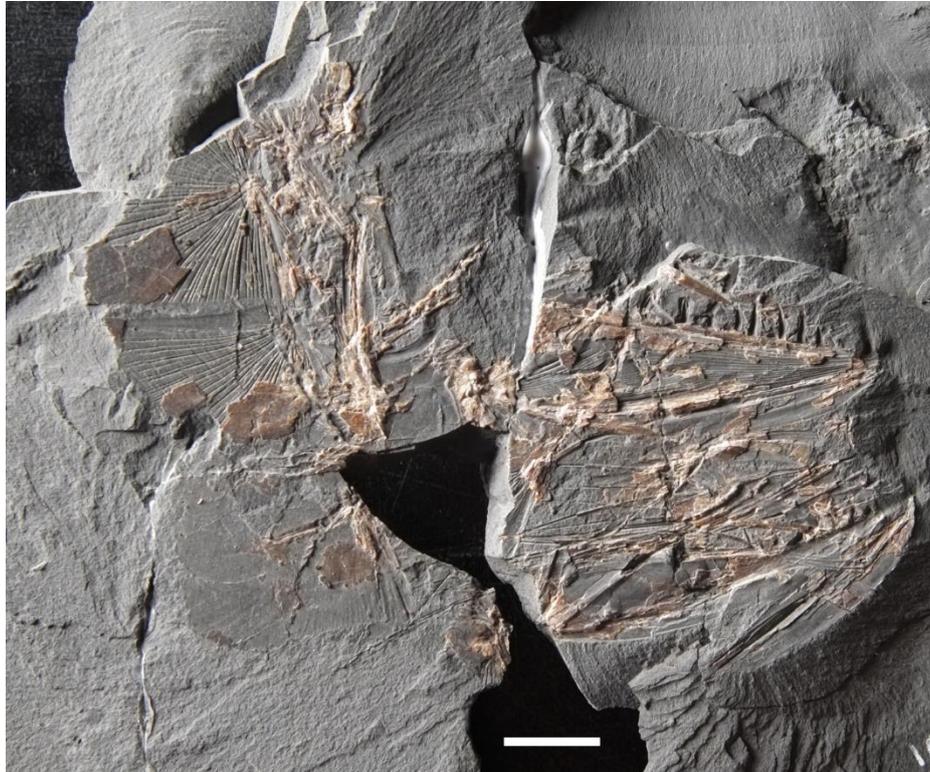


Fig. 60. *Enchodus venator*. MCSNVR IG37498 and MGCB IG37499 (part and counterpart). Detail of MGCB IG37499. Scale bar equals 10 mm.

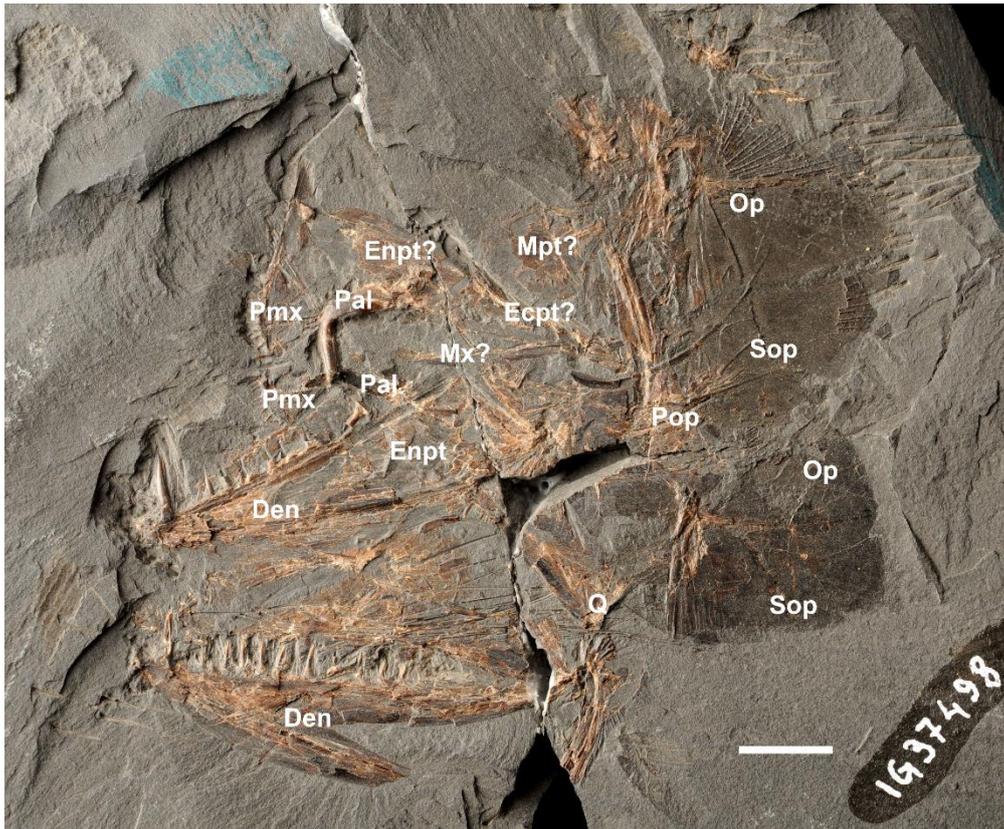


Fig. 61. *Enchodus venator*. MCSNVR IG37498 and MGCB IG37499 (part and counterpart). Detail of MCSNVR IG37498 with bones identification. Scale bar equals 10 mm. Abbreviations: **Den**: dentary; **Ecpt**: ectopterygoid; **Enpt**: ento pterygoid; **Mpt**: metapterygoid; **Mx**: maxilla; **Op**: opercle; **Pal**: palatine; **Pmx**: premaxilla; **Pop**: preopercle; **Q**: quadrate; **Sop**: subopercle.

Family Enchodontidae Lydekker, 1889

Genus *Enchodus* Agassiz, 1835

Enchodus venator Arambourg, 1954

Fig. 59-61

1976 *Enchodus* cfr. *venator* Arambourg 1954 - Sorbini, p. 513, fig. 16-19, pl.26.

1980 *Paravinciguerrria praecursor* - Sorbini, p. 119.

1990 *Enchodus* cfr. *venator* Arambourg - Astolfi and Colombara, p. 150.

1994 *Enchodus venator* Arambourg, 1954 - Sirna et al., p. 271.

2005 *Enchodus* cf. *E. venator* - Dalla Vecchia et al., p. 106.

2010 *Enchodus* cfr. *venator* - Khalloufi, p. 48.

Referred material. MCSNVR IG37498 and MGCB IG37499; MGCB IG37500-37501, U3S1/1; MCSNVE 24577, 24578, MCSNVR IG37512-37513, 37490.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. All the available specimens are poorly preserved. MCSNVR IG37498 and MGCB IG37499 (Fig. 59-61) are the most informative ones and represent part and counterpart of a single individual. They consist of partially complete articulated cranial remains, especially of the jaws and the opercular series. A combination of characters allows to refer the specimen to the species *Enchodus venator*, including (see Fielitz, 2004): vomerine teeth absent, preopercle with an anterior and posterior ventral broadening (see Fielitz, 2004: fig. 2), dermal pattern of mandibular and opercular bones represented by radiating ridges with tubercles along each ridge. palatine teeth curved and showing two offset cutting edges in cross section (see also Arambourg, 1954: fig. 61); premaxilla deep anteriorly without ascending process. The other specimens are poorly preserved and considerably incomplete but are referred to *Enchodus venator* for the peculiar pattern of dentary teeth, with the teeth posterior to the longest anterior tooth decreasing in size posteriorly (Fielitz, 2004: character 39). This character is also present in *E. shumardi* and *E. marchesetti* (see Fielitz, 2004). However, these species can be excluded, since *E. shumardi* is restricted to North America as a geographically vicariant species of *E. venator* (Fielitz, 2004; Cavin, 2008; Silva and Gallo, 2011; Cavin et al., 2012), while *E. marchesetti* has a completely different dermal pattern of opercular bones (see Fielitz, 2004: character 50). MCSNVR IG37490, which consists of a completely disarticulated and fragmentary skeleton, was referred by Sorbini (1976) to *Thrissops microdon*, although it clearly shows the characters of the opercular bones and dentary teeth typical of *Enchodus venator*.

Genus *Rharbichthys* Arambourg, 1954

Rharbichthys ferox Arambourg, 1954

Fig. 62

1976 *Rharbichthys* cfr. *ferox* - Sorbini, p. 509, fig. 15, pl. 24.

1980 *Rharbichthys* cfr. *ferox* - Sorbini, p. 119.

1990 *Rharbichthys* cfr. *ferox* Arambourg - Astolfi and Colombara, p. 149, fig. 214.

2005 *Rharbichthys* cf. *R. ferox* - Dalla Vecchia et al., p. 106.

2010 *Rharbichthys* cfr. *ferox* - Khalloufi, p. 48.

Referred material. MGCB IG37525.

Locality. Bomba Quarry (Cinto Euganeo, Padova).

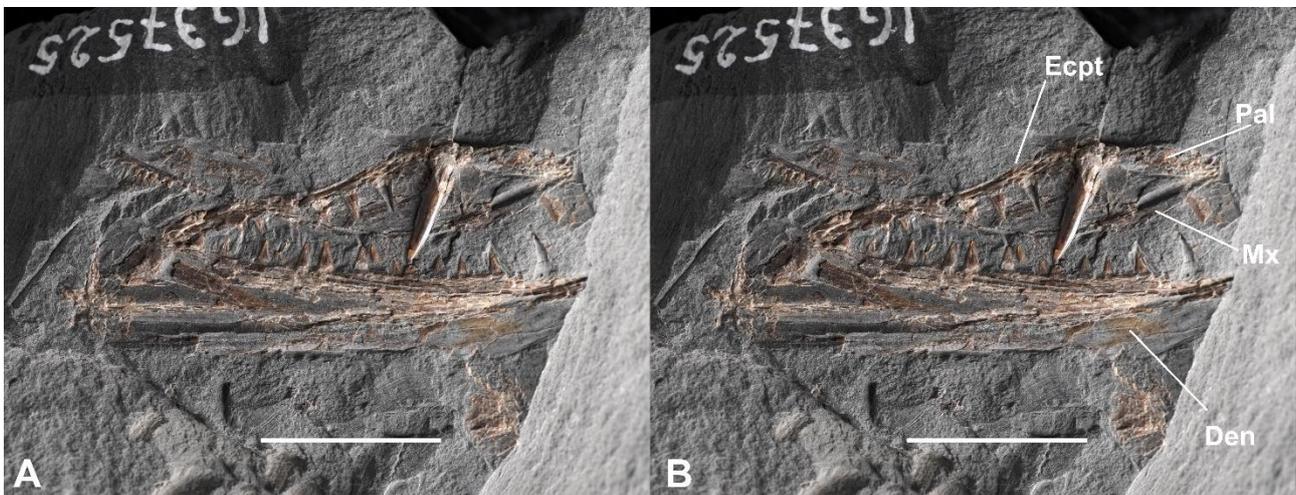


Fig. 62. *Rharbichthys ferox*. MGCB IG37525. **A.** Detail of the specimen. **B.** Detail with bones identification. Scale bars equal 10 mm. Abbreviations: **Den**: dentary; **Ecpt**: ectopterygoid; **Mx**: maxilla; **Pal**: palatine.

Description and remarks. The only specimen (Fig. 62) referred herein to *Rharbichthys ferox* includes only partial remains of the jaws and suspensorium, showing a long and narrow premaxilla, maxilla excluded from the gape of the mouth, and a single large dermopalatine tooth with an elliptical cross section and an anterior cutting edge. This combination of characters fits well the definition of *Rharbichthys ferox* provided by Fielitz (2004).

Sept Acanthomorpha Rosen, 1973 (*sensu* Johnson and Patterson, 1993)

Order Polymixiiformes Rosen and Patterson, 1969 (*sensu* Johnson and Patterson, 1993)

Polymixiiformes indet.

Fig. 63

1976 *Omosoma simum* Arambourg 1954 - Sorbini, p. 524, fig. 23, pl. 31.

1980 *Paravinciguerrria praecursor* - Sorbini, p. 119.

1990 *Omosoma simum* Arambourg - Astolfi and Colombara, p. 149, fig. 214.

2005 *Omosoma simum* - Dalla Vecchia et al., p. 106.

2010 *Omosomipsis simum* - Khalloufi, p. 48.

Referred material. MCSNVR IG37524 and MGCB IG37523.

Locality. Bomba Quarry (Cinto Euganeo, Padova).



Fig. 63. Polymixiiformes indet. MCSNVR IG37524 and MGCB IG37523 (part and counterpart). Detail of MCSNVR IG37524. Scale bar equals 10 mm.

Description and remarks. The specimens MCSNVR IG37524 and MGCB IG37523 represent part and counterpart of an incomplete specimen represented by part of the axial skeleton. It includes also a hemaxanal complex, a typical feature of acanthomorphs (Patterson, 1993; Davesne et al., 2014). The specimens exhibit two series of intermuscular bones. The presence of the epipleurals may support an assignment to the Polymixiiformes (Johnson and Patterson, 1993). Sorbini (1976) referred the remains to the extinct polymixiid species *Omosoma simum* known from the Cenomanian of Jebel

Tselfat (Arambourg, 1954). However, due to the considerable incompleteness of the specimen and the consequent absence of relevant diagnostic features, we are confident that a more detailed taxonomic attribution is not possible.

Order Beryciformes Regan, 1909

?Beryciformes indet.

Fig. 64

Referred material. MGCB VT 002.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Sinigaglia Quarry (Villa di Teolo, Padova).



Fig. 64. ?Beryciformes indet. MGCB VT 002. Scale bar equals 20 mm.

Description and remarks. The specimen MGCB VT 002 (Fig. 64) consists of the anterior portion a spinous dorsal fin. Dorsal-fin spines represents an apomorphic character of Acanthomopha (Johnson and Patterson, 1993). There are six robust and pointed dorsal-fin spines with a marked lateral groove supported by five pterygiophores. The first pterygiophore bears a supernumerary spine. An additional spine was probably present in origin, supported by the sixth pterygiophore of the series mostly preserved as impression only. It exhibits also a chain-link articulation of dorsal fin-spines, a

characteristic shared by beryciforms and percomorphs (Johnson and Patterson, 1993). Due to the paucity of genuine Cenomanian percomorph, we tentatively refer this spinous dorsal fin to an indeterminate beryciform fish.

Suborder Trachichthyoidei Parr, 1933 (*sensu* Patterson, 1993)

Family Hoplopterygiidae, Jordan 1923 (*sensu* Patterson, 1993)

Genus *Hoplopteryx* Agassiz, 1838

***Hoplopteryx* sp.**

Fig. 65



Fig. 65. *Hoplopteryx* sp. MGCB U3S1/2. Scale bar equals 5 mm.

Referred material. MGCB U3S1/2.

Locality. Bomba Quarry (Cinto Euganeo, Padova); Sinigaglia Quarry (Villa di Teolo, Padova).

Description and remarks. The specimen consists of an isolated opercle. It is deeper than long, with two strong spines along the posterior margin. The dorsal margin of the opercle is rounded, followed by a concavity and by an oblique and crenulated posteroventral margin converging with an acute angle with the anterior margin. The opercle exhibits a marked horizontal ridge ending with a spine

posteriorly plus some other shallow ridges also diverging from the articular condyle. The overall morphology of the opercle is very similar to that of the tranchichthyoid genus *Hoplopteryx* (Patterson, 1964). This is the first report of the genus from the Bonarelli Level of northeastern Italy.

Discussion

The fish assemblage of the Bonarelli Level from northeastern Italy appears to be rather diverse. The list of the taxa provides an insight into the results of our study (see Tab. 1). There are at least 28 taxa, versus 23 recognized by Sorbini (1976, 1980) and 16 reported by Khalloufi (2010). Khalloufi (2010) did not consider the chondrichthyans, but even considering only the actinopterygians our studied evidenced the presence of at least 21 taxa. The chondrichthyans are much more diverse than previously thought.

Tab. 1. Taxa identified in the present study.

Chondrichthyes	
<p>Lamniformes</p> <p>Mitsukurinidae</p> <ul style="list-style-type: none"> • <i>Scapanorhynchus raphiodon</i> <p>Cretoxyrhinidae</p> <ul style="list-style-type: none"> • <i>Cretoxyrhina mantelli</i> • <i>Cretalamna appendiculata</i> <p>Archaeolamnidae</p> <ul style="list-style-type: none"> • <i>Archaeolamna kopingensis</i> <p>Anacoracidae</p> <ul style="list-style-type: none"> • <i>Squalicorax falcatus</i> <p>Ptychodontidae</p> <ul style="list-style-type: none"> • <i>Ptychodus decurrens</i> 	<ul style="list-style-type: none"> • <i>Heckelichthys vexillifer</i> <p>Elopiformes</p> <ul style="list-style-type: none"> • ?Elopiformes indet. • <i>Davichthys lacostei</i> <p>Crossognathiformes</p> <p>Pachyrhizodontidae</p> <ul style="list-style-type: none"> • <i>Pachyrhizodus</i> indet. • <i>Pachyrhizodus subulidens</i> <p>Tselfatiiformes</p> <p>Plethodidae</p> <ul style="list-style-type: none"> • <i>Tselfatia formosa</i> • <i>Dixonanogmius dalmatius</i> <p>Tselfatiiformes?</p> <ul style="list-style-type: none"> • ‘<i>Protosphyraena</i>’ <i>stebbingi</i> <p>Protostomidae</p> <ul style="list-style-type: none"> • <i>Protostomias maroccanus</i> <p>Aulopiformes</p> <p>Ichthyotringidae</p> <ul style="list-style-type: none"> • <i>Ichthyotringa africana</i> <p>Dercetidae</p> <ul style="list-style-type: none"> • <i>Rhynchodercetis</i> sp. • <i>Enchodus venator</i> • <i>Rharbichthys ferox</i> <p>Polymixiiformes</p> <ul style="list-style-type: none"> • Polymixiiformes indet. <p>Beryciformes</p> <ul style="list-style-type: none"> • ?Beryciformes indet. • <i>Hoplopteryx</i> sp.
<p style="text-align: center;">Actinopterygii</p> <p>Pycnodontiformes</p> <p>Pycnodontidae</p> <ul style="list-style-type: none"> • <i>Paranursallia gutturosa</i> • ‘<i>Nursallia</i>’ <i>tethysensis</i> <p>Pachycormiformes</p> <p>Pachycormidae</p> <ul style="list-style-type: none"> • <i>Protosphyraena ferox</i> <p>Aspidorhynchidae</p> <ul style="list-style-type: none"> • <i>Belonostomus</i> sp. • <i>Belonostomus cinctus</i> • <i>Belonostomus</i> sp. <p>Ichthyodectiformes</p> <ul style="list-style-type: none"> • Ichthyodectoidei indet. <p>Ichthyodectidae</p>	

We identified three taxa never reported before from the BL (*Scapanorhynchus raphiodon*, *Cretalamna appendiculata* and *Archaeolamna kopingensis*). *Scapanorhynchus raphiodon* was found in the 1988 excavation carried out at Bomba Quarry and therefore the taxon was not included in previous studies. There are some additional differences between this study and that of Sorbini (1976) also concerning the identification of bony fishes i.e. *Heckelichthys microdon*, *Clupavus* cfr. *maroccanus*, *Pachyrhizodus intermedius*, *Paravinciguerrria praecursor*. In our analysis these taxa have been identified as *Heckelichthys vexillifer* (already correctly identified by Taverne, 2006), *Ichthyotringa africana*, *Pachyrhizodus subulidens* and *Protostomias maroccanus* (already referred by Khalloufi, 2010), respectively. We also identified some previously unreported taxa among the bony fishes, such the pycnodontiform ‘*Nursallia*’ *tethysensis*, at least two species of *Belonostomus*, *Dixonanogmius dalmatius*, ‘*Protosphyraena*’ *stebbingi* and *Hoplopteryx* sp. The presence of the aspidorhynchiform genus *Belonostomus* was already reported by Bassani (1880, 1882) from the bituminous shales cropping out near Crespano del Grappa (Treviso).

As regards the composition (Fig. 66), although it should be considered that it might be altered by sampling or preservation biases (Sorbini, 1976; Patterson, 1993), the ichthyofauna is apparently dominated by crossognathiforms, tselfatiiforms and aulopiforms. Ptychodontids and lamniforms also compose a rather significant part of the assemblage. The ichthyofauna contains apparently no clupeomorphs and very few pycnodonts, that are typically shallow-water fishes (Forey et al., 2003). Aulopiforms and other groups are usually interpreted by modern analogy as deep- or more open-water fishes (Forey et al., 2003). Therefore, the ichthyofauna mainly includes open water taxa. This is consistent with the general depositional environment of the BL in northeastern Italy.

Despite this study is based on material deriving from museum collections, it is possible to discuss some qualitative taphonomical aspects. The preservation of the specimens is generally poor, and the high grade of disarticulation of the fish remains, evidenced especially by the high number of isolated caudal remains of pachyrhizodontids, is possibly the product of some environmental disturbance on the sea floor. The best-preserved specimens are usually small-sized fishes, which are buried more quickly than the carcasses of larger individuals, which was exposed on the sea floor for a long period before burial. In fact, extensive disarticulation could be related to a prolonged residence time of the fish carcasses on the sea floor before the definitive burial by sediment or the development of microbial mats (Fürsich et al., 2007; Chellouche et al., 2012). In undisturbed environments the grade of disarticulation due to simple decay (e.g. by escaping gases from the body or settling of hard-parts into gravitationally stable positions after decay of soft tissues holding them in place) is directly proportional to the residence time of a fish carcass on the water-sediment interface (Lyman, 1994;

Chellouche et al, 2012). Other possibility to produce strongly disarticulated carcasses are currents or predation/scavenging activities. There is no direct evidence of this kind of biological disturbance on the fish remains. Therefore, we could not conclusively rule out this kind of disturbance that might cause disarticulation. There are also no clear tractive patterns on the fish remains that could imply strong currents, but disarticulation may be also produced by a bloating-and-floating mechanism or weak currents that scattered the remains on the sea floor. The high number of caudal remains in some contexts has been elegantly discussed and explained by Chellouche et al. (2012: p. 109) with a differential sequence of burial of the different components of the carcass after bloating-and-floating. This scenario perfectly matches also with the occurrence of isolated caudal portions of the body pertaining to pachyrhizodontids and other taxa in the BL. The same mechanism could explain the presence of isolated cranial remains or segments of vertebral columns, depending of the grade of adhesion or articulation within different body regions (e.g., more/less loosely attached skeletal elements, skin and soft part decomposition effects; see Chellouche et al., 2012). We do not have any direct evidence of hyperextended backward bending, but isolated skeletal portion could be a direct consequence of this mechanism occurring on the carcasses. The depositional context in anoxic conditions surely promoted the preservation but fully anoxic condition do not explain such decomposition processes occurring on the carcasses, therefore there could have been an alternation of oxic and anoxic condition at the water-sediment interface and in the superficial layers of the sea floor.

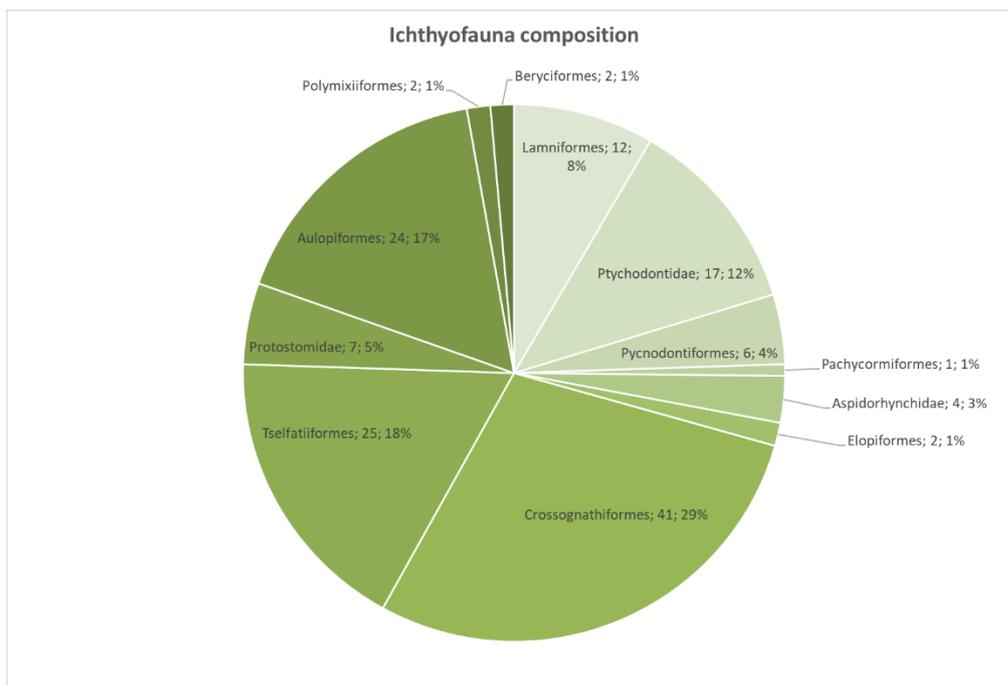


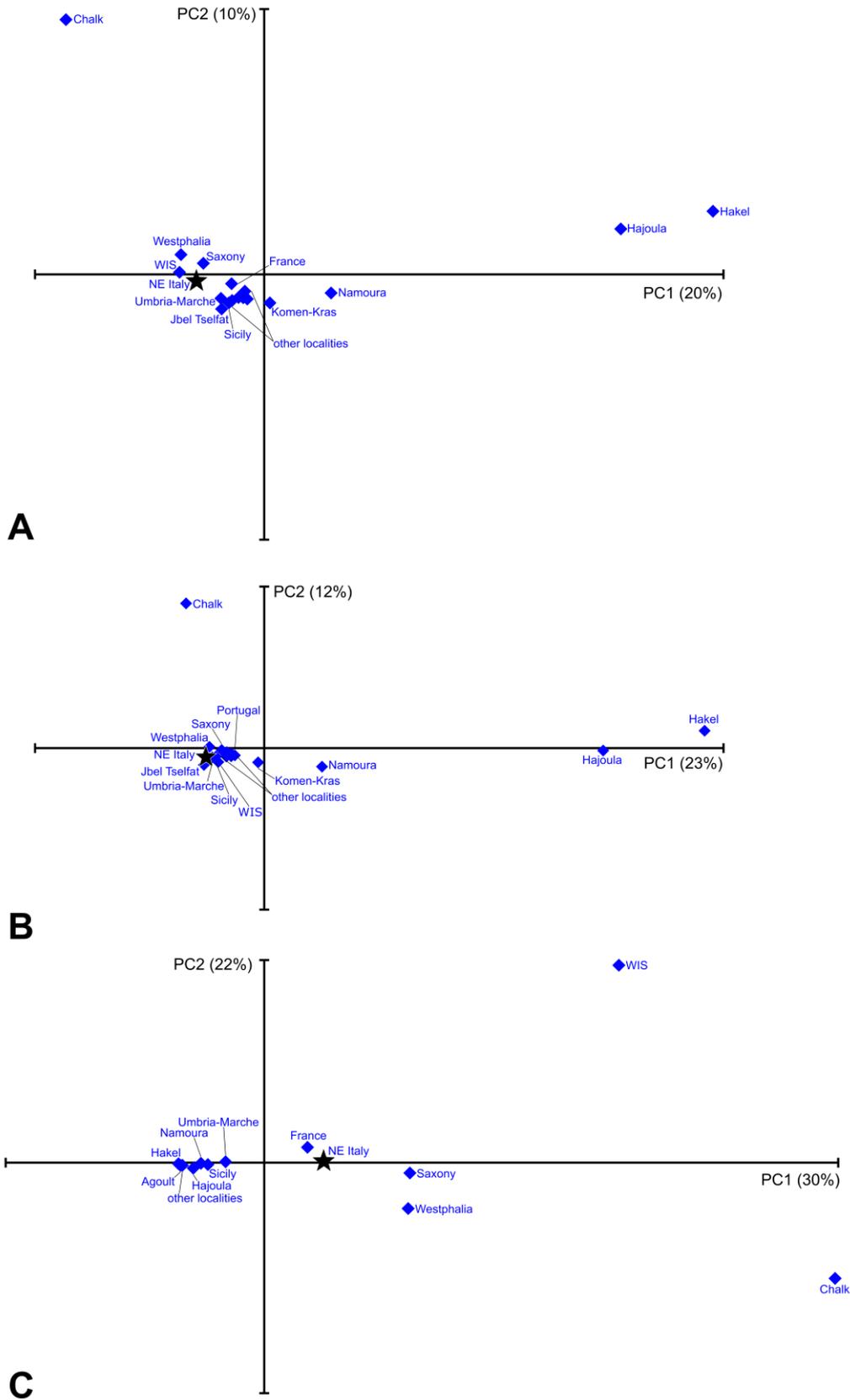
Fig. 66. The composition of the ichthyofauna from the Bonarelli Level of Northeastern Italy. The numbers refer to the amount of specimen referred to each group, followed by the percentage. The total number of specimens examined is 143.

Paleobiogeographic remarks

The study of the composition of the BL ichthyofauna from NE Italy allows to make some paleobiogeographic remarks. Forey et al. (2003) had already compared the Lebanese localities of Hakel, Hajoula and Namoura to other Cenomanian Tethyan localities but did not consider the NE Italy assemblage. Their study evidenced that, taking it as a whole, the Lebanon fauna appeared to be more closely similar to the fish faunas from Komen and Morocco (and perhaps Middle East, Portugal and Israel) than to that from the English Chalk. Forey et al. (2003) suggested that it was a real phenomenon, not affected by collecting or taphonomic artifacts. The difference might have been related to the difference to the marked boundary of distribution running at 30°N identified by Voigt (1996) for inoceramids and rudists. Forey et al. (2003) suggested that the boundary reflected cool, humid conditions to the north, that contrasted to arid conditions of the south, which experienced higher temperatures and formation of carbonate platforms (for a general overview on Cretaceous climate see Hay and Floegel, 2012). Forey et al. (2003) also presumed that the boundary could only be maintained through the Cenomanian by distinct ocean circulation, which would imply faunal separation. However, there are numerous recent studies that evidenced a rather dynamic oceanic circulation during the Cenomanian and especially during the OAE2 (see McLeod et al., 2008; Trabucho et al., 2010; Jarvis et al., 2011; Martin et al., 2012; Zheng et al., 2013, 2016; De Vivier et al., 2014; Jenkins et al., 2017). The analyses performed by Silva and Gallo (2016) on the paleobiogeography of enchodontoid fishes may support this assumption, because they evidenced during the Cenomanian a generalized NW-SE track probably related to a cold current from North reaching North Africa and Middle East. However, as more fossil deposits are found around the world, the similarities among the faunas from distant areas become apparent (Murray et al., 2013). Many of these fishes seem to represent geographically wide-ranging families, and even genera, especially considering elasmobranchs (see, e.g., *Cretoxyrhina* and *Ptychodus* from the BL level of northeastern Italy); however, at the lower taxonomic level they may appear much more restricted in their range. The Cenomanian paleobiogeography of the ichthyofaunas is characterized by vicariance and dispersal events. Patterns observed by Cavin (2008) concerned east-west events rather than north-south events. Such patterns are confirmed also in more recent studies on single clades (i.e., enchodontoid fishes) by Silva and Gallo (2016). This is probably because the separation between Laurasia and Gondwana was already underway in the Late Jurassic and affects only weakly the Cretaceous faunas (Cavin, 2008). The east-west pattern concerns mainly taxa from Africa versus South America and Central versus Western Tethys in the mid-Cretaceous and the results are in accordance with the time of the

opening of the Atlantic Ocean starting in the South then extending northwards (Cavin, 2008). Within this framework, we performed PCA and neighbor joining cluster analyses to compare several ichthyofaunas from the Cenomanian/Turonian boundary (CTB) to investigate their affinities (see Tab. A.1 in Appendices S. 2.3). Considering chondrichthyans and bony fishes together (Fig. 67A), the PCA evidences that the Lebanese and the English Chalk assemblages are completely different from the other assemblages. All other western Tethys assemblages are grouped together. This would suggest a strong endemism in the English Chalk assemblage. This fact was already evidenced by Forey et al (2003), Cavin (2008) and Friedman et al. (2016) as regards the English Chalk assemblages, but what concerns the Western Tethys localities considered as a whole could represent a new information. The datum of the Lebanese localities in our analysis is strongly affected by their enormous diversity, probably enhanced by Lagerstätte-effect and collection biases, already evidenced in other studies (e.g., Guinot and Cavin, 2016). The BL ichthyofauna is very close to the other localities from the Western Tethys domain, especially to Jbel Tselfat (Morocco). Their similarities were already evidenced by Sorbini (1976), Khalloufi (2010) and Khalloufi et al. (2010). However, it exhibits also a close affinity to the German assemblages (Westphalia and Saxony). This trend reflects the geographic proximity to these regions and evidences an apparent absence of strong physical barriers (currents, basins, etc.) between them. All trends evidenced are confirmed by the neighbor joining cluster analysis (Fig. A.3A). Considering the bony fishes alone (Fig. 67B, A.3B), the PCA and cluster analyses almost perfectly match the bony fishes+chondrichthyans analysis. It is noteworthy to evidence that the analysis of the chondrichthyan dataset alone (Fig. 67C, A.3C) evidences a strong separation between chondrichthyan assemblages of the English Chalk and the North American Western Interior Seaway (WIS), that would imply a strong provincialism in these two assemblages. Also removing the Lebanese localities and the English Chalk from the data set (Fig. 68), the WIS assemblages is completely separated from the other localities, resulting close to the other localities in the previous analyses probably for the sampling bias. The analyses depict an overall strong provincialism during the Cenomanian/Turonian, already reported also in other fossil groups (e.g., Kaufman, 1973; Hallam, 1974). Whether this reflects their true distributions, or merely a bias caused by lack of fossils (sampling or preservation bias) or even a lack of systematic revisions (e.g., the revision of the complex *Rhacolepis-Pachyrhizodus-Goulmimichthys*; see Cavin, 2008), may become clear with increased interest driving new finds and more excavations in Cretaceous deposits throughout the world (Murray et al., 2013). Our remarks should be tested furtherly and we hope that more intensive studies utilizing more specimens of all Tethyan localities will help to clarify the

paleobiogeography of Cretaceous ichthyofaunas and the factors (climatic, tectonic, etc.) driving their dynamics.



[previous page] **Fig. 67.** PCA analysis of the CTB assemblages. **A.** ‘fish’ (chondrichthyans+bony fishes) data set plot; **B.** bony fish data set plot; **C.** chondrichthyan data set plot. The names in the plots refers to the localities listed in Tab. A.1. The black star indicates the ichthyofauna from this study. Abbreviations: WIS, Western Interior Seaway (North America).

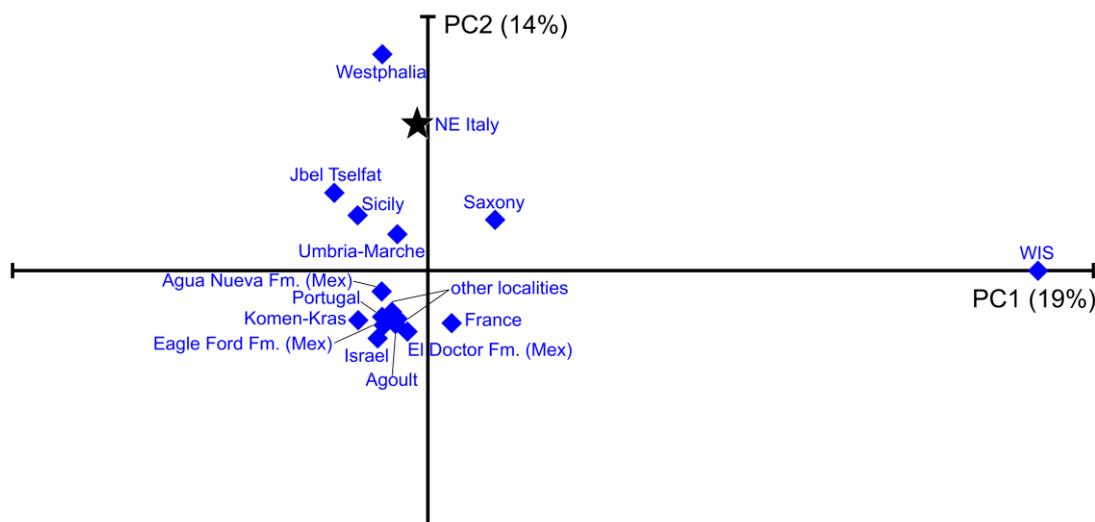


Fig. 68. PCA analysis of the CTB assemblages excluding the Lebanese and English Chalk assemblages. The names in the plots refers to the localities listed in Tab. A.1. The black star indicates the ichthyofauna from this study. Abbreviations: Fm., Formation; Mex, Mexico; WIS, Western Interior Seaway (North America).

Concluding remarks

The BL ichthyofauna from northeastern Italy was in need of a revision also to integrate the new material that was collected after the publication of the seminal paper on the Cinto Euganeo ichthyofauna by Sorbini (1976). Our revision considered the findings coming from three new fish-bearing localities: Carcoselle Quarry, Valdagno-Schio tunnel and Quero. We identified a total of at least 28 taxa, including six new additions (*Scapanorhynchus raphiodon*, *Cretalamna appendiculata*, *Archaeolamna kopingensis*, ‘*Nursallia*’ *tethysensis*, at least two species of *Belonostomus*, *Dixonanogmius dalmatius*, ‘*Protosphyraena*’ *stebbingi* and *Hoplopteryx* sp.). The overall assemblage is primarily composed by crossognathiforms, tselfatiiforms and aulopiforms. Therefore, the ichthyofauna mainly includes oceanic taxa, with a minor epipelagic component. The degree of preservation seems to be consistent with the depositional setting. A brief comparison with coeval assemblages evidences a general similarity with nearby western Tethyan fish assemblages and especially with the Jbel Tselfat (Morocco) ichthyofauna and the German assemblages. It is noteworthy to introduce that during the late Cenomanian a pattern of brief invasions of

boreal/northern faunas from the high latitudes caused by the oceanic circulation disturbances induced by the cooling phases of the OAE2 is observed in other groups (see Jefferies, 1962; Gale and Christensen, 1996; Jarvis et al., 2011; Zheng et al., 2013; Jenkins et al., 2017), that also follows the same path evidenced by the paleobiogeographic study by Silva and Gallo (2016) on the enchodontoid fishes. However, there is a consistent record of vicariance and events during the Cretaceous (Cavin, 2008) that implies faunal separations, and our analyses of the Cenomanian ichthyofaunas indicate an overall strong provincialism, therefore additional information would be necessary to more properly define the main global ichthyogeographic patterns during the Late Cretaceous.

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Chapter 3.

The Scaglia Rossa Formation ichthyofauna from northeastern Italy

3.1. First skeletal remains of the giant sawfish *Onchosaurus* (Neoselachii, Sclerorhynchiformes) from the Upper Cretaceous of northeastern Italy

Amalfitano et al., 2017. Cretaceous Research, 69, 124-135

3.2. Amalfitano, J., Dalla Vecchia, F. M., Giusberti, L., Fornaciari, E., Luciani, V., Roghi, G. (2017). Direct evidence of trophic interaction between a large lamniform shark, *Cretodus* sp., and a marine turtle from the Cretaceous of northeastern Italy

Amalfitano et al., 2017. Palaeogeography, Palaeoclimatology, Palaeoecology, 469, 104-121

3.3. First associated tooth set of a high-cusped *Ptychodus* (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of northeastern Italy, and resurrection of *Ptychodus altior* Agassiz, 1835

Amadori et al., 2019. Cretaceous Research, 93, 330-345

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

Amalfitano et al., 2019. Cretaceous Research, 98, 250-275

3.5. A revision of the Upper Cretaceous shark *Ptychodus mediterraneus* Canavari, 1916 from Italy, with a reassessment of *P. latissimus* and *P. polygyrus* Agassiz, 1835 (Chondrichthyes; Elasmobranchii)

Amadori et al. Accepted on Cretaceous Research.

3.1.

First skeletal remains of the giant sawfish *Onchosaurus* (*Neoselachii*, *Sclerorhynchiformes*) from the Upper Cretaceous of northeastern Italy

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Abstract

Sclerorhynchiform sawfishes are a diverse and extinct clade of elasmobranchs that is restricted to the Cretaceous. Most taxa are known only by isolated rostral spines, whereas skeletal remains are rare and have been reported from a small number of Upper Cretaceous localities. Here, we describe skeletal remains of the giant sclerorhynchiform *Onchosaurus pharao* for the first time, which provides new morphological information. The single specimen comes from middle-basal upper Turonian strata of the Lessini Mountains in northeastern Italy and represents the first record of this genus from Italy. The specimen consists of unidentifiable cranial remains, several diagnostic rostral spines, the rostrum with fragments of tessellated calcified cartilage, and 87 disarticulated vertebrae. The rostrum preserves the characteristic sensory system of sclerorhynchiforms. It is devoid of any lateral sockets indicating that rostral spines were attached laterally to its surface. This pattern is identical to most sclerorhynchiforms and extant pristiphoriformes implying also similar replacement patterns as in most other sclerorhynchiforms with the exception for *Schizorhiza*. Additionally, the bases of two longitudinally arranged rows of ventral rostral spines are identifiable concurring with patterns seen in *Sclerorhynchus*. The axial skeleton is partly preserved. Re-arranging the disarticulated vertebrae according to their life position in combination with measures of the size and thickness of preserved vertebral centra, and the ratio rostrum length/body size depending on the number of vertebral centra indicate that the specimen was ca. 450 cm long. Growth rings in the vertebral centra show that the specimen was about four years old and thus probably not yet fully sexual mature when it died. This age assumption corresponds well with the calculated size when compared with complete skeletons of extinct sclerorhynchiforms and extant pristiforms. The size of the specimen and its occurrence in hemipelagic rocks corroborates previous assumptions that this sclerorhynchiform was a large and pelagic sawfish.

Introduction

Upper Cretaceous chondrichthyans from northern Italy are known since the 19th century and are mainly represented by isolated teeth of ptychodontid and lamniform sharks, recovered from hemipelagic rocks of the Scaglia Rossa Formation (e.g., Catullo, 1827, Catullo, 1842, Lioy, 1865, Bassani, 1877, Pellegrini, 1883, D'Erasmus, 1922, Sirna et al., 1994, Dalla Vecchia et al., 2005). After a few initial studies aimed to describe some well-preserved and partially articulated specimens (e.g., Bassani, 1888, Canavari, 1916, Cigala Fulgosi et al., 1980), this chondrichthyan assemblage was neglected and remained practically unknown to the scientific community (Amalfitano et al., unpublished data). In the framework of a comprehensive project aimed to revise the entire vertebrate marine fauna of Scaglia Rossa Formation and its stratigraphic and paleoenvironmental context, we report here the first record of the extinct sawfish, *Onchosaurus pharao* (Dames, 1887a) from this unit and from the Cretaceous of Italy in general. *Onchosaurus* is placed traditionally into the Sclerorhynchidae, a clade that includes all extinct Cretaceous sawfish-like batoids with a cosmopolitan distribution during the Late Cretaceous (Corral et al., 2012, Kriwet and Klug, 2012). Sclerorhynchids possess an elongated rostrum with rostral spines that are not homologous to oral teeth (Smith et al., 2015, Welten et al., 2015). These spines are laterally attached to the rostral cartilage by connective tissue and replacement spines are formed parallel to the edge of the rostrum before being rotated into functional position (Cappetta, 1987, Wueringer et al., 2009). The pattern of rostral spine replacement in most sclerorhynchids is identical to that of living pristiphorid sawsharks, but differs from that seen in pristid sawfishes, in which spines grow continuously and are inserted into sockets along the lateral rostrum cartilage (e. g., Welten et al., 2015). The replacement mode, however, also seemingly differs between taxa included in the Sclerorhynchidae (Smith et al., 2015). It has been suggested that both sclerorhynchids and pristids are closely related with shovelnose rays, thus basal “modern” batoids (Cappetta, 1974, Wueringer et al., 2009, Cappetta, 2012, Underwood et al., 2015), while pristiphorids are squalomorph sharks (Cappetta, 2012, Underwood et al., 2015). According to the phylogenetic analysis by Kriwet (2004), all extinct sawfishes from the Cretaceous fall within the clade Sclerorhynchiformes. Currently, two clades, the Sclerorhynchidae and the Ptychotrygonidae are included in Sclerorhynchiformes. The different rostral spine replacement modes, however, suggest that Sclerorhynchidae and possibly Sclerorhynchiformes, as currently understood, might be paraphyletic.

The aim of this paper is to describe the skeletal remains of the giant sclerorhynchid *O. pharao* from the Scaglia Rossa Formation consisting of disarticulated vertebrae, several diagnostic rostral spines, the rostrum with fragmentary tessellated calcified cartilage and other fragmentary cranial remains. The specimen is not only the first documented record of this genus from Italy, but also the most

complete specimen of this taxon that has been recovered worldwide so far. Up to now, this species has been known only from isolated rostral spines. The new remains allow us to estimate the age and size of the specimen, using the rostrum length and vertebrae measurements, and to discuss its paleoecology. This information significantly contributes to our understanding of sclerorhynchid life history traits and lifestyles.

2. Locality and stratigraphic setting

The specimen was recovered from the “lastame”, a peculiar lithozone of the Upper Cretaceous Scaglia Rossa Formation (lithozone 2 of Lozar and Grosso, 1997), which crops out in the Lessini Mountains (western Veneto Region, northeastern Italy) (Fig. 1). This lithostratigraphic unit, which is ca. 7-8 m in thickness, consists of reddish, pinkish and whitish nodular hemipelagic limestones and marly limestones deposited during the early Turonian-early Santonian in open marine conditions on a pelagic rise, the “Trento Plateau” (Lozar and Grosso, 1997, Palci et al., 2013). The microfacies usually consists of wackestone with planktonic foraminifera, pithonellids, radiolarians and benthic foraminifera (Lozar and Grosso, 1997). “Lastame” is a package of 70-72 nodular/flaser beds intensively quarried for decorative and building purposes, especially in the surroundings of the village of S. Anna d'Alfaedo (about 30 km north of Verona). In the Veneto Region, “lastame” is renowned for its paleontological content consisting of invertebrates (echinoids, inoceramids, ammonites and rudists) and rare vertebrate remains, which are dominated by sharks associated with rare marine

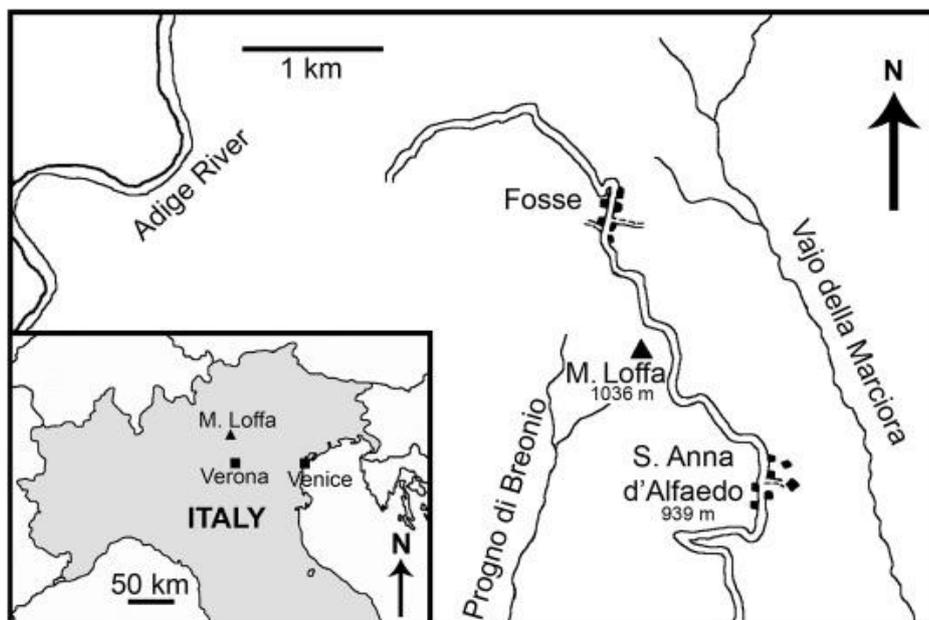


Fig. 1. Map of the surroundings of S. Anna d'Alfaedo and Mount Loffa. In the small box, the location of Mount Loffa in northern Italy is reported.

turtles and mosasaurs (e.g., Capellini, 1884, Cigala Fulgosi et al., 1980, Ginevra et al., 2000, Dalla Vecchia et al., 2005, Trevisani and Cestari, 2007, Roghi, 2010, Palci et al., 2013). Among sharks, the most common fossils are isolated teeth of *Ptychodus* and remains of lamniform sharks (e.g., *Cretoxyrhina mantelli*). These taxa are

represented by both isolated teeth and teeth associated with vertebrae and calcified cartilage remains (Cigala Fulgosi et al., 1980, Dalla Vecchia et al., 2005; Amalfitano et al., unpublished data).

The sawfish described here was found by Mr. Luigi Benedetti in 1981 in his quarry at Mount Loffa, close to the village of S. Anna d'Alfaedo (Verona Province). Although the finding dates back some 35 years ago, the specimen never received proper attention and was only recently mentioned as “Pristidae” in a list of fossils from the “lastame” compiled by Trevisani and Cestari (2007, p. 75).

Materials and methods

The skeletal remains described herein (rostrum, rostral spines, cranial remains and vertebrae) are preserved on two slabs of nodular/sub-nodular limestone (IGVR 45303 and IGVR 45304), both on exhibit in the Prehistorical and Paleontological Museum of S. Anna d'Alfaedo, northern Italy. The main slab (IGVR 45303) has an irregular polygonal outline and measures 340 cm in maximum length, 147 cm in maximum width and 10.5 cm in maximum thickness; the counter-slab (IGVR 45304) is smaller than the main slab and has an irregular polygonal shape, with its maximum length of about 172 cm, its maximum width of about 145 cm and its maximum thickness of 8 cm (see Fig. S1 of Supplementary material for more detailed measurements). The specimen was photographed with different digital cameras: a Nikon Coolpix L120, a Sony α 200 mounting 18-70 mm lens, and a Fuji XE1 mounting 18-55 mm lens. The specimen was also subjected to ortho-photography and macro-photography. The images were edited using the freeware GIMP (v. 2.8) and Inkscape (v. 0.91). Illustrative drawings using GIMP were produced to highlight or underline some morphological features, if difficult to identify in photographs alone. After this first step, we employed a UV light lamp (Way Too Cool, 95 Watt, Triple UVC-UVB-UVA-4608 West Bluefield Avenue, Glendale, Arizona, USA, AZ85308) to better observe morphological details of the rostrum. UV light has been widely used in paleontology (e.g., Haug et al., 2009, Trevisani and Cestari, 2007). This technique exploits the property of fluorescence of calcium carbonate, calcium phosphate (fluorapatite) and fossils with traces of organic material or remains. Delicate skeletal elements, including some bones, scales, and remains of soft parts, are sometimes poorly or not discernible at all in visible light, but are revealed under UV light. Furthermore, the contrast between the matrix and the fossil is enhanced considerably (Tischlinger and Arratia, 2013).

The measurements of the specimen were taken using the freeware ImageJ. The images used for the image analysis were orthophotos and detail photos of the specimen with metric scale. For the description of the rostral spines, their peculiar terminology and orientation, we used Corral et al., 2012, Kriwet and Klug, 2012 and Cappetta (2012) as references.

Two small limestone nodules detached from IGVR 45303 were processed for micropaleontological analyses. One nodule was processed following the cold acetolysis method of Lirer (2000) for isolating planktonic foraminifera of the >63 µm fraction, the other was utilized for thin section and for a preparation of a smear slide for calcareous nannofossils analysis.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, U.S.A.; **MB.f.**: Museum für Naturkunde, Berlin, Germany; **BMNH**: The Natural History Museum, London, UK (former British Museum of Natural History); **IGVR**: Inventario Generale Verona, Verona, Italy; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France.

Results

Systematic paleontology

Remarks. Controversy exists about the systematic rank of sclerorhynchoid batoids. Corral et al. (2012) and Cappetta (2012) consider this clade as a member of the Rajiformes using a traditional phenotypic approach for systematic arrangement of taxa, whereas Kriwet (2004) and Kriwet and Klug (2012) consider this clade to be of equal rank to the Rajiformes employing cladistics methods. Here, we follow the systematics based on Kriwet (2004), although the Sclerorhynchiformes might be paraphyletic (see Smith et al., 2015). A diagnostic feature of sclerorhynchiform batoids is the presence of tooth-like structures that are laterally aligned along the rostrum, which are not inserted in sockets similar to the condition seen in sawsharks (Pristiophoriformes), but conversely to the condition in extant sawfishes (Pristiformes). These structures are often named as “teeth” (e.g., “rostral teeth” in Cappetta, 2012, or “saw-teeth” in Welten et al., 2015), which might be misleading, seemingly implying that they are homologous to oral teeth. Recently, however, Smith et al. (2015) showed that these structures develop differently from oral teeth and are in serial homology with dermal denticles, as previously suggested by other authors (e.g., Cappetta, 1980). Consequently, we refer to these rostral elements as “rostral spines” here.

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
 Infraclass Neoselachii Compagno, 1977
 Superorder Batomorphii Cappetta, 1980
 Order Sclerorhynchiformes Kriwet, 2004
 Family Sclerorhynchidae Cappetta, 1974

Genus *Onchosaurus* Gervais, 1852

Type species: *O. radicalis* Gervais, 1852 from the Campanian of Meudon near Paris, France.

Referred species: *O. pharao* (Dames, 1887a)

Diagnosis (emended from Kriwet and Klug, 2012). Sclerorhynchiform sawfish characterized by a combination of the following characters: rostral spines large and dorso-ventrally flattened; dorsal peduncle face slightly convex in anterior and posterior views forming an obtuse downwardly inclined angle with peduncle basal face; ventral peduncle face concave in anterior and posterior views; crown low in relation to peduncle, smooth, and asymmetrically triangular with well-developed cutting edge; anterior margin of crown oblique, slightly sigmoidal and basally extending on peduncle; posterior margin of crown straight and almost vertical, may bear a single basally directed barb; dorsal crown face with very shallow basal depression; crown-peduncle junction well-marked and obliquely directed; peduncle high with flaring and strongly folded base, otherwise smooth; base rectangular with median depression in basal view; posterior margin of peduncle concavely notched along its entire length; rostrum bi-convex in dorsal view with greatest width in the middle portion; tectospondyl-type vertebral centra, slightly higher than wide; vertebral centra sizes diminish with a regular pattern posteriorly.

Onchosaurus pharao (Dames, 1887a).

Fig. 2-8

†1887a *Titanichthys pharao* Dames: 69, figs 1-2.

1887b *Gigantichthys pharao* (Dames, 1887a, Dames, 1887b): 137.

1917 *Onchosaurus pharao* (Dames, 1887a); Eastman: 95.

1921 *Onchosaurus pharao* (Dames, 1887a); Stromer: 121, fig. 11.

1940 *Onchosaurus pharao* (Dames, 1887a); Arambourg: 142, fig. 4; pl. 3, figs 6-9.

1943 *Onchosaurus pharao* (Dames, 1887a); Arambourg and Joleaud: 33, fig. 1; pl. 1, figs 1-7, 12.

1943 *Onchosaurus pharao* (Dames, 1887a); Darteville and Casier: 166, pl. 14, fig. 9.

1951 *Onchosaurus pharao* (Dames, 1887a); Dunkle: 346.

1986 *Ischyrhiza iwakiensis*, Uyeno and Hasegawi: 68, figs 1-2.

1987 *Onchosaurus pharao* (Dames, 1887a); Cappetta: 154.

1989 *Onchosaurus pharao* (Dames, 1887a); Lehman: 553, fig. 1.1.

2003 *Onchosaurus pharao* (Dames, 1887a); Al Maleh and Bardet: 392, 398.

2004 *Onchosaurus pharao* (Dames, 1887a); Suarez and Cappetta: 93.

2006 *Onchosaurus pharao* (Dames, 1887a); Jacobs et al.: 95, tab. 1.

2006 *Onchosaurus pharao* (Dames, 1887a); Cappetta: 179.

2007 Pristidae; Trevisani and Cestari: 75.

2012 *Onchopristis pharao* (Dames, 1887a); Martill and Ibrahim: 74, fig. 4.

2012 *Onchosaurus pharao* (Dames, 1887a); Corral et al.: 215, figs 2D-G.

2012 *Onchosaurus pharao* (Dames, 1887a); Kriwet and Klug: 53, fig. 2.

2012 *Onchosaurus pharao* (Dames, 1887a); Cappetta: 383.

Syntypes. MB.f.11217a-c and MB.f.11223 (Museum für Naturkunde Berlin, Germany) from the Santonian (Upper Cretaceous) of Gizeh, Egypt. The holotype is lost (see Kriwet and Klug, 2012).

Diagnosis. For species diagnosis see Kriwet and Klug (2012).

Material. Slabs IGVR 45303 and 45304 (slab and counterslab), housed at the Prehistorical and Paleontological Museum of S. Anna d'Alfaedo (Verona, northeastern Italy).

Locality and Horizon. The specimen was recovered from the Luigi Benedetti's Quarry at Mount Loffa, near S. Anna d'Alfaedo, and comes from the basal portion (beds 61-62) of the “lastame” lithozone of the Upper Cretaceous Scaglia Rossa Formation of Lessini Mountains. The microfacies of a nodule detached from slab IGVR 45303 is a wackestone/packestone with pithonellids, planktonic foraminifera and sparse crinoidal ossicles. Planktonic foraminifera, examined both in thin section and residue, are mainly represented by marginotruncanids and dicarinellids; the assemblage can be referred to the *Marginotruncana schneegansi* Zone according to Sliter (1989), due to the absence of *Helvetoglobotruncana helvetica* and *Dicarinella concavata*, which are biostratigraphic markers of the underlying and overlying zones, respectively. According to the zonal scheme of Ogg and Hinnov (2012), this zone corresponds to the middle and basal upper Turonian (Fig. S2 of Supplementary material). The smear slide contains few and poorly preserved calcareous nannofossils with no biostratigraphically useful taxa (Eliana Fornaciari, pers. com.).

Description

General description. The specimen (Fig. 2, Fig. 3) comprises a partially preserved elongated rostrum on the main slab (IGVR 45303) and an additional endocast (= internal mould) on the counterslab (IGVR 45304) with the tessellated calcified cartilage layer being preserved, seven rostral spines, two rows of small rostral ventral denticles, 87 disarticulated vertebrae and some fragmentary cranial remains. Jaw elements with oral teeth are seemingly not preserved or completely covered by rocky matrix and thus not accessible. Consequently, the morphology of oral teeth in this species remains unknown.

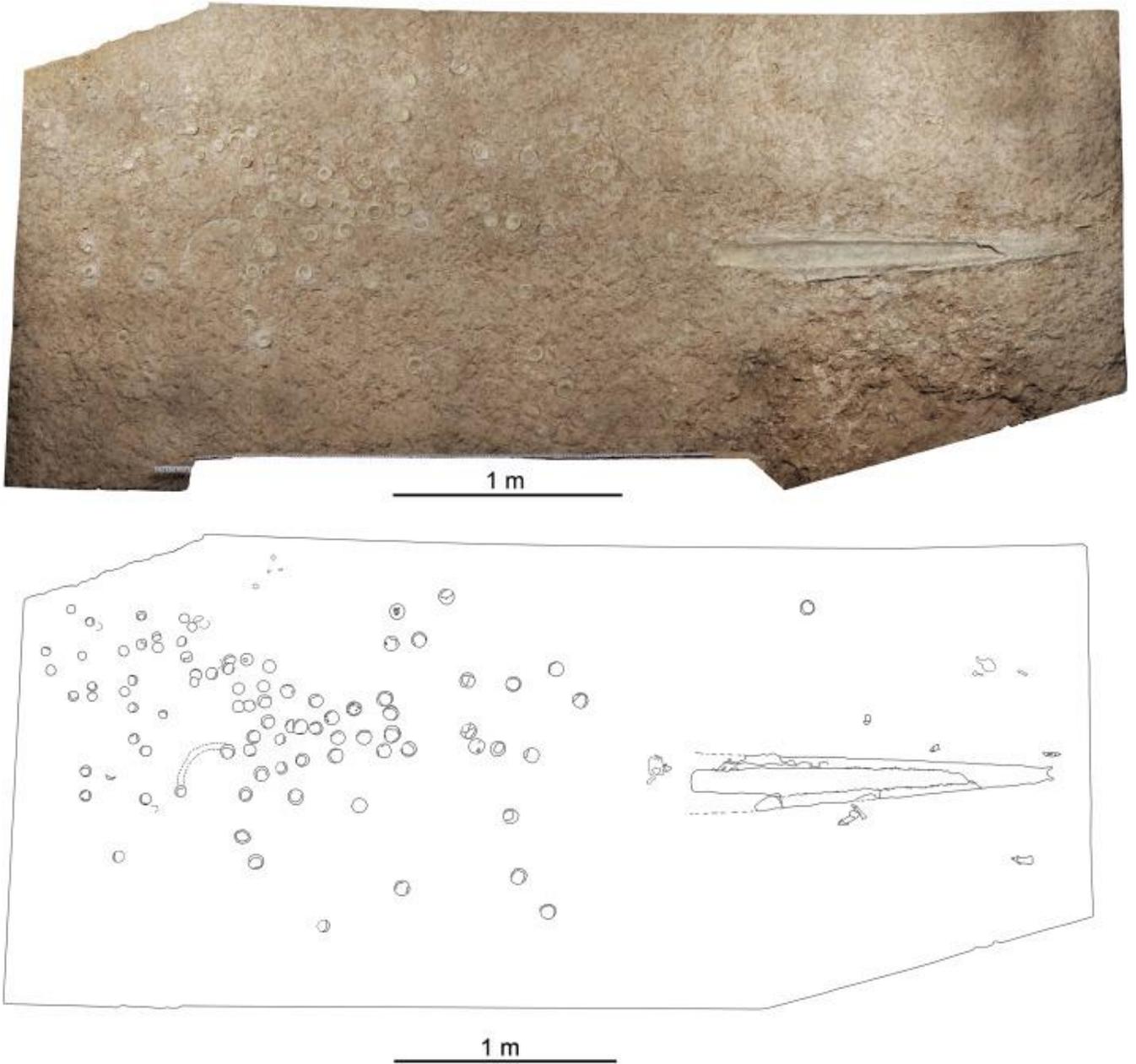


Fig. 2. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. The main slab, IGVR 45303, with the interpretative drawing.

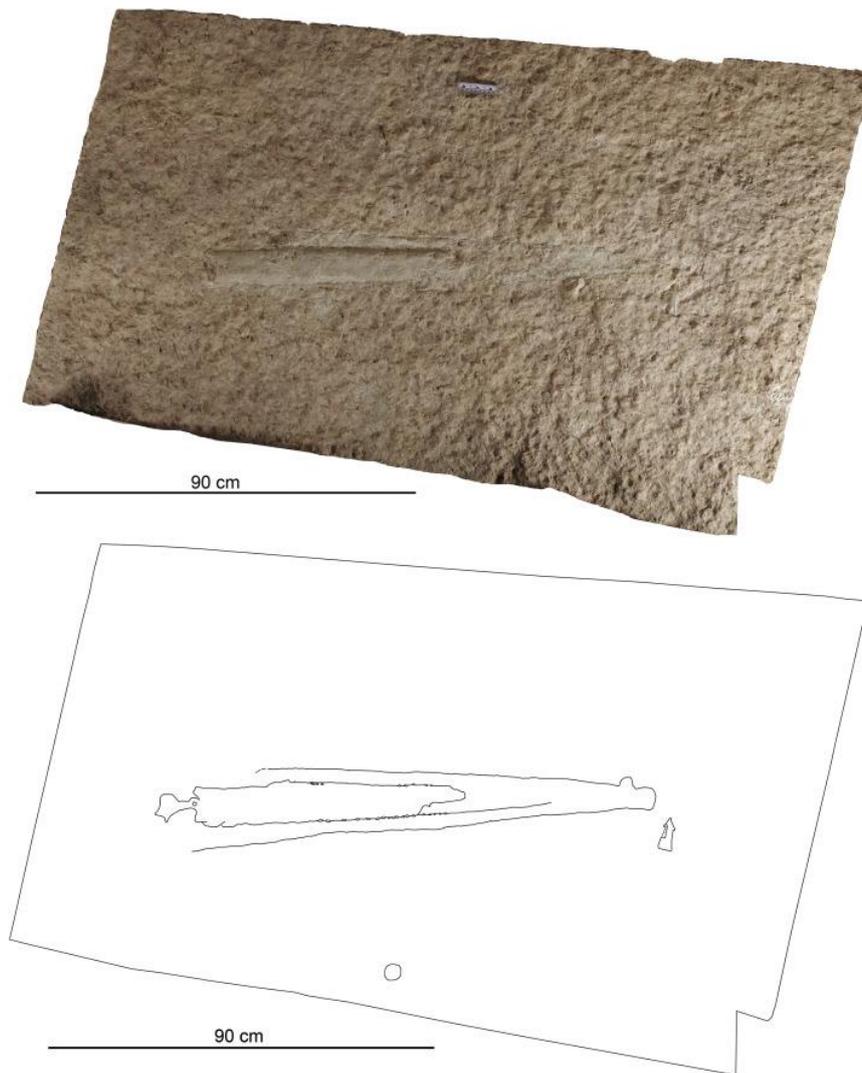


Fig. 3. *Onchosaurus pharao* from the Upper Cretaceous S. Anna d'Alfaedo. The counter-slab, IGVR 45304, with the interpretative drawing.

Cranium. Some fragments of tessellated calcified cartilage are preserved close to the base of the rostrum, which might be parts of the chondrocranium and of the nasal capsulae, respectively because of their position immediately posterior to the rostrum.

Rostrum. The rostrum, which is preserved on the main slab (IGVR 45303), is almost flat. The anterior tip and the posterior base are not well-preserved, and, for this reason, measurements were taken in correspondence of the phosphatic remains that delimit the rostrum outline. Accordingly, it measures 115 cm in length, 19 cm in width at the base, and ca. 3.5 cm in width at the tip. This rostrum displays a medial canal and two, nearly parallel grooves that extend close to its lateral edge converging towards the tip. The medial canal is 7 cm wide at the base of the rostrum, expands towards about a third of the entire length (maximum width: 7.5 cm), and then narrows towards the tip again (minimum width: 2.5 cm). Its preserved depth ranges from 1.2 to 1.5 cm. The lateral grooves narrow in width towards

the tip from ca. 3.5 cm to 2 cm. The internal mould is 64 cm long and 7.5 cm wide at its base. It expands towards the middle of its length (maximum width: 9 cm) and then narrows again towards the rostrum tip (5.5 cm). Its thickness is 2 cm. The visible surface of the mould corresponds to the ventral side of the rostrum.

Under UV and raking lights (Fig. 4, Fig. 5, Fig. 6) the rostrum and its internal mould reveal remains of the tessellated calcified cartilage of the ventral side of the rostrum. These remains are patchy and concentrated at the base and at about 2/3 of the length, at the tip of the rostrum and along one side of the internal mould and at its base. The UV and raking lights also reveal two rows of regularly spaced (ca. 5 mm) oval or nearly circular marks lateral to the medial canal; a partial row is also detectable on one side of the internal mould (Fig. 4, Fig. 5, Fig. 6). These marks represent the bases of two rows of additional small rostral denticles, which are arranged perpendicularly on the ventral surface of the rostrum, pointing ventrally.



Fig. 4. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. UV-photographs of a portion of the rostrum, IGVR 45303. Black arrows indicate the nearly circular marks interpreted as the bases of additional ventral spines.

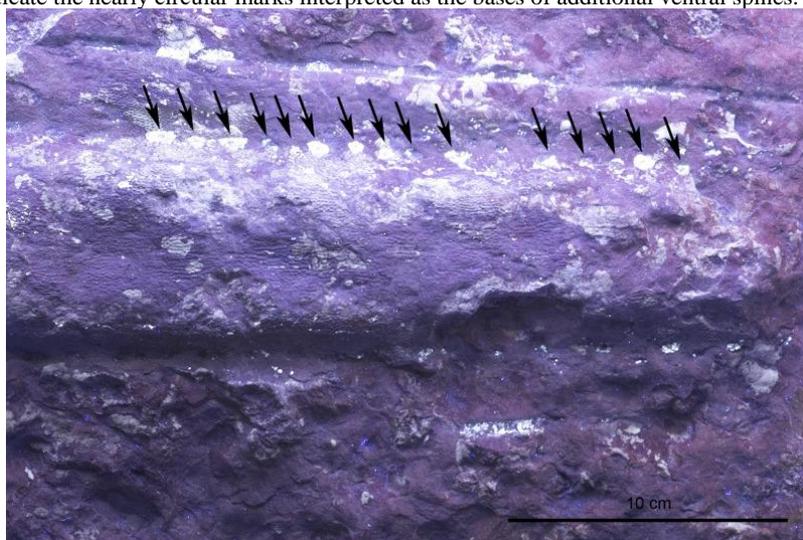


Fig. 5. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. UV-photographs of a portion of the rostrum internal mould, IGVR 45304. Black arrows indicate the marks interpreted as the bases of additional ventral spines.

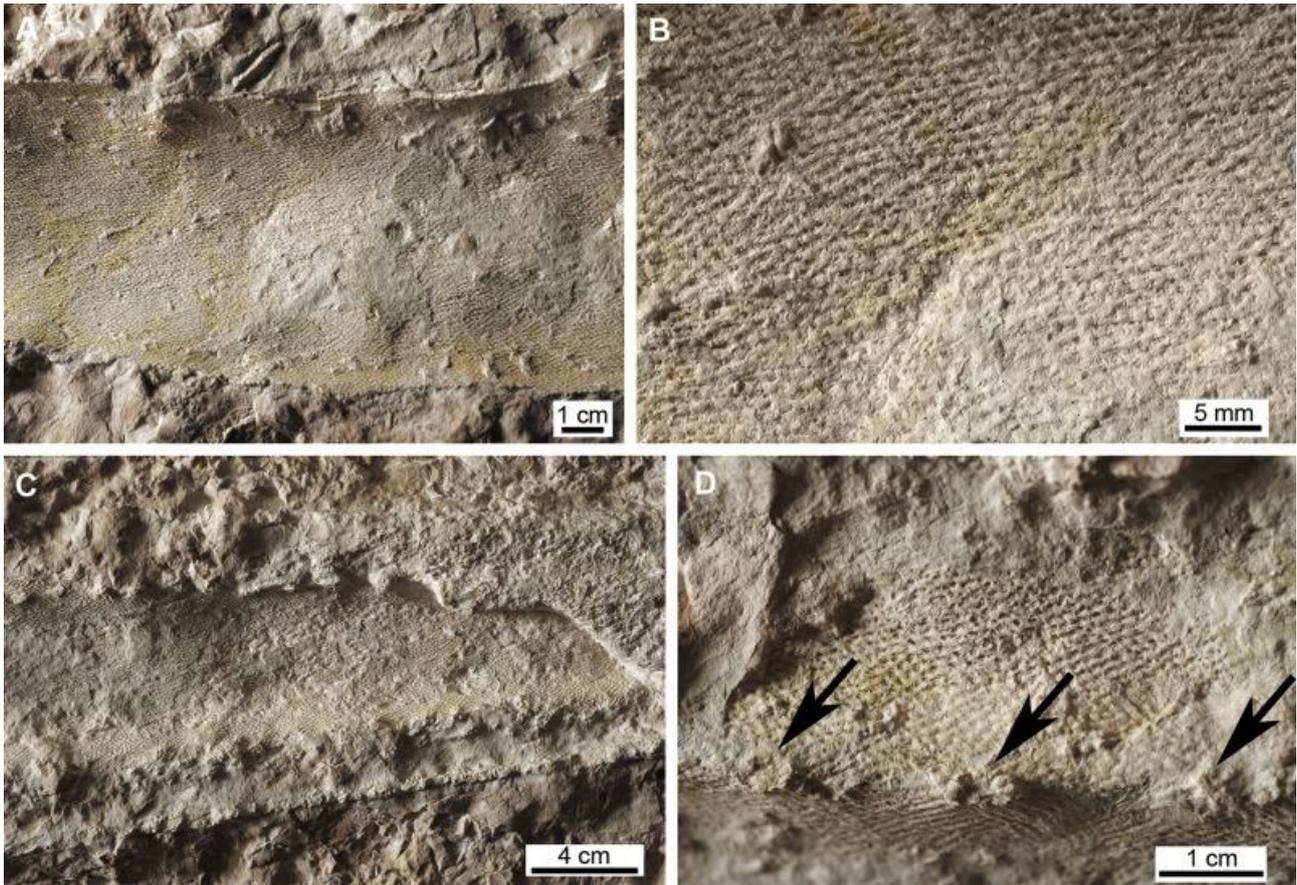


Fig. 6. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. Photographs of the rostrum under raking light, IGVR 45303. **A.** Base of the rostrum. **B.** Detail of the tessellated calcified cartilage of the base of the rostrum. **C.** The anterior part of the rostrum with the nearly circular marks in relief on both the sides of the medial canal that are interpreted as the bases of additional ventral spines. **D.** Detail of the bases of the additional ventral spines, with arrows indicating their position.

Rostral spines. Seven disarticulated rostral spines can be identified, six of which are preserved on the main slab (IGVR 45303) and one on the counter-slab (IGVR 45304). The spines are numbered arbitrarily from one to seven (see Fig. S1 of Supplementary material for their location). They all are embedded in the matrix and visible in different views. The state of preservation differs in every spine. Identification of ventral and dorsal faces is based on the concavity and convexity, respectively of the peduncle.

All spines (Fig. 7 and Fig. S3 of Supplementary material) are quite robust, apicobasally elongated, dorsoventrally flattened and present a peduncle, which is significantly longer than the crown. The upper portion of the anterior and posterior margins of the peduncle is nearly straight, but flares basally. Consequently, the peduncle tends to widen towards its base. The posterior margin of the peduncle is slightly concave. The base of all spines is either not well preserved or still embedded in the matrix. Therefore, the characteristic folding of the basal margin is not ascertainable.

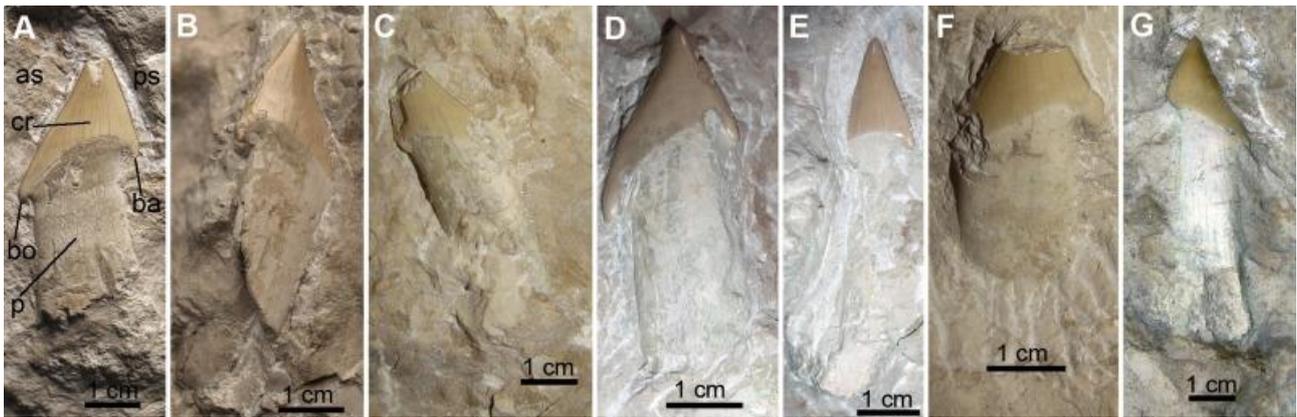


Fig. 7. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. Rostral spines. **A.** Spine no. 1. **B.** Spine no. 2. **C.** Spine no. 3. **D.** Spine no. 4. **E.** Spine no. 5. **F.** Spine no. 6. **G.** spine no. 7. Abbreviations: as, anterior side; ps, posterior side; cr, crown; p, peduncle; bo, boss; ba, barb.

The crown has a straight and nearly vertical posterior margin, with a posteriorly projected base forming a small barb. The anterior margin is slightly sigmoid (slightly concave in the upper and slightly convex in the lower part) and oblique. It extends basally to the anterior margin of the peduncle with a prominent boss, almost forming an anterior barb. The enameloid cover is smooth with an asymmetrical triangular shape in dorsal and ventral views and a slightly rounded apex. The cutting edge is continuous across the crown and distinct. The basal enameloid margin of the crown forms a narrow arc pointing backwards. The notches between the barb and the posterior peduncle margin and between the anterior margin and the boss display both a hook-like shape. A detailed description of every spine, including measurements, follows below.

Spine no. 1 (Fig. 7A) is on the main slab and exhibits its dorsal convex face. Its crown apex is partially broken, and the lower portion of the peduncle is partially eroded or dissolved. The total length of the spine as preserved is 6.2 cm. The crown is 2.5 cm high, measured from the base of the boss to the apex, and 2.2 cm wide. The anterior margin of the crown measures 3.1 cm in length and the posterior one 2.2 cm. The angle formed by both anterior and posterior margins is about 50°. The peduncle is 1.5 cm wide in its upper portion and 2.5 cm at the base. The anterior and posterior margins of the peduncle are 3.3 and 4.1 cm long, respectively. Six delicate ridges are preserved in the upper portion of the peduncle and extend to its middle part. The barb is almost completely covered by rocky matrix, while the boss is very evident.

Spine no. 2 (Fig. 7B) is situated close to the rostrum on the main slab and displays its posterior and ventral concave faces. The barb is very evident. The lower part of the peduncle is broken, but its partial imprint is still visible in the rock. The spine is 6.2 cm long, including the imprint. The crown is 2.1 cm high (from the apex to the lower end of the barb) and 1.8 cm wide in its exposed parts.

Spine no. 3 (Fig. 7C) is located at about 2/3 of the rostrum length, above the rostrum, exposing only the dorsal face. Most of the apical part of the crown is lacking. The anterior margin is partially

preserved, while the posterior one is not visible. The crown is almost 2 cm wide. The upper part of the peduncle is exposed, while the lower one still is embedded in the rock. The preserved part of the spine is 3.7 cm long. The upper part of the peduncle is 1.5 cm wide.

Spine no. 4 (Fig. 7D) is one of the best-preserved rostral spines. It is exposed near the rostrum with the crown pointing towards the supposed posterior part of the association and most likely shows its dorsal face. The crown is very well preserved, with undamaged boss and barb. Parts of the posterior margin of the crown are fractured and seem to have been glued to the slab. The base of the peduncle and parts of its posterior margin still are covered by matrix. The exposed part of the spine is 5 cm long, so it was probably longer. The crown is 2.6 cm high and 2 cm wide. The anterior and posterior margins of the crown are 3.1 and 2 cm long, respectively. The angle formed by the margins is about 50°. The exposed part of the anterior margin of the peduncle is 2.6 cm long; the upper part of the peduncle is 1.5 cm wide.

Spine no. 5 (Fig. 7E) has a well-preserved crown, while most of the peduncle is still embedded in the rock and its base is broken. This spine is situated very close to spine no. 4 and is oriented perpendicularly to the rostrum, with the crown pointing towards it. The exposed face is probably the ventral one, because it is slightly concave. The total length is 6.3 cm. The posterior margin of the crown, which is the only completely visible one, measures 2 cm. The posterior barb is visible. The anterior part of the spine is completely embedded in the rock.

Spine no. 6 (Fig. 7F) is exposed dorsally. The apical part of the crown and the boss are broken and absent; only parts of the anterior and posterior margins of the lower part of the crown are preserved. The barb is visible and well developed. The peduncle is mostly covered by matrix, showing only its upper part. No measurements were taken due to its poor state of preservation.

Spine no. 7 (Fig. 7G) is the most complete and largest spine of the sample. It is preserved on the counter-slab (IGVR 45304), near the tip of the internal mould of the rostrum and shows its slightly convex dorsal face. It is almost intact. Basally near the anterior margin, the peduncle shows just a depression with an irregular outline that probably represents a post-mortem damage. The boss is very evident, while the barb is covered by matrix, as also are parts of the posterior margin of the peduncle. The total length measures 7 cm. The crown is 2.5 cm high and almost 2 cm wide. The exposed part of the anterior and posterior margins of the crown is 2.8 and 1.5 cm long, respectively. The angle formed by the margins is about 50°. The anterior margin of the peduncle is 4.4 cm long, while the posterior one, as can be measured in its exposed parts, is 5 cm long. The upper and lower parts of the peduncle are 1.4 and 2.4 cm wide, respectively.

Vertebral centra. A total of 87 disarticulated vertebral centra are preserved on the main slab (IGVR 45303). Twelve of them are damaged or incompletely preserved. Except for one, they are all partly or almost completely covered by rock or by other vertebrae (Fig. 8). For this reason, no reliable

measurements of those vertebrae could be taken. The measurements of the other vertebrae are reported in Table S1 of Supplementary material (see Fig. S1 of Supplementary material for the numeration).



Fig. 8. *Onchosaurus pharao* from the Upper Cretaceous of S. Anna d'Alfaedo. Vertebral centra. **A.** One centrum in lateral view (no. 33). **B-C.** Some centra in anteroposterior view (no. 2, 31-33-34), with black asterisks indicating the growth bands and the white asterisk indicating the birth band. **D.** Detail of the cross-section of a broken centrum (no. 13).

The vertebrae display the tectospondylous mineralization pattern *sensu* Hasse (1879) that is characteristic of batoids. Most preserved vertebral centra are slightly higher than wide. The smallest vertebral centrum (no. 80) measures about 2.5 cm in width and 2.6 cm in height, while the widest (no. 11) measures 4.6 cm in width and 4.3 cm in height. The highest vertebral centrum measures 4.6 cm (centrum no. 18). Differences between width and height of similarly sized vertebral centra result from taphonomic biases. Seemingly, vertebral centra diminish in size posteriorly following a very regular pattern (Fig. 2).

Age and maturity

Different mineralization zones can be identified on the vertebral centra and in the cross-section of a fractured centrum (Fig. 8C, D), corresponding to growth rings or annuli. Narrow bands indicate slower growth periods and adjacent broader zones indicate faster growth periods, suggesting episodic growth (Frederickson et al., 2015). A total of four, probably five zones are identifiable indicating that the specimen was at least four, but not more than five years old and probably not yet fully sexual mature when compared to living pristids (see below).

Body size estimate

Precise measuring of the width and height of the vertebral centra is hampered by the fact that at least some centra might have been compacted during fossilization and are thus slightly irregular in shape and thickness. Nevertheless, even though only a part of the total vertebrae are preserved, they allow a rough estimate of the vertebral column length using a linear regression model assuming that vertebral centra decrease in size regularly in caudal direction. Thickness of vertebral centra (where it could be measured) indicates that it is almost the same for all and only slightly decreases posteriorly. This allows to re-arrange the vertebral centra into a vertebral column based on their measurements. The graph (see Fig. S4 of Supplementary material) illustrates well that seemingly only vertebral centra from the anterior part of the body are preserved, while smaller ones from the posterior part are missing. Living pristids (e.g., Thorburn et al., 2007; JK, pers. obs.) and extinct sclerorhynchids such as *Libanopristis* and *Sclerorhynchus* from the Upper Cretaceous of Lebanon (JK, pers. obs.) have a total of 213-240 vertebral centra, most common counts being around 230 vertebral centra. Although it was impossible to measure the thickness of all preserved vertebral centra in IGVR 45303-45304, it is possible to use the mean of the five measured centra, which is 15 mm for roughly estimating the length of the vertebral column. Accordingly, the length of the vertebral column of this specimen was 345 cm, assuming 230 vertebral centra as approximate estimate in comparison with living pristids. Combining this with the length of the rostrum length would amount to 460 cm, keeping in mind that no measurements of the cranium can be included.

Applying a linear regression model shows, furthermore, that the preserved vertebrae occupy almost the upper half of the best-fit line. Calculating the possible number for the remaining space (assuming that vertebrae diminish in size regularly with no or only few vertebrae being of the same size) results in 98 possible additional vertebral centra (185 vertebrae in total). Accordingly, the total postcranial size amounts to 322 cm.

Additional information about the total body length of this specimen can be derived from the length of the rostrum alone. In living pristids, the rostrum accounts for 30% and 20-25% of the total body size in juveniles and adults, respectively (Thorson, 1982, Miller, 1995, Thorburn et al., 2007). Similarly, the rostrum constitutes about 25% of the total body size in various sclerorhynchiforms from Lebanon (JK, pers. obs.). Thus, this specimen was ca. 460 cm long assuming similar relationships between rostrum length and total body size as in living pristids.

Discussion

IGVR 45303-45304 is the most complete specimen of the extinct sawfish *Onchosaurus*. This genus has been known so far only by isolated and generally large rostral spines providing the only diagnostic characters, such as generally flattened shape of the spines, shape and outline of the crown and the cutting edges, shape and outline of the peduncle and its base, and the peduncle size in relation to the crown. Currently, two species, *O. pharao* and *O. radicalis*, are distinguished (Cappetta, 2012). For a review of the diagnostic features of the two species see Corral et al. (2012) and Kriwet and Klug (2012). The robust aspect of the rostral spines of IGVR 45303-45304, their near vertical peduncle margins, which flare basally, and the presence of a posterior barb (Fig. 7) allow their assignment to *O. pharao*. In *O. radicalis*, conversely, the spines are more slender, the posterior margin of the peduncle is more concave and the posterior crown barb is absent. Moreover, the basal enamel margin of the crown of the spines of the “lastame” specimen forms a posteriorly pointing arc, which is a diagnostic feature of *O. pharao* (see Corral et al., 2012), though this is not detectable in all the specimens described and figured by Kriwet and Klug (2012).

Another important feature of the rostral spines of the sample is the prominent boss that almost forms an anterior barb (Fig. 7). This feature is shared with the syntype of *O. pharao* MB.f.11217a from Egypt (Corral et al., 2012: fig. 2E) and the Peruvian specimen figured in Kriwet and Klug (2012: fig. 2). Additionally, the size of the rostral spines of the specimen herein described is similar to the size of the spine from Peru, which measures 6.3 cm in length. The same applies to the measurements of the crown and peduncle.

The rostral spines of IGVR 45303-45304 are morphologically very similar to those housed in the MNHN (without number) (Kriwet and Klug, 2012: fig. 3J-M), which come from the Turonian of Damergou (Niger), and BMNH P.28478a-b (Kriwet and Klug, 2012: fig. 3Q-S), which is from the Santonian of Sinai (Egypt). All share the shape of the peduncle with near vertical margins and the overall shape of the crown. These African spines, however, differ from those of the specimen IGVR 45303-45304 in the morphology of the anterior crown boss, which is only slightly prominent and is not separated from the upper portion of the peduncle by a notch. In IGVR 45303-45304, the similar

size of all spines could be indicative of their provenance from very similar positions in the rostrum. We hypothesize that all the preserved spines come from the middle portion of the rostrum. In fact, the rostral spines from the median part of the rostrum of the Sclerorhynchidae are more or less of the same size (Cappetta, 2012).

Partially or completely preserved rostra are relatively scarce in the sclerorhynchiform fossil record and occur in complete skeletons from the Upper Cretaceous (Cenomanian) of Lebanon (e.g., *Libanopristsis*, *Micropristsis* and *Sclerorhynchus*) (e.g., Arambourg, 1940, Cappetta, 1980, Kriwet, 2004, Cappetta, 2012, Underwood et al., 2015); in *Onchopristsis* from the Cretaceous of Europe, North America and North Africa (e.g., Kriwet and Kussius, 2001, Cappetta, 2012); and in *Schizorhiza* (traditionally assigned to the sclerorhynchids, but still with uncertain position) from the Upper Cretaceous of Africa, America, and Near East (e.g., Cappetta, 2012, Smith et al., 2015). Fossil rostra are known from the pristiform sawfishes *Pristis* from the Paleogene of Africa (e.g., Cappetta, 2012) and *Propristsis* from the Eocene of North America and Africa, of which a 2.15 m-long rostrum is known (e.g., Cappetta, 1987).

The specimen reported here is the first record of skeletal remains of a Cretaceous sawfish from Europe and it displays the general features typical for sclerorhynchiforms.

The rostrum of the large *Onchosaurus* from Italy not only allows a general description of its morphology but also provides additional information about the internal structure of rostra in sclerorhynchiform sawfishes, described for the first time in *Libanopristsis* (Cappetta, 1980). Three cartilaginous bands encrusted with calcite form the rostrum in sclerorhynchid sawfishes (Arambourg, 1940, Cappetta, 1980). These cartilages include one medial unpaired canal, a pair of parallel dorsal grooves on the surface of the rostrum, where the superficial ophthalmic nerve was located, and a pair of parallel ventral grooves also on the surface of the rostrum, for the bucco-pharyngeal nerve (Wueringer et al., 2009). A thin sheet of cartilage is assumed to have covered the ventral grooves (Cappetta, 1987, Werner, 1989, Kirkland and Aguillon-Martinez, 2002, Wueringer et al., 2009). These structures also occur in the specimen described here and are encrusted with tessellated calcified cartilage, in particular the medial canal (Fig. 7). The tessellated calcified cartilage presents a peculiar kind of mineralization (prismatic calcification), typical of chondrichthyans, and characterize the axial and appendicular skeleton, differing from the vertebral calcified cartilage (areolar calcification) (Dean and Summers, 2006). The grooves on both surfaces of the rostrum undoubtedly correspond to the grooves for the bucco-pharyngeal nerve.

In all known sclerorhynchids, the rostrum starts at the nasal capsulae, regularly widening until it reaches a maximum width, and then tapers towards the tip (e.g., *Libanopristsis*; Cappetta, 1980). We can observe the same trend in the rostrum described here. The width of the medial canal follows that of the rostrum and its maximum is reached in the middle portion of the rostrum, where also the largest

rostral spines are located. The functional significance of these structures remains unclear at the moment. The superficial arrangement of the ophthalmic superficial and buccal nerves in IGVR 45303-4, which corresponds to the pattern seen in other sclerorhynchiforms, supports the interpretation that this is the general arrangement for this extinct clade. In this, the sclerorhynchiforms differ significantly from living sawfishes, where these nerves are included in ducts in the rostrum, and are more similar to the condition seen in living sawsharks (Pristiophoriformes).

The new specimen reported herein is exceptional, because it displays two parallel rows of regularly spaced and nearly circular marks that are visible under the UV or raking light on the rostrum and its internal mould (Fig. 4, Fig. 5, Fig. 6). They have been reported only recently from another sclerorhynchiform, *Sclerorhynchus atavus* (see Underwood et al., 2015, Welten et al., 2015). These marks correspond to the bases of additional rostral denticles that extend along the entire length of the ventral surface of the rostrum. These additional ventral denticles also occur in the sawshark *Pristiophorus* (Welten et al., 2015), but not in other sawfishes.

Onchosaurus shares with the sclerorhynchiforms *Pucapristis* and *Schizorhiza* a distinct rostral spine histotype, which consists of a core of osteodentine, while in some other sclerorhynchiforms, a core of orthodentine surrounds the pulp cavity (e.g., Kriwet and Klug, 2012, Smith et al., 2015). This supports the hypothesis that the Sclerorhynchidae and possibly even the whole Sclerorhynchiformes might not represent a monophyletic group, pending further studies. The importance of the histotype of the rostral spine for systematic purposes, however, remains ambiguous momentarily because not all taxa have been studied so far. Moreover, the differences in rostral spine histotypes recorded by Cappetta (2012) might be related to biased samples comprising spines of different developmental stages that also can be misinterpreted as divergences within congeneric taxa as recorded by Slaughter and Steiner (1968) (Underwood et al., 2015).

Both body size estimate procedures employed here (vertebral column length + rostrum length; length of rostrum as proportion of total body size) result in similar values providing a reliable minimum body length of more than 400 cm, probably as much as 460 cm for this specimen. Using a threshold of 25% for the proportion that the rostrum contributes to the total body length agrees with the assumption that the specimen was around four to five years old and thus probably not yet fully grown, if compared to extant pristids. In fact, in adult living pristids, the rostrum only contributes 20-22% to the total body length (Thorson, 1982). This would indicate that *Onchosaurus* could have grown up to about 520-575 cm in total body length. Using a simple regression for presuming missing vertebral centra seemingly does not yield any realistic counts since complete sclerorhynchiforms from Lebanon display more than 200 vertebrae conversely to the calculated number being smaller than 200 in *Onchosaurus*. However, this can provide a rough estimate of the total body length of the described specimen. Nevertheless, it could be argued that large sclerorhynchiforms had fewer vertebral centra,

which then could also indicate different mobility abilities. The specimen seemingly is not yet fully sexual mature despite its size. Available information for living elasmobranchs including batoids indicates a two-phased growth model (Arraya and Cubillos, 2006) in which growth is fast until maturity but decreases when maturity is reached (e.g., Licandeo et al., 2006, Smith et al., 2007).

Conclusions

Onchosaurus has a Turonian-Campanian range. In particular, remains of *O. pharao* occur in upper Turonian to middle Campanian strata (corresponding to a time span of over 10 Myr) of Africa, Middle East, North America, South America, and Japan (Antunes and Cappetta, 2002, Corral et al., 2012, Kriwet and Klug, 2012), so entirely in the Tethyan domain, not in northern Europe nor in the northern part of North America, as far as we know, despite lots of offshore sediments of this age. The specimen reported herein is between middle and (basal) late Turonian in age and fossilized in a hemipelagic setting, corroborating the previous assumptions of *Onchosaurus* distribution and paleoecology. Kriwet and Klug (2012) considered this sclerorhynchiform a large, cosmopolitan and pelagic sawfish based on its geographic distribution and the size of its rostral spines. Most likely, *Onchosaurus* was not a benthic batoid as most other sclerorhynchids but a highly migratory and open water sclerorhynchid similar to living mobulids. The Italian specimen is the first report of associate skeletal remains and rostral spines of this genus. Other sclerorhynchiforms were previously known from exceptionally well-preserved specimens (especially from Lebanon), but did not reach the size of the described specimen, which represents the largest individual ever reported of this group. The only other sclerorhynchid that seemingly also grew to very large sizes was *Onchopristis numidus* (Haug, 1905) for which Stromer (1921) assumed a length up to 8 m. Furthermore, *Onchosaurus* is a further addition to the vertebrate assemblage from the “lastame”, which appears to be more diverse than previously assumed. Further studies will allow highlighting the patterns of palaeobiodiversity through the time in the “lastame”, which needs an overall stratigraphic revision.

Acknowledgments

We thank Roberto Zorzin (Natural History Museum of Verona) for the permission to study the specimen under his care and for precious information. All necessary permits were obtained from Veneto Region Archaeological Soprintendenza; prot. no. 156 08/01/2016. The photographs of IGVR 45303 and 45304 (Fig. 2, Fig. 3, Fig. 4, Fig. 5, Fig. 6, Fig. 7, Fig. 8 and Fig. S3 of Supplementary material) are printed and made available under permission of Ministero per i Beni e le Attività Culturali - Veneto Region Archaeological Soprintendenza (prot. no. 9454 PD-RE 08/09/2016). All rights reserved. Thanks also to Elisa Marchesini (Associazione Culturale Officina 3) for favouring the access to the specimen housed and exhibited at the Prehistorical and Paleontological Museum of S. Anna d'Alfaedo. Stefano Castelli (Department of Geosciences of University of Padova) is deeply acknowledged for his help with photographs and images preparation. Thanks to Eliana Fornaciari for the personal communication on the calcareous nannoplankton. We are also grateful to Valeria Luciani (Department of Physics and Earth Sciences of the University of Ferrara) for her help with the determination of the planktonic foraminifera.

Funding for this research to FMDV and LG was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled “Reappraisal of two key Fossil-Lagerstätten in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach”, assigned to Eliana Fornaciari). JA's stay in Vienna was funded by six months post-graduate grant provided by Fondazione “Aldo Gini” (Padova) (prot. 57/15). We are grateful to two anonymous reviewers and to the editor, E. Koutsoukos, who gave very detailed and constructive reviews that improved the paper.

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3.2.

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 m) is a pellet-like accumulation of partially broken bones belonging to a large chelonioid 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.

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, 1885, 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.

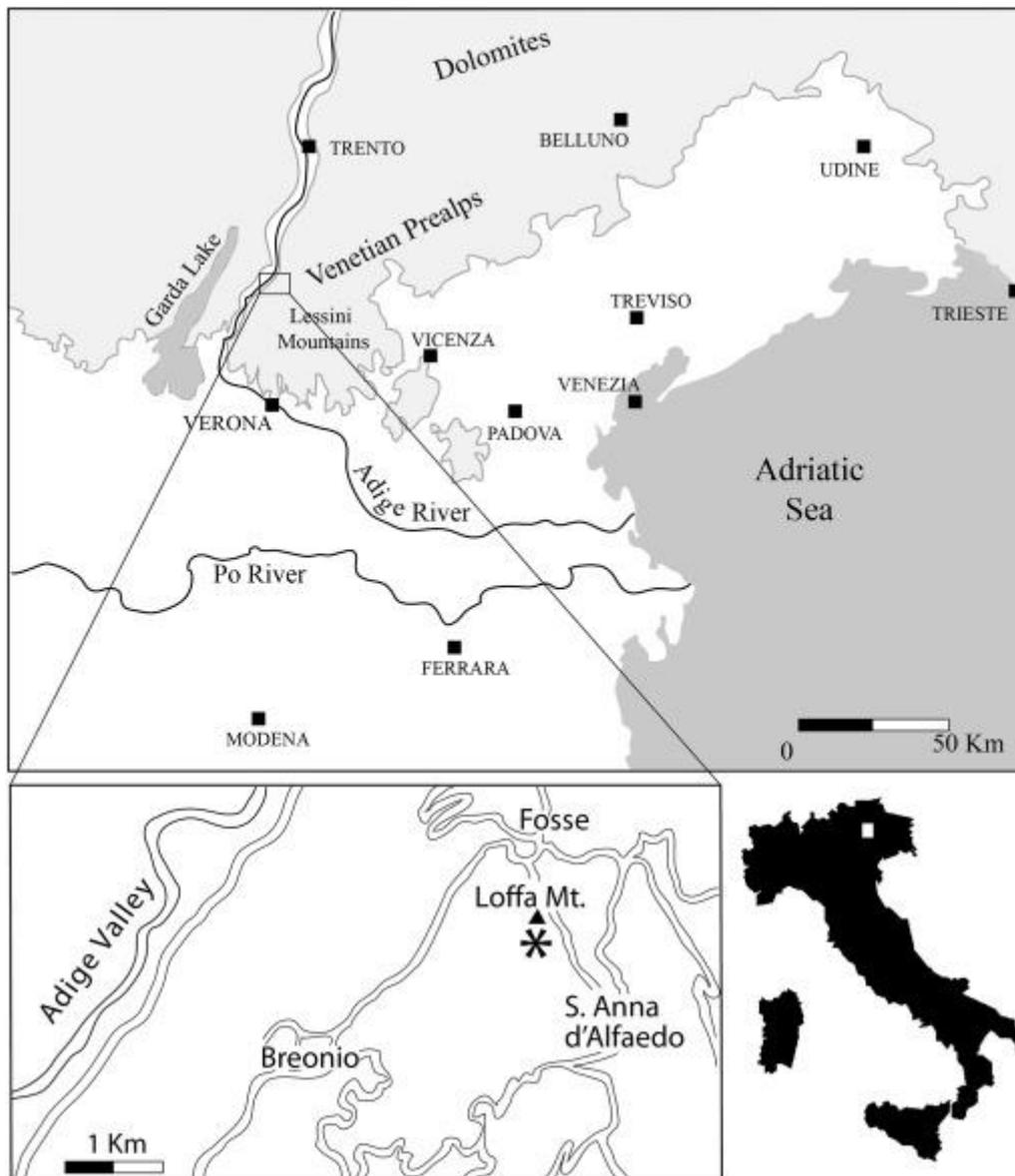


Fig. 1. Location of the site. The quarry that yielded the specimen IGVR 91032 in the surrounding of Sant'Anna D'Alfaedo (Verona) is indicated by an asterisk.

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 m 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 to 100 m 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.

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.

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.

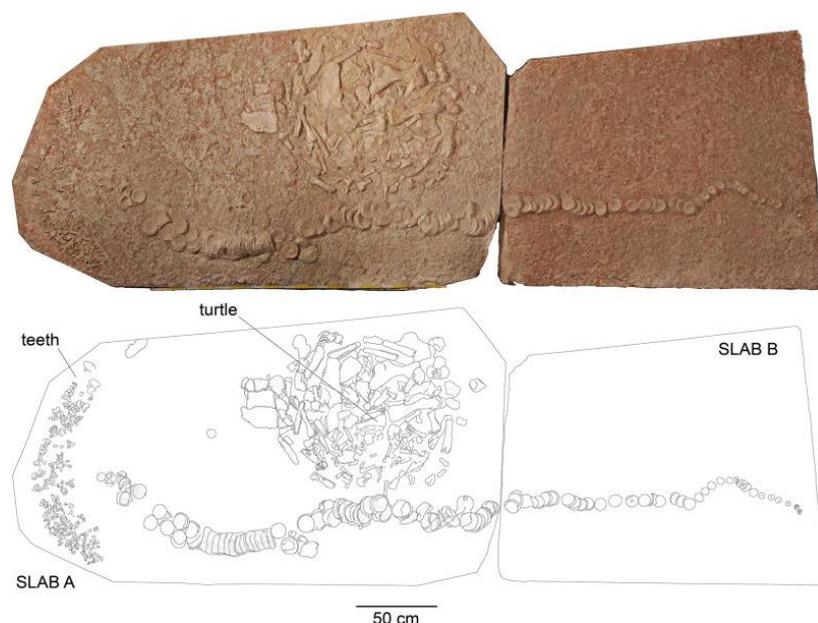


Fig. 2. The specimen IGVR 91032. Above: orthophoto; below: interpretative drawing. Photograph printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved.

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 and 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.

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*, heterohelicidids and hedbergellids (Fig. 3B).

Methods

Micropaleontology

Foraminifera

Semiquantitative analysis of planktic and small benthic foraminifera was performed in washed residues of the > 63 µm fraction obtained from a sample removed from slab A (A3 sample), and processed following the cold acetolysis method of Lirer (2000) as described in Luciani et al. (2007).

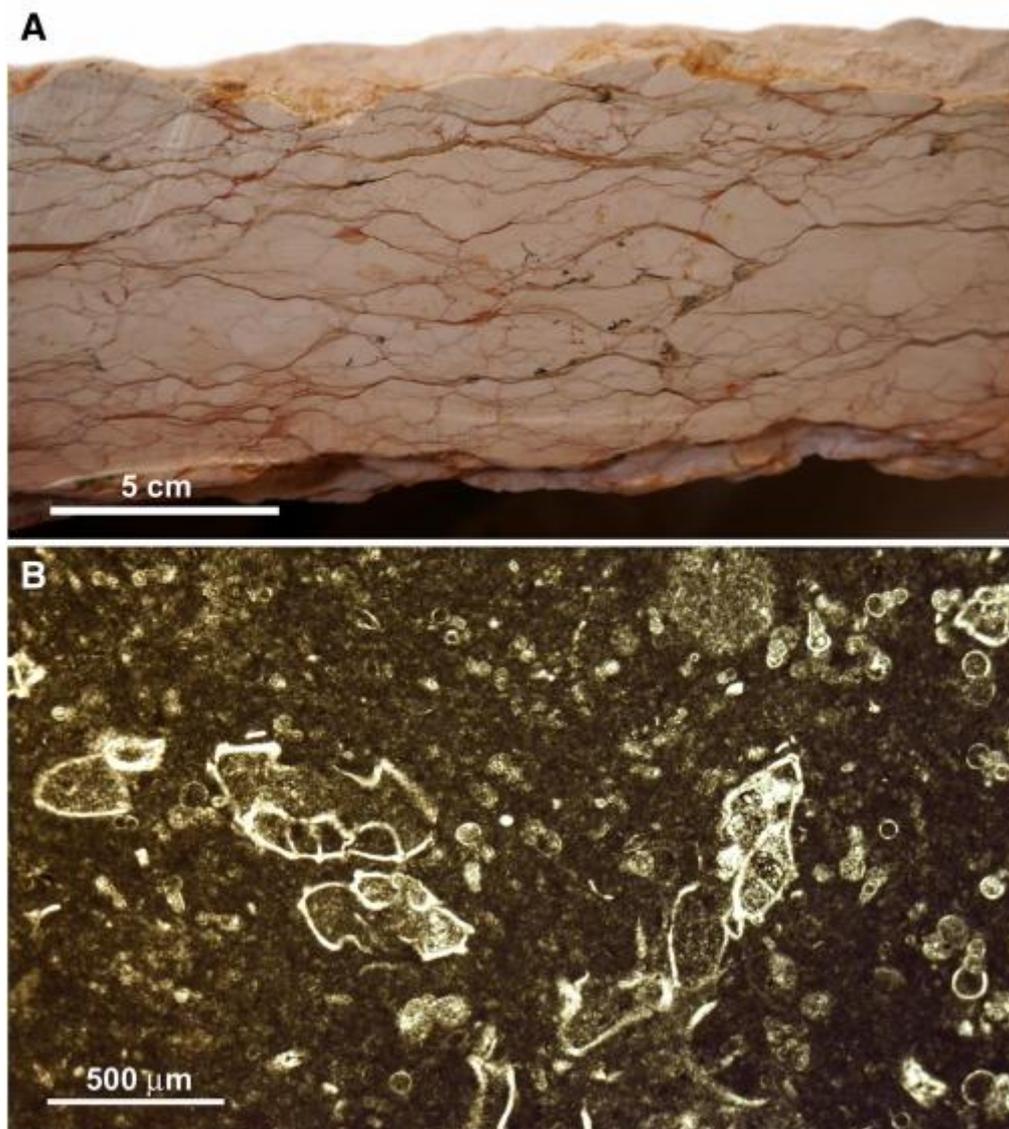


Fig. 3. Lithology of the slab IGVR 91032A. **A.** Transverse section of the slab showing the flaser-nodular texture that is characteristic of the 'lastame' interval of the Scaglia Rossa from Lessini Mountains. The vertebrate remains are preserved at the upper surface of the slab within a layer of reddish calcareous marl. **B.** Thin section of sample A7 showing the microfacies of a calcareous nodule: planktonic foraminiferal wackestone with marginotruncanids, *Dicarotella hagni*, heterohelicidids 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.

The studied residues are deposited in the micropaleontological collections of the Department of Geosciences, Padova 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 1250 × 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 Padova University (Italy) and labeled with the sample number assigned during the specimen matrix extraction.

Shark and turtle

The specimen was photographed with several digital cameras: Nikon Coolpix L120, Sony α200 mounting 18-70 mm lens and Fuji XE1 mounting 18-55 mm 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, Cappetta, 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 µm of the six samples processed following the cold acetolysate method of Lirer (2000). The placoid scales are deposited in the micropaleontological collections of the Department of Geosciences, Padova University (Italy) and labeled with the sample number assigned during the sampling from slab A of IGVR 91032.

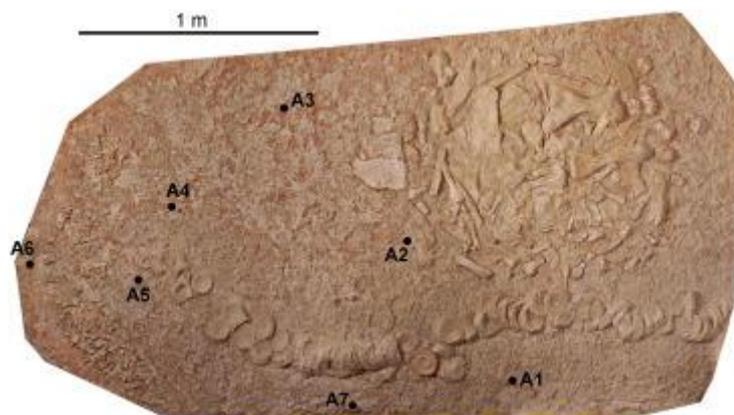


Fig. 4. Location of the samples on slab IGVR 91032A. Samples (from A1 to A6) were collected for placoid scales extraction and micropaleontological analyses. Photograph printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence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

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, Capellini, 1898, Hay (1908), Hirayama, 1992, Hirayama, 1994, Hirayama, 1997, Kapuścińska and Machalski (2015), Lehman and Tomlinson (2004), Młynarsky (1976), Mulder (2003), Parris et al. (2014), Villa et al. (2014), Wieland, 1900, Wieland, 1906, Wyneken, 2001, Wyneken, 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.

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.

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 praeglobotruncanids 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).

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

Cretodus sp.

Fig. 4, 6-10, 15

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.

Description

Teeth

The specimen preserves 120 teeth, at different growth stages (Fig. 6, Fig. 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 artifact produced by the person who did it, although the teeth are all from this specimen as we explained in the Materials and Methods section.

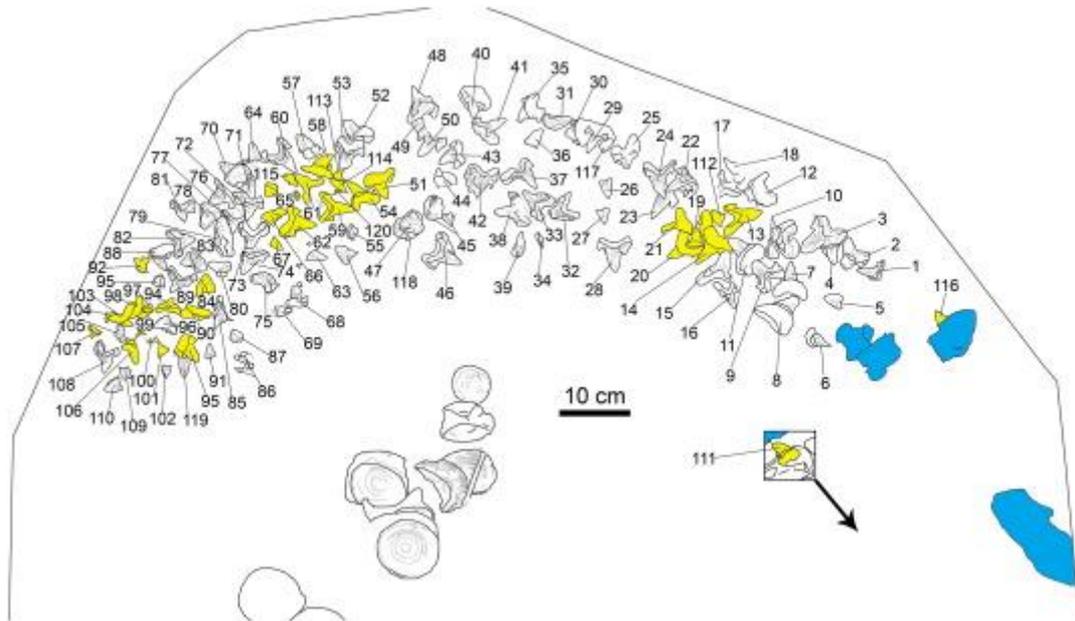


Fig. 6. Teeth of *Cretodus* sp. (IGVR 91032). Graphic sketch of the specimens indicative of the position of the skeletal elements. Color code: blue, calcified cartilage remains; yellow, *in situ* teeth. Non-colored teeth were glued to the slab. Numbers are progressive from no. 1 to no. 120. Tooth no. 111 (box) is preserved within the turtle remains.

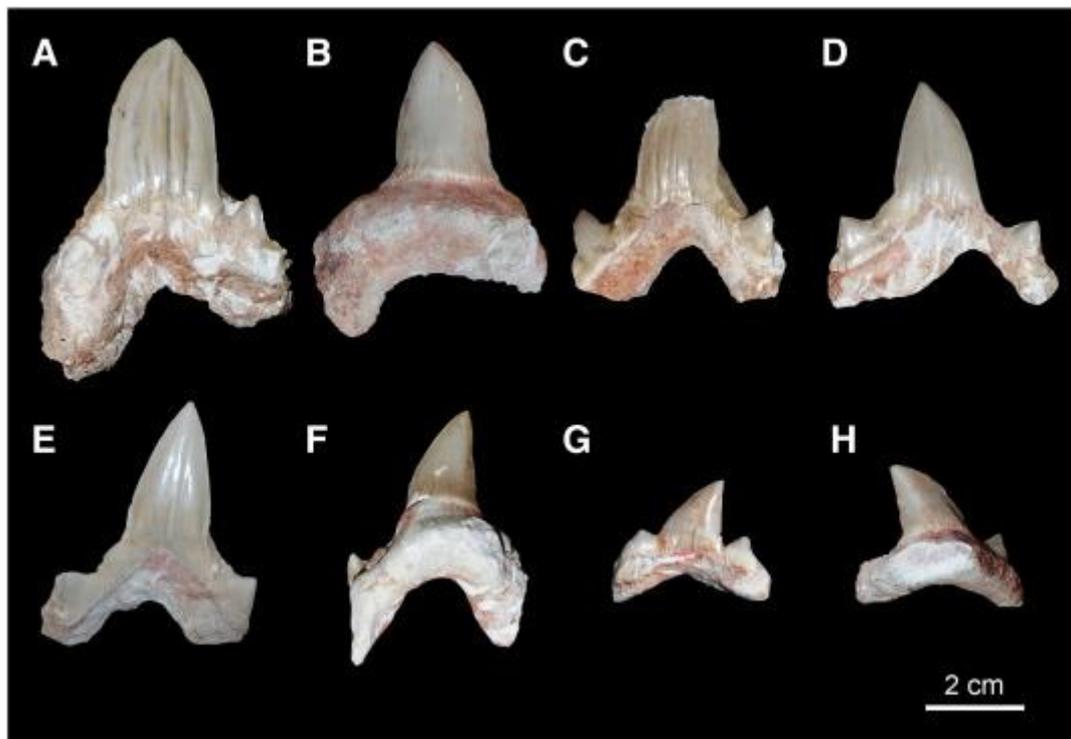


Fig. 7. Representative teeth of *Cretodus* sp. (IGVR 91032). **A.** anterior tooth (no. 3), labial view; **B.** anterior tooth (no. 11), lingual view; **C.** anterior tooth (no. 9), labial view; **D.** lateral tooth (no. 61), labial view; **E.** lateral tooth (no. 59); **F.** lateral tooth (no. 20), 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.

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).

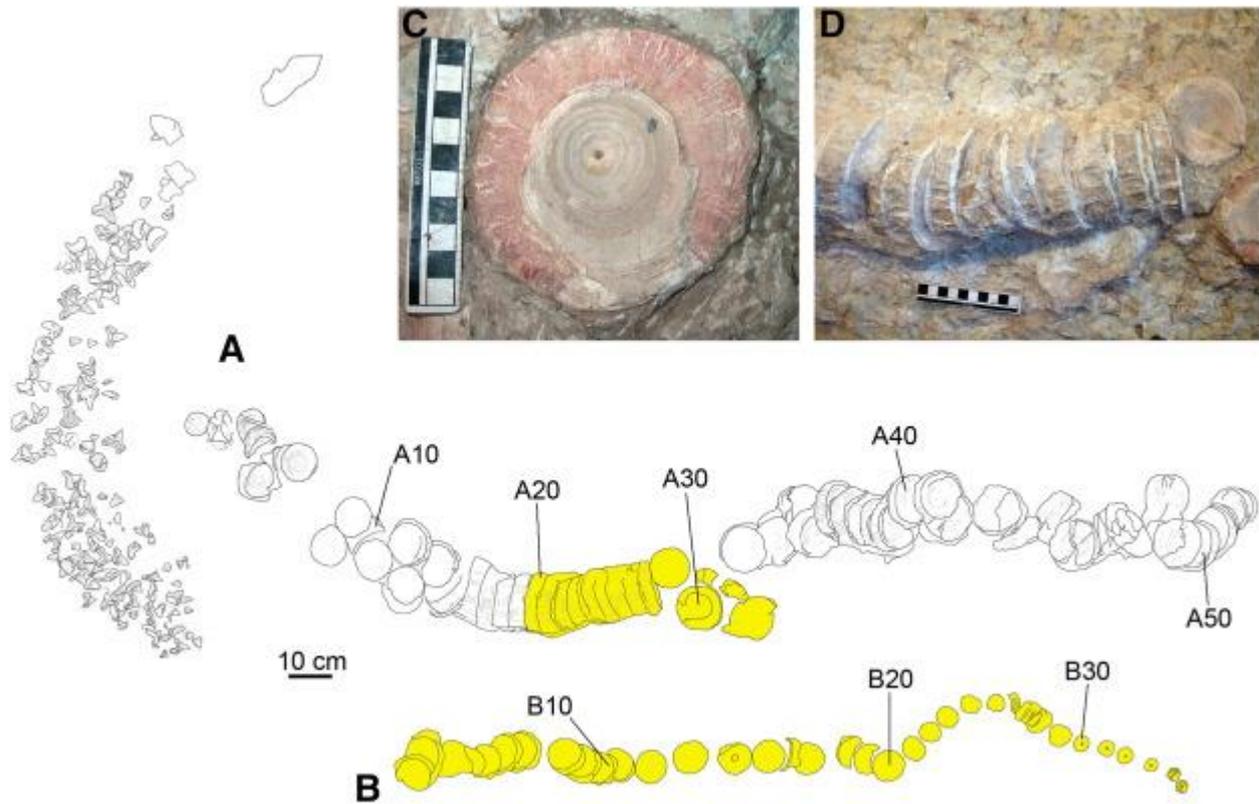


Fig. 8. Vertebral column of *Cretodus* sp. (IGVR 91032). Drawing of the shark remains on slab A (**A**) and slab B (**B**) with the vertebrae glued to the slab that are highlighted in yellow. Particular of vertebra A30 in anterior view (**C**) and segment of vertebral column A21-29 (**D**). Photographs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

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 astrospondylic 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 $> 63 \mu\text{m}$ 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.

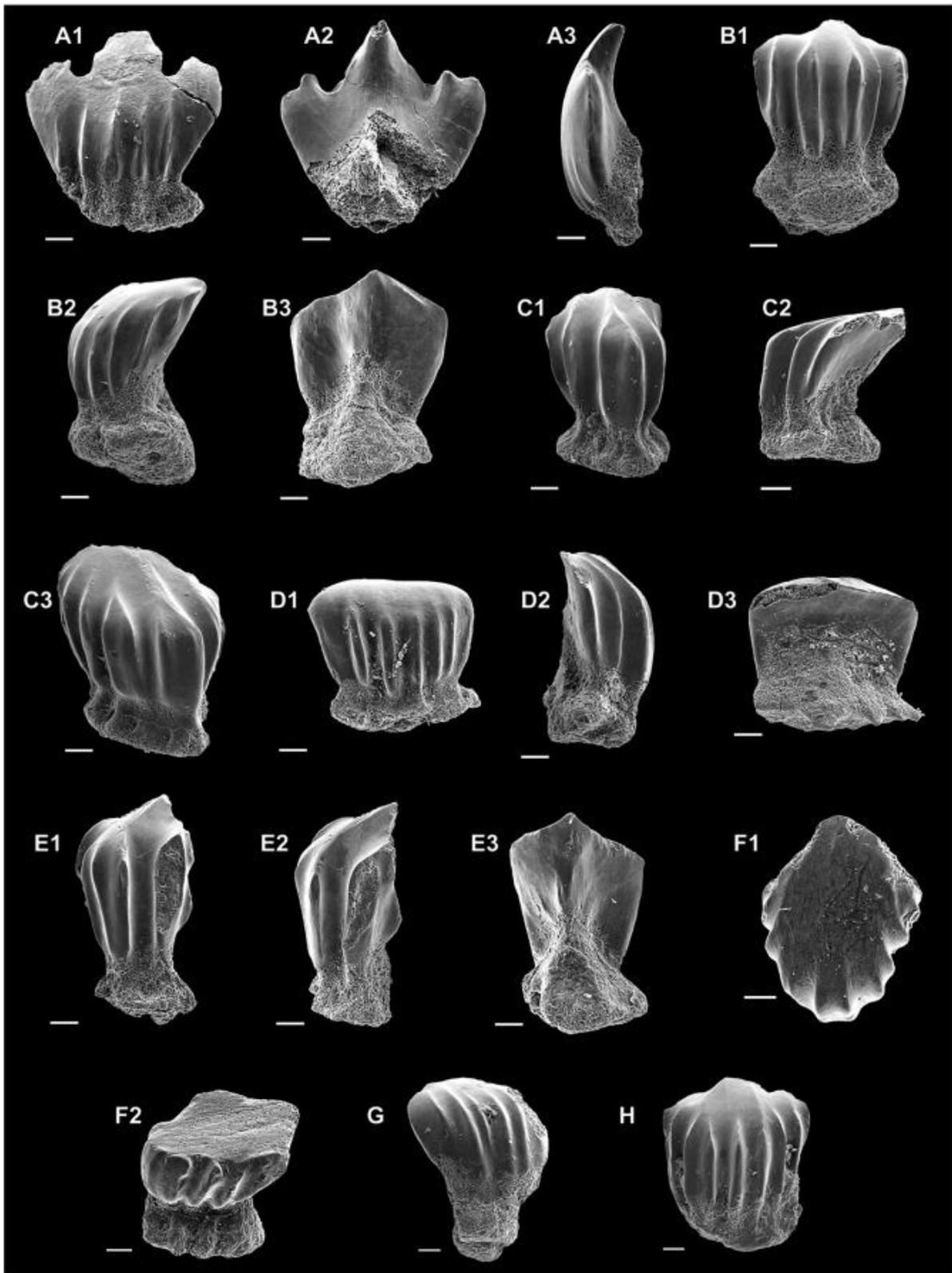


Fig. 9. Placoid scales of *Cretodus* sp. (IGVR 91032). **A1-3.** tricuspid scale, with broad rhomboid crown, anterior, posterior and lateral views; **B1-3.** single cusp scale, with rhomboid crown, anterior, lateral and posterior views; **C1-3.** single cusp scale, with slender rhomboid crown, anterior, 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 μm . 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.



Fig. 10. Calcified cartilage of *Cretoodus* sp. (IGVR 91032). **Left:** fragment glued within the turtle remains (scale bar = 1 cm); **Right:** the largest fragment close to the teeth accumulation. 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.

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, Siversson, 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. (2012), 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.

The turtle

Class Reptilia Laurenti, 1768

Subclass Diapsida Osborn, 1903

Order Testudines Linnaeus, 1758

Superfamily Chelonioidea Baur, 1893

Chelonioidea indet.

Fig. 4, 11-14-

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 be 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 femora, 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).

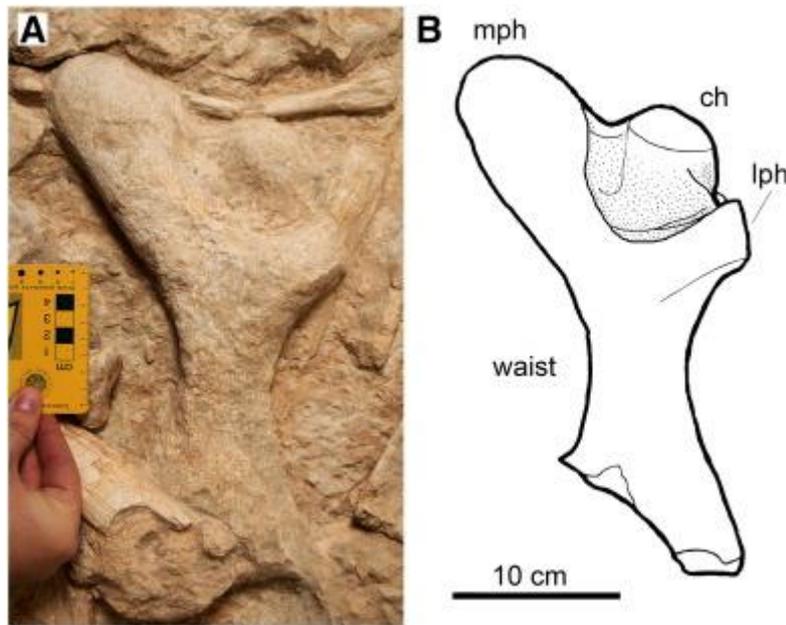


Fig. 12. Chelonioid turtle of IGVR 91032, left humerus in ventral view. **A.** photo of specimen; **B.** drawing. Abbreviations: ch, caput humeri; lph, lateral process; mph, medial process. Photograph printed and made available under permission of Italian Ministry of Cultural Heritage and Activities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

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 chelonioid 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 chelonioids). 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 prog.). 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 chelonioid turtles from 'lastame'. The morphology of the humerus of IGVR 91032 is typical for the Chelonioidea (the thalassic type humeri as described by Wieland, 1900; see also Młynarsky, 1976, Hirayama, 1994, Hirayama, 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, Hirayama, 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, Fig. 1, Fig. 2, Fig. 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).

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.

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.

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.

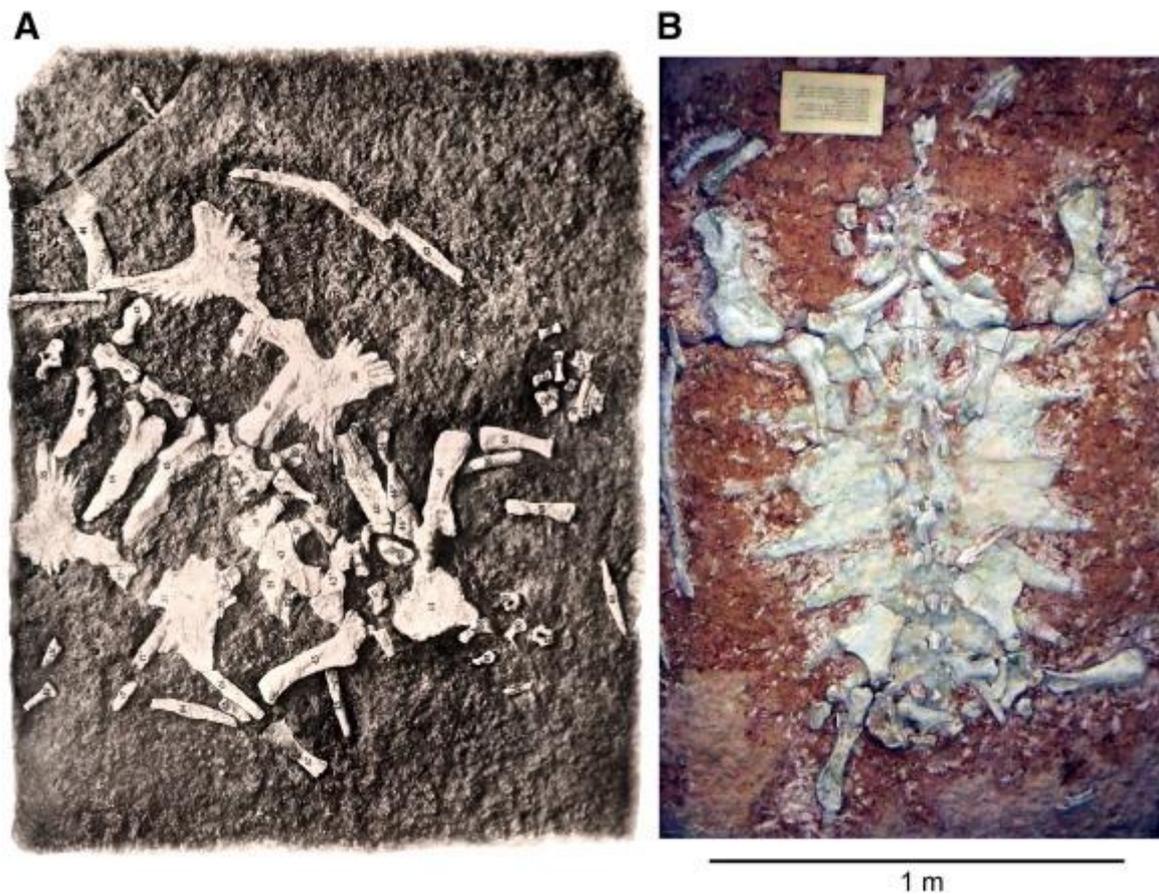


Fig. 13. Marine turtles from the ‘lastame’ of Sant’Anna d’Alfaedo (Verona). **A.** MGGC 8841, holotype of *Protosphargis veronensis* (from Capellini, 1884, pl. 2), the slab measures 150 × 185 cm; **B.** MSNV V.10670, Chelonioidea indet. Scale bar = 1 m. Photograph B printed and made available under permission of Italian Ministry of Cultural Heritage and Activities and Tourism - Veneto Region Superintendence for Archaeological Heritage, all rights reserved.

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, 2012, 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 accommodate large preys and its maximum capacity is about 10% of the shark's total weight (Aidan Martin, 2003). A 6.4 m-long white shark is reported to weight about 3300 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.

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.

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, Myhrvold, 2012).



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.

A shark tooth embedded within the accumulation

A lateral *Cretodus* tooth is embedded within the turtle bone accumulation (Fig. 11, Fig. 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, Myhrvold, 2012).



Fig. 15. Lateral tooth of *Cretodus* sp. (IGVR 91032) preserved within the turtle bones (see Fig. 11B). Photograph 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.

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.

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 chelonioid 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, Stancyk, 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, 1997a). 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).

Conclusions

A large, over 6.5 m-long lamniform shark *Cretodus* from middle Turonian of Italy is preserved with closely associated remains of a big cheloniod turtle (estimated length about 2 m) 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.

Acknowledgements

We thank Roberto Zorzin and Anna Vaccari (MSNV) for the permission to study the specimens under their care. We are grateful also to Giovanni and Gianfranco Benedetti (quarry owners and discoverers of the specimen) for the information about the specimen and to Elisa Marchesini (Associazione Culturale Officina 3) for the access to the specimens exhibited at the MPPS. We would like to thank an anonymous reviewer and the editor for the constructive reviews that strongly improved the manuscript. Other thanks go to the MGPC and Luigi Ambrosi, for further information about the specimens from the Scaglia Rossa Formation. Thanks to Kenshu Shimada (DePaul University, Chicago, USA), Mikael Siverson (Western Australian Museum, Perth, Australia), Massimo Delfino, Andrea Villa, and Márton Rabi (University of Torino, Italy) for the information and advices about fossil sharks and turtles; Carlo Sarti (University of Bologna, Italy) for the information about the holotype of *Protosphargis veronensis*. Stefano Castelli (Department of Geosciences of University of Padova) is acknowledged for his precious help with photographs and figures preparation. This work was carried out in the context of a wide project aimed to study the vertebrate fauna of the Scaglia Rossa Formation from the Veneto Region of NE Italy. Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled 'Reappraisal of two key *Fossil-Lagerstätten* in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach', assigned to Eliana Fornaciari).

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3.3.

First associated tooth set of a high-cusped *Ptychodus* (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of northeastern Italy, and resurrection of *Ptychodus altior* Agassiz, 1835

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Abstract

Dental remains of the elasmobranch *Ptychodus* from the Upper Cretaceous of northeastern Italy are described herein. This material, consisting of two slabs containing a partially associated tooth set and additional detached teeth with similar morphological features, derives from different lithozones of the Scaglia Rossa Formation, known as the ‘lastame’ and ‘Pietra di Castellavazzo’. All of these teeth are characterized by an unusual high and narrow cusp. The tooth set exhibits elements with different morphologies although they are clearly referable to a single taxon. Based on the species-specific characters of the teeth and according to the Principle of Priority of the International Code of Zoological Nomenclature, we propose herein to resurrect the species *Ptychodus altior* Agassiz, 1835 as a valid taxon that can easily be separated from *P. rugosus* Dixon, 1850. Moreover, we designate a neotype of *Ptychodus altior* Agassiz, 1835 since the type series seemingly is lost. Although similarly developed cusps are observed also in the species *Ptychodus rugosus* Dixon, 1850 and *P. whipplei* Marcou, 1858, the material described herein is assigned to *Ptychodus altior* because of the presence of a narrow cusp with smooth lateral cusp faces. The narrow high-cusped morphology characterizing this species probably indicates a different target prey compared to low-crowned congeneric species. *Ptychodus altior* is solely known from the Turonian-Coniacian of Europe; we review the distribution and paleobiogeography of this species, extending its range to the Angola region. The fossils described herein represent the first record of *Ptychodus altior* from Italy and significantly contribute to the knowledge of this species and, more generally, of the paleobiodiversity of the genus *Ptychodus* in the central Tethys area.

Introduction

Ptychodus Agassiz, 1835 is a Cretaceous elasmobranch genus, belonging to the family Ptychodontidae, whose systematic affinities have been extensively debated up to now and remain controversial. Ptychodontids have been variously interpreted as batoids, hybodontids or, more recently, neoselachian sharks (see Cuny, 2008, Shimada et al., 2009, Shimada, 2012, Brignon, 2015, Hoffman et al., 2016, Hoffman et al., 2016). Two genera are generally included in this family, namely *Ptychodus* and *Heteroptychodus* (Cappetta, 2012). Recently, Hamm (2015) introduced a new genus, *Parapterychodus*, with the species *P. washitaensis*, for teeth from the Cretaceous of Texas that previously have been assigned to *Ptychodus decurrens*.

Ptychodus occurs in Upper Cretaceous marine deposits of North and South America, Europe, Africa and Asia (Cappetta, 2012, Shimada, 2012, Hamm, 2017). Teeth arranged in dental plates in both upper and lower jaws, adapted for crushing or grinding shelled macroinvertebrates (e.g., Kauffman, 1972, Ozanne and Harries, 2002, Shimada et al., 2009), characterize this durophagous taxon (Cappetta, 2012, Shimada, 2012, Verma et al., 2012). Although several associated specimens including skeletal fragments and articulated sets of teeth were previously found (Williston, 1900, Dibley, 1911, Canavari, 1916, Cigala Fulgosi et al., 1980, MacLeod, 1982, Shimada et al., 2009, Shimada et al., 2010, Hamm, 2010, Hamm, 2017, Shimada, 2012), the genus *Ptychodus* is mostly known from isolated teeth (Cappetta, 2012). The teeth of *Ptychodus* have generally a bulky and flat-top cusp rising from a nearly flat and broad marginal area forming low and broad crowns. A very narrow and high cusp, conversely, is a character shared by two peculiar species of *Ptychodus*, the European *P. altior* Agassiz, 1835 (Dixon, 1850; Fossa-Mancini, 1921), and the North American *P. whipplei* Marcou, 1858 (Lucas and Johnson, 2003, Siverson and Lindgren, 2005, Lucas, 2006). However, *Ptychodus altior* Agassiz, 1835 is either regarded as a junior synonym of *P. mammillaris* Agassiz, 1835 (e.g., Giebel, 1848, Woodward, 1889, Woodward, 1912; Priem, 1896) or a phenotypic variation of *P. rugosus* Dixon, 1850 (e.g., Woodward, 1889, Woodward, 1912, Leriche, 1906, Leriche, 1909), for which Leriche (1929) introduced the name “*elevatus*”. Herman (1977) even considered the “*elevatus*” morphotype as a valid distinct species, thus suppressing de facto the previously instituted name *P. altior*.

Here, we describe an associated tooth set and additional isolated specimens of *P. altior* from the Scaglia Rossa Formation. This material represents the first Italian record of this species. The nomenclature and taxonomy of this high-cusped species are discussed and we provide evidence that *Ptychodus altior* Agassiz, 1835 is a valid species. A detailed comparison between this taxon and the morphologically similar *Ptychodus rugosus* Dixon, 1850 and *P. whipplei* Marcou, 1858 is also presented.

The Italian record of high-cusped *Ptychodus*

In 1818, the Italian naturalist, zoologist, and paleontologist, Tommaso Antonio Catullo described the first record of *Ptychodus* teeth from Italy (Catullo, 1818). Later various authors documented isolated, associated, and even articulated remains of *Ptychodus* from several Italian localities (Lioy, 1865, Bassani, 1876, Bassani, 1888, De Zigno, 1883, Canavari, 1916, D'Erasmus, 1922, Sorbini, 1976, Cigala Fulgosi et al., 1980, Astolfi and Colombara, 1994, Astolfi and Colombara, 2003). More recently, remains of *Ptychodus* from northeastern Italy were reported by Dalla Vecchia et al., 2005, Trevisani and Cestari, 2007, Trevisani, 2009, Trevisani, 2011, Roghi, 2010, Palci et al., 2013 and Amalfitano et al. (2017a). However, only sporadic occurrences of high-cusped *Ptychodus* teeth have been reported from Italy so far.

Bassani (1886) reported eight teeth from Castellavazzo (Belluno) referred to an indeterminate species of *Ptychodus* with a very high and narrow central cusp and compared them to *Ptychodus trigeri* Sauvage, 1878. However, Bassani (1886) pointed out that those teeth exhibit a smooth crown, thereby resembling those of *P. altior* rather than those of *P. trigeri*. These specimens (Fig. 1) are currently considered lost.

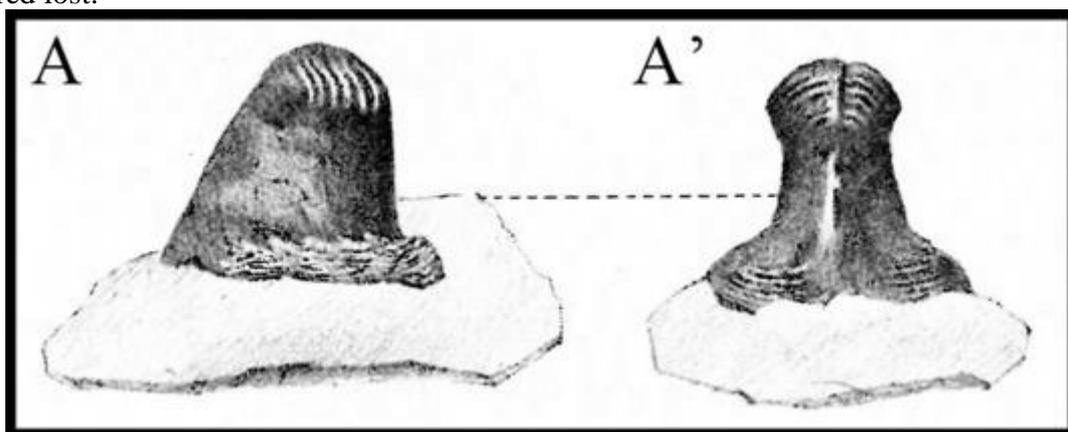


Fig. 1. High-cusped *Ptychodus* tooth from Castellavazzo (Belluno) figured by Bassani (1886), probably assignable to *P. altior* Agassiz, 1835. This specimen is currently lost. Excerpt from Bassani (1886).

Sorbini (1978) reported the occurrence of *Ptychodus whipplei* from Upper Cretaceous deposits cropping out in the surroundings of Monte Loffa (S. Anna d'Alfaedo, Verona, north-eastern Italy). Based on the figures published by Sorbini (1978), it is evident that he was referring to the associated set of teeth that is described in detail herein.

Geological setting

The Upper Cretaceous hemipelagic deposits of the Scaglia Rossa Formation of northeastern Italy are generally poor in macrofossils (Giusberti et al., 2005), with the exception of peculiar lithozones,

commercially known as ‘lastame’ and ‘Pietra di Castellavazzo’ (Castellavazzo Stone; Amalfitano et al., 2017c). The specimens described herein come from these specific stratigraphic intervals.

The ‘lastame’ is a condensed and nodular/subnodular package of reddish to whitish limestone, 7-8 m thick, extensively quarried around Sant'Anna d'Alfaedo (Verona Province), in the Lessini Mountains (Roghi and Romano, 2009, Trevisani and Cestari, 2007, Amalfitano et al., 2017a; Fig. 2). According to Lozar and Grosso (1997), this lithozone (‘lithozone’ 2) spans stratigraphically from the lower Turonian to the lower Santonian, while other authors assigned a Turonian-Coniacian age to it (e.g., Cigala Fulgosi et al., 1980). The fossil content of the Lessinian ‘lastame’ consists of invertebrates (echinoids, inoceramids, ammonites and rudists) and rare vertebrate remains, primarily of sharks and subordinately of rare marine turtles and mosasaurs (e.g., Capellini, 1884, Cigala Fulgosi et al., 1980, Ginevra et al., 2000, Dalla Vecchia et al., 2005, Trevisani and Cestari, 2007, Roghi, 2010, Palci et al., 2013, Amalfitano et al., 2017b).

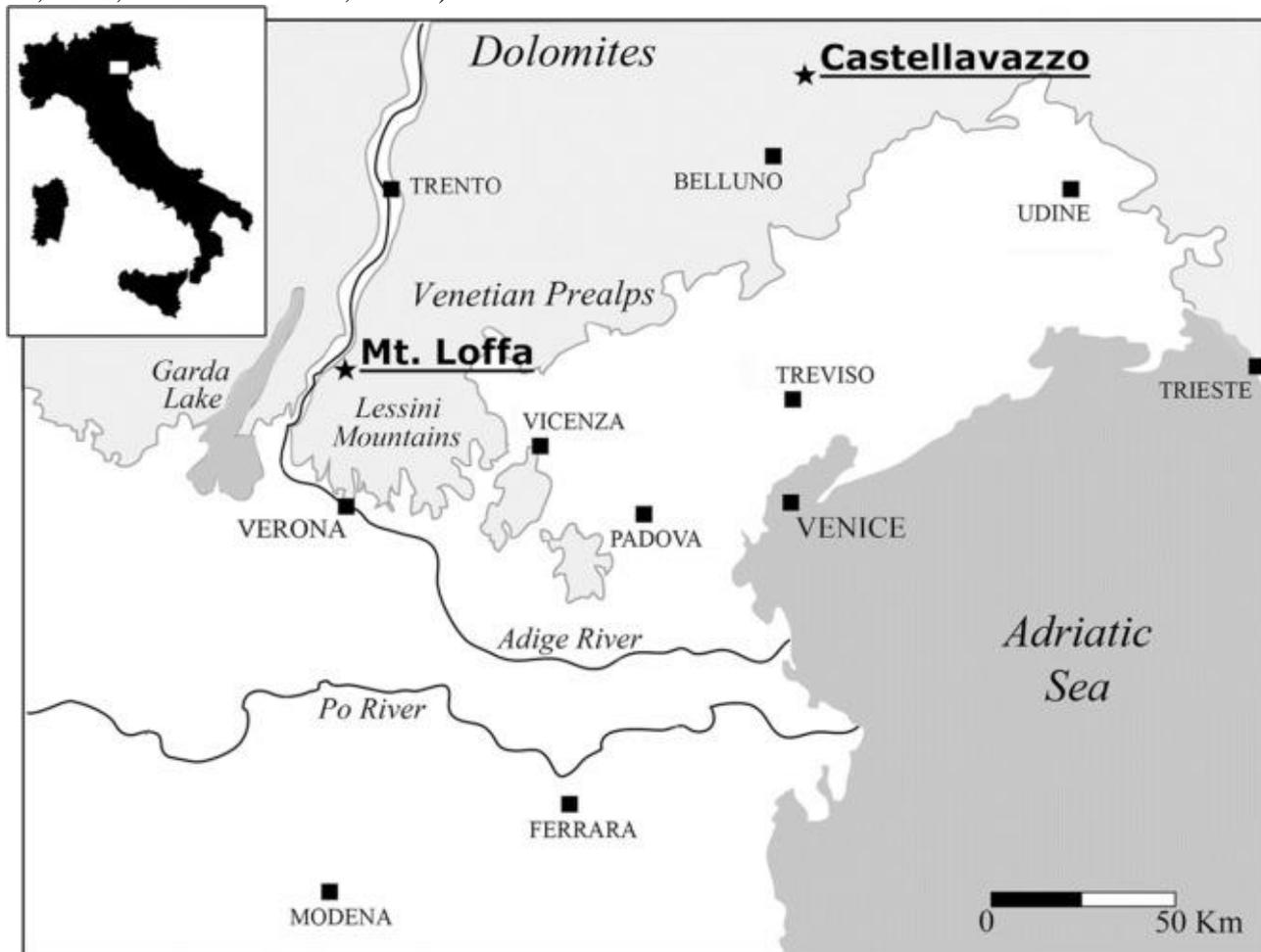


Fig. 2. Location map of the sites in northeastern Italy that yielded the *Ptychodus* remains described in this paper (modified from Amalfitano et al., 2017a). The black stars indicate the fossiliferous sites.

The ‘Pietra di Castellavazzo’ is another condensed interval within the Scaglia Rossa Formation characterized by relatively common macrofossils (Bassani, 1886, Bassani, 1888, Trevisani and

Cestari, 2007, Amalfitano et al., 2017c). This lithozone, very similar in thickness and paleontological content to the ‘lastame’, is exposed in the surroundings of the village of Castellavazzo (north of Longarone, Piave Valley, Belluno; Amalfitano et al., 2017c; Fig. 2). The ‘Pietra di Castellavazzo’ consists of a 6-7-m-thick interval of nodular micritic limestone, whose color varies from reddish to gray-greenish (Trevisani, 2011). Thin dark-red clay interlayers separate the micritic beds (of variable thickness, generally 10-20 cm; Trevisani, 2011). Based on correlation with the ‘lastame’, the ‘Pietra di Castellavazzo’ has been referred to early-middle Coniacian (Colleselli et al., 1997, Trevisani, 2011), pending ongoing stratigraphic revisions.

The macrofossil assemblage of the ‘Pietra di Castellavazzo’ consists of chondrichthyans (e.g., *Scapanorhynchus subulatus*, *Cretoxyrhina mantelli*, *Ptychodus* spp.; Bassani, 1886, Bassani, 1888, Amalfitano et al., 2017a), bony fishes (*Lepidotes?* sp. and *Protosphyraena? ferox?*; Bassani, 1886, Bassani, 1888, Amalfitano et al., 2017c), ammonites, echinoids, inoceramids and rudists (radiolitids; Trevisani, 2009, Trevisani, 2011). Generally, the fossils are less common compared to that of the ‘lastame’ probably because of the lower number of outcrops (especially quarries) occurring in the Belluno area (Trevisani, 2009, Trevisani, 2011), and in many cases poorly preserved.

Materials and methods

The fossils described and figured herein comprise five specimens housed in the Museo di Preistoria e Paleontologia di S. Anna d'Alfaedo (specimen numbers MCSNV v.3994-3995) and the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (specimen numbers MGP-PD 7344, MGP-PD 14044, MGP-PD 14031, MGP-PD 32066). The specimen MCSNV v.3994-3995 (slab and counterslab of the same associated specimen), currently housed in the Museo Paleontologico e Preistorico di S. Anna d'Alfaedo, actually belongs to the paleontological collections of the Museo Civico di Storia Naturale di Verona and for this reason is catalogued with the acronym ‘MCSNV’. The specimen comes from Monte Loffa, close to the village of S. Anna d'Alfaedo (Verona Province), and was acquired by the museum in 1973 and referred to as *Ptychodus whipplei* in the museum catalogue. The specimens from the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova are represented by isolated teeth coming from the Castellavazzo quarries (Belluno Province) and an isolated tooth of *P. whipplei* from Kamp Ranch Formation, Dallas County, Texas (U.S.A.). The specimens were photographed using a Nikon D810 camera mounting a 60-90 mm lens and a Canon PowerShot SX720 HS camera. The teeth were measured with image analysis software ImageJ (v. 1.47). The tooth surface was coated with ammonium chloride in order to enhance the contrast of morphological crown features (“smoking”; see Amalfitano et al., 2017c and Scovil, 1996). This methodology guarantees a uniform coverage and the persistence of surfaces fidelity.

Illustrative drawings and images of the specimens were prepared using the software packages GIMP (v. 2.8.16) and Photoshop CS5 (v.12.0 x32).

A millimetric tungsten carbide spherical drill bit mounted on an electric drill was used to sample the matrix of the specimens MCSNV v.3995, MGP-PD 14044, and MGP-PD 14031. A smear slide, for calcareous nanofossil analysis, has been prepared with the powder obtained from the embedding rock. A small portion of the limestone from MCSNV v.3995 was utilized for preparing a thin section for planktic foraminiferal analysis.

The morphological terminology used herein mostly follows Cappetta, 2012, Shimada, 2012, and Hamm (2017), with some modifications (see Fig. 3). Open nomenclature follows the standard proposed by Matthews, 1973, Bengston, 1988 and Sigovini et al. (2016).

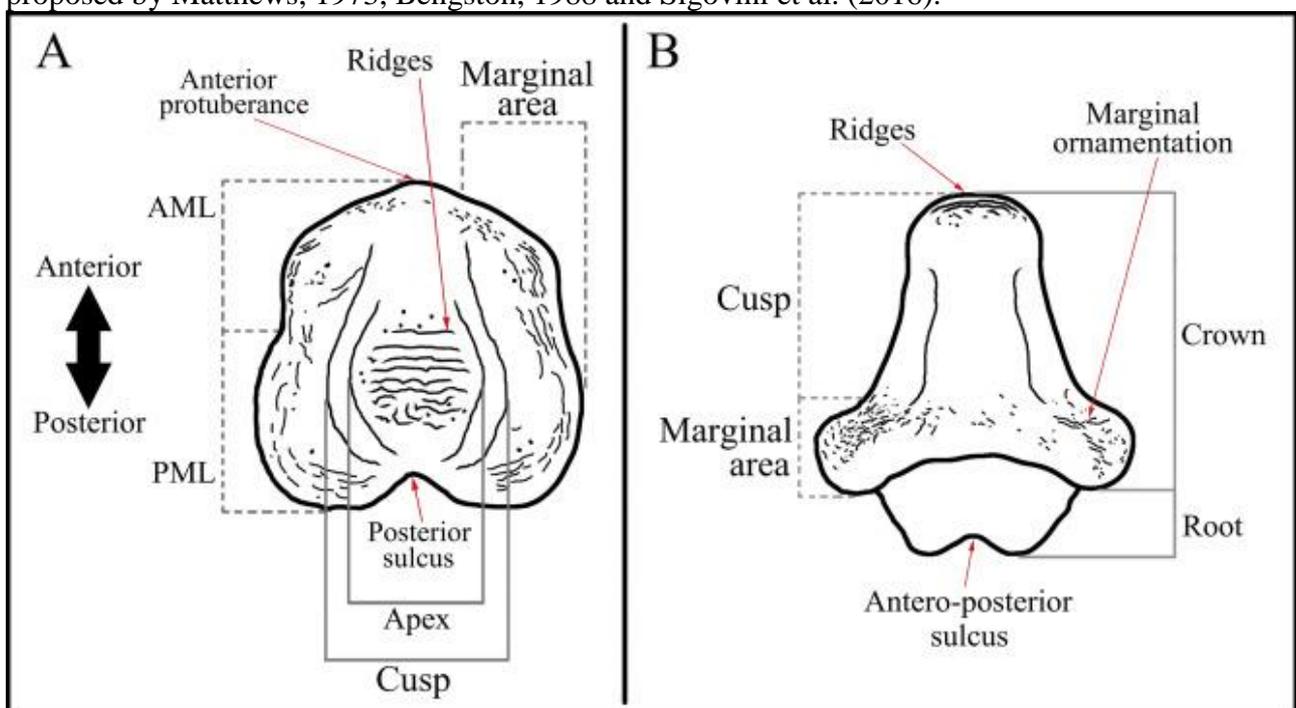


Fig. 3. Line drawing of a lower symphyseal tooth of *Ptychodus altior*. **A**, occlusal view; **B**, anterior view; AML = anterior marginal lobe; PML = posterior marginal lobe.

Results

Systematic paleontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order *incertae sedis*

Family Ptychodontidae Jaekel, 1898

Genus *Ptychodus* Agassiz, 1835

Diagnosis. See Woodward (1912).

***Ptychodus altior* Agassiz, 1835 emended**

Fig. 1, 3-11, 13-14.

- p.1822 Teeth allied to *Diodon* - Mantell, p. 231, t. 32, figs. 17, 21, 27 (non figs. 18-10, 23-25, 29).
†1835 *Ptychodus altior* Ag. - Agassiz, Feuilleton additionnel, p. 54.
p.1838 *Ptychodus decurrens* Agass. - Agassiz, p. 154, t. 25b, figs. 5-5' (non figs. 1-4, 6-8).
non1838 *Ptychodus altior* Agass. - Agassiz, atlas, vol. III, t. 25, fig. 9, 10.
non1839 *Ptychodus altior* Agass. - Agassiz, vol. III, p. 155.
p.1845 *Pt. mammillaris* Ag. - Reuss, p. 2, t. 2, figs. 11, 12 (non fig. 13).
non1848 *Pt. altior* Ag. - Giebel, p. 333.
1850 *Ptychodus altior* - Dixon, p. 362, t. 30, fig. 10.
1886 *Ptychodus* sp. - Bassani, p. 146, t. 9, fig. 10.
1888 *Ptychodus* cfr. *decurrens* - Bassani, p. 5 (footnote).
p.1889 *Ptychodus rugosus* Dixon - Woodward, p. 136 (non syn.), figs. 2, 3 (non fig. 1).
p.1896 *Ptychodus rugosus* Dixon - Priem, p. 289, t. 9, figs. 13-17, 22 (non figs. 1-12, 18-21, 23-25).
p.1902 *Ptychodus rugosus* Dixon - Leriche, p. 94, t. 2, figs. 16, 17 (non figs. 13-15, 18).
1906 *Ptychodus rugosus* variété *altior* Dixon - Leriche, p. 68.
1909 *Ptychodus rugosus* Dixon var. *altior* Dixon - Leriche, p. 57.
p.1912 *Ptychodus rugosus* Dixon - Woodward, p. 231, t. 48, figs. 6, 7 (non figs. 1-5, 8-11) (non syn.).
1929 *P. rugosus* mut. *elevatus* - Leriche, p. 217.
1977 *Ptychodus elevatus* Leriche M. 1929 - Herman, p. 62, text fig., p. 63, t. 2, figs. 6a-b.
1978 *Ptycodus* (sic) *whipplei* - Sorbini, p. 69, fig. 10.
1984 *Ptychodus whipplei* - Aspes and Zorzin, p. 14.
1987 *P. rugosus* Dixon 1850 - Cappetta, p. 38, figs. 4I-K.
2002 *Ptychodus whipplei* Marcou 1858 - Antunes and Cappetta, p. 106, t. 2, figs. 11a-d (non syn.).
2012 *P. elevatus* Leriche 1929B - Cappetta, p. 78.
2013 *Ptychodus rugosus* Dixon 1850 - Guinot et al., p. 594, figs. 3G-L.
2017 *Ptychodus rugosus* (Dixon, 1850) (sic). Trif and Codrea, p. 8, fig. 2.
2017 *Ptychodus mammillaris* - Fischer et al., p. 15, fig. 2c.

Original type series. The three teeth originally figured by Mantell (1822; Fig. 11) coming from the Chalk of South Downs, southern England, without any indication of the precise locality of finding. We tried to locate the original material in the Mantell's collection of the Natural History Museum, London (NHMUK), but unfortunately it seems to be lost (Emma Bernard, pers. comm.). For this reason, we designate below a neotype of *Ptychodus altior* Agassiz, 1835.

Neotype. NHMUK PV P28347 (see Figs. 14B-B'), a detached tooth coming from the Chalk of Sussex (southern England) and belonging to the "Dixon Collection", is designated herein as neotype of *Ptychodus altior* Agassiz, 1835. This definition meets the qualifying conditions specified in the article 75.3 of the International Code of Zoological Nomenclature (ICZN Code, 1999). NHMUK PV P28347 (Figs. 14B-B'), housed in Natural History Museum, London, is characterized by an extremely elevated narrow cusp with smooth lateral faces (see also Woodward, 1912: p. 232). In occlusal view, the tooth shows a quadratic outline and six apical ridges, which characterize the apex; a concentric ornamentation covers the thin marginal area. We designate this specimen as neotype owing its

completeness and English Chalk provenance from a geographical area close to the type area of the type series. Moreover, the selected neotype exhibits all the morphological characters of *Ptychodus altior* and it is consistent with the original illustrations of the type series by Mantell (1822). NHMUK PV P28347 has been erroneously reported as NHMUK PV P28247 by Woodward (1912: pl. 48, fig. 7; Fig. 14) and, subsequently, by Cappetta (1987: text figs. 4I-K).

Diagnosis (emended). Symphyseal teeth with very high cusps and symmetric, quadratic crown in occlusal view. Cusp with smooth lateral faces, narrowing towards the apex. Pronounced enameloid folds confined to the apex of the cusp. Fine granulations anterior and posterior to the ridges commonly present. Concentric, thin and rugose ornamentation covering the marginal area of the crown. Lateral teeth differ from symphyseals by having a bilaterally asymmetric cusp. Cusp height decreasing mesio-distally throughout the dental plate. It mainly differs from the morphologically similar high-cusped *Ptychodus whipplei* Marcou, 1958, by lacking ridges that extend transversally across the entire cusp.

Referred material. An associated tooth set belonging to a single individual, MCSNV v.3994-3995 (Fig. 4-8), and two moderately preserved isolated teeth, MGP-PD14044 (Figs. 9D, D') and MGP-PD14031 (Figs. 9A-C').

Locality and horizon. All the referred specimens come from the Upper Cretaceous Scaglia Rossa Formation. Slabs MCSNV v.3994-3995 were collected from the 'lastame' of Monte Loffa in the Lessini Mountains (Verona province, Fig. 2). The isolated teeth MGP-PD14044 and MGP-PD14031 were found in the so-called "Pietra di Castellavazzo" in the surroundings of Longarone (Belluno, Fig. 2). Calcareous nannofossil content of MCSNV v.3994-3995 indicates the UC8-UC9 zones of Burnett (1999). The planktic foraminiferal assemblage is referable to the *Dicarinella primitiva*/*Marginotruncana sigali* Zone of the zonal scheme by Coccioni and Premoli Silva (2015). This zone is equivalent to the *Marginotruncana schneegansi* Zone Auctt. The calcareous plankton biostratigraphic results suggest a middle-upper Turonian age of specimens coming from 'lastame' (see Supplementary Table A.1), according to the correlation between calcareous plankton zones and stages by Ogg and Hinnov (2012). Matrix samples from "Pietra di Castellavazzo" were almost devoid of calcareous nannoplankton and the amount of sedimentary rock was inadequate to analyze planktic foraminifera.

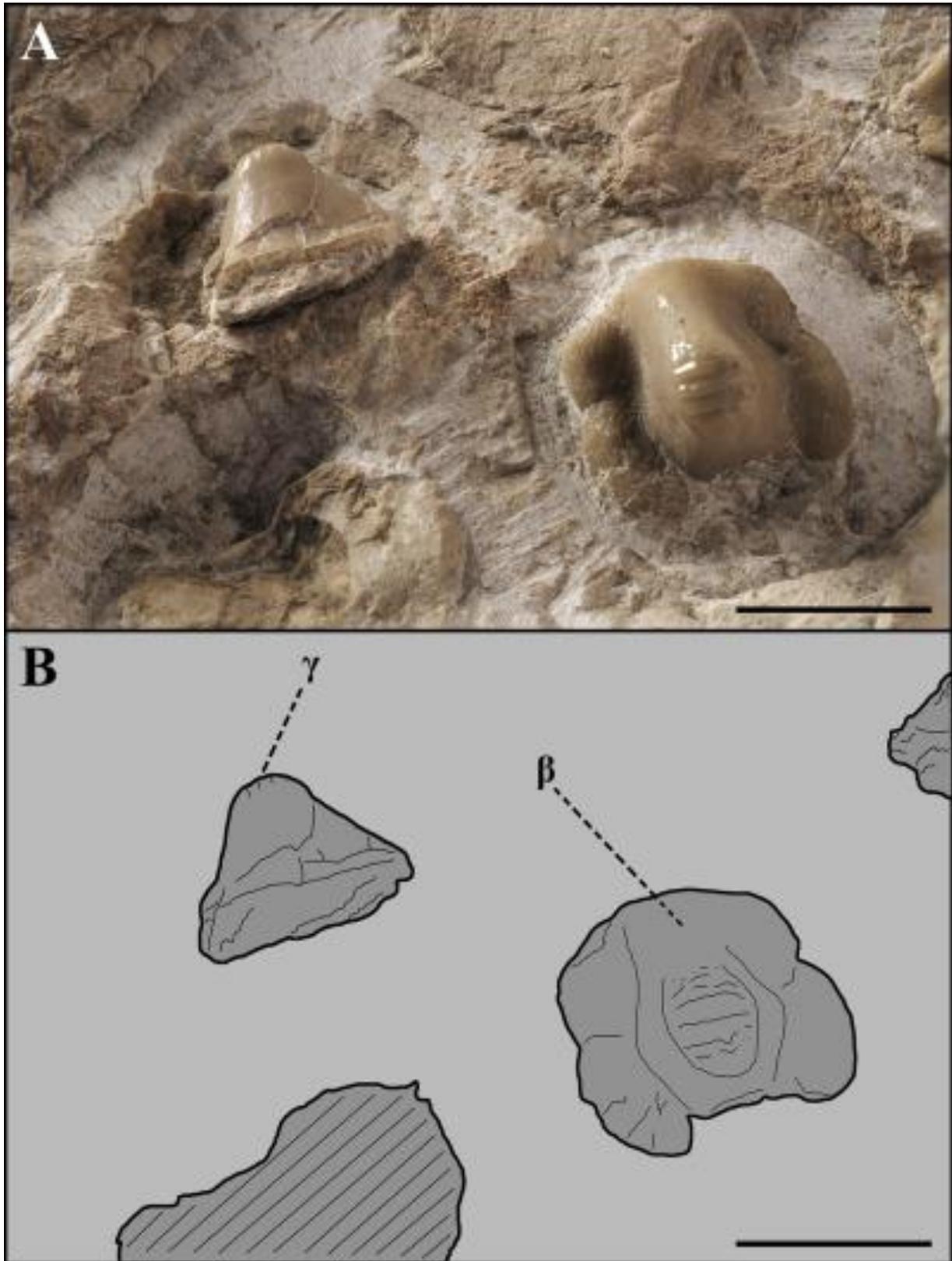


Fig. 4. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. The slab MCSNV v.3995, (A) photo and (B) interpretative line drawing, showing two of five teeth; the striated area indicates tooth fragments. β = MCSNV v.3995 β ; γ = MCSNV v.3995 γ . Scale bars equal 5 mm.



Fig. 5. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. The slab MCSNV v.3995. Scale bar equals 10 mm.

Description. The specimen MCSNV v.3994-3995 consists of two slabs that comprise a total of 38 associated teeth of small size. In addition, several tooth fragments and some dental impressions are also preserved on the surface of the two slabs (Fig. 6, Fig. 7). The teeth slightly differ from each other in their overall size, height, and bilateral asymmetry of the cusps. MCSNV v.3995 contains five teeth that are well exposed on the slab surface. One of them (labeled herein as “MCSNV v.3995 α ”, Figs. 8A-C') was removed in order to allow detailed morphological observations. Three teeth still embedded in the matrix exhibit a complete crown, whereas a fourth one only consists of the cusp (Fig. 4, Fig. 5). Moreover, at least four additional fragmentary teeth and several tooth impressions are also recognizable on the slab.

The dental crown of MCSNV v.3995 α (Figs. 8A, C') has a quadratic and symmetrical outline in occlusal view. The tooth exhibits both the characteristically high central cusp and the well-developed marginal area. The mesial and distal marginal areas are bilobate (Figs. 8A, A') with the posterior marginal lobe (PML; see Fig. 3) being wider and more rounded than the anterior one (AML; see Fig. 3). Fine wrinkles and concentric granulations cover the surface of the marginal area. Both the posterior sulcus and the anterior protuberance are weakly developed. Three ridges, preceded by a weak granulation and followed by evident rugosities, cross transversely the dental apex. The cusp is considerably elevated, with a smooth lateral faces, and is mesio-distally compressed (Figs. 8B-C'). The anterior profile of the cusp is oblique, whereas its posterior profile is vertical. Anteriorly, the base of the crown is thin and arched, with the concavity directed downwards. The crown is covered with enameloid wrinkles. The tooth also possesses remains of the root (Figs. 8C, C'). One of the teeth

preserved on slab MCSNV v.3995 is much smaller and bilateral asymmetric compared to MCSNV v.3995 α , also showing a well-developed distal marginal area and a low and slightly pointed cusp.

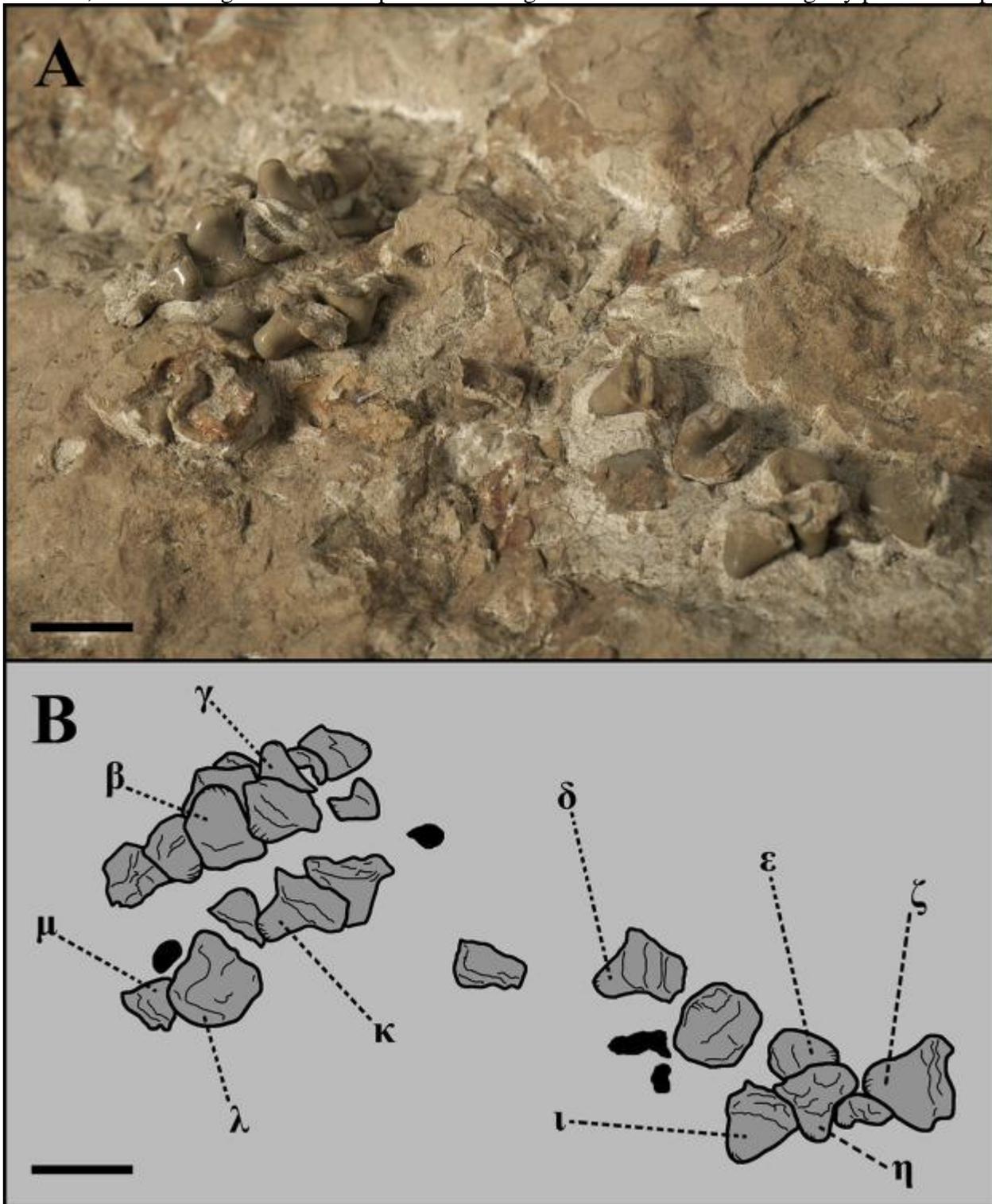


Fig. 6. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. Slab MCSNV v.3994, (A) photo and (B) interpretative line drawing, showing several teeth and some impressions of detached teeth (black areas). β = MCSNV v.3994 β ; γ = MCSNV v.3994 γ ; δ = MCSNV v.3994 δ ; ϵ = MCSNV v.3994 ϵ ; ζ = MCSNV v.3994 ζ ; η = MCSNV v.3994 η ; ι = MCSNV v.3994 ι ; κ = MCSNV v.3994 κ ; λ = MCSNV v.3994 λ ; μ = MCSNV v.3994 μ . Scale bars equal 20 mm.

The slab MCSNV v.3994 comprises 33 teeth, most of which are damaged with the root being almost never preserved (Fig. 6). Some of the preserved teeth in MCSNV v.3994 exhibit a marked bilateral asymmetry and two of them are also very small in size (e.g., MCSNV v.3994 μ ; Fig. 6, Fig. 7). The associated teeth are similar in size although the height of the cusps displays some variability (see Table 1 and Fig. 7). The tooth MCSNV v.3994 δ (Fig. 6) has a bilobate root.

Table 1. Measurements of the teeth of *Ptychodus altior*. MCSNV v.3995 α and MCSNV v.3994 α : see Fig. 8. MCSNV v.3994 β , MCSNV v.3994 γ , MCSNV v.3994 δ , MCSNV v.3994 ϵ , MCSNV v.3994 ζ , MCSNV v.3994 η , MCSNV v.3994 ι , MCSNV v.3994 κ , MCSNV v.3994 λ and MCSNV v.3994 μ : see Fig. 6, Fig. 7. MCSNV v.3995 β and MCSNV v.3995 γ : see Fig. 4. CRH = Crown height; CRW = Crown width; CRL = Crown length; CUH = Cusp height; CUW = Cusp width; CUL = Cusp length.

Tooth	CRH	CRW	CRL	CUH	CUW	CUL
MCSNV v.3994 α	~10 mm	~18 mm	~14 mm	~8 mm	~9 mm	~12 mm
MCSNV v.3994 β	~14 mm	~13 mm	~14 mm	~ mm	~ mm	~ mm
MCSNV v.3994 γ	~11 mm	-	~11 mm	-	-	-
MCSNV v.3994 δ	~10 mm	~13 mm	~12 mm	-	-	-
MCSNV v.3994 ϵ	-	~12 mm	~12 mm	-	-	-
MCSNV v.3994 ζ	~7 mm	~10 mm	~11 mm	-	-	-
MCSNV v.3994 η	~12 mm	~10 mm	~13 mm	-	-	-
MCSNV v.3994 ι	~8 mm	~11 mm	-	-	-	-
MCSNV v.3994 κ	~14 mm	~13 mm	~12 mm	-	~7 mm	-
MCSNV v.3994 λ	~12 mm	~13 mm	~13 mm	-	-	-
MCSNV v.3994 μ	~7 mm	~8 mm	~9 mm	~4 mm	~3 mm	~7 mm
MCSNV v.3995 α	~12 mm	~13 mm	~14 mm	~10 mm	~6 mm	~11 mm
MCSNV v.3995 β	~10 mm	~18 mm	~13 mm	-	~6 mm	~11 mm
MCSNV v.3995 γ	-	-	-	~9 mm	-	~12 mm
MCSNV v.14044	-	-	-	~8 mm	~9 mm	~6 mm
MCSNV v.14031	-	-	-	~5 mm	~4 mm	~7 mm

Three teeth, still associated, have been detached from the slab (Figs. 8D-H'). This tooth association comprises a well-preserved tooth (labeled herein "MCSNV v.3994 α ", Figs. 8F-H'), a single dental cusp (Figs. 8D, E) and a bilaterally asymmetric fragmentary tooth (Fig. 7E). The tooth MCSNV v.3994 α (Figs. 8F-H') is very similar in size and overall morphology to MCSNV v.3995 α (Figs. 8A-

C'), although notably asymmetric. Moreover, MCSNV v.3994 α has the mesial marginal area more developed than the distal one (Figs. 8F, F', H, H'). See Table 1 for tooth measurements.

Specimen MGP-PD 14044 (Figs. 9D, D') from Castellavazzo (Belluno) consists of an isolated and incomplete tooth, solely represented by the apical part of the cusp, still partially embedded in the matrix. This tooth, rather abraded, exhibits two ridges limited to the apex of the cusp, whose extremities only are visible. MGP-PD 14031 (Figs. 9A, C') is a laterally compressed tooth, which consists of a thin and high cusp, whose basal portion is embedded in a thin matrix layer. Six feebly pronounced ridges limited to the apex characterize the asymmetric cusp. The lateral and posterior faces of the cusp are completely smooth, whereas the anterior face of the cusp displays faint granulations (Figs. 9C, C'). Posteriorly, the crown profile is perpendicular to the horizontal axis of the tooth, whereas the anterior profile is much more inclined.

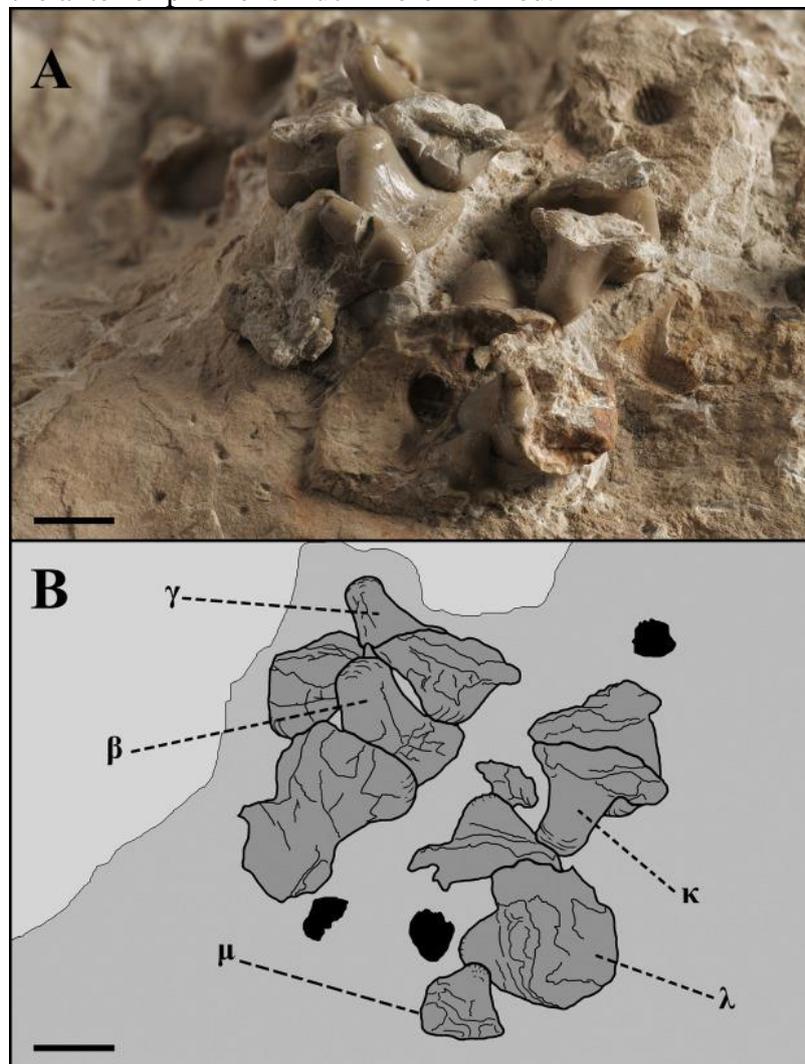


Fig. 7. *Ptychodus altior* Agassiz, 1835, from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. MCSNV v.3994 (A) photo and (B) interpretative line drawing, showing teeth characterized by different size and height. The black areas indicate the imprints of detached teeth. β = MCSNV v.3994 β ; γ = MCSNV v.3994 γ ; κ = MCSNV v.3994 κ ; λ = MCSNV v.3994 λ ; μ = MCSNV v.3994 μ . Scale bars equal 10 mm.

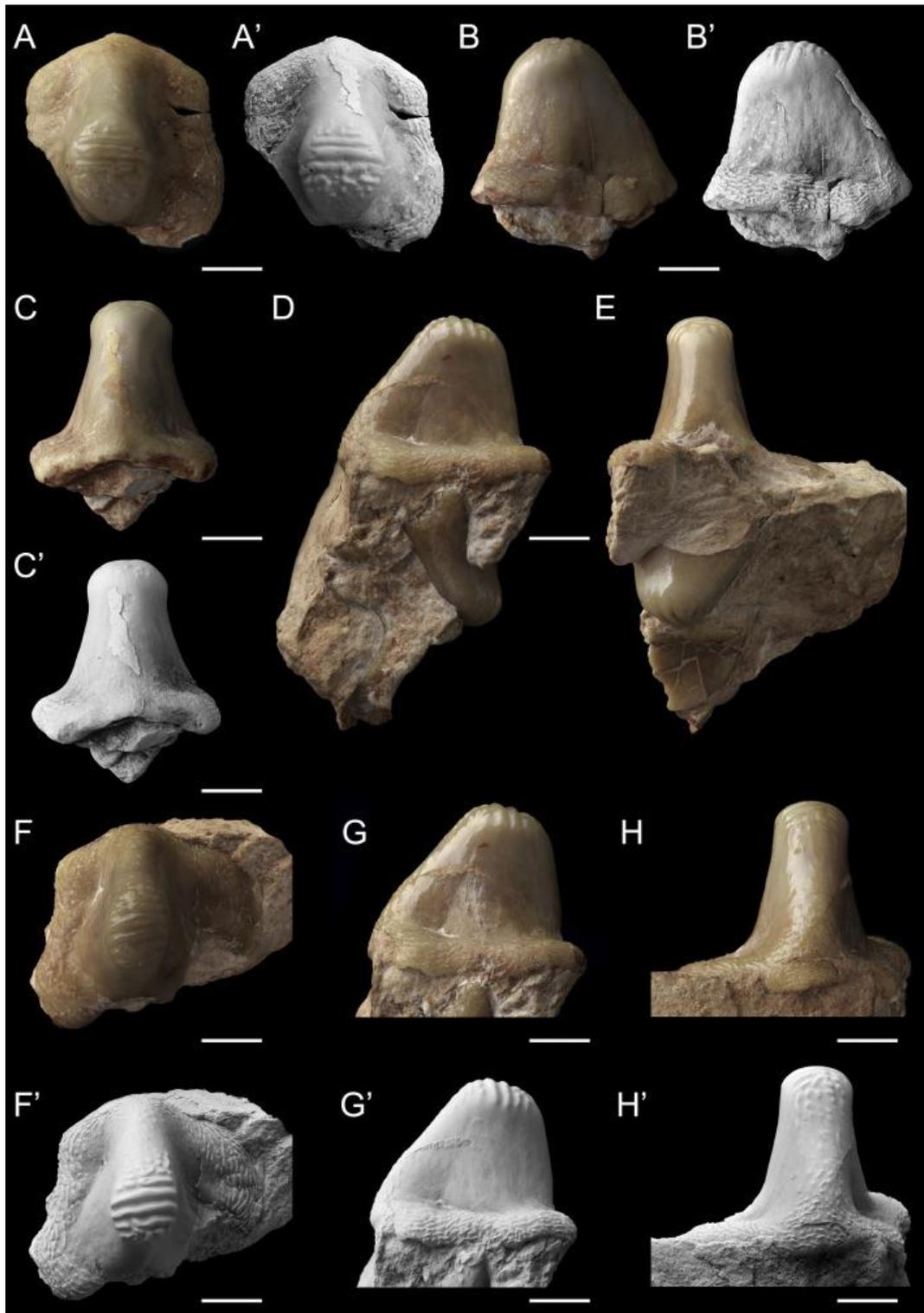


Fig. 8. Dental remains of *Ptychodus altior* Agassiz, 1835. Detached teeth from slabs MCSNV v.3994 (**D-H'**) and MCSNV v.3995 (**A-C'**); Specimens documented by color photos (**A-H**) and photos after 'smoking' treatment (**A'-C'**, **F'-H'**). Overview of the associated teeth of the specimen MCSNV v.3994 (**D, E**). Occlusal (**F, F'**), lateral (**G, G'**) and anterior (**H, H'**) views of MCSNV v.3994 α . Occlusal (**A, A'**), lateral (**B, B'**) and anterior (**C, C'**) views of NHMVR-3995 α . Scale bars equal 5 mm. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

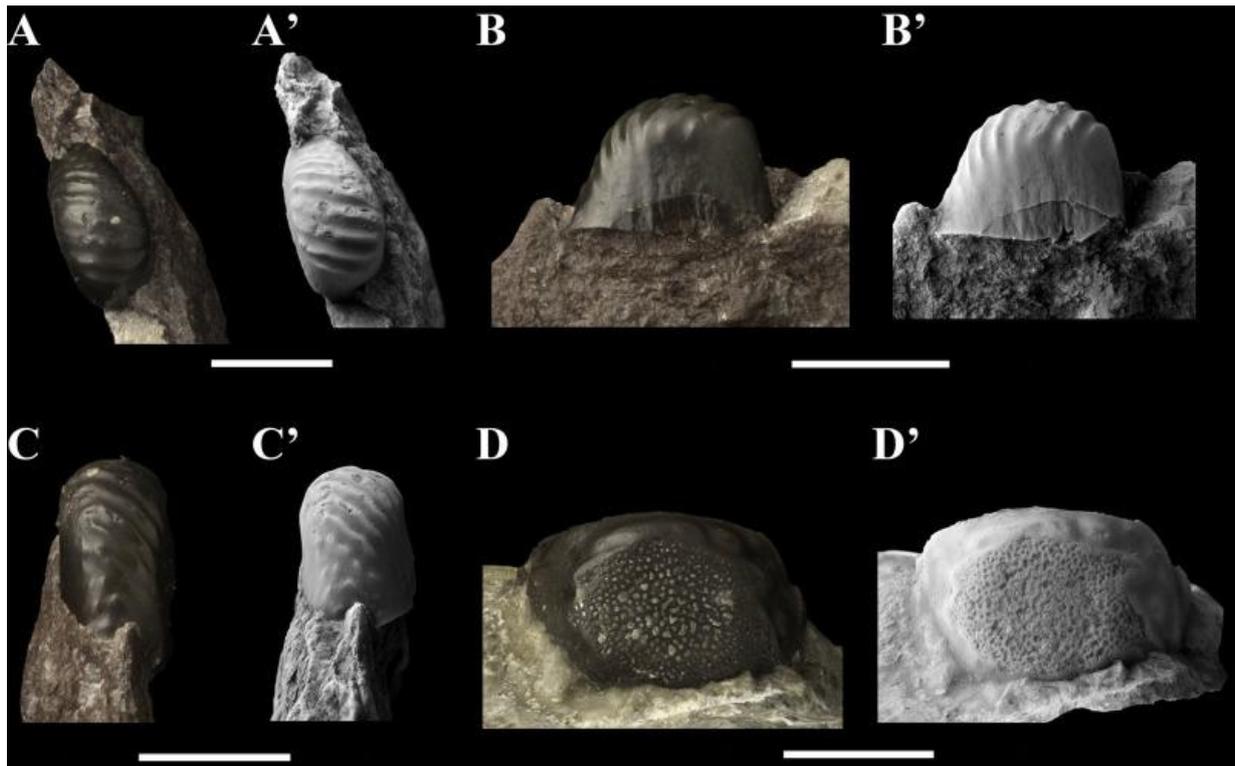


Fig. 9. Isolated teeth of *Ptychodus altior* Agassiz, 1835 from Castellavazzo (Belluno). Specimens documented by color photos (**A-D**) and photos after smoking treatment (**A'-D'**). MGP-PD-14031 (**A, A'**, occlusal view; **B, B'**, lateral view; **C, C'**, anterior view) and MGP-PD-14044 (**D, D'**, occlusal view), the latest markedly abraded on the dental cusp. The fossils show typical reddish or gray-greenish matrix of the “Pietra di Castellavazzo” limestone. Scale bars equal 5 mm. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

Remarks. The tooth labeled MCSNV v.3995 α (Figs. 8A-C') has a symmetric and high crown, and possibly represents a symphyseal tooth (Fig. 10S). MCSNV v.3994 α (Figs. 8F-H') represents a lateral tooth (Fig. 10L), because of the asymmetric development of its marginal area. MCSNV v.3994 μ (Fig. 6, Fig. 7) is the smallest tooth of the set and is considerably bilaterally asymmetric; it probably occupied one of the outer rows of the dental plate. The other teeth are too fragmentary to confidently establish their position within the jaws. There is no evidence of the upper symphyseal teeth. The different heights of the many teeth along with their similar size may indicate the presence of both lower and upper jaw teeth (Fig. 7). MGP-PD 14044 (Figs. 9D, D') is too fragmentary to identify its original position within the dental plate. The cusp MGP-PD 14031 (Figs. 9A-C') is asymmetric, probably because this tooth occupied one of the lateral rows of the dental plate.

As mentioned above, on both slabs MCSNV v.3994-3995, several teeth are broken or only poorly preserved (Fig. 4, Fig. 5, Fig. 6, Fig. 7). In his description of *Ptychodus altior* sensu Agassiz, 1835, Dixon, 1850 assumed that a direct relationship exists between the reduced thickness of the enameloid layer and occurrence of damaged teeth. Several specimens from the Upper Chalk of England, housed in the Natural History Museum, London, display damaged enameloid and seem to support Dixon's assumption. Several detached teeth coming from two tooth sets housed in the Naturhistorisches

Museum, Wien (NHMW) exhibit morphologies that are fully consistent with the lateral and symphyseal teeth described herein; the only difference is their much smaller size (one third as wide in average) compared to those preserved on the slabs MCSNV v.3994-3995. Such difference in size could be an indication of different ontogenetic stages, pending further findings of associated or articulated tooth sets of this poorly known species.

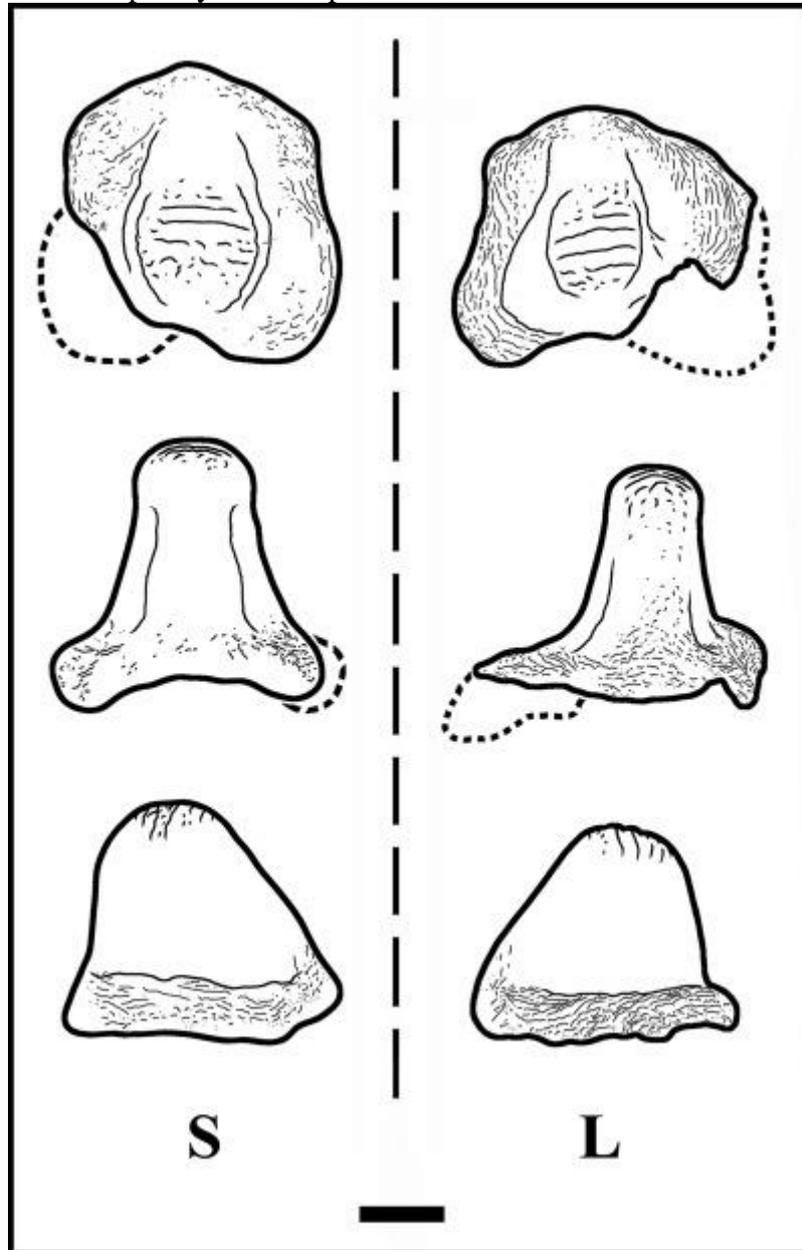


Fig. 10. Interpretative illustrations of lower teeth of *Ptychodus altior* Agassiz, 1835. Symphyseal (S) and lateral (L) teeth; reconstruction based on MCSNV v.3994 α (L) and MCSNV v.3995 α (S). Scale bar equals 5 mm.

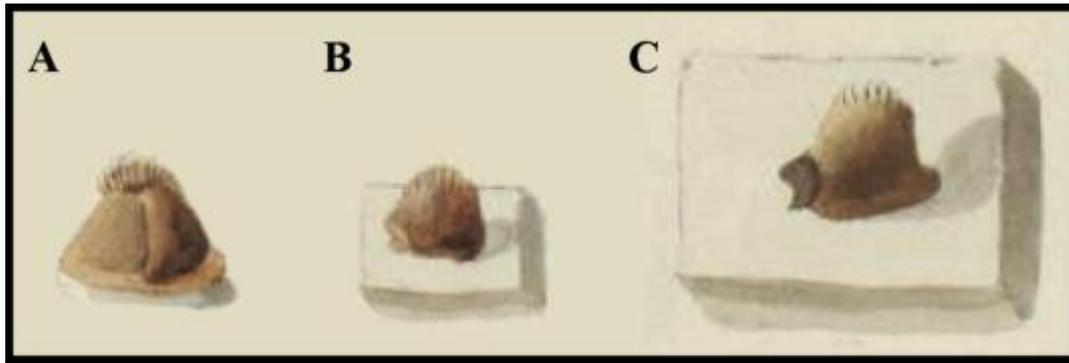


Fig. 11. First illustration of *Ptychodus altior* Agassiz, 1835 teeth. Figures (A-C) by Mantell (1822: t. 32, figs. 17, 21, 27). Mantell initially identified these fossil teeth as pertaining to a teleost close to the porcupine fish genus *Diodon*. Excerpt from Mantell (1822), ETH-Bibliothek Zürich, Rar 2452, <http://doi.org/10.3931/e-rara-16021/Public Domain Mark>.

Nomenclatural notes. High-cusped *Ptychodus* teeth with smooth cusp faces were figured for the first time by Gideon Mantell (1822: pl. 32, figs. 17, 21, 27; Fig. 11) based on material collected from the English Chalk of South Downs. Subsequently, Agassiz (1835, p. 54) introduced the species *Ptychodus altior*, referring explicitly to the teeth figured by Mantell (1822), in the “Feuilleton additionnel” of the “Recherches sur les Poissons Fossiles” (Brignon, 2015). Therefore, according to Article 12.2.7 of the Code of Zoological Nomenclature (ICZN Code, 1999, names published before 1931), 1835 must be regarded as the year of the original description of *P. altior* (Brignon, 2015: p. 14). After the publication of the “Feuilleton”, Agassiz attributed two additional teeth, figured and described in the third volume of the “Recherches” (Agassiz, 1838: pl. 25b, figs. 9, 10 and Agassiz, 1839; Fig. 12), to *P. altior*. However, the teeth figured by Agassiz (1838) strongly differ from those presented in Mantell’s figure, to which Agassiz referred in 1835. Subsequently, several authors (e.g., Giebel, 1848; Priem, 1896; Woodward, 1889, Woodward, 1912) considered *Ptychodus altior* as figured in Agassiz, 1838, Agassiz, 1839 to be a junior synonym of *Ptychodus mammillaris* Agassiz. However, according to Dixon (1850), *Ptychodus altior* represents a “very characteristic species”. The specimen figured by Dixon (1850: pl. 30, fig. 10; Fig. 13E), which is fully consistent with the specimens described herein, is probably NHMUK PV P49851 (Figs. 13A-D), currently part of the “Capron Collection” housed in the Natural History Museum, London. This specimen is also very similar to the three teeth originally figured by Mantell (1822) and assigned to *P. altior* by Agassiz (1835). Woodward, 1889, Woodward, 1912 considered *P. altior* sensu Dixon (1850) to be a phenotypic variation of *P. rugosus* Dixon 1850, and figured two specimens exhibiting the peculiar high-cusped morphology in his 1912 publication (Fig. 14). Since then, most authors followed this interpretation and Leriche, 1906, Leriche, 1909 used the name “*altior*” to indicate a variety of *P. rugosus* with elevated cusp and smooth lateral cusp faces. The same author later renamed this peculiar morphotype and introduced the name “*elevatus*” for it (Leriche, 1929). Since Dixon (1850), *P. altior* was mentioned as a valid

species solely by Fossa-Mancini (1921: p. 209). Herman (1977) considered the “morphotype” *elevatus* as a separate and valid species (*Ptychodus elevatus*), returning to the initial *Ptychodus altior* concept of Dixon (1850) and Agassiz (1835). Finally, Cappetta (2012) used the specific name *elevatus* for *Ptychodus* teeth characterized by a high and narrow cusp. According to the Article 23.1 of the International Code of Zoological Nomenclature (ICZN Code, 1999), the valid name of a taxon is the oldest available name. As a consequence, we consider *Ptychodus elevatus* Herman 1977 as a junior synonym of *Ptychodus altior* Agassiz, 1835.

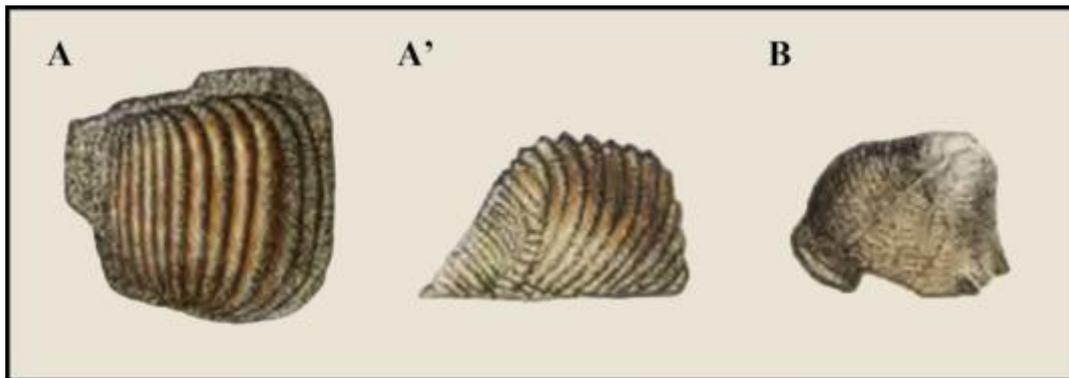


Fig. 12. Teeth assigned by Agassiz (1838: t. 25b, figs. 9, 10) to *Ptychodus altior*, figured in the third volume of “Recherches sur les poissons fossiles”, subsequently re-determined by other authors as *P. mammillaris*. Excerpt from Agassiz (1838). **A**, occlusal view; **A'**, **B**, lateral view.

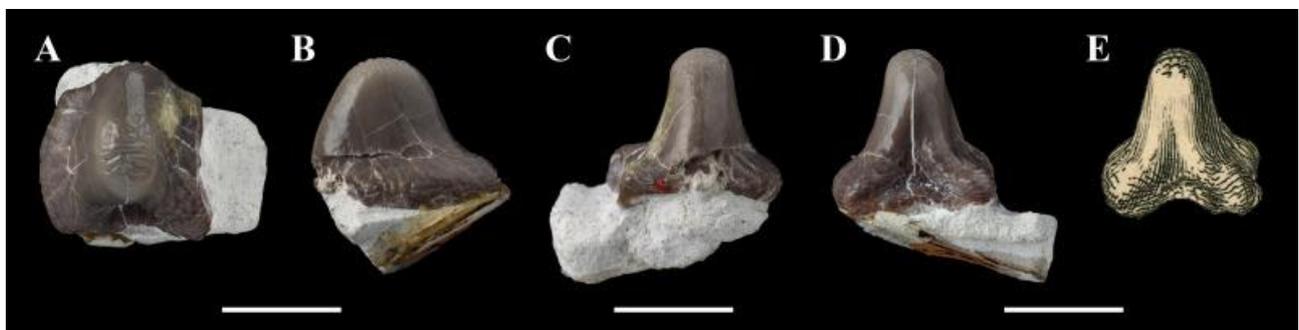


Fig. 13. NHMUK PV P49851, specimen of *Ptychodus altior* Agassiz, 1835 belonging to the “Capron Collection” (associated to another teeth). **A**, occlusal view; **B**, lateral view; **C**, anterior view; **D**, posterior view. It probably corresponds to the specimen (E) originally figured by Dixon (1850: t. 30, fig. 10). Scale bars equal 10 mm. Fig. 13E is an excerpt from Dixon (1850).

Discussion

Comparison with similar species

As discussed above, several authors assigned *Ptychodus* teeth with high cusps and smooth faces to the species *P. rugosus* (e.g., Woodward, 1912, Hamm, 2010). Priem (1896) interpreted the small and narrow teeth formerly referred to *P. altior* as pertaining to the upper symphyseal row of *P. rugosus*.

This hypothesis is, however, not acceptable since the upper symphyseal teeth of *P. rugosus* (Figs. 15B, B') are characterized by a scarcely developed or almost absent cusp (Case et al., 1990; Hamm, 2010). Moreover, as evidenced herein, both specimens MCSNV v.3994-3995 comprise bilateral asymmetric (lateral, Figs. 8F-H', 10L) as well as symmetric (symphyseal, Figs. 8A-C', 10S) teeth and both of them are notably different from those characteristic of *Ptychodus rugosus* (e.g., Hamm, 2010; MGP-PD 7344, Figs. 15A-A").

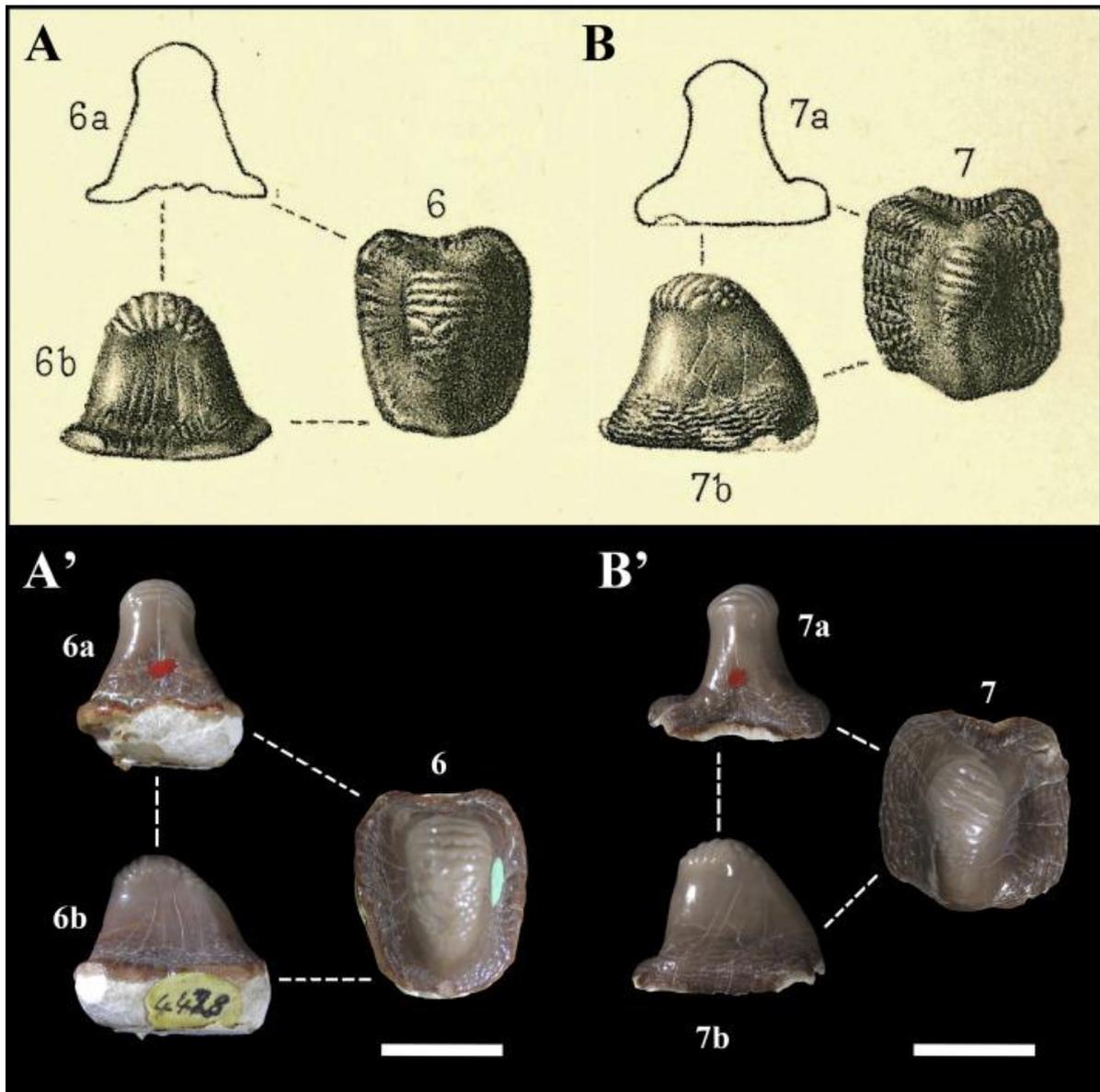


Fig. 14. Teeth of *Ptychodus altior* Agassiz, 1835. Specimens NHMUK PV P4428 (**A**, **A'**) from the “Mantell Collection” and NHMUK PV P28347 (**B**, **B'**) from the “Dixon Collection”. NHMUK PV P28347 (**B**, **B'**) is designated herein as neotype of *Ptychodus altior* Agassiz, 1835. Woodward (1912: t. 48, figs. 6-7b) originally figured both these teeth, and referred them to *Ptychodus rugosus*. 6, 7 = occlusal view; 6a, 7a = posterior view; 6b, 7b = lateral view. Scale bars equal 10 mm. Fig. 14A-B excerpt from Woodward (1912).

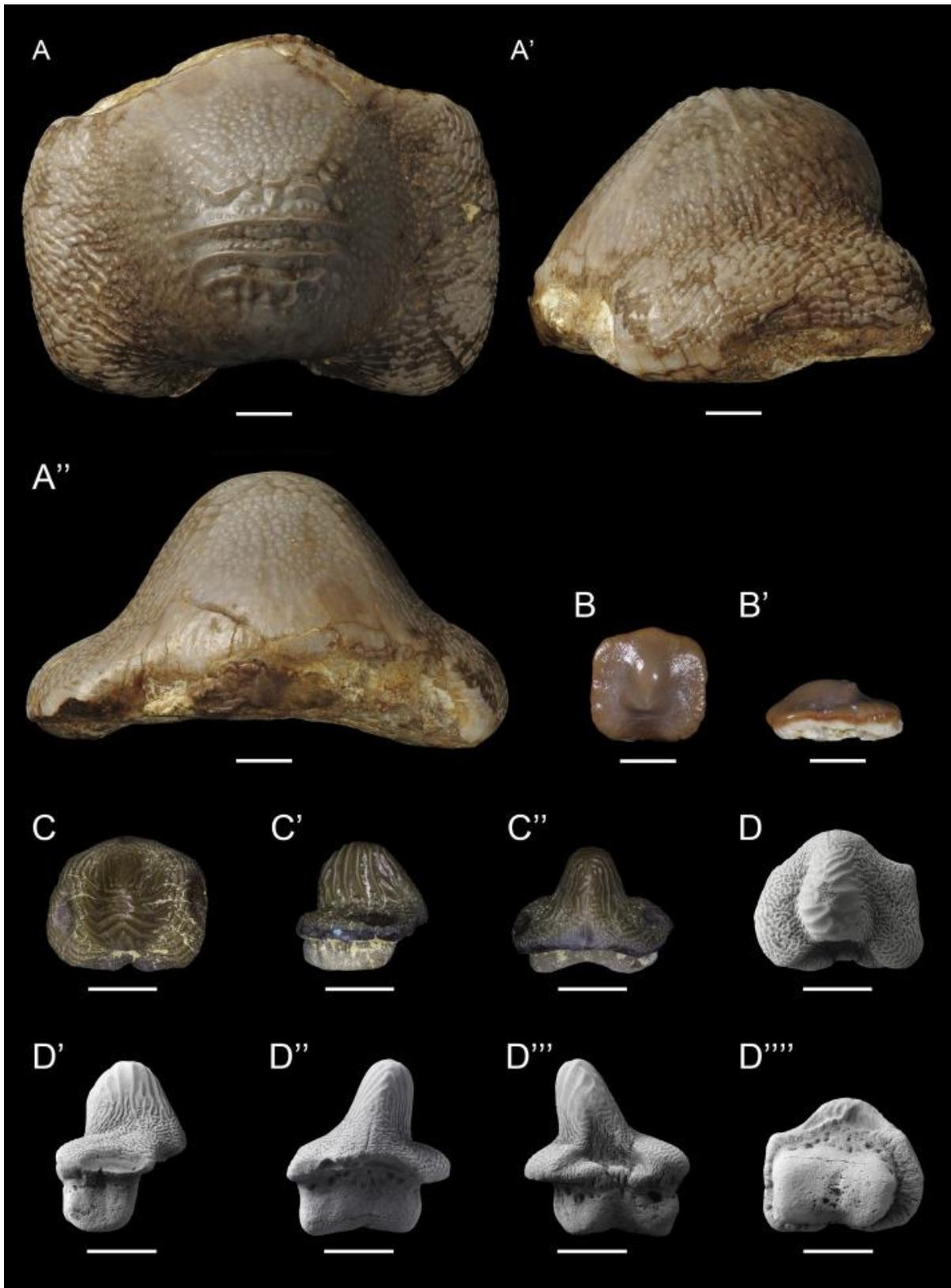


Fig. 15. Teeth of high-cusped *Ptychodus*. Central rows tooth (MGP-PD-7344; **A**, occlusal view; **A'**, anterior view; **A''**, lateral view) of *Ptychodus rugosus* from the Santonian of Valdagno (Vicenza province, Northern Italy); scale bars equal 10 mm. Upper symphyseal tooth of *Ptychodus rugosus* (**B**, occlusal view; **B'**, lateral view) belonging to an associated tooth set (NHMUK PV P61143-49), Sussex (English Chalk); scale bars equals to 5 mm. FHSM VP-18451 (**C**, occlusal view; **C'**, lateral view; **C''**, anterior view) ascribed to *P. whipplei*, Northern Kansas (U.S.A.) and

housed in Fort Hays State University's Sternberg Museum of Natural History (FHSM); scale bars equals to 5 mm. MGP-PD 32066 (**D**, occlusal view; **D'**, lateral view; **D''**, anterior view; **D'''**, posterior view; **D''''**, inferior view) ascribed to *P. whipplei* coming from Kamp Ranch Fm., Dallas County, Texas (U.S.A.).

Woodward (1912) hypothesized that the *Ptychodus altior* morphotype might belong to immature specimens of *P. rugosus* Dixon (1850). Later, other authors (e.g., Leriche, 1929) accepted the opinion of Woodward (1912), based on some similarities between the teeth of *P. altior* and *P. rugosus*, as for example the presence of ridges confined to the cusp apex, which occur only in these two taxa (Figs. 7, 14A-A"). Moreover, the stratigraphic ranges of the two taxa are partially overlapping. *Ptychodus altior* seems to be restricted to the interval Turonian-Coniacian (Leriche, 1929, Herman, 1977), whereas *P. rugosus* ranges from the Coniacian to the Santonian (Herman, 1977, MacLeod, 1982, Hamm, 2010). Furthermore, the central teeth of *P. rugosus* have more rounded and large cusps (Figs. 15A-A") than those of *P. altior* (Figs. 8A-C') and their lateral marginal areas are never bilobate (see Hamm, 2010).

High cusps similar to those of *Ptychodus altior* (e.g., Fig. 8) are also present in the North American species *P. whipplei* (Figs. 15C-C", D-D'''). *Ptychodus whipplei* is characterized by narrow and high tooth cusps, which are nearly cylindrical in cross section, unlike those of other *Ptychodus* species, which have a more oval or conical cusp cross section (see Lucas, 2006). The two species, however, can be easily separated based on different ridge morphologies and distributional pattern since *P. whipplei* has ridges that extend transversally across the entire cusp (Figs. 15C-C", D-D'''; see also Williston, 1900).

Possible dietary preference of *Ptychodus* with high and narrow-cusped teeth

The wide and flat molariform teeth of *Ptychodus* (e.g., *P. decurrens*, *P. latissimus* and *P. polygyrus*) are commonly regarded as durophagous feeding adaptations and benthic, thick-shelled macroinvertebrates are traditionally considered target preys of *Ptychodus* (e.g., Compagno, 2002, Everhart and Caggiano, 2004, Everhart, 2005, Cappetta, 2012, Shimada, 2012, Kolmann et al., 2014). A few possible lines of evidence supporting this assumption are represented by putative tooth marks on inoceramid bivalves (Kauffman, 1972). Stewart (1988) also reported some *Ptychodus* teeth found associated with presumed remains of inoceramid bivalves and fragments of cirriped crustaceans. The peculiar cusp morphology shared by *P. altior* and *P. whipplei* (see above) may be related to peculiar target preys, possibly different from those of the other congeneric species. Cappetta (2012) therefore suggested that the narrow-cusped species *Ptychodus whipplei* and *P. elevatus* (= *P. altior*) probably preyed mostly on thin-shelled invertebrates (e.g., ammonites). However, there is no direct evidence of predator-prey relationships between *Ptychodus* and any invertebrate yet. Shimada et al. (2009) hypothesized an alternative diet for *Ptychodus occidentalis* based on articulated specimen exhibiting

laterally narrow dentitions with high-crowned teeth. According to Shimada et al. (2009), the dentition could have also had a grasping function in although the dental plates of this species were suitable for crushing. The species *P. occidentalis* may have been an opportunistic generalist, which occasionally preyed on crustaceans and mollusks that not necessarily were protected by hard shell (Shimada et al., 2009).

In addition, several extant chondrichthyans with relatively narrow and cusped teeth feed on thin-shelled prey (see Talent, 1982, Wilga and Motta, 2000, Compagno et al., 2005, Shimada et al., 2009, Mara et al., 2010, Herbert and Motta, 2018). For example, in the bonnethead shark (*Sphyrna tiburo*) the high-cusped anterior teeth are relatively small and narrow and are used for grasping, while the posterior molariform teeth are suitable for crushing and processing food (Wilga and Motta, 2000, Mara et al., 2010). Smooth-hound sharks (*Mustelus* spp.) have rounded cusped teeth as well and feed on crustaceans (Compagno, 1984, Rountree and Able, 1996). Moreover, some Rajidae, such as *Dipturus chilensis* and *Bathyraja brachyurops*, or Potamotrygonidae, such as *Potamotrygon motoro*, grasp its preys (e.g., crustaceans) using their narrow-cusped teeth (Belleggia et al., 2008, Koen Alonso et al., 2001, Shibuya et al., 2012.). Although these extant chondrichthyans and *Ptychodus altior* are not closely related, some of the dental characters shared by most of them may indicate similar diet preferences. Indeed, the peculiar dental morphology with narrow-cusped teeth in *P. altior* suggests a grasping function.

Nevertheless, based on the marked abrasion patterns observed on occlusal surfaces of some of the teeth described here (see for example Fig. 9 D, D') and on those observed on teeth housed in the collections of the museums of London and Vienna, it is evident that *P. altior* was also able to crush and fragment its preys.

Therefore, it is possible that within the genus *Ptychodus* generalists (e.g., *P. altior* and *P. occidentalis*) and specialists (e.g., *P. mortoni*, see Shimada, 2012; *P. latissimus* and *P. polygyrus*) evolved probably to minimize competition. *Ptychodus altior* may represent a peculiar evolutionary lineage, in which new feeding adaptations evolved, with a dental morphology more similar to a mixed grinding/grasping-type dentition, in analogy with some extant rays or sharks that target mostly crustaceans (see above).

Distribution and paleobiogeography

Most specimens referred to *Ptychodus altior* come from the Upper Cretaceous English Chalk (e.g. Kent, Sussex, Surrey; Dixon, 1850, Mantell, 1822, Woodward, 1889, Woodward, 1912). The Chalk of Sussex, England (see Mantell, 1822) also provided the original type series on which Agassiz (1835) based this species (see also Brignon, 2015). Reuss (1845) and Fischer et al. (2017) described some

teeth belonging to *P. altior* from Germany, erroneously referred to as *P. mammillaris*. Several other isolated teeth from Germany are housed in the collections of the Naturhistorisches Museum, Wien. Material referred to *P. altior* also occurs in Turonian deposits of northwestern France (Priem, 1896; Leriche, 1902, Leriche, 1906, Leriche, 1929, Guinot et al., 2013), and two teeth from the Coniacian of Belgium (Maisières Chalk Fm) were described and figured by Herman (1977). More recently, an isolated tooth, attributable to *P. altior* was described from the Upper Cretaceous of Romania (Trif and Codrea, 2017). The Late Cretaceous configuration of Europe as an archipelago (see Dalla Vecchia et al., 2005, Martin and Delfino, 2010, Scotese, 2014) probably promoted the broad distribution of *Ptychodus altior* in this area. Antunes and Cappetta (2002: figs. 11a-d) described and figured a single tooth, assigned to *P. whipplei* but clearly attributable to *P. altior*, from Angola, which currently is the only record of this species outside Europe. The presence of a “Trans-Saharan Seaway” (Scotese, 2014) could have constituted a passage between southern Europe and Angola region.

Concluding remarks

The Late Cretaceous elasmobranch *Ptychodus altior* had a dominantly European distribution with the exception of a single record from Angola (Africa). All records indicate that the stratigraphic range of the species is confined to the Turonian-Coniacian and the micropaleontological analyses of the sedimentary rock sample obtained from the matrix of MCSNV v.3995 are consistent with this datum. According to the International Code of Zoological Nomenclature (ICZN Code, 1999), *Ptychodus altior* Agassiz, 1835 must be considered valid and consequently represents a senior synonym of *P. elevatus* Herman, 1977. The presence of MCSNV v.3994-3995 in the Lessini Mountains area represents the first associated occurrence of this species in Italy providing new information about its dental pattern (e.g., the narrow teeth of *P. altior* do not represent upper symphyseal teeth of *P. rugosus* as previously hypothesized). The Italian specimens are similar, but still clearly different from the teeth of *Ptychodus rugosus* and *P. whipplei*. The different size of Italian specimens and those housed at the Natural History Museum of Wien may be an indication of different ontogenetic stages. The narrow high-cusped morphology characterizing *Ptychodus altior* and *P. whipplei* probably indicates a different target prey compared to low-crowned *Ptychodus* species.

Author contributions

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

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

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

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

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

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

Acknowledgements

This paper is dedicated to Anna Vaccari (curatorial technician of the paleontological section of the Museo Civico di Storia Naturale di Verona), taken from us too soon.

The authors deeply thank Elisa Marchesini (Associazione Culturale Officina 3; Museo Paleontologico e Preistorico di S. Anna d'Alfaedo), Roberto Zorzin (Museo Civico di Storia Naturale di Verona), Mariagabriella Fornasiero (Museo di Geologia e Paleontologia dell'Università di Padova), Emma Bernard (Natural History Museum of London, NHMUK) and Ursula Göhlich (Naturhistorisches Museum, Wien) for access to the specimens and to the information about the collections. We would also acknowledge Stefano Castelli (Dipartimento di Geoscienze dell'Università di Padova) for accurate photographic documentation and figures preparation of the Italian specimens and Kevin Webb (NHMUK) for the accurate photos of the English Chalk specimens housed in the NHMUK. The copyright of the NHMUK photos is reserved to the NHMUK ("NHM") and Kevin Webb. We thank also Christina Byrd (Sternberg Museum of Natural History, Fort Hays State University) for photographs and collection data about *Ptychodus whipplei* from the U.S.A. Special thanks are due to Giuseppe Marramà (University of Wien) for useful suggestions. We thank Alberto Collareta and an anonymous reviewer for helpful comments and suggestions. Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled 'Reappraisal of two key Fossil-Lagerstätten in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach', assigned to Eliana Fornaciari). V.L. was also financially supported by the Ferrara University FAR 2016-2017 grants.

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3.4.

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

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Abstract

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

Introduction

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

Isolated teeth are so far the most common remains of *C. mantelli* reported from Italy (e.g., Bassani, 1876, D'Erasmus, 1922), although some partial skeletons were found in the Scaglia Rossa Formation of Lessini Mountains (Verona Province, Veneto Region) during the 1970s (Amalfitano et al., 2017b, Amalfitano et al., 2017c, Cigala Fulgosi et al., 1980, Dalla Vecchia et al., 2005; Ginevra et al., 2000). The majority of these skeletal remains consist of teeth associated with calcified vertebral centra and fragments of calcified cranial cartilage; in some cases, they include also placoid scales.

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

Geological background

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

The ‘lastame’ (‘lithozone’ 2 of the Scaglia Rossa Formation of Lozar and Grosso, 1997) crops out in the surroundings of S. Anna d'Alfaedo village (Verona Province) (Fig. 1), on Loffa Mount (western

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



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

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

(Colleselli et al., 1997, Trevisani, 2011), pending revisions, which are currently being carried out (Federico Fanti, pers. comm.). The fossil content of the ‘Pietra di Castellavazzo’, is similar to that of the ‘lastame’, including chondrichthyans and bony fishes, mostly represented by isolated teeth, and occasionally by more complete remains (e.g., Bassani, 1876, Bassani, 1888, Trevisani, 2009, Trevisani, 2011).

Historical background

The first report of isolated teeth of *Cretoxyrhina mantelli* from the Upper Cretaceous Scaglia Rossa Formation of the Lessini Mountains was that by Bassani (1876). However, teeth of this species have been found in northern Italy from at least the first half of the 19th century, as testified by the presence of four specimens in the collection of Tommaso Antonio Catullo (1782-1869) housed in the Museum di Geology and Paleontology of the University of Padova (pers. obs.; see Table 1 for details and D’Erasmus, 1922; Fig. 2 and supplementary material Fig. A.10-λ). Other teeth from the ‘Pietra di Castellavazzo’ were initially misidentified as *Lamna* (= *Sphenodus*) *longidens* (Bassani, 1876, D’Erasmus, 1922). De Zigno (1883: p. 9) reported several localities of the Scaglia Rossa Formation yielding isolated teeth of *C. mantelli*, including the Valpolicella, Agno Valley, Follina Hills, and the surroundings of the towns of Feltre and Belluno.

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

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

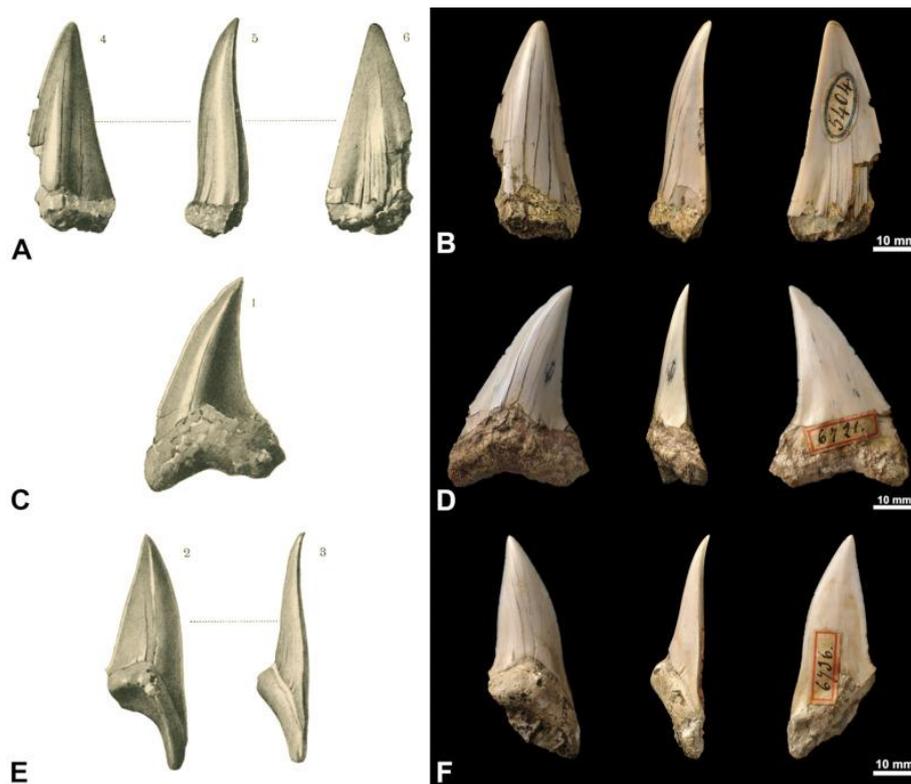


Fig. 2. *Cretoxyrhina mantelli* (Agassiz, 1835). Isolated teeth housed in the historical collections of the Museum of Geology and Paleontology of the University of Padova. **A.** MGP-PD 5404 as figured by D'Erasmus (1922: pl. 3, figs. 4-6), coming from Spilecco (VR) and erroneously attributed to the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

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

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

Material and methods

Institutional abbreviations

CE.A.S.C.: Centro di Analisi e Servizi Per la Certificazione, University of Padova, Padova, Italy; **FHSM:** Sternberg Museum of Natural History, Hays, Kansas, USA; **NHM:** The Natural History Museum, London, UK; **MCSNV:** Museo Civico di Storia Naturale di Verona (Civic Museum of Natural History), Verona, Italy; **MGC:** Museo Geopaleontologico di Camposilvano (Geopaleontological Museum), Camposilvano, Italy; **MGP-PD:** Museo di Geologia e Paleontologia (Museum of Geology and Paleontology), University of Padova, Padova, Italy; **MPPSA:** Museo Preistorico e Paleontologico di S. Anna d'Alfaedo (Prehistoric and Paleontological Museum), S. Anna d'Alfaedo, Italy.

Material

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

Methods

The specimens were documented with different photographic techniques depending on the size of the slabs (e.g., MPPSA IGVR 36371 and MPPSA IGVR 45305 were photographed with the photogrammetric technique and then the images were elaborated to obtain an orthophoto) using digital cameras (a Canon PowerShot SX720 HS and a Fuji X-E1 mounting 18-55 mm lens). Images and interpretative drawings of the specimens were obtained using the freewares GIMP (v. 2.10.2) and ImageJ (v. 1.47). The synonymy list and open nomenclature follow the standards proposed by Matthews, 1973, Bengtson, 1988 and Sigovini et al. (2016).

We refer to papers concerning *Cretoxyrhina* dentition (e.g., Bourdon and Everhart, 2011, Cappetta, 2012, Shimada, 1997a, Shimada, 2002) for tooth position identification, general dental characters and technical terms. The identification of tooth position in lamniform sharks is a debated matter related to the tooth rows arrangement on the palatoquadrate and Meckel's cartilage, as well as to the structure of these cranial elements (e.g., presence/absence of intermediate bar *sensu* Shimada, 2002 and the two hollows present on each side of the jaw *sensu* Siverson, 1999). 'Intermediate teeth' is probably the most controversial term. Siverson (1999) and Shimada (2002) proposed two alternative indications, based on homologous/non-homologous tooth positions. Later on, Cook et al. (2011: p. 9-

10) summarized the arguments discussed in the debate. We refer to Cook et al. (2011) and Kriwet et al. (2015). We follow Shimada (1997d) for general skeletal anatomy and Newbrey et al. (2015) for the vertebral morphology of *C. mantelli*. The terminology used for placoid scales follows Reif (1985). As for other fossil chondrichthyans (see Cappetta, 1987, Cappetta, 2012), the diagnosis of *Cretoxyrhina mantelli* is essentially based on dental characters. Herein, we propose an emended diagnosis of *C. mantelli* that integrates all of the dental characters reported by Bourdon and Everhart, 2011, Cappetta, 2012 and Shimada (1997a), in order to complete and better formalize it.

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

Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977
Superorder Galeomorphii Compagno, 1973
Order Lamniformes Berg, 1937
Family Cretoxyrhinidae Glikman, 1958
Genus *Cretoxyrhina* Glikman, 1958

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

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

Cretoxyrhina mantelli (Agassiz, 1835).

Fig. 2-12, Fig. 15, supplementary material Figs. A.1α-δ, θ-λ.
(selected synonyms)

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

- 1993 *Cretoxyrhina mantelli* (Agassiz, 1843) - Welton, Farish, p. 101, text-figs. 1-12 p. 101, 1-2 p. 102.
- 1996 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson, p. 819, pl. 1, figs. 1-18.
- 1997a *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 269, figs. 1-10.
- 1997b *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 926, figs. 1-2, 5-6.
- 1997c *Cretoxyrhina mantelli* - Shimada, p. 233, fig. 1.
- 1997d *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 642, figs. 1-11.
- 1997e *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada, p. 139, fig. 1.
- v2000 *Cretoxyrhina mantelli* (*sic*) - Ginevra et al., p. 31, fig. 6.1.
- v2000 Denti di squalo - Ginevra et al., p. 33, fig. 6.3.
- v2001 *Cretoxyrhina mantelli* - Zorzin, p. 98 (including text-fig.).
- v2003 *Isurus mantelli* (Agassiz) - Astolfi, Colombara, p. 144, fig. 205.
- 2005 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson, Lindgren, p. 303, fig. 2.
- v2005 *Cretoxyrhina mantelli* - Dalla Vecchia et al., p. 108, fig. 81.
- 2006 *Cretoxyrhina mantelli* (Agassiz, 1843) - Shimada et al., p. 185, figs. 1-6.
- 2008 *Cretoxyrhina mantelli* (Agassiz) - Shimada, p. 21, figs. 1-2, 6-7.
- 2011 *Cretoxyrhina mantelli* Agassiz - Bourdon, Everhart, p. 15, figs. 2, 4-7.
- 2012 *Cretoxyrhina mantelli* (Agassiz, 1838) - Cappetta, p. 236, figs. 216E-I.
- 2013 *Cretoxyrhina mantelli* (Agassiz, 1843) - Cook et al., p. 568, fig. 10.
- 2013 *Cretoxyrhina mantelli* (Agassiz, 1843) - Siverson et al., p. 3, fig. 10.
- vp.2013 Vertebre di selaceo squaloideo (*sic*) - Colombara, p. 40 (text-fig.).
- 2014 *Isurus denticulatus* Glickman (1957) - Diedrich, p. 8, figs. 4, 5A-D, 7A-F, N—V.
- 2015 *Cretoxyrhina mantelli* (Agassiz, 1843) - Newbrey et al., p. 878, figs. 7A-C, 8.
- 2017 *Cretoxyrhina mantelli* - Everhart, fig. 13.3.

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

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

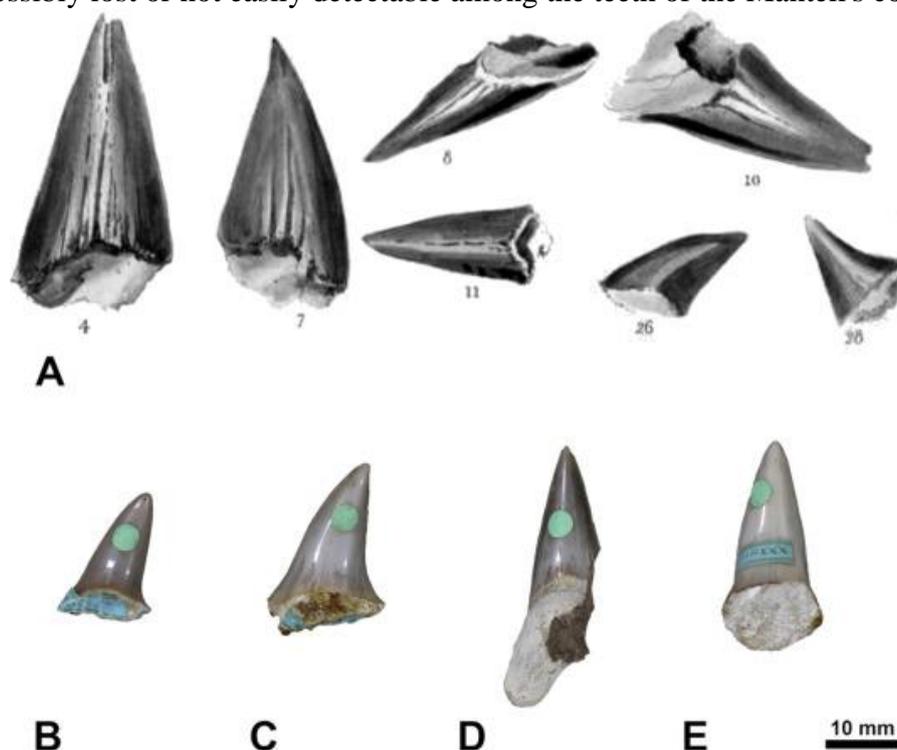


Fig. 3. Syntypes of *Cretoxyrhina mantelli* (Agassiz, 1835). **A.** Isolated teeth figured by Mantell (1822: pl. 32, figs. 4, 7, 8, 10, 11, 26, 28) to which Agassiz (1835, p. 54) referred when created *Lamna Mantellii* (subsequently *Oxyrhina mantelli* and *Cretoxyrhina mantelli*). Woodward (1889) identified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

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

Emended diagnosis. Lamniform shark unique in having the following apomorphic combination of dental characters: dental formula: 4S-2A-4I-11(+x)L/1s?-2a-1i-15(+x)l; monognathic heterodonty, strongly disjunct in upper teeth, slightly gradational in lower teeth; teeth with usually narrow, blade-like, asymmetrical and distally curved or sloped crown, extending above the mesial branch of root (especially in anterior teeth); cusp sharply pointed; symphyseal teeth strongly asymmetrical, with crown higher than wide, and distal root lobe generally more developed than the mesial one; first symphyseal teeth distally inclined, other symphyseal teeth mesially curved; anterior teeth nearly symmetrical; lower anterior teeth with very high cusp, higher than wide, particularly the second lower anterior tooth; first anterior teeth (upper and lower) usually the most symmetrical, with the second anterior tooth characterized by a slight distal inclination; crown tending to be labiolingually thicker and more sigmoidal (labially directed) in lower than in upper teeth, which are flatter and thinner, with the point of the cusp labially curved; lower teeth with more massive roots than uppers; intermediate teeth with crown height greater or similar to crown width, cusp inclined distally, with the sole first upper intermediate tooth distally curved; lateral teeth generally with crown wider than high, slightly to strongly distally inclined, decreasing in size distally, their inclination increases distally; enameloid smooth and cutting edges continuous; enameloid may form weak basoapical ripples, mainly on the labial side; lingual face convex, labial face nearly flat or only weakly convex; basal part of crown characterized by small oblique heels (shoulders), with continuous cutting edges on the sides of the cusp; both heels may occasionally bear a lateral cusplet in distolateral and commissural teeth; tooth neck marked; root strongly bilobated, becoming more splayed distally; concavity of the basal margin of the root low (lateral teeth) to high (anterior-intermediate teeth); mesial branch of the root usually pointed, the distal one rounded and expanded; lingual protuberance developed, lacking a nutrient groove and usually bearing one nutrient foramen.

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

Based on calcareous nannofossils and planktic foraminifera biostratigraphy, the specimens are dated to the middle-late Turonian (for more details see Table 2) according to the correlation between calcareous plankton zones and stages by Ogg, Hinnov (2012) (UC7-UC9 Zones, Burnet, 1998 and *Dicarinella primitiva*/*Marginotruncana sigali* Zone, Coccioni, Premoli Silva, 2015).

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



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

Table 2. Biostratigraphic data from *Cretoxyrhina mantelli* specimens. Main calcareous plankton taxa and biostratigraphic classification of samples obtained from three partially articulated specimens of *Cretoxyrhina mantelli* (Agassiz, 1835).

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

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

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

F). Other teeth are fragmentary. The highest tooth measures 67 mm in total height (52 mm in crown height on the labial side), while the lowest tooth is ca. 28 mm high.

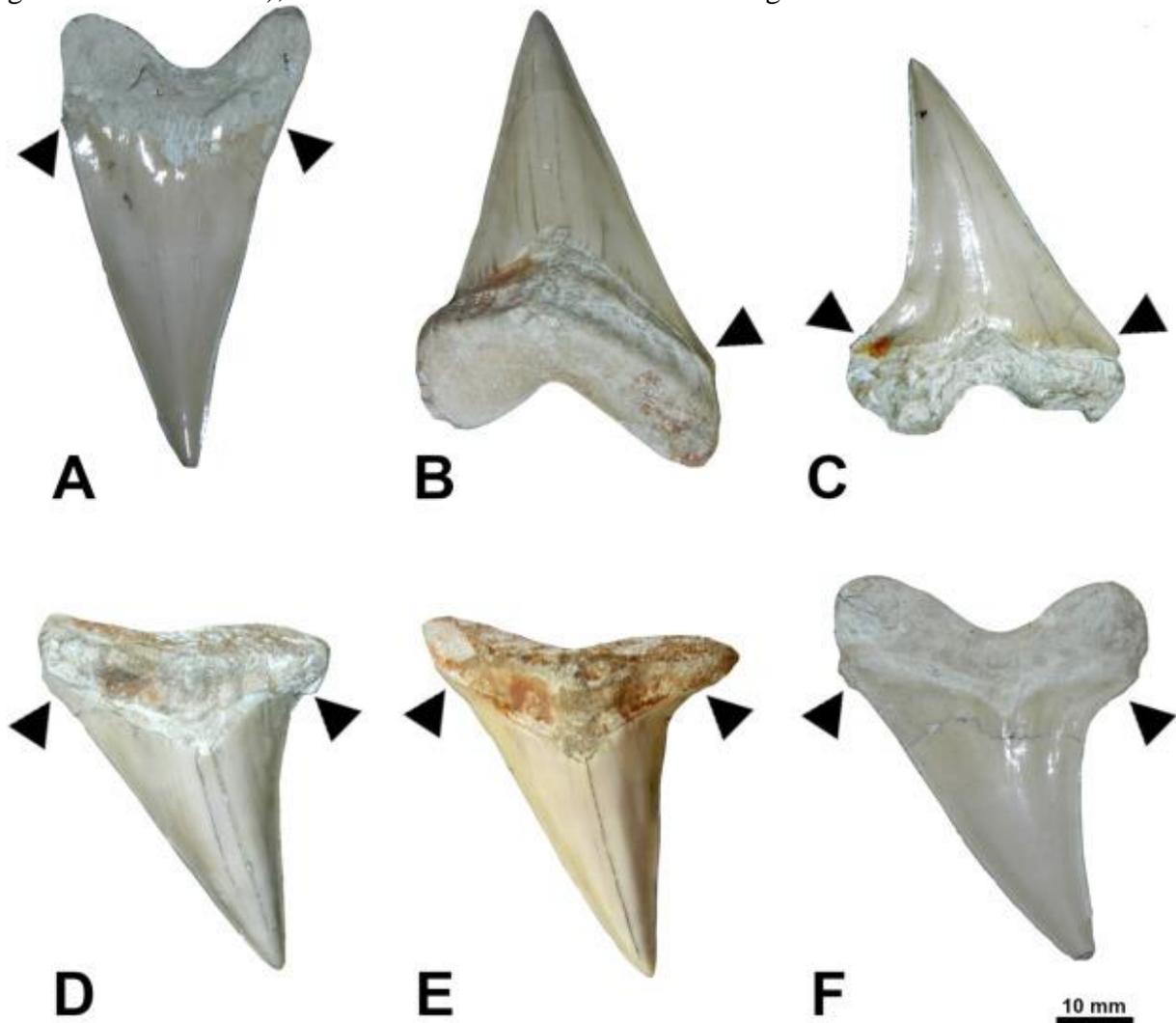


Fig. 5. *Cretoxyrhina mantelli* (Agassiz, 1835). Teeth of the specimen MPPSA-IGVR 36371. **A.** First upper anterior tooth (A1) (left palatoquadrate), labial view. **B.** Second lower anterior tooth (a2) (left Meckel's cartilage), lingual view. **C.** Intermediate tooth/third lower anterior? tooth (i?/a3),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

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

while the smallest one has a maximum diameter of ca. 40 mm. The antero-posterior length ranges from 14 mm to ca. 40 mm.

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

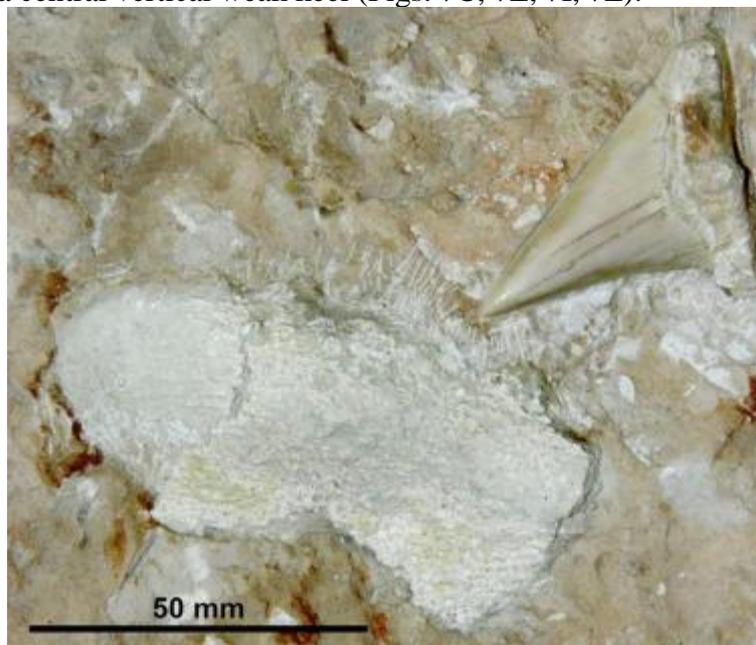


Fig. 6. *Cretoxyrhina mantelli* (Agassiz, 1835). Tessellated calcified cartilage of MPPSA-IGVR 36371. Photo of a fragment of cranial calcified cartilage associated to a tooth. Scale bar = 50 mm.

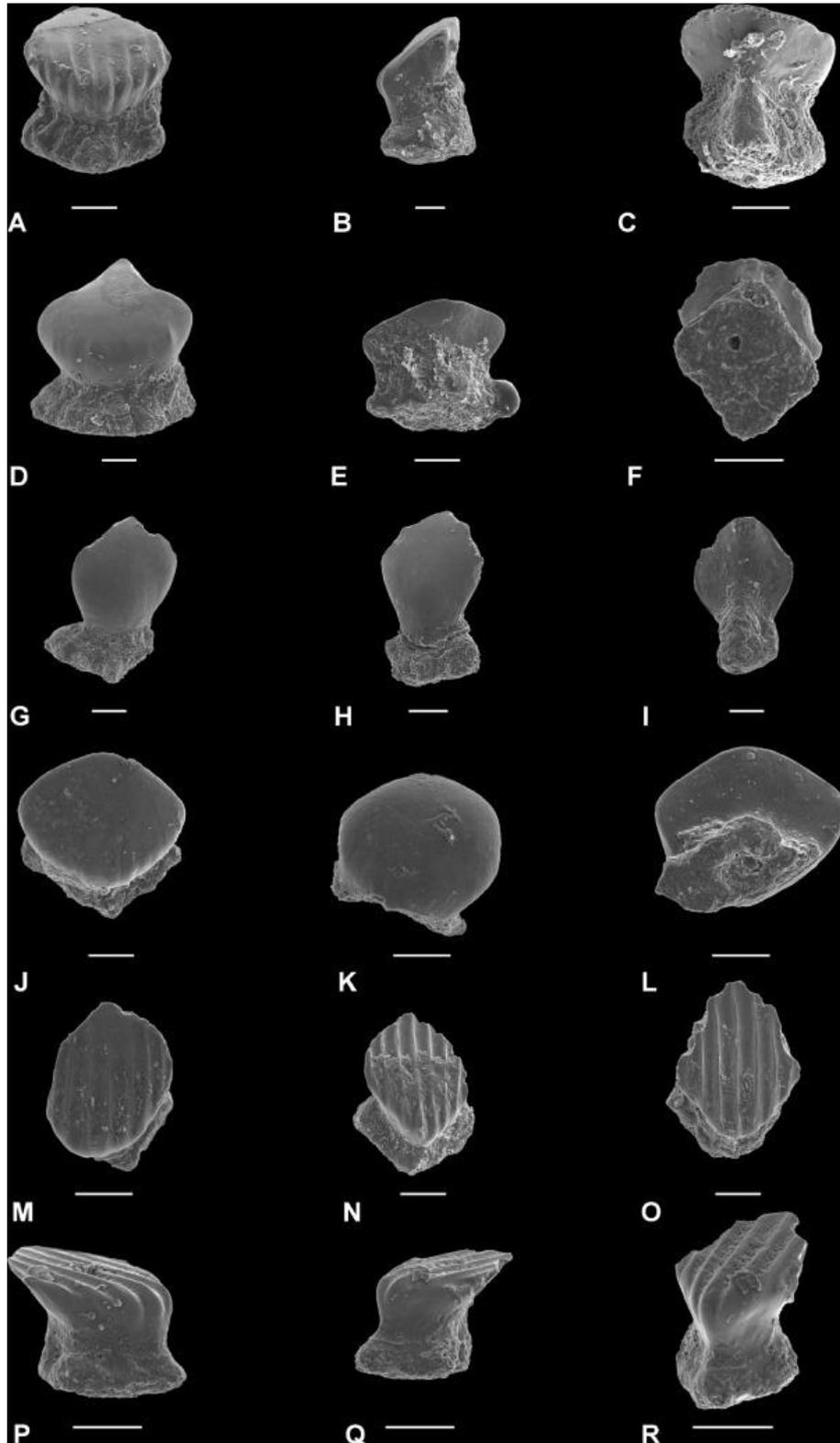


Fig. 7. *Cretoxyrhina mantelli* (Agassiz, 1835). SEM images of placoid scale from MPPSA-IGVR 36371. **A.** Frontal view. **B.** Lateral view. **C.** Posterior view. **D.** Anterior view. **E.** Posterior view. **F.** Inferior view. **G.** Anterior view. **H.** Anterior view. **I.** Posterior view. **J.**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

Specimen MPPSA-IGVR 45305 (Fig. 5B) is preserved on four slabs and comprises 131 vertebral centra, 55 teeth, and is associated with fragments of tessellated calcified cartilage. All teeth are

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

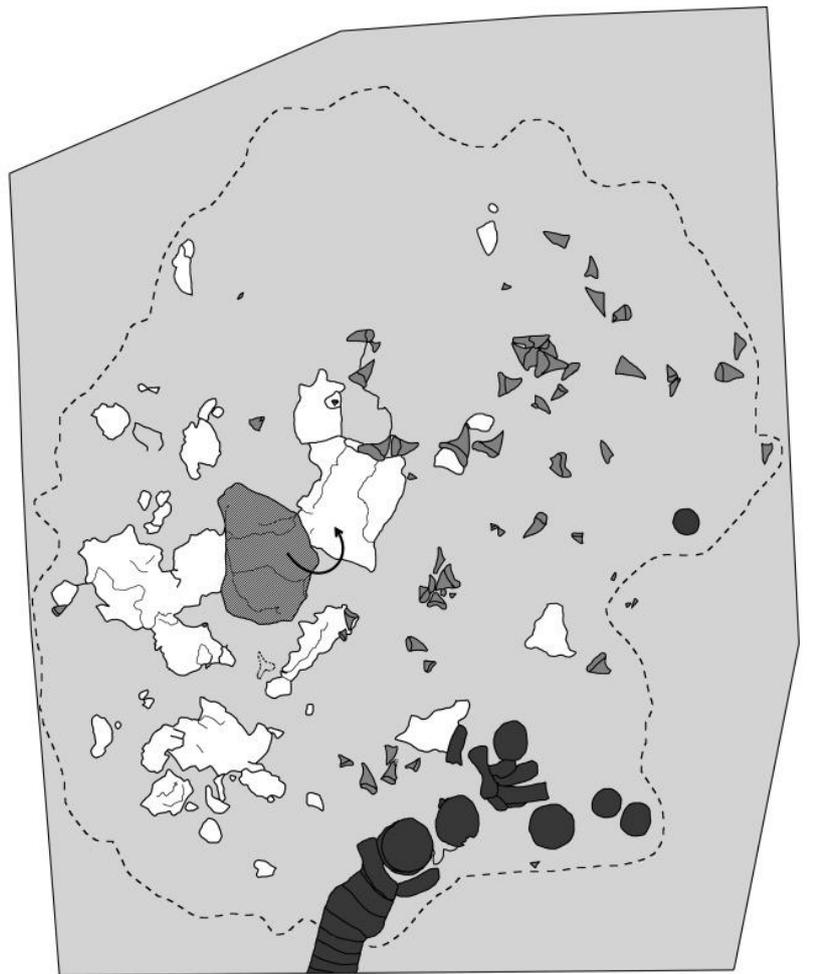


Fig. 8. Line drawing of the head region of the specimen of *Cretoxyrhina mantelli* (Agassiz, 1835) MPPSA-IGVR 45305. Colors map: dark gray = vertebral centra; gray = teeth; light gray = rocky matrix; white = fragments of

tessellated cartilage. The barred area represents a glued fragment which contains the counterpart of the cranial cartilage indicated by the arrow. The dashed line delimits the area where can be detected the fragments (tesseræ) of cranial calcified cartilage. Scale bar = 100 cm.

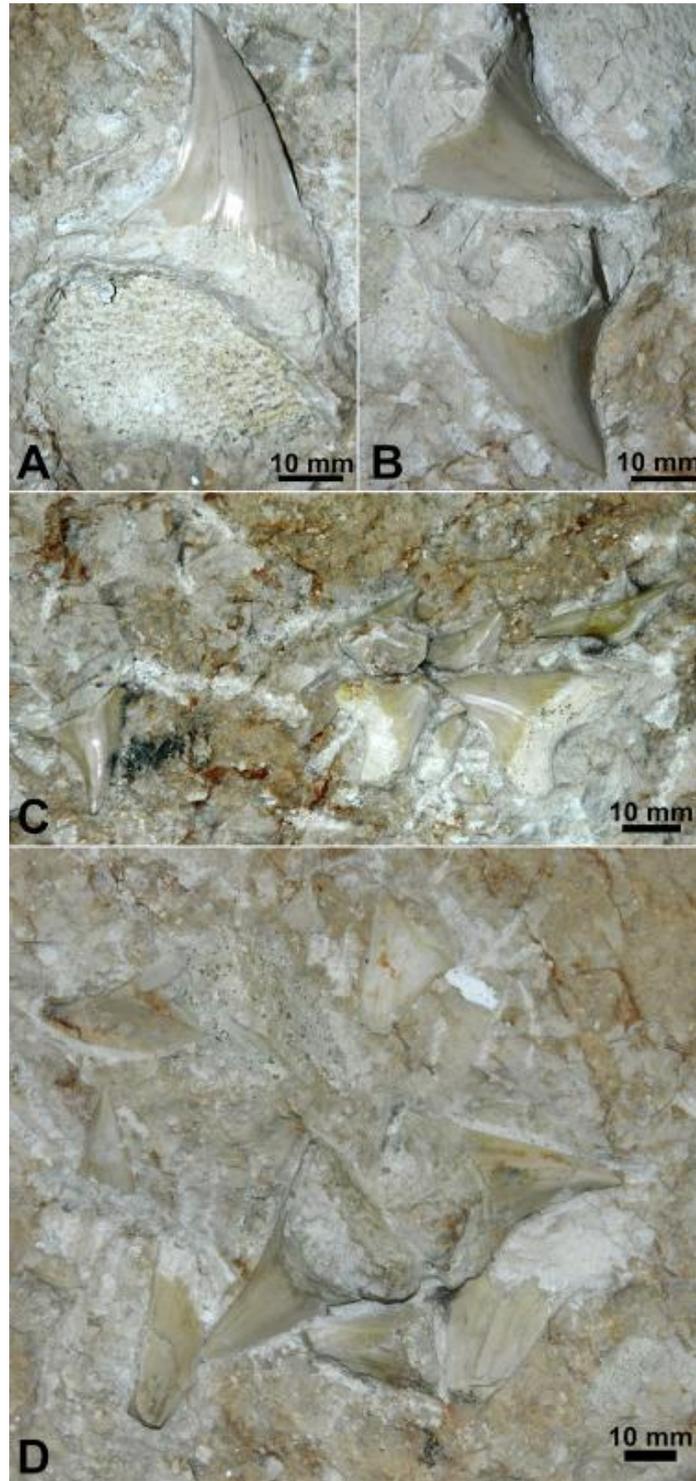


Fig. 9. *Cretoxyrhina mantelli* (Agassiz, 1835). Teeth from MPPSA-IGVR 45305. **A.** Teeth articulated to a fragment of tessellated mandibular cartilage. **B.** Two lateral teeth with poorly preserved roots. **C-D.** Partially associated tooth sets. Scale bars = 10 mm.

Other skeletal remains include segments of partially articulated vertebral columns associated with teeth and cranial cartilage fragments (MPPSA-IGVR 45324, MPPSA-IGVR 45326, MPPSA-IGVR

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

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

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

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

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

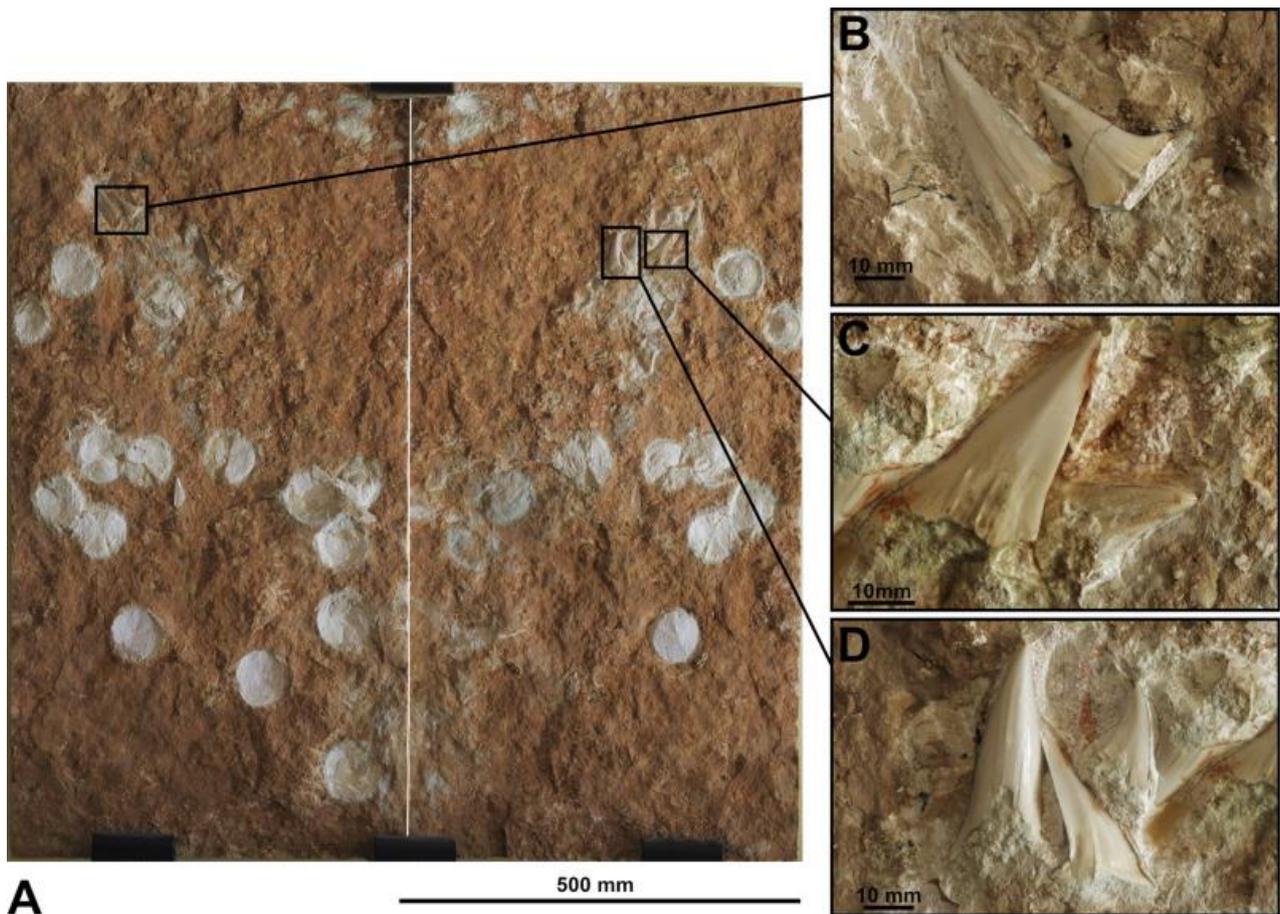


Fig. 10. *Cretoxyrhina mantelli* (Agassiz, 1835). MPPSA-IGVR 45344-45345. **A.** MPPSA-IGVR 45345 (left slab) and MPPSA-IGVR 45344 (right counterslab). Scale bar = 500 mm. **B.** Detail of the labial side of the teeth. Scale bar = 10 mm. **C.** Detail of the labial side of teeth. Scale bar = 10 mm. **D.**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

Specimen MGC-IGVR 81375-81376 (Fig. 11) is preserved on a slab and its counterpart with 80 teeth, 33 vertebral centra, and many fragments of tessellated cranial cartilage. The total height of the highest tooth is 67 mm, whereas the smallest one measures 12 mm. In this tooth set, the maximum crown height on the labial side is 47 mm. The maximum diameter of the largest vertebral centrum is 86 mm, while that of the smallest one is 45 mm. A total of 142 placoid scales was found in a sample extracted from specimen MGC-IGVR 81375, exhibiting morphologies very similar to those observed in MPPSA-IGVR 36371 (Fig. 12).

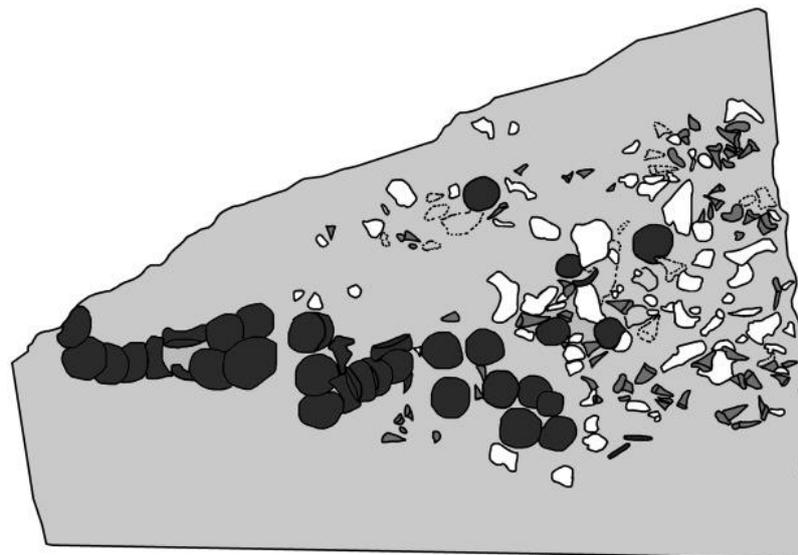
Discussion. The shark specimens from the ‘lastame’ lithozone of the Scaglia Rossa Formation can be unquestionably referred to the genus *Cretoxyrhina*, because of the presence of narrow and blade-like crowns. The oblique heels on the side of the cusp, the absence of the lateral cusplets, and the asymmetric, sharp pointed and rather robust crown (if compared to other congeneric species) support the assignment of the specimens to *Cretoxyrhina mantelli*. *Cretoxyrhina mantelli* had a cosmopolitan distribution, since it has been reported in Europe, Russia, Africa, North America and Brazil (Cappetta,

2012). The genus *Cretoxyrhina* includes also the species *C. denticulata* (Glickman, 1957) and *C. agassizensis* (Underwood, Cumbaa, 2010), both of which are diagnosed by the presence of lateral cusplets (with sharp apices in *C. agassizensis*, and rounded apices in *C. denticulata*) in many of the lateroposterior teeth (see Underwood and Cumbaa, 2010, Newbrey et al., 2015). *C. agassizensis* teeth also exhibit a slender and generally straight cusp (also in lateroposterior teeth) than *C. mantelli* and *C. denticulata* (see Underwood, Cumbaa, 2010), and incomplete cutting edges on small juvenile anterior teeth (Newbrey et al., 2015). The latter character, however, cannot be taken into account to compare and differentiate adult teeth from the other species. Some associated dentitions of *C. mantelli* exhibit almost upright crown on lateroposterior teeth (e.g., Eastman, 1894), but this condition may be related to gynandric heterodonty (Siverson M., pers. comm.). Two of the three species have partially overlapping stratigraphic distributions, because *C. denticulata* ranges from the lower Cenomanian to the lower middle Cenomanian, *C. agassizensis* ranges from the upper middle Cenomanian to lower middle Turonian (Newbrey et al., 2015), whereas *Cretoxyrhina mantelli* is reported globally from the upper Cenomanian to the Campanian (Bourdon, Everhart, 2011; Cappetta, 2012, Shimada, 1997e). Another species of *Cretoxyrhina*, the upper Albian-lower Cenomanian *C. vracensis* (Zhelezko, 2000), was revised by Siverson et al. (2013) and clearly differs from *C. mantelli* in having cusplets and different tooth morphologies in corresponding dental positions (for details see Siverson et al., 2013: p. 14). The species of the genus *Cretoxyrhina* might possibly represent chronospecies of a single evolutionary lineage (see Newbrey et al., 2015). This evolutionary lineage was characterized by the progressive reduction of lateral cusplets and the progressive increasing size and robustness of teeth throughout its temporal range (see Underwood and Cumbaa, 2010, Cook et al., 2013; Siverson, Lindgren, 2005). An increase in tooth size (probably corresponding to an increase in body size; see “Paleobiological Remarks” for individual length estimates), a significant decrease of crown height-crown width ratio and a loss of lateral cusplets are recorded in the upper Cenomanian-Coniacian interval (see Shimada, 1997e, Siverson and Lindgren, 2005) and the size of the teeth of the Italian specimens indicates that the teeth from the middle-upper Turonian had already reached a size similar to those of the Coniacian specimens.



A

500 mm



B

500 mm

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

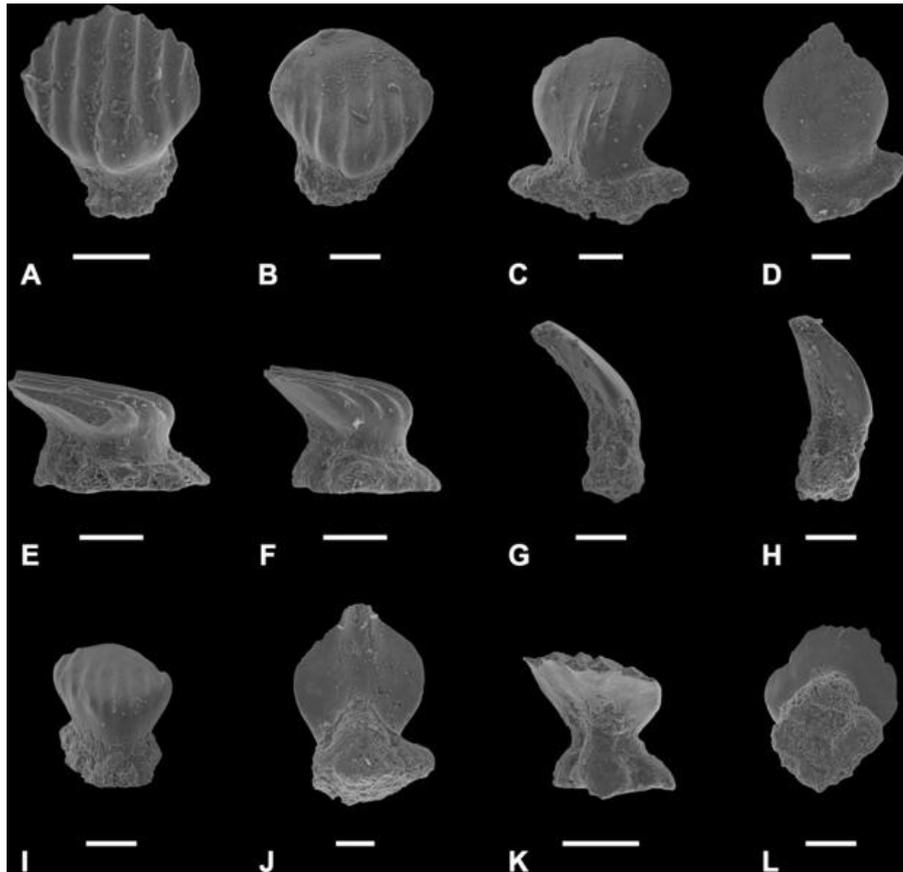


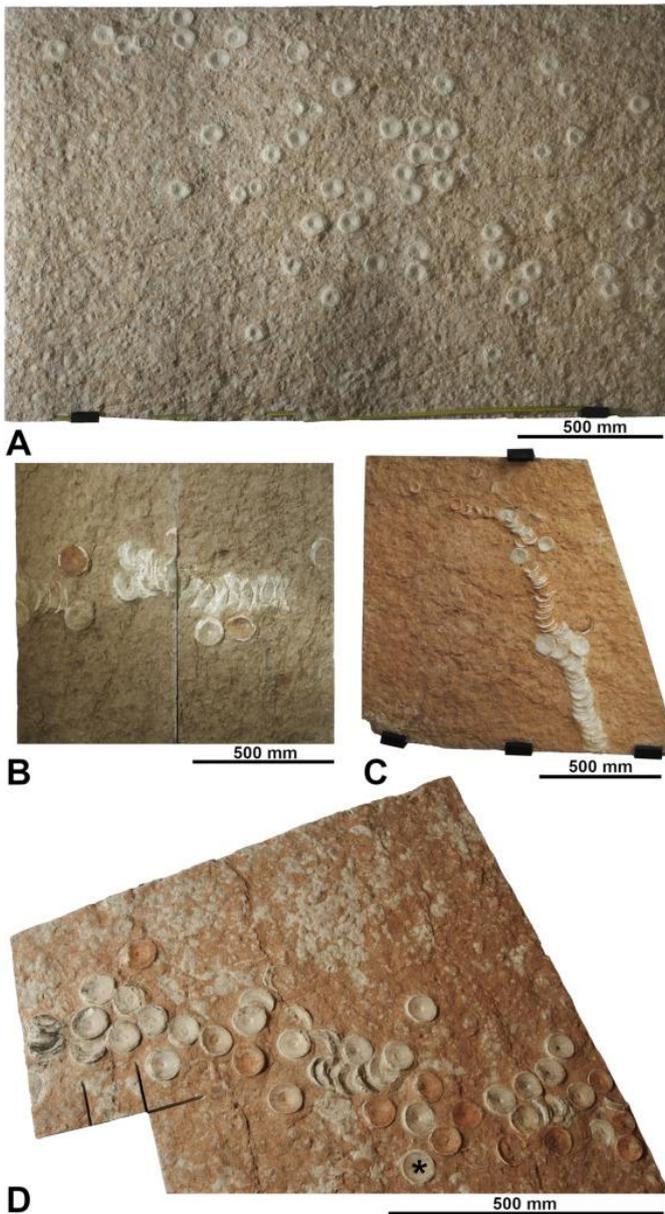
Fig. 12. *Cretoxyrhina mantelli* (Agassiz, 1835). Placoid scale from MGC-IGVR 36371. SEM imaging of selected placoid scales, from different views, coming from the residual of detached samples. **A-D.** Anterior views. **E-H.** Lateral views. **I.** Anterior view. **J-K.** Posterior views. **L.** Inferior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

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

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

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

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



Cretoxyrhina? sp

Fig. 13-14, supplementary material Figs. A.1ε-η

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

Referred material. MPPSA-IGVR 45308, MPPSA-IGVR 45319-45320, MPPSA-IGVR 45321-45322, MPPSA-IGVR 45323, MPPSA-IGVR 45337, MGC-IGVR 47789, MGP-PD 31960.

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

Locality and horizon. All these specimens come from the ‘lastame’ of Scaglia Rossa Formation of Loffa Mount and other surrounding sites (Lessini Mountains, Verona Province, Italy).

Description. The material described here consists of portions of vertebral columns of lamniform sharks with different degrees of disarticulation. The vertebral centra are of lamnoid type *sensu* Applegate (1967). Specimen MPPSA-IGVR 45308 (Fig. 13A) consists of 55 scattered vertebral centra with diameters ranging from 38 to 81 mm. Specimens MPPSA-IGVR 45319 and 45320 (Fig. 13B) are preserved on two slabs with portions of vertebral columns that included a total of 25 vertebral centra (12 and 13 centra, respectively). Centra are partially embedded in the rock and are moderately articulated, arranged in a

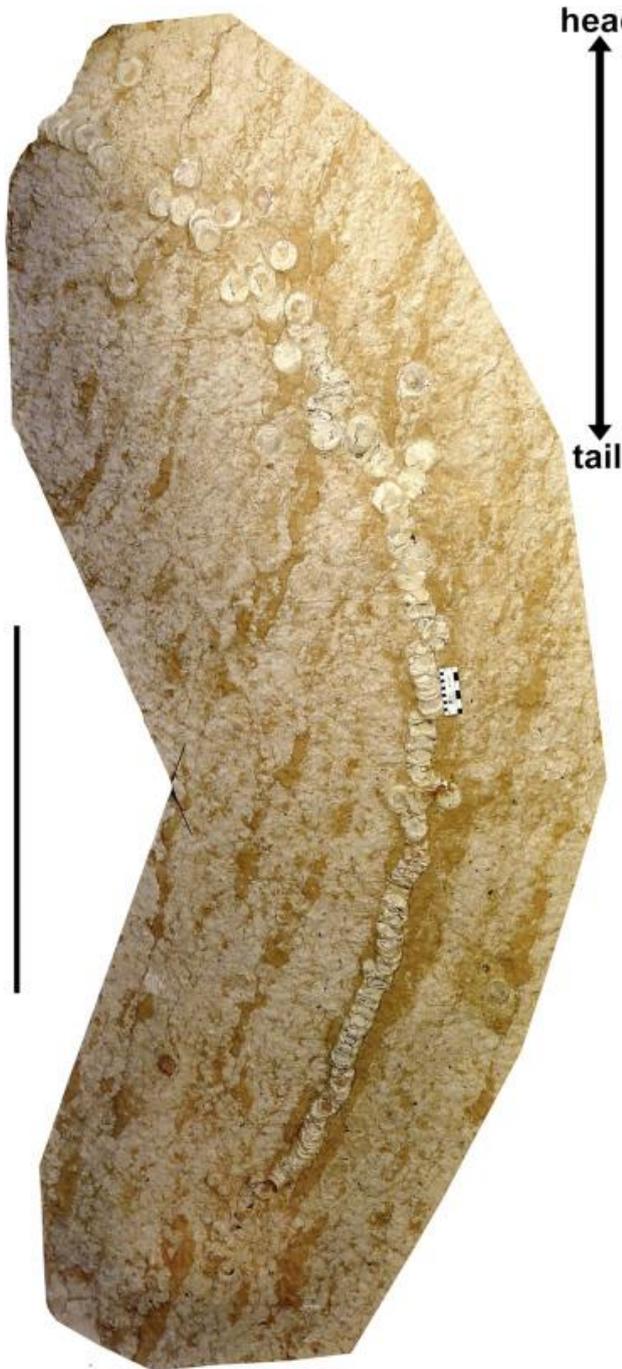


Fig. 14. *Cretoxyrhina?* sp. Vertebral column. Photo of MGC-IGVR 47789. Scale bar = 100 cm.

nearly linear row mostly showing the lateral side. These elements likely belong to a single individual as the vertebral diameter gradually decreases along the vertebral rows. Specimens MPPSA-IGVR 45321 and MPPSA-IGVR 45322 (see supplementary material Figs. A.1ε-ζ) represent two portions of the vertebral column containing 17 and 12 centra, respectively. Centrum diameters range from 92 to 98 mm. The portions probably belong to two distinct individuals, because all centra have similar diameters and there is no decrease in diameter along the vertebral rows.

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

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

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

centra is 84 mm.

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

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

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

Paleobiological Remarks

Length and longevity estimates

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

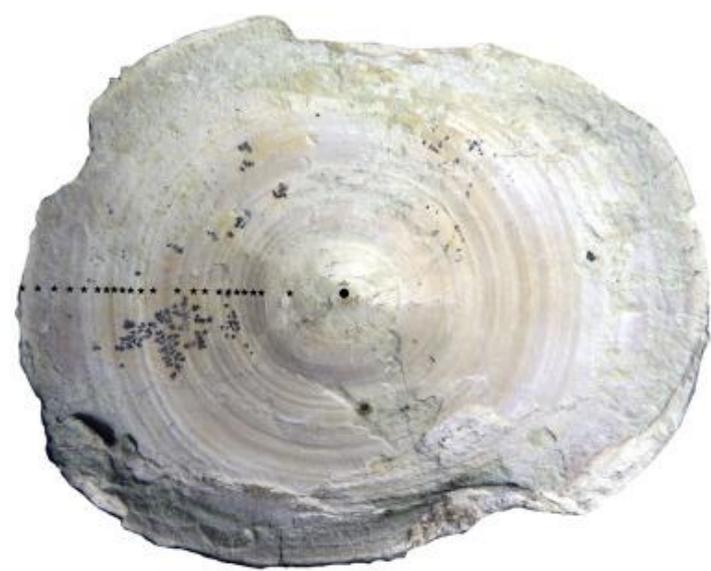
The incremental bands of the vertebral centra (couplets of translucent and opaque bands that correspond to annual growth) allow the estimation of the individual longevity in extant and extinct elasmobranchs (e.g., Cailliet and Goldman, 2004, Shimada, 2007, Shimada, 2008, Goldman et al., 2012, Newbrey et al., 2015, Amalfitano et al., 2017c). These bands can be observed in the vertebral centra of specimens IGVR 36371 and 45305. Other than the birth band, it is possible to observe 26 incremental bands in MPPSA-IGVR 36371 (Fig. 15A) and 21 in MPPSA-IGVR 45305 (Fig. 15B),

thereby suggesting an estimated age of at least 26 and 21 years, respectively. The incremental band counting is consistent with the results obtained from the equation by Shimada (2008) that uses the number of bands to estimate the individual total length. The equation, $TL = 119(BN+1)^{0.522}$, in which BN refers to the band number (with 0 referring to the birth band and the outermost band assumed to represent the maximum BN), provides total length estimates (ca. 665 cm for MPPSA-IGVR 36371, 597 cm for MPPSA-IGVR 45305) that are only slightly larger than those obtained using the vertebral and dental measurements (615-650 cm for MPPSA-IGVR 36371 and 525-565 cm for MPPSA-IGVR 45305).



A

10 mm



B

10 mm

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

Swimming behavior and paleoecology

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

The swimming capabilities of sharks can be estimated also through the morphological analysis of the placoid scales (e.g., Reif, 1985). Scale morphology suggests that *Cretoxyrhina mantelli* was a fast swimming shark (Shimada, 1997d). According to Reif and Dinkelacker (1982), keels (= ridges or riblets) and grooves on the scales that run approximately parallel to the body axis, as observed in *Cretoxyrhina mantelli*, are characteristic of fast swimming sharks (see also Shimada, 1997d). Reif (1985) recognized six ecological groups of sharks based on their locomotory habits, in which placoid scales have different functions that correlate to the ecology of the various shark species. Only in two groups, the fast swimming pelagic sharks and the large near-shore predators/moderate speed pelagic predators, the morphology of the placoid scales shows an evident hydrodynamic function. Fast swimming pelagic sharks have flat, usually overlapping scale crowns that form a dense pavement (Reif, 1985). Crowns exhibit a rounded posterior end or short cusps. The surface of the crown in this group of sharks is ornamented with fine parallel ridges that have average distances between 40 and 80 μm with U-shaped grooves separating the ridges. The placoid scales of *Cretoxyrhina mantelli* show all of these features. When found articulated, such as those figured in Shimada (1997d: fig. 8), they have a pavement-like arrangement to reduce hydrodynamic drag. As far as the scale ornamentation is concerned, placoid scales from MPPSA-IGVR 36371 and MGC-IGVR 81375 exhibit a pattern of ridges and grooves nearly identical to that observed by Shimada, 1997d, Shimada et al., 2006 and Diedrich (2014) in *Cretoxyrhina mantelli* from other localities. The distance between the ridges in the specimens described herein ranges between 33 μm and 60 μm , with the mean value falling within the range of fast swimming sharks (Reif, 1985). Moreover, we employed a method utilized by Reif (1985) that was recently used for other fossil sharks (e.g., Marramà et al., 2018), which takes into account the ridge spacing and the scale width. We plotted the average ridge spacing and average crown width from a few individuals (FHSM VP-2187, MPPSA-IGVR 36371, MGC-IGVR 81375; see Tab. A.3) and compared the results with those of fast pelagic hunting sharks and

large near-shore hunters/pelagic predators of moderate speed (see Reif, 1985). The results are shown in Fig. 16, in which *Cretoxyrhina mantelli* clearly falls within the fast pelagic hunting shark group, in particular the ridge spacing is very similar to that of *Isurus oxyrinchus* and *Sphyrna tudes*. The average crown width, however, differs from those observed in these two taxa, but it is more similar to that of *Lamna nasus*. Comparing the morphology and arrangement of placoid scales of *Cretoxyrhina mantelli* and those of extant lamniform sharks, the scales of *Cretoxyrhina mantelli* (see Shimada, 1997d: fig. 8) nevertheless differ from those of *Isurus oxyrinchus* (see Reif, 1985: pl. 20, 21), which is a very fast hunter adapted to chasing fast moving fishes, such as swordfishes and tunas, in that the placoid scales have a looser arrangement. Actually, the placoid scales arrangement in *C. mantelli* is more similar to that in *Carcharodon carcharias* (see Reif, 1985: pl. 23). However, the number of ridges in the scales of *C. mantelli* (up to nine; Shimada, 1997d) is greater than that observed in *I. oxyrinchus* (up to five ridges; Reif, 1985) and *Carcharodon carcharias* (up to three ridges). Reif (1985) hypothesized that new ridges were added with the expansion of the crown width to maintain constant the distance between the ridges.

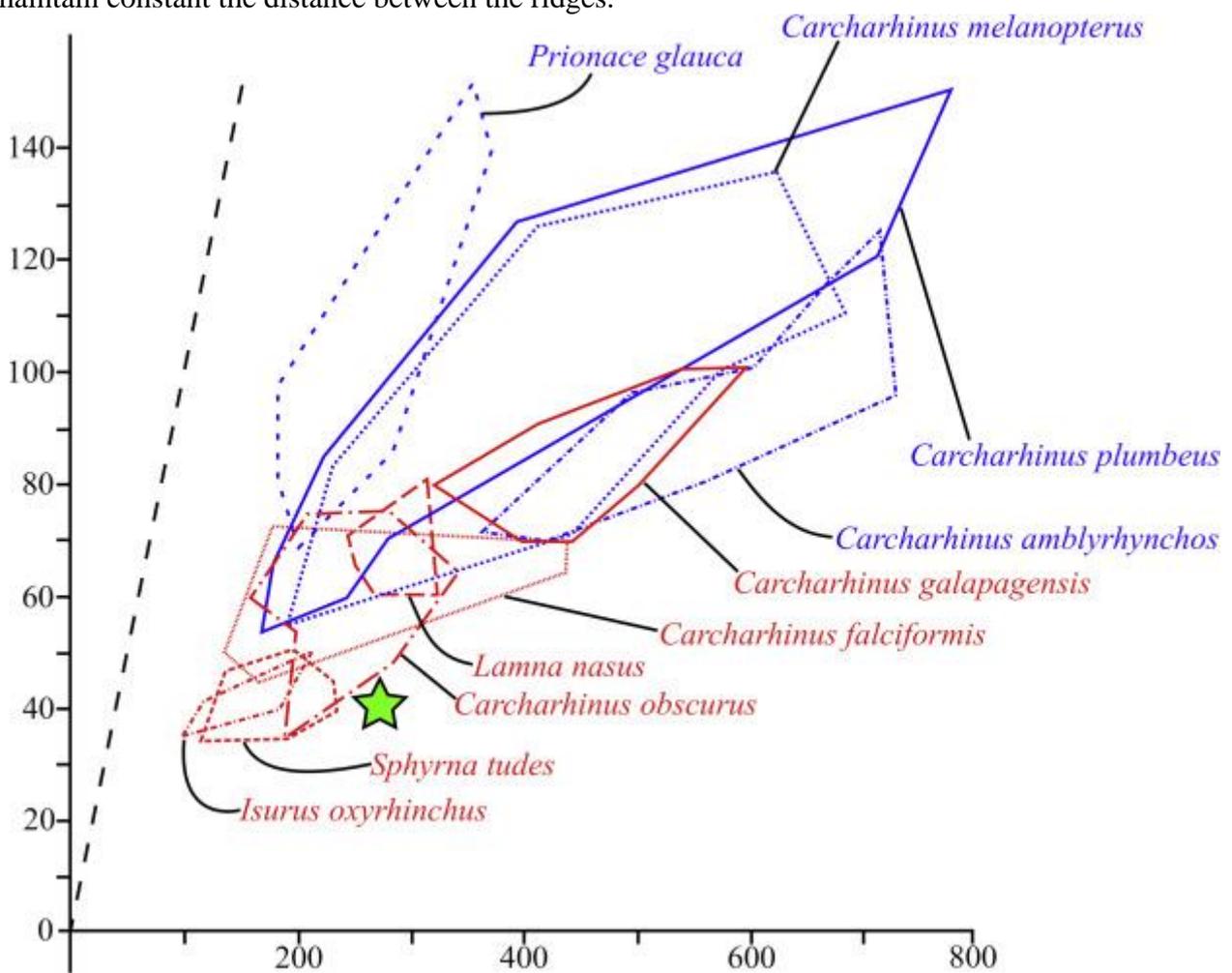


Fig. 16. Correlation diagram of scale crown width (x axis) and ridge distance (y axis) (in μm). The black dashed line indicates the slope of 1.0. The red labeled taxa are from the group of fast pelagic hunting sharks, while the blue

labeled taxa are from the group of large nearshore predators/moderate speed pelagic predators. Note that the *Cretoxyrhina mantelli* average (green star) falls in the clouds of correlation of fast pelagic hunting sharks, in the lower part of the diagram. The diagram is modified after Reif (1985). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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

Taphonomic Remarks

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

All of the specimen from the ‘lastame’ documented herein are preserved within the limestone beds or on their bedding surfaces, sometimes draped with calcareous marly sediments. Lamniform sharks represent the most represented taxonomic group within associated or at least partly articulated vertebrate skeletal remains found in the ‘lastame’, with 15 specimens out of a total of at least 39 determined specimens, including four other chondrichthyans (Ptychodontidae, *Creodus*, and *Onchosaurus*), 13 marine turtles, six mosasaurs and a bony fish. Other skeletal remains of lamniform sharks consisting of segments of vertebral columns (at least three) are housed in the collections of the MCSNV and probably come from the ‘lastame’ lithozone (Zorzin R., pers. com.), thereby confirming the great abundance of lamniform shark remains.

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

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

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

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

The more or less rapid decay of non-mineralized tissues, differential sinking in the unconsolidated calcareous nannoplankton-foraminiferal ooze that characterized the sea floor during the deposition of the 'lastame' and the different exposure intervals on the seafloor before burial could explain the different conditions of the skeletal remains, from the better preserved and fully articulated vertebral columns, MPPSA-IGVR 45305 and MGC-IGVR 47789, to the largely disarticulated vertebral column of MPPSA-IGVR 45308. Some articulated specimens, such as IGVR 36371, 45305 and 47789 (Fig. 4, Fig. 14), show an arched arrangement of the vertebral column, which could be explained as a possible product of peri-mortem or post-mortem deformations of the carcasses (see e.g., Faux and Padian, 2007; Viohl, 1994). The limited displacement of adjacent vertebral centra in partially articulated skeletons was probably caused by the limited decay of the thin fibrous intervertebral cartilages that firmly connect consecutive centra (Cappetta, 1987). Such limited disarticulation of the chondrichthyan axial structures was observed in cases of experimental taphonomy of chondrichthyan material (e.g., Samson et al., 2013). Fully disarticulated skeletons were probably exposed to the biological activity on the seafloor for longer periods. The partial sinking of the carcasses in the carbonate ooze is supported by the presence of centra and teeth partially or totally

embedded in the rock and slightly displaced from the main plane of arrangement of the skeletal remains on the bedding surface (e.g., MGP-PD 31960, Fig. 17, and supplementary material Fig. A.1η). The centra exposing one of the articular surfaces may have had slower sinking, floating for hydrostatic thrust, because they exposed the largest surface to the underlying calcareous nannoplankton-foraminiferal ooze, and did not totally sink because of the precocious lithification of the underlying substrate.



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

Bioerosive fossil traces

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

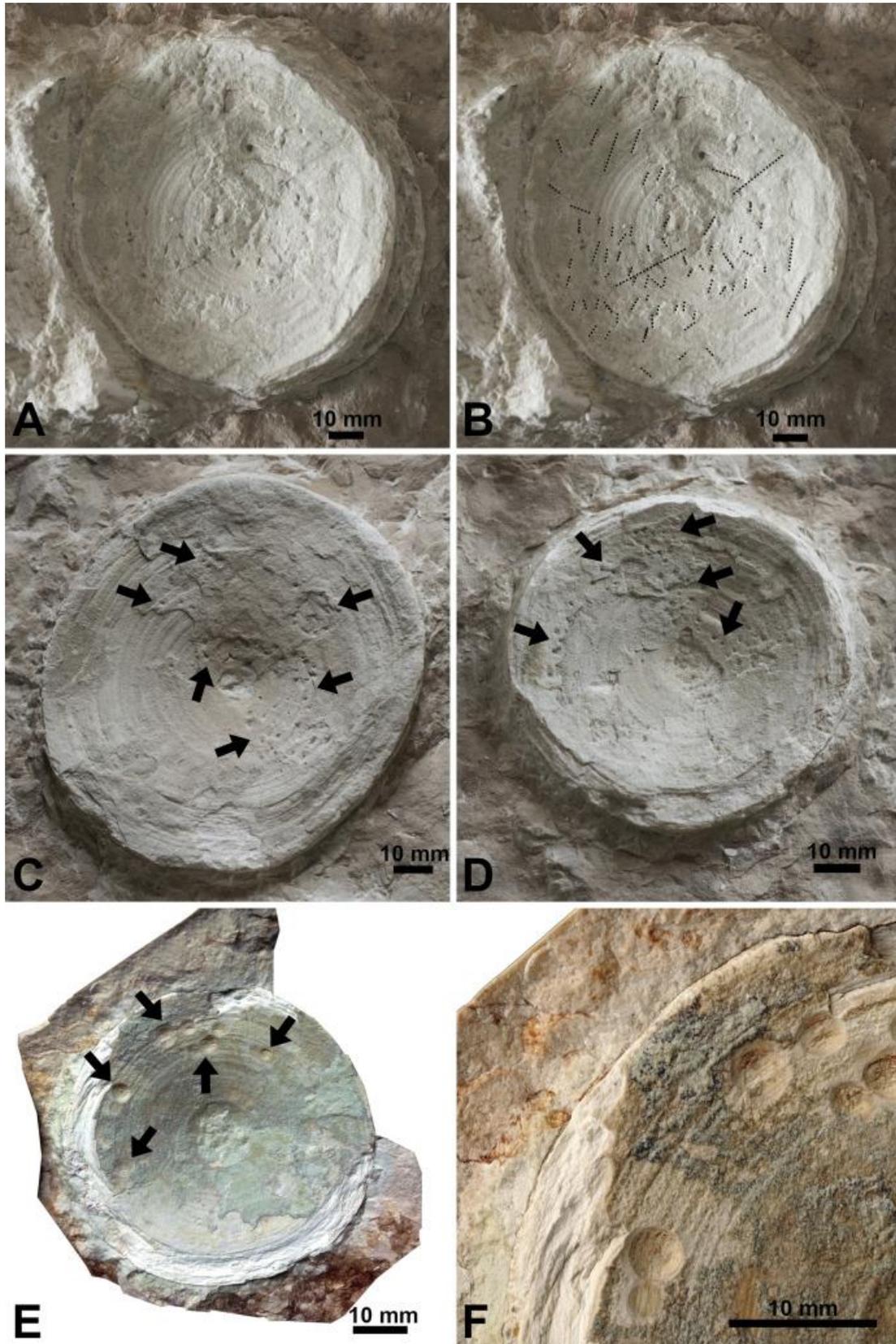


Fig. 18. *Cretoxyrhina mantelli* (Agassiz, 1835) and *Cretoxyrhina?* sp. bioerosive fossil traces on vertebral centra. **A.** Photo of a vertebra with short grooves from MPPSA-IGVR 36371. **B.** Same as in A, with the grooves highlighted by dashed lines. **C.** Photo of small circular openings and collapsed areas on a vertebra from IGVR 36371, indicated by the black arrows, here interpreted as putative *Osedax* borings. **D.** Another photo of a vertebral centrum from MPPSA-

IGVR 36371 with putative *Osedax* borings. **E.** Photo of a vertebra from MGP-PD 31960, with lenticular borings with a *Gastrochaenolites*-like structure. **F.** Detail of the lenticular borings from the vertebra of MGP-PD 31960. Scale bars = 10 mm [2-column width].

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

Small circular borings on MPPSA-IGVR 36371 vertebral centra are similar to the fossil traces of *Osedax*, a marine worm (Siboglinidae, Anellida) thriving on vertebrate deadfalls (Rouse et al., 2004). Among siboglinids, *Osedax* has developed a unique metazoan-bacteria symbiosis that exploits the organic material sequestered within the bones of dead vertebrates as an energy source (Danise, Higgs, 2015). *Osedax* and *Osedax*-like fossil traces were found on diverse vertebrate remains (e.g., whales, marine birds, bony fishes, marine turtles, and plesiosaurs; Danise and Higgs, 2015, Muñiz et al., 2010, Kiel et al., 2010, Kiel et al., 2011, Kiel et al., 2013); the oldest one dates back to the Albian-Cenomanian (Danise, Higgs, 2015). There is no record of *Osedax* borings in chondrichthyans, and also experimental studies on extant vertebrate remains (e.g., Rouse et al., 2011) did not report colonization by *Osedax* on chondrichthyan remains. However, the use of juvenile *Isurus oxyrinchus* vertebrae (diameter 5 mm) in the experiment carried out by Rouse et al. (2011) does not provide a definitive support to exclude any possible colonization of adult chondrichthyan deadfalls, which show more calcified skeletal components and, thereby, represent a potential site for *Osedax* colonization. However, it is not possible to demonstrate whether these borings were actually produced by *Osedax* worms or not, mostly because the vertebral centra of the larger slabs are still embedded in the rock, thereby preventing a tomographic analysis (like that carried out on other fossil vertebrate remains, e.g. Danise and Higgs, 2015). In any case, coalescent *Osedax* borings originating from colonization of multiple individuals may often collapse into small irregular pits (Danise S., pers. comm.) surrounded by some individual borings. This feature is evident in two vertebral centra, supporting a tentative attribution to *Osedax* colonization and likely representing the first one reported from chondrichthyan remains.

The borings on the bioeroded vertebra of specimen MGP-PD 31960 have a *Gastrochaenolites*-like structure, representing only a superficial boring stage. In fact, these borings resemble the borings produced by pholadid bivalves reported from fossil whale bones affected by clavate bivalve borings (see Belaústegui et al., 2012 and references therein). *Gastrochaenolites* borings were also described

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

Concluding remarks

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

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

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

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

The specimens of *C. mantelli* from the ‘lastame’ lithofacies of the Scaglia Rossa Formation show features that allow to interpret the taphonomic processes that affected the carcasses before their final

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

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

Author contribution statement

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

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

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

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

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

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Acknowledgements

We thank Roberto Zorzin and †Anna Vaccari (MCSNV) and Mariagabriella Fornasiero (MGP-PD) for the permission to study the specimens under their care. We are grateful also to Elisa Marchesini (Associazione Culturale Officina 3) and Marta Castagna and Francesco Sauro (Associazione Museo dei fossili della Lessinia) for the help and the access to the specimens exhibited at the PPMSA and GMC. Stefano Castelli (Department of Geosciences of University of Padova) is acknowledged for his precious help with photographs. We are also deeply grateful to Guido Roghi (CNR-Padova) for his precious help and photos. We thank Massimo Varese, Luca Deflorian and Daniela Vecchiato for assistance in an early phase of study of some of the specimens here investigated. We deeply thank Todd Cook and Mikael Siverson for their constructive and precious comments and suggestions. This work was carried out in the context of a wide project aimed to study the vertebrate fauna of the Scaglia Rossa Formation from the Veneto Region of NE Italy. Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled 'Reappraisal of two key Fossil-Lagerstätten in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach', assigned to Eliana Fornaciari) and ex 60% (L.G.). The research of G.C. was also supported by grants (ex-60% 2017 and 2018) of the Università degli Studi di Torino. V. L. was also financially supported by the University of Ferrara (FAR 2017-2018).

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3.5.

A revision of the Upper Cretaceous shark *Ptychodus mediterraneus* Canavari, 1916 from Italy, with a reassessment of *P. latissimus* and *P. polygyrus* Agassiz, 1835 (Chondrichthyes; Elasmobranchii)

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Abstract

Dental and skeletal remains of *Ptychodus mediterraneus* from the Upper Cretaceous Scaglia Rossa Formation of northeastern Italy are described and discussed herein, together with isolated teeth of *P. latissimus* and *P. polygyrus* from the English Chalk of Sussex, southern England. The redescription of the holotype of *Ptychodus mediterraneus* and lectotype fixations for *P. latissimus* and *P. polygyrus* allow the systematic reassessment of the three low-crowned *Ptychodus* species. In addition, these taxa are compared with other morphologically similar species, such as *P. martini* and *P. marginalis*. Micropalaeontological analyses suggest a Turonian age for the low-crowned *P. mediterraneus*. Based on articulated tooth sets of *P. mediterraneus*, the pavement-like dentitions of this durophagous taxon are reconstructed herein, revealing a marked dignathic heterodonty. Imbricated dentitions observed in articulated specimens of *Ptychodus mediterraneus* also suggest broad distributions of bite-induced load on tooth plates; the dental features of this low-crowned durophagous shark indicate a high specialization for grinding thick-shelled bivalves (e.g., inoceramids and rudists). Fragments of cranial mineralized cartilages (e.g., a ‘V-shaped’ jaw portion) and asterospondylic vertebral centra of *P. mediterraneus* are consistent to those commonly occurring in fusiform sharks. Evidences of scavenging on *Ptychodus* recorded on cartilages and tooth-bioerosion are also reported herein. Moreover, a posterior-to-anterior tooth replacement is hypothesized for *Ptychodus* based on the abrasion patterns observed in articulated dental sets. New insights on the palaeoecology and palaeobiology of *Ptychodus* are also provided.

Introduction

Ptychodus is an extinct genus of durophagous elasmobranchs mostly known through dental and, more rarely, skeletal remains (e.g., vertebral centra, portion of mineralized cartilages and placoid scales; MacLeod 1982; Everhart and Caggiano 2004; Shimada et al. 2009, 2010). Associated and isolated teeth of *Ptychodus* are common in the Upper Cretaceous of Africa, Asia, Europe and North and South America (e.g., Cappetta 2012; Shimada 2012; Hamm 2017). The polygonal teeth of *Ptychodus* are arranged in antero-posteriorly elongated rows in both jaws, forming maxillary and mandibular dental plates with the thickness and height of the dental crown exhibiting species-specific patterns (see Woodward 1912; Herman 1977; Shimada 2012; Amadori et al. 2019b). Moreover, the rare known articulated specimens exhibit a marked dignathic heterodonty (Williston 1900a,b; Woodward 1887, 1904; MacLeod 1982; Williamson et al. 1991; Shimada 2012). Although recent studies of the dental enameloid seem to place *Ptychodus* within the elasmobranchs *sensu* Maisey (2012) (= neoselachians) (e.g., Hoffman et al. 2016), the systematic placement of the genus within the group remains elusive. The palaeoecology and palaeobiology of this enigmatic shark genus also are still poorly known, primarily because of the rarity of articulated *Ptychodus* remains. Recently, Shimada et al. (2009) described the replacement teeth in an articulated specimen of a high-crowned *Ptychodus* species for the first time and also discussed some palaeobiological issues, such as body size and feeding specialization (see also Shimada 2012). *Ptychodus* species are commonly regarded to be durophagous predators able to feed mainly on hard-shelled macroinvertebrates (e.g., Quenstedt 1885; Williston 1900a,b; Canavari 1916; Fossa-Mancini 1921; Casier 1953; Kauffmann 1972; Wolberg 1985; Everhart and Caggiano 2004; Cappetta 2012; Shimada 2012; Diedrich 2013; Everhart 2017; Amadori et al. 2019b).

The species *Ptychodus mediterraneus* Canavari, 1916 was erected based on a single specimen, comprising articulated upper and lower jaw dentitions, from northeastern Italy. Although widely known in the literature (e.g., D'Erasmus 1922; Herman 1977; Hamm 2010b; Hoffman et al. 2016; Amalfitano et al. 2017b), this exceptionally preserved specimen has never been discussed in detail and not reanalyzed since its original description. *P. mediterraneus* exhibits a clear morphological affinity with other low-crowned congeneric species, including *P. latissimus* Agassiz, 1835 and *P. polygyrus* Agassiz, 1835 (see Canavari 1916). More specifically, the similar dentitions of *P. latissimus* and *P. mediterraneus* led some authors to consider the latter species name as junior synonym of the former (e.g., Diedrich 2013). *P. latissimus* is characterized by flat or gently raised dental crown with thick and sharp ridges on the occlusal surface ('crushing type' dentition; see

Cappetta 2012) and often has been confused with *P. polygyrus*, which in turn is characterized by thin ridges usually fused at their ends to form lateral ‘loops’ (e.g., Dixon 1850; Woodward 1912; Canavari 1916; Longbottom and Patterson 1987).

In this paper, we provide a detailed comparative analysis of *Ptychodus latissimus*, *P. mediterraneus* and *P. polygyrus* in order to disentangle the taxonomic confusion generated and accumulated over the years. Our revision mostly relies on three well-preserved articulated tooth sets and a number of isolated teeth coming from Upper Cretaceous of northeastern Italy and southern England, including the ‘type material’ of the three species. Lectotypes and paralectotypes of *P. latissimus* and *P. polygyrus* are designated herein to better clarify the taxonomic status of the species by fixing their names and avoid confusion among very similar species. Moreover, most of the documented specimens are reassigned by comparison of tooth sets and several detached teeth from Upper Cretaceous of northeastern Italy. We also propose a reconstruction of the arrangement of teeth into dental plates in *Ptychodus mediterraneus* based on a detailed study of the Italian articulated specimens and provide further inferences about its possible feeding specialization and tooth replacement patterns. Some of the cartilaginous remains preserved in the articulated specimens are interpreted as jaw portions. The careful examination of these remains, as well as of associated vertebral impressions, allowed us to highlight similarities with extant groups of elasmobranchs and led to the recognition of possible bioerosional traces due to scavenging and microboring.

Historical notes

Most of the Italian *Ptychodus* remains come from the Upper Cretaceous stratigraphic succession of the Veneto region (NE Italy) and mainly consist of isolated teeth, with few remarkable exceptions. The first reports date back to the first half of the XIXth century, when Brocchi (1814) and Catullo (1818) cited the occurrence of both isolated and associated teeth from the Belluno province (see Amadori et al., 2019a). The first significant finding of an associated tooth set, however, dates back to Pellegrini (1883) who reported a slab with several teeth coming from Prun (Lessini Mountains), later figured by Nicolis (1889). The geologist Mario Canavari (1914, 1916) created the species *P. mediterraneus* based on an exceptionally well-preserved articulated tooth set. This specimen, consisting in five portions, was found during basement excavations of the house of Mr. Domenico Segafredo, located in the Contrà Eck (Gallio, Asiago plateau, Vicenza province, Fig. 1A). The last comprehensive work on *Ptychodus* records of northeastern Italy was published by D’Erasmus (1922), who reported the presence of eight species of *Ptychodus*, including *P. latissimus*, *P. mediterraneus*

and *P. polygyrus*. More recently, another well-preserved and articulated finding coming from the Lessini Mountains and provisionally referred to *Ptychodus* cf. *latissimus* was cursorily documented and figured by Cigala-Fulgosi et al. (1980).

Isolated teeth reassigned here to *Ptychodus mediterraneus*, from the Upper Cretaceous of Tuscany, Sicily and Emilia-Romagna regions, previously were described and figured by De Stefani (1885), Seguenza (1900) and Canestrelli (1910). Some isolated teeth referred to *P. latissimus* and *P. polygyrus* were found in Cretaceous deposits of the northern Apennines (Parma and Piacenza provinces, Emilia-Romagna region) and in the ‘Cretaceous Scaglia’ of the eastern Madonie (central-northern Sicily; Sacco 1905; Coggi 1964).

Geological setting

Most of the specimens described herein come from the ‘Lastame’ and ‘Pietra di Castellavazzo’ (Castellavazzo Stone), two lithozones pertaining to the Upper Cretaceous Scaglia Rossa Formation of northeastern Italy (Fig. 1A). Unlike from other stratigraphic intervals of this formation, these two lithozones are relatively rich in macrofossils (Amalfitano et al. 2017c; Amadori et al. 2019b). The ‘Lastame’ is a nodular/subnodular package of whitish and reddish limestones quarried in the Lessini Mountains, Verona province (Trevisani and Cestari 2007; Roghi and Romano 2009; Amalfitano et al. 2017a). The stratigraphic range of this lithozone is still object of debate: Cigala-Fulgosi et al. (1980) reported a Turonian-Coniacian age for the ‘Lastame’, while Lozar and Grosso (1997) proposed an early Turonian-early Santonian age. The ‘Lastame’ is characterized by abundant echinoids, inoceramids, ammonites and rudists, but also by vertebrate remains, such as sharks, marine turtles and mosasaurs (e.g., Cigala-Fulgosi et al. 1980; Dalla Vecchia et al. 2005; Trevisani and Cestari 2007; Roghi 2010; Palci et al. 2013; Amalfitano et al. 2017a,b, 2019; Amadori et al. 2019b). The ‘Pietra di Castellavazzo’ is a condensed stratigraphic interval outcropping in the surroundings of the village of Castellavazzo (Belluno; Fig. 1A) mostly consisting of grey-greenish and reddish nodular and subnodular limestones very similar in thickness and palaeontological content to the ‘Lastame’ (Bassani 1886, 1888; Trevisani and Cestari 2007; Amalfitano et al. 2017c; Amadori et al. 2019b). Exposures in the Castellavazzo area were historically referred to the upper Turonian-upper Campanian based on calcareous nannofossils and planktic foraminifera (Larocca Conte et al. 2019). The macrofossil assemblage of the Pietra di Castellavazzo consists of ammonites, echinoids, inoceramids and rudists (radiolitids; Trevisani 2009, 2011) and, more rarely, chondrichthyans (e.g., lamniforms and ptychodontids; Bassani 1886, 1888; Amalfitano et al. 2017a; Amadori et al. 2019a,b;

Larocca Conte et al. 2019) and bony fishes (e.g., pachycormids; Bassani 1886, 1888; Amalfitano et al. 2017c).

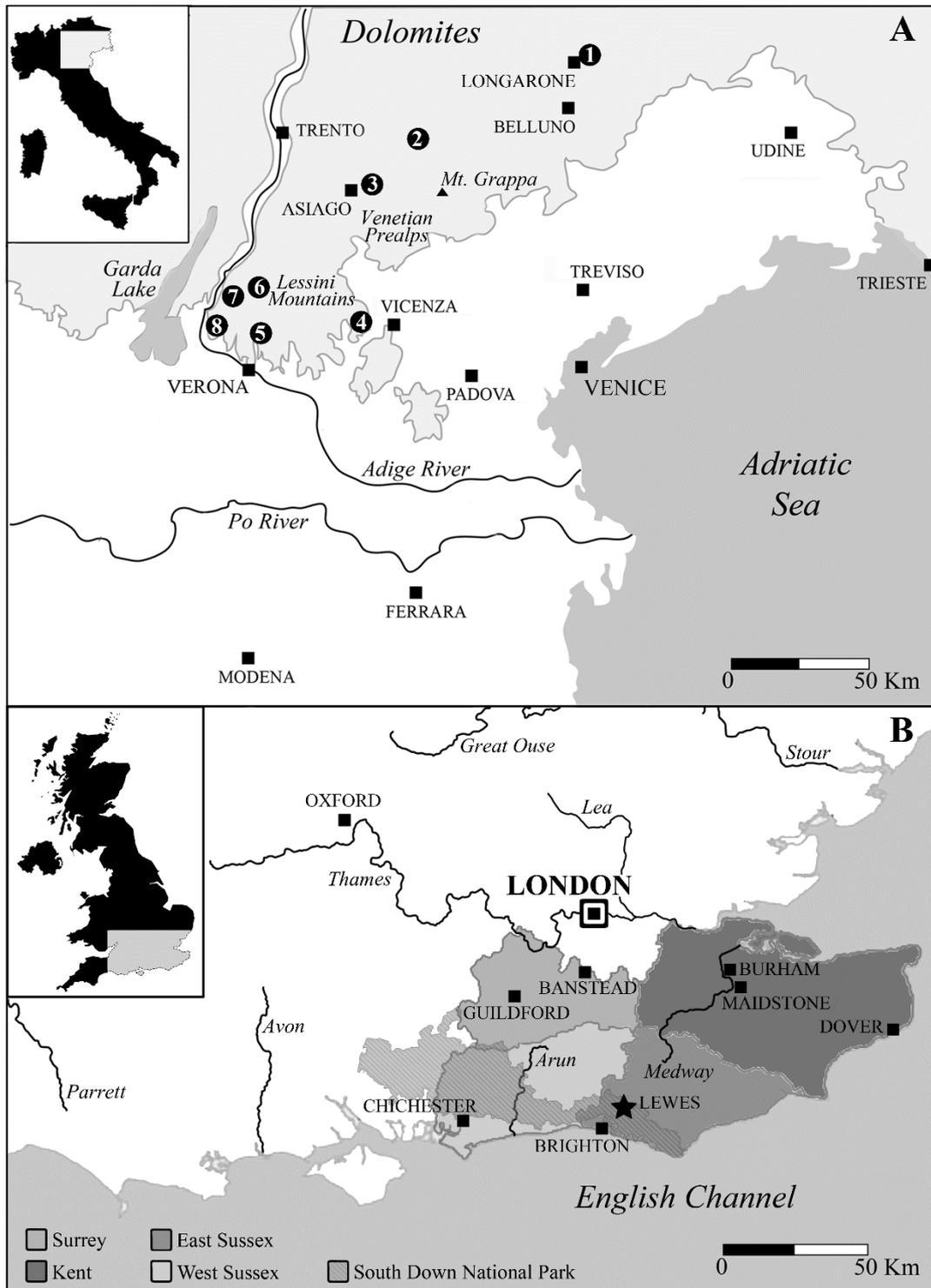


Fig. 1. Location map of the sites in northeastern Italy (A, modified from Amalfitano et al., 2017a) and southeastern England (B, modified from Nuttall et al. 1901). The black dots in A indicate the fossiliferous sites that yielded remains of *Ptychodus mediterraneus* Canavari, 1916. 1, Castellavazzo; 2, Val Cismon; 3, Gallio; 4, Chiampo; 5, Negrar; 6, Mt. Loffa (S. Anna d’Alfaedo); 7, Breonio; 8, Mazzurega. The black star in B indicates the fossiliferous site in the surroundings of Lewes that yielded the specimens studied by Agassiz (1835, 1837, 1838, 1839) and here redescribed.

Some isolated teeth examined herein come from the Upper Cretaceous Chalk outcropping in the surroundings of Lewes (eastern Sussex, UK; Fig. 1B). The lithological succession cropping out at this locality consists of a ca. 80 m of nodular chalks referred to as the Lewes Chalk Member (Mortimore 1986). This member belongs to the White Chalk Formation, corresponding to the traditional Middle and Upper Chalk of England (for more details see Gale and Kennedy 2002; Kriwet 2002). This formation deposited in the north-western part of the Anglo-Paris Basin and is subdivided in different members (Mortimore 1986; Mortimore and Pomerol 1987; Gale et al. 2000; Kriwet 2002). In particular, the Lewes Chalk Member spans from the upper Turonian to the middle Coniacian and its palaeontological content includes both invertebrates and vertebrates (e.g., Gale and Kennedy 2002). Echinoids (e.g., *Micraster*), brachiopods (e.g., *Cretirhynchia*), bivalves (e.g., *Mytiloides*, *Cremnoceramus*) and rare ammonites (e.g., *Romaniceras*) primarily represent the invertebrate assemblage (Mortimore 1986). The Chalk succession (Chalk group) of southern England is well known for its abundant fossil fishes (see Mantell 1822; Woodward 1912; Kriwet 2002; Friedman et al. 2016); in particular, the Cretaceous ichthyofauna therein includes a large variety of actinopterygians (e.g., Dixon 1850; Woodward 1909; Kriwet 2002) and several cartilaginous fishes (e.g., *Cretoxyrhina* and *Ptychodus*; Dixon 1850; Woodward 1912; Longbottom and Patterson 1987). The Chalk of Sussex yielded also remains of marine reptiles (e.g., *Plesiosaurus*, *Polyptychodon* and *Mosasaurus*) coming from the surroundings of Lewes (Dixon 1850).

Materials and methods

Institutional abbreviations

MGP-PD: Museo di Geologia e Paleontologia dell'Università di Padova, Italy; **NHMUK:** Natural History Museum, London, UK; **MCSNV:** Museo Civico di Storia Naturale di Verona, Italy; **MPPSA:** Museo Preistorico e Paleontologico di Sant'Anna d'Alfaedo (Verona), Italy; **MSNUP:** Museo di Storia Naturale dell'Università di Pisa, Italy; **MMC:** Museo 'Padre Aurelio Menin' di Chiampo (Vicenza), Italy; **MCBL:** Museo Civico di Belluno, Italy; **MCBG:** Museo Civico di Bassano del Grappa (Vicenza), Italy.

Materials

Here we describe and figure several dental and skeletal remains of *Ptychodus* from the Upper Cretaceous of the Veneto region (northeastern Italy) and Sussex (southern England). The following

Italian findings, including articulated specimens, detached tooth sets and several isolated teeth, were examined: MSNUP I-17373, slab with articulated dental plate portions, several disarticulated teeth and few skeletal remains; MPPSA IGVR 91031, slab with articulated and disarticulated teeth plus several skeletal remains; MCBG 4048, a few articulated teeth; MCBG 4050, associated and isolated teeth; MGP-PD 6720, MGP-PD 13531, MGP-PD 13532 and MSNUP 274, associated tooth sets; MCBL 677, MCSNV v.11791, MCSNV v.12507, MCSNV v.12508, MCSNV v.12528, MGP-PD 6717, MGP-PD 6718, MGP-PD 7345, MGP-PD 8494, MGP-PD 8497, MGP-PD 13533, MGP-PD 13534, MGP-PD 13535, MGP-PD 13536, MGP-PD 14040, MGP-PD 23539, MMC PTY01 and MMC PTY02, isolated teeth. We consider MGP-PD 13531-13534 and MGP-PD 13536 as part of a unique tooth set because of their consistent dental morphologies (see below), same locality of origin, as indicated by historical curatorial labels, and identical preservation style. Five isolated teeth represent the English material examined and included in this study: NHMUK PV OR P4369, NHMUK PV OR P4372, NHMUK PV P4408, NHMUK PV P4410 and NHMUK PV P75453. For more details see. Tab. A.1 (Appendices).

Methods

The specimens were photographed using a Nikon D810 camera mounting 60-90 mm lens and a Canon PowerShot SX720 HS. The teeth were measured through the image analysis software Image J (v. 1.47). The Italian specimens were coated with a thin layer of white ammonium chloride sublimate ('smoking') with the aim to enhance the morphological characters of the dental crown (e.g., Teichert, 1948; Scovil 1996; Amalfitano et al. 2017b). The GIMP (v. 2.8.16) and Photoshop CS5 (v.12.0 x32) softwares have been used to prepare the illustrative drawings and images of the specimens. Smear slides were prepared from matrix powder from the specimens for calcareous nannofossil study (see Amalfitano et al. 2017c, Amadori et al. 2019b). The anatomical and odontological terminology used herein (see Fig. 2) represents a modified version of that of Cappetta (2012), Shimada (2012) and Hamm (2017). Open nomenclature follows the standards proposed by Matthews (1973), Bengtson (1988) and Sigovini et al. (2016).

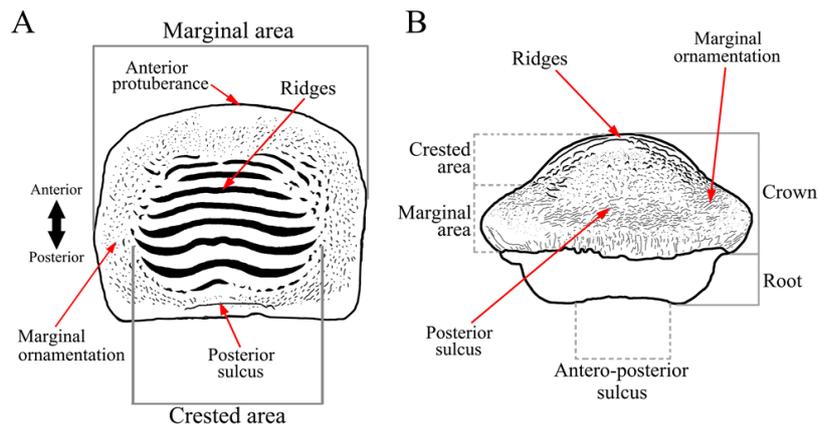


Fig. 2. Line drawing of a lower symphyseal tooth of low-crowned *Ptychodus*. **A.** occlusal view; **B.** anterior view.

Results

Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order *Incertae sedis*

Family †Ptychodontidae Jaekel, 1898

Genus †*Ptychodus* Agassiz, 1834

Type species. *Ptychodus schlotheimii* Agassiz, 1834 (nomen oblitum), senior synonym of *Ptychodus latissimus* Agassiz, 1835 (nomen protectum); see Giusberti et al. (2018).

Diagnosis. See Woodward (1912).

Nomenclatural remarks on the species erected by Agassiz. Agassiz (1835) originally established the nominal species *Ptychodus altior*, *P. latissimus*, *P. mammillaris* and *P. polygyrus* by indication (Art. 12 of the ICZN Code, 1999) in his ‘Feuilleton additionnel’ of the ouvrage ‘Recherches sur les poissons fossiles’ (see Brignon, 2015, 2019 and Amadori et al., 2019b). In fact, Agassiz (1835) referred these names were to specimens previously illustrated by Mantell (1822: pl. 32, figs. 17-29) and coming from South Downs (south-eastern Sussex, southern England). As recently established by Brignon (2019: p. 29, 69-72), however, the type series of each taxon includes not only the specimens figured by Mantell (1822), but also the specimens from the Mantell’s collection figured by Agassiz in 1837, 1838 and 1839 (Agassiz, 1837, pl. 25a; Agassiz, 1838, pl. 25b; Agassiz, 1839; pl. 25).

†*Ptychodus latissimus* Agassiz, 1835 emended

Fig. 3

- 1737 “dens molans piscis majoris marini”; Brückmann: 116, pl. 4, fig. 5.
p.1752 “Dentem seu palatum piscis Ostracionis”; Brückmann: 116, pl. 5, fig. 3 (non fig. 4; non pl. 6, fig. 4).
1769 “ein versteinter fischzahn”; Walch: 235, pl. H.1.a, fig. 4
1811 “species of unknown fish”; Parkinson: 262, pl. 19, fig. 18
1814 “palati di pesce”; Brocchi: 174.
1818 “palati”; Catullo: 20.
1820 *Diodon*; Catullo: 390, pl.7, fig. C.
1822 “einer der hintern Kieferzähne eines grossen Fisches”; Schlotheim: 70, pl. 13, figs 2a-c.
p.1822 ‘Teeth allied to *Diodon*’; Mantell: 231, pl. 32, fig. 19 (non figs 17, 18, 20, 21, 23-25, 27, 29).
p.1827 *Diodon*; Catullo: 149, pl. 3, fig. C (non figs A,B).
1827 “fossil fish tooth”; von Sternberg: 98, pl. 1, fig. 1.
p.1832 “appareils dentaires de poissons”; Passy: 8, pl. 15, fig. 5 (non figs 2-4), atlas.
1833 “fish related to the *Diodon*”; Mantell: 132, text fig. p. 133.
1834 *Ptychodus Schlottheimii* (sic); Agassiz: 69 (nomen oblitum).
†1835 *Ptychodus latissimus* Ag.; Agassiz: 54, Feuilleton additionnel.
1837 *Ptychodus*; Buckland: 46, pl. 27d, fig. B4, 5.
p.1837 *Ptychodus latissimus* Agass.; Agassiz: pl. 25a, figs 5, 6 (non figs 1-4, 7, 8), atlas vol. III
1838 *Pt. latissimus* Agass.; Agassiz: pl. 25b, figs 24-26, atlas vol. III.
1840 *Ptychodus latissimus*; Owen: 10, pl. 17, figs 1,2, atlas vol. II.
p.1842 *P. latissimus* Ag.; Geinitz: 63, pl. 7, fig. 5a-c; pl. 17, figs 1-3 (non fig. 11).
1842 *P. Schlottheimii* Ag.; Geinitz: 63, pl. 17, figs 4, 5.
1843 *Ptychodus latissimus* Ag.; Agassiz: 156, vol. III (non syn.).
1845 *Pt. latissimus* Ag.; Reuss: 1, pl. 2, figs 5-8.
1850 *Ptychodus paucisulcatus*, new; Dixon: 362, pl. 30, fig. 3.
1870 *Ptychodus latissimus* Ag.; Roemer: pl. 36, fig. 7, atlas.
(1872-75) *Pt. latissimus* Ag.; Geinitz: 212, pl. 40, figs 16-22.
1878 *Ptychodus latissimus*, Ag.; Fritsch: 15, text fig. 36.
1885 *Ptychodus latissimus*; Quenstedt: pl.21 fig. 65, atlas.
1886 *Ptychodus latissimus* Agassiz; Bassani: 145, pl. 9, fig. 11.
1889 *Ptychodus latissimus* Agass.; Nicolis: 61, pl. 1.
1902 *Ptychodus latissimus* Agassiz; Leriche: 91, pl. 2, figs 1-7.
1905 *Ptychodus latissimus* Ag.; Sacco: 255, pl. 8, figs 11a-c.
1906 *Ptychodus latissimus* L. Agassiz 1843; Leriche: 54, pl. 5, figs 1, 2.
1906 *P. paucisulcatus*; Leriche: 75, pl. 5, figs 3-9.
p.1911 *Ptychodus latissimus* Agassiz; Dibley: 268, pl. 20, figs 3-5.

- p.1912 *Ptychodus latissimus* Agassiz; Woodward: 235, text figs 74, 75, pl. 50, figs 4, 6-8, 11, 12 (non figs 1-3, 5, 9, 10 13-16).
- v1916 *Pt. latissimus* Agass.; Canavari: 67, pl. 12, fig. 17.
- vp.1922 *Ptychodus latissimus* Ag.; D'Erasmus: 17, pl. 2, figs 9, 10, 12-14 (non figs 11, 15).
- vp.1922 *Ptychodus polygyrus* Ag.; D'Erasmus: 20, pl. 2, figs 16 (non figs 17-20).
- 1935 *Ptychodus latissimus* Agassiz 1843; Dalinkevičius: 262, pl. 3, fig. 61.
- 1949 *Ptychodus latissimus* Agassiz; Tan: 18, text figs 1, 2.
- 1953 *Ptychodus latissimus* L. Agassiz; Casier: 8, text fig. 1.
- 1964 *Pt. latissimus* Ag.; Coggi: 119, text fig. 1.
- p.1977 *Ptychodus paucisulcatus* Dixon F. 1850; Herman: 67, text fig. p. 71, pl. 2, fig. 10c (non figs 10a, b) (non syn.).
- 1984 “pesci fossili simili alle razze”; Aspes and Zorzini: 16, text fig. p. 16.
- 1987 *Ptychodus latissimus* Agassiz; Longbottom and Patterson: 254, pl.54, fig. 15.
- 1987 *Ptychodus latissimus* Agassiz 1843; Cappetta: 38, fig. 41F,G.
- 1993 *Ptychodus*; Walker and Ward: 200, text fig. p. 200.
- 1993 *Ptychodus latissimus* Agassiz 1843; Welton and Farish: 60, text figs 1-8, p. 60.
- 2001 *Ptychodus latissimus*; Zorzini: 97, text fig. p. 97.
- 2002 *Ptychodus latissimus* Agassiz 1838; Antunes and Cappetta: 104, pl. 1, fig. 3.
- p.2002 *Ptychodus paucisulcatus* Agassiz 1838; Antunes and Cappetta: 105, pl. 1, fig. 8 (non figs 4-7, 9).
- 2003 *Ptychodus latissimus* Agassiz 1843; Niedźwiedzki and Kalina: 16, fig. 3.1.
- 2003 *Ptychodus polygyrus* Agassiz 1843; Niedźwiedzki and Kalina: 20, fig. 5.1.
- 2004 *P. latissimus* Agassiz; Wiese et al: 332, fig. 4a.
- 2012 *P. latissimus* Agassiz 1837 (1843B); Cappetta: 81, text fig. 66F-K.
- 2012 *Ptychodus latissimus*; Klug and Bolliger: 373, text fig. 2 (top left).
- 2013 *Ptychodus latissimus* Agassiz 1835; Diedrich: 23, figs 5C, 8.
- 2015 *Ptychodus latissimus* Agassiz 1835; Brignon: 6.
- 2015 *Ptychodus schlotheimii* Agassiz 1834; Brignon: 7, text-fig. 1.
- 2017 *Ptychodus latissimus*; Fischer et al.: 14, fig. 2b.
- 2019 *Ptychodus*; Brignon: fig. 21C.19.
- 2019 *Ptychodus* cf. *latissimus* Agassiz, 1835; Brignon: fig. 32D-G.
- p.2019 *Ptychodus latissimus* Agassiz, 1835; Brignon: text-fig. p. 2 (below), fig. 13B, 18B,D,E, 22 line C, 23B,D, 26C-H, 30B, 37A, 41B-D, 54 (p. 70) first and second line (not third line).
- 2019 *Ptychodus* sp.; Brignon: figs. 8C, 11C, 22 (line E).
- p.2019a *Ptychodus* cf. *latissimus*; Amadori et al.: 236, pl. III, figs A-B¹ (non fig. C).

Type series. The single specimen roughly sketched in Mantell (1822: pl. 32, fig. 19; Fig. 3A) and recently traced back by Brignon (2019; p. 33, fig. 22C; NHMUK PV P 75453), and the seven specimens from the ‘Mantell collection’ figured in Agassiz (1837; pl. 25a, figs. 1-7), of which three (NHMUK PV OR 4369, 4372 and 4355a) are figured in Brignon (2019; p. 70, fig. 54). According to

the Art. 74 of the ICZN Code (1999), we designate herein the lectotype of *Ptychodus latissimus* Agassiz, 1835 with the aim of fixing the species name and differentiate this taxon from the other similar low-crowned species *P. polygyrus* Agassiz, 1835 and *P. mediterraneus* Canavari, 1916.

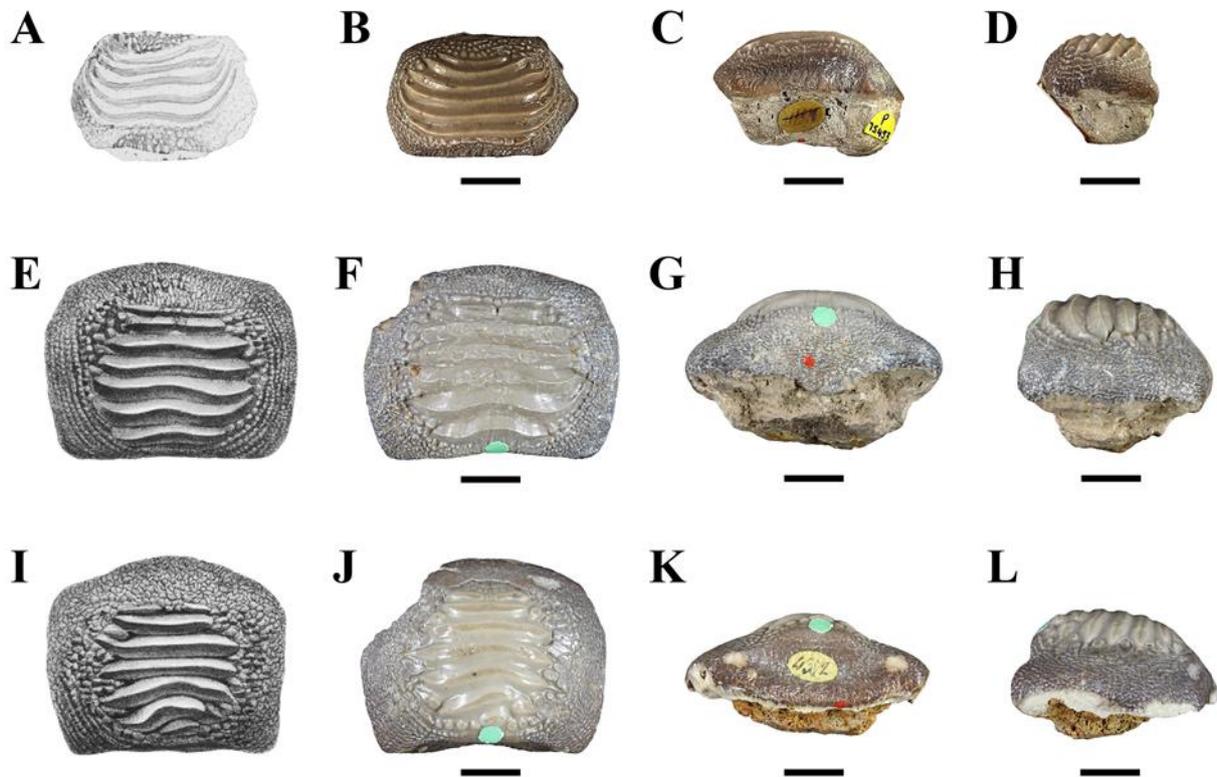


Fig. 3. Isolated specimens of *Ptychodus latissimus* Agassiz, 1835 from Lewes Chalk Member (southern England) belonging to ‘Mantell collection’. **A-D.** syntype NHMUK PV P75453: **A**, occlusal view from Mantell (1822); **B**, occlusal view; **C**, posterior view; **D**, lateral view. **E-H.** syntype NHMUK PV OR P4369 designated herein as lectotype of the species: **E**, occlusal view from Agassiz (1837); **F**, occlusal view; **G**, posterior view; **H**, lateral view. **I-L.** syntype NHMUK PV OR P4372: **I**, occlusal view from Agassiz (1837); **J**, occlusal view; **K**, posterior view; **L**, lateral view. All scale bars equal 10 mm.

Lectotype. NHMUK PV OR P4369 (Fig. 3E-H) is an isolated tooth from the Mantell’s collection housed in the Natural History Museum, London and it is designated herein as lectotype. The specimen corresponds to the tooth originally illustrated by Agassiz (1837) in plate 25a, fig. 5, 5a (Fig. E). NHMUK PV OR P4369 (Fig. 3E-H) has an almost quadratic shape with symmetrical outline; the crown is characterized by a slight anterior protuberance and a shallow posterior sulcus. In occlusal view (Fig. 3F), six thick and sharp transversal ridges cross the crown. These are anteriorly preceded by an interrupted, very thin seventh ridge. The ends of the posteriormost ridges are curved, continuing anteriorly into fine granulations. Around the crested area there are coarse granules, while the granulation becomes very thin in the marginal area. The occlusal ridges are damaged but not abraded.

In posterior view (Fig. 3G), the crested area is slightly raised, and the lateral edges are externally inclined. The specimen shows a partially preserved root, which is completely overhung by the crown. NHMUK PV OR P4369 clearly exhibits the main dental features of the species. In addition, Woodward (1912: p. 237) interpreted this finding as a lower symphyseal tooth; the symphyseals are considered as the most diagnostic elements within the *Ptychodus* dentition (Hamm 2010a, 2017; Shimada 2012).

Paralectotypes. As part of the original type series, the other specimens of *Ptychodus latissimus* from the ‘Mantell collection’ figured by Agassiz (1835, 1837), including NHMUK PV OR P4372 (Fig. 3I-L) and NHMUK PV P 75453 (Fig. 3A-D), should be considered as the paralectotypes for this taxon (Art. 74.1.3 of the ICZN 1999 Code; see also Brignon 2019). However, we reject as paralectotypes the original syntypes illustrated in pl. 25a, figs 1-4 and 7 by Agassiz (1837), because they show diagnostic features of *P. polygyrus* Agassiz, 1835. The rejected specimens (isolated teeth and associated tooth sets), currently housed in Natural History Museum, London, exhibit dental morphologies consistent with each other; in addition, one of the associated sets shows lateral teeth and a large lower symphyseal (see Agassiz 1837: pl. 25a, fig. 7), the latter being completely different from the other symphyseals belonging to the type material (NHMUK PV OR P4369 in Fig. 3E-H and NHMUK PV OR P4372 in Fig. 3I-L). Conversely, the rejected symphyseal teeth share most of the occlusal features (e.g., the ‘lateral loops’, see below) with the symphyseals of *P. polygyrus*.

Emended diagnosis. A *Ptychodus* species with almost quadratic dental crown, flattened or slightly bulged in central area and crossed by very thick, transversally short and sharp ridges; ridges with little or no curvature at their lateral ends, terminating abruptly but never forming loops; crested area never reaching the tooth edges; transition between marginal and crested area often characterized by large granules; marginal area well developed and covered by fine granulations; granules sometimes extending to the ridges ends and curving anteriorly.

Referred material. Three isolated teeth: NHMUK PV OR P4369, NHMUK PV OR P4372 and NHMUK PV P 75453; the first two specimens were figured by Agassiz (1837: pl. 25a, fig. 5-6a), while NHMUK PV P 75453 was previously figured by Mantell (1822: pl. 32, fig. 19).

Occurrence. NHMUK PV OR P4369, NHMUK PV OR P4372 and NHMUK PV P 75453 come from the Lower or Upper Chalk of Lewes (East Sussex, UK; see Woodward 1889: p. 148). Woodward

(1912: p. 238) assigned all the specimens attributed to *Ptychodus latissimus* from the vicinity of Lewes to the ‘Turonian zones’.

Description. NHMUK PV P4369 (see above; Fig. 3E-H) and NHMUK PV OR P4372 (Fig. 3I-L) are very similar to each other, except for the ridge pattern. The occlusal surface of NHMUK PV OR P4372 (see Fig. 3J) is crossed by seven ridges without curved ends. The first and the last ridges are thinner than the others and interrupted. Both ridges and coarse granules are markedly worn out; also, the anterior marginal area is completely abraded (see Fig. 3J). A small portion of the dental root can be observed in posterior and lateral view (Fig. 3K,L). NHMUK PV P 75453 (Fig. 3A-D) exhibits polygonal and asymmetrical outlines with both anterior protuberance and posterior sulcus being poorly developed. In occlusal view (Fig. 3B), two ‘articular facets’ on the right side of the crown form an ‘acute-shaped’ margin. Moreover, six marked ridges cross the dental crown, which curve anteriorly, fading into a fine granulation; however, they are not reaching the lateral tooth edges. Coarse granules cover the marginal areas. In posterior view (Fig. 3C), the ‘acute-shape’ margin on the right is lower than the opposite one. NHMUK PV P 75453 exhibits the dental root, which measures approximately 29 mm in width, 17 mm in length and 8 mm in height. The dental root has a shallow antero-posterior sulcus with the right lobe more developed than the left one (see Fig. 3C). In lateral view (Fig. 3D), the occlusal ridges have sharp outline and the root exhibits a posteriorly inclined anterior side.

Measurements and other details of the teeth are reported in Tab. 1.

Tab. 1. Measurements of teeth of *Ptychodus* housed at Natural History Museum, London. **CW**, Crown width; **CL**, Crown length; **CH**, Crown height; **nTR**, number of transverse ridges.

<i>Ptychodus latissimus</i> Agassiz, 1835				
Catalogue Number	CW	CL	CH	nTR
NHMUK PV OR P4369	~ 43 mm	~ 33 mm	~ 19 mm	7
NHMUK PV OR P4372	~ 42 mm	~ 33 mm	~ 16 mm	6
NHMUK PV P 75453	~ 33 mm	~ 22 mm	~ 13 mm	6
<i>Ptychodus polygyrus</i> Agassiz, 1835				
Catalogue Number	CW	CL	CH	nTR
NHMUK PV P4408	~ 37 mm	~ 28 mm	~ 13 mm	8
NHMUK PV P4410	~ 37 mm	~ 28 mm	~ 13 mm	8

Remarks. Woodward (1912) published the last revision of *Ptychodus latissimus* Agassiz, 1835, examining several isolated and associated European specimens (e.g., tooth set NHMUK PV OR P5603, see Woodward 1912: pl. 50 fig. 6-8) and compared them with the material previously figured and discussed by Agassiz (1835, 1837, 1838, 1843; e.g., Fig. 3). *Ptychodus latissimus* was considered

a large-sized species by Woodward (1912: p. 236) and Dixon (1850: p. 362). Quenstedt (1885: p. 282) reported very large *P. latissimus* teeth, measuring about 78 mm in width, from Westphalia (northwestern Germany; see also Fossa-Mancini 1921).

Although Agassiz (1837: pl. 25a, fig. 5-6a) figured these two teeth as nearly intact, NHMUK PV OR P4369 (Fig. 3E-H) and NHMUK PV OR P4372 (Fig. 3I-L) actually lack a small portion of their marginal area on the left anterior side. Considering their symmetrical outline and ornamentations, both NHMUK PV OR P4369 and NHMUK PV OR P4372 should be considered symphyseal teeth belonging to the lower dentition (see also Woodward 1912: p. 237). The bulged, crested area of NHMUK PV OR P4372 (see Fig. 3K) is less raised than that of NHMUK PV OR P4369 (see Fig. 3G). These variations of the configuration of the crown suggest that teeth belonging to the same antero-posterior row can have different degrees of occlusal convexity. The well-developed ridges and the observed wear traces indicate a durophagous specialization, as also suggested for many other *Ptychodus* species (e.g., Cappetta 2012, Shimada 2012). The asymmetrical outline of NHMUK PV P 75453 (see Fig. 3B) suggests that it could belong to a lateral tooth row, not placed on the outer edge of the dental plate.

Woodward (1889: p. 148) discussed the geographic distribution of *Ptychodus latissimus* in Europe, documenting material from England, Germany, ‘Bohemia’ and Russia. Actually, tooth sets of *P. latissimus* from ‘Teplitz’ (Teplice, Czech Republic) are housed in the Naturhistorisches Museum, Vienna; these latter findings are currently under revision together with another well-preserved associated specimen from northern Italy (e.g., see Nicolis 1889; Amadori et al. 2019a).

†*Ptychodus polygyrus* Agassiz, 1835 emended

Fig. 4

1769 “zahn eines seefisches”; Wilkens: 80, pl. 8, fig. 45-47.

p. 1822 ‘Teeth allied to *Diodon*’; Mantell: 231, pl. 32, figs. 23, 24 (non figs 17-21, 25, 27, 29).

†1835 *Ptychodus polygyrus* Ag.; Agassiz: 54, Feuilleton additionnel.

p.1837 *Ptychodus latissimus* Agass.; Agassiz: pl. 25a, figs 1-4, 7, 8 (non figs 5, 6), atlas vol. III

1837 *Ptychodus polygyrus*; Buckland: 48, pl. 27f, fig. 1.

p.1838 *Pt. polygyrus* Agass.; Agassiz: pl. 25b, fig. 22, 23 (non fig. 21), atlas vol. III.

p.1839 *Ptychodus polygyrus* Agass.; Agassiz: pl. 25, figs 4, 7, 8, 10, 11 (non figs 5, 6, 9), atlas vol. III.

1850 *Ptychodus latissimus*; Dixon: 362, pl. 30, figs 1, 2, pl. 31, fig. 3.

1850 *Ptychodus polygyrus*; Dixon: 362, pl. 31, fig. 10, 10a.

1863 *Ptychodus polygyrus*; Mackie: 161, pl. 9, fig. 1.

1887 *P. paucisulcatus*; Woodward: 130, pl. 10, fig. 12.

- 1889 *Ptychodus polygyrus* Agassiz; Woodward: 143, pl. 5, fig. 7 (non syn.).
- 1896 *Ptychodus latissimus* Ag.; Priem: 9, pl.1, figs 1, 3 (non 2, 4).
- 1899 *Ptychodus Belluccii* (sic) n. f.; Bonarelli: 6, pl. 1, fig. 7.
- 1902 *Ptychodus polygyrus* Agassiz; Leriche: 97, pl. 2, figs 21-23.
- 1905 *Pt. polygyrus* Ag.; Sacco: 255, pl. 8, figs 12a,b.
- p.1911 *Ptychodus polygyrus* Agassiz; Dibley: 268, pl. 20, fig. 1, 2, pl. 21, fig. 1-3, pl. 22, fig. 2, 9 (non pl. 22, fig. 1).
- 1911 *Ptychodus dixony*, sp. nov. Agassiz; Dibley: 270, pl. 20, figs 1, 2.
- p.1912 *Ptychodus latissimus* Agassiz; Woodward: 235, pl. 50, figs 1-3, 9, 10, 13-16 (non figs 4-8, 11, 12).
- p.1912 *Ptychodus polygyrus* Agassiz; Woodward: 232, pl. 48, figs 12, 15, 16, pl. 49 (non pl. 48, figs 13, 14).
- vp.1922 *Ptychodus latissimus* Ag.; D'Erasmus: 20, pl. 2, figs 17-19 (non figs 16, 20).
- 1934 *Ptychodus Belluccii* Bonarelli; Leriche: 77, pl. 1, figs 1, 1a (non syn.).
- 1958 '*Ptychodus*-Zähnen'; Hantke: 62, pl. 1, figs 1, 2.
- 1958 *Ptychodus polygyrus*; Hantke: 61, pl. 1, figs 3a-d.
- 1977 *Ptychodus Belluccii* Bonarelli G. 1899; Herman: 76 (non syn.).
- p.1977 *Ptychodus latissimus* Agassiz L. 1843; Herman: 67, text fig. p. 69 (non pl. 2, figs 9a,b) (non syn.).
- p.1977 *Ptychodus paucisulcatus* Dixon F. 1850; Herman: 67, pl. 2, fig. 10a, b (non text fig. p.71, pl.2, fig.10c) (non syn.).
- 1977 *Ptychodus polygyrus* Agassiz L. 1843; Herman: 74, text fig. p. 75, pl. 2, fig. 12 (non syn.).
- 1987 *Ptychodus marginalis* Agassiz; Longbottom and Patterson: 256, pl. 55, fig. 5.
- 1987 *Ptychodus polygyrus* Agassiz; Longbottom and Patterson: 255, pl. 55, fig. 3.
- 1993 *Ptychodus polygyrus* Agassiz 1843; Welton and Farish: 65, text figs 1a-e, p. 65.
- 2010a *P. polygyrus*; Hamm: 540, fig. 2.
- 2013 *Ptychodus polygyrus* Agassiz 1835; Diedrich: 23, fig. 6.11-18.
- p.2013 *Ptychodus polygyrus* Agassiz 1839; Hamm and Harrell: 107, figs 3, 4C (non figs 4A, B).
- 2019 *Ptychodus*; Brignon: fig. 21C.23, 21C.24.
- 2019 *Ptychodus marginalis* Agassiz, 1843; Brignon: fig. 54 (p. 70) fourth line.
- 2019 *Ptychodus polygyrus* Agassiz, 1835; Brignon: text-fig. p. 2 (above), fig. 22 (line A,B), 27B-E, 52F-H, 53A,B.
- 2019 *Ptychodus* sp.; Brignon: figs. 10C-E.

Type series. The two specimens illustrated by Mantell (1822: pl. 32, fig. 23, 24; Fig. 4A,E) and recently reported by Brignon (2019; p. 31, fig. 22A,B; NHMUK PV OR 4408 and 4410), and the five specimens from the 'Mantell collection' figured by Agassiz (1839; pl. 25, figs. 4-8). The fig. 4, 4a of plate 25 in Agassiz (1839) illustrates the specimen NHMUK PV OR 4408, previously figured by Mantell (1822: pl. 32, fig. 23; see also Woodward 1889: p. 143). According to Brignon (2019, p. 63), also two teeth from the chalk of Kent belonging to the 'Regley collection' figured by Agassiz (1839, pl. 5, fig. 10, 11) should be considered part of the type series of *P. polygyrus*. Mantell (1822) did not provide precise information about the provenance of the syntypes NHMUK PV OR 4408 and 4410,

merely indicating South Downs (near Sussex, southern England); nevertheless, Woodward (1889: p. 143-144) reported Lewes (Sussex, southern England) as the original locality for both the specimens belonging to the ‘Mantell collection’. We designate below the lectotype of *P. polygyrus* with the aim of enhancing the nomenclatural stability of this species.

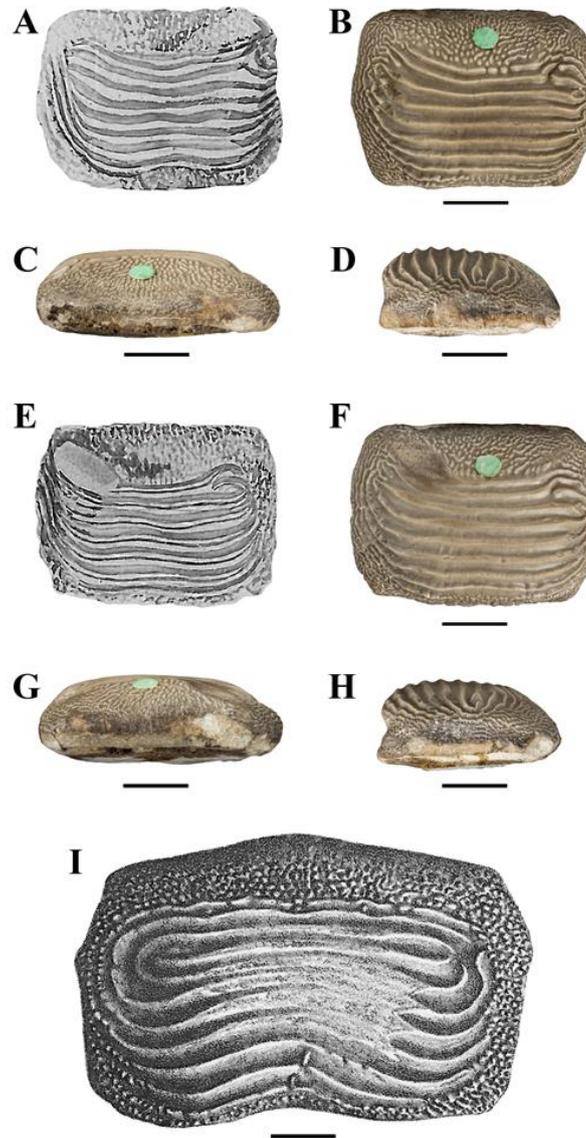


Fig. 4. Isolated teeth of *Ptychodus polygyrus* Agassiz, 1835 in occlusal (**A, B, E, F, I**), anterior (**C, G**) and lateral (**D, H**) view. **A–H.** Syntypes NHMUK PV P4408 (**A–D**, designated herein as lectotype) and NHMUK PV P4410 (**E–H**) of *P. polygyrus* from Lewes Chalk Member (southern England) originally figured (**A, E**) by Mantell (1822); **I.** lower symphyseal tooth NHMUK PV P10771 α , belonging to the dental set NHMUK PV P10771, coming from Banstead (Surrey, southern England) and originally figured and described by Woodward (1912: p. 233; pl. 49, fig. 2). All scale bars equal 10 mm.

Lectotype. The specimen NHMUK PV P4408 (Fig. 4A-D) from Lewes (East Sussex, southern England; see Woodward 1889, 1912) is designated herein as the lectotype of *Ptychodus polygyrus*. NHMUK PV P4408 (Fig. 4A-D) exhibits a flat and thin crown with rectangular outline. Both the

anterior protuberance and the posterior sulcus are poorly developed. The occlusal surface is transversally crossed by eight thick ridges, which extend to the lateral edges. Laterally, the ridges taper off and curve anteriorly anastomosing to form non-concentric loops. The marginal area is not well developed except anteriorly, and is covered by granulation. Although NHMUK PV P4408 lacks the root (see Fig. 4C,D), the specimen clearly exhibits the main occlusal features of the species (see Fig. 4B).

Paralectotypes. As part of the original type series (see above), the other specimens of *Ptychodus polygyrus* from the ‘Mantell collection’ figured by Mantell (1822) and Agassiz (1839), including NHMUK PV P4410 (Fig. 4E-H), should be considered the paralectotypes of this species (Art. 74.1.3 of the ICZN 1999 Code; see also Brignon 2019). Among the original syntypes, however, we discard the two isolated specimens figured in Agassiz (1839: pl. 25, figs 5, 6) as paralectotypes having diagnostic features typical of *P. mammillaris* Agassiz, 1835 (see also the emended diagnosis in Hamm 2017: p. 20). The first specimen (NHMUK PV OR 4413, see also Brignon 2019: fig. 22, line D), figured by Mantell (1822: pl. 32, fig. 29) and originally assigned to *P. mammillaris* by Agassiz (1835) exhibits a raised dental cusp with flat apex crossed by several thin ridges not reaching the poorly preserved dental edge. The second tooth exhibits a flat cusp similar to that of NHMUK PV OR 4413 together with a shelf-like marginal area.

Emended diagnosis. A *Ptychodus* species with flattened rectangular dental crown; occlusal aspect in lower symphyseals teeth markedly convex; occlusal surface crossed by thick, transverse ridges with thin lateral ends curved towards the anterior edge, almost completely covering the dental crown and often forming loops mainly on both antero-lateral sides of the teeth; narrow marginal area, only well-developed anteriorly, not clearly distinct from the ridges; coarse and fine granulations without a distinct arrangement covering the marginal area; ridges decreasing in size and number mesio-distally; ridges becoming thinner, sometimes developing loops, only on the distal side of the dental crown (modified from Woodward 1912).

Referred material. Two isolated teeth: NHMUK PV P4408 (Fig. 4A-D) and NHMUK PV P4410 (Fig. 4E-H).

Occurrence. Both NHMUK PV P4408 and NHMUK PV P4410 come from the Lower or Upper Chalk of Lewes (East Sussex, UK; see Woodward 1889: p. 143-144). Woodward (1912: p. 235) assigned

all the NHMUK specimens attributed to *Ptychodus polygyrus* from the vicinity of Lewes to the ‘Turonian zones’.

Description. NHMUK PV P4408 (see above; Fig. 4A-D) and NHMUK PV P4410 (Fig. 4E-H) exhibit identical dental features, including outline, ornamentation pattern and degree of preservation. Both the teeth lack their root. Moreover, NHMUK PV P4410 (see Fig. 4F) exhibits marked wear traces, mainly concentrated on the left side of the ridges, as well as on the anterior marginal area. Measurements and other morphological details of the teeth are reported in Tab. 1.

Remarks. *Ptychodus polygyrus* is characterized by a remarkable intraspecific variability (e.g., Agassiz 1839, 1843; Dibley 1911; Woodward 1912). According to Woodward (1912: p. 223), some of the teeth commonly assigned to *P. polygyrus* may actually belong to different species. Woodward (1912: pl. 49, fig. 1-3) described and figured a tooth set (NHMUK PV P10771) housed in Natural History Museum, London and assigning it to *P. polygyrus*. Among these teeth, originally associated, Woodward (1912) recognized also the lower symphyseals (labelled herein to as NHMUK PV P10771 α , Fig. 4J; see also Hamm and Harrell 2013). However, articulated specimens of this taxon are currently unknown.

NHMUK PV P4408 (Fig. 4A-D) and NHMUK PV P4410 (Fig. 4E-H), probably belong to the first lateral rows of the upper dentition, because of their rectangular outline, flat crown and ridge number. The ornamental loops in the lateral teeth of *P. polygyrus* seem to be more marked and complete on the distal side of the crown (e.g., Woodward 1912: pl. 49, fig. 1-3; Hamm and Harrell 2013: fig. 4C). The ridge pattern, including the lateral loops, suggests that the teeth were originally placed in the right upper side of the jaw.

Nomenclatural remarks. After the original creation of *Ptychodus polygyrus* in 1835 (see above), Agassiz (1839: p. 156; 1843: p. 157) described the species, recognizing three different ‘variétés’ (varieties), which he named *P. polygyrus* ‘proprement dit’ (‘stricto sensu’), *P. concentricus* and *P. sulcatus*, respectively. Later, Agassiz (1843) added a further variety that he named *marginalis* (see also Brignon 2015). Woodward (1912, p. 233) hypothesized that var. *P. concentricus* could be an abnormal form of *P. mammillaris* Agassiz, 1835 and he also noted relevant morphological similarities between var. *P. sulcatus* and *P. decurrens* Agassiz, 1838 (see also Hamm 2010a). Nevertheless, the two varieties were not synonymized by Woodward (1912) with the species *P. decurrens* and *P.*

mammillaris. Currently, only *P. polygyrus* ‘stricto sensu’ and *P. marginalis* are considered valid species (e.g., Herman 1977; Hamm 2010a; Hamm and Harrell 2013).

Woodward (1889, 1912) also described an associated tooth set of *Ptychodus polygyrus* (NHMUK PV P. 10771) found in a single block of Chalk in Surrey (southern England). This specimen, currently housed in Natural History Museum, London, consists of 76 detached teeth, which properly show ‘the typical form of *P. polygyrus*’ (Woodward 1912: p. 233; see also Hamm 2010a: fig. 2). Hamm and Harrell (2013) recently provided what they called a ‘revised diagnosis of type’ of *P. polygyrus* based on NHMUK PV P. 10771. Indeed, not being aware of what is reported in the subsequent nomenclatural reconstruction by Brignon (2015, 2019; see above), Hamm and Harrell (2013) erroneously considered the Woodward’s tooth set (NHMUK PV P. 10771) as the holotype of *P. polygyrus* (see also Hamm 2010a). Although NHMUK PV P. 10771 shows the main morphological features of the species (e.g., NHMUK PV P. 10771 α in Fig. 4J), this tooth set from Banstead (Surrey, southern England) does not belong either to the ‘Mantell collection’ or to the ‘Regley collection’, and it cannot be considered as part of the original type series of *P. polygyrus* (see above).

†*Ptychodus mediterraneus* Canavari, 1916 emended

Figs 5-20

1837 *Ptychodus* Agassiz; Bronn: 745, pl. 33, fig. 19a,b.

p.1838 *Pt. latissimus* Agass.; Agassiz: pl. 25b, fig. 26 (non figs 24, 25), atlas vol. III.

1842 *Ptychodus latissimus* Ag.; Catullo: 10.

p.1845 *Pt. decurrens* Ag.; Reuss: 1, pl. 2, fig. 10 (non fig. 9).

1863 *Ptychodus polygyrus*; Mackie: 162, pl. 9.

1885 *Ptychodus* (sic) *polygyrus* L. Agassiz; De Stefani: 118, pl. 2, fig. 13.

1896 *Ptychodus latissimus* Ag.; Priem: 9, pl. 1, figs 2, 4 (non 1, 3).

1900 *Ptychodus latissimus* Ag.; Seguenza: 475, pl. 5, fig. 19 (non syn.).

1900a *Ptychodus polygyrus*; Williston: 31, pl. 11, fig. 9, pl. 12, fig. 14.

1900b *Ptychodus polygyrus*; Williston: 240, pl. 29, fig. 9, pl. 30, fig. 14.

1900a *Ptychodus* sp.; Williston: 34, pl. 11, figs 1-3, pl. 13, fig. 53.

1900b *Ptychodus* sp.; Williston: 243, pl. 29, figs 1-3, pl. 31, fig. 53.

1906 *Ptychodus polygyrus* L. Agassiz 1839, var. *marginalis* L. Agassiz, 1839; Leriche: 76, pl. 6, fig. 1-17.

1910 *Ptychodus latissimus* Agassiz; Canestrelli: 112, pl. 1, fig. 3-5.

†v1916 *Ptychodus mediterraneus*; Canavari: 98, text figs 1-4, pls 5-11, pl.12, figs 1-16, pls 13, 14.

vp.1922 *Ptychodus latissimus* Ag.; D'Erasmus: 17, pl. 2, figs 11, 15 (non figs 9, 10, 12-14).
v1922 *Ptychodus mediterraneus* Canavari; D'Erasmus: 19, pl. 2, fig. 21.
1966 *Ptychodus mediterraneus* Can.; Dal Piaz and Malaroda: 37, fig. 36a,b.
1970 *Ptychodus polygyrus* Agassiz; Applegate: 393, text fig. 149A.
p.1977 *Ptychodus latissimus* Agassiz L. 1843; Herman: 67, pl. 2, figs 9a, b (non text fig. p. 69) (non syn.).
v1980 *Ptychodus* cf. *latissimus*; Cigala-Fulgosi et al.: 126, text fig., p. 124.
1985 *Ptychodus polygyrus* Agassiz 1843; Wolberg: 9, fig. 3/5.
1999 *Ptychodus* cf. *latissimus* Agassiz 1843; Trbušek: 54, pl. 1, fig. 5.
v2000 *Ptychodus* (sic); Ginevra et al.: 35, fig. 6.5.
p.2002 *Ptychodus paucisulcatus* Agassiz 1838; Antunes and Cappetta: 105, pl. 1, figs 4-7, 9 (non fig. 8).
2004 *Ptychodus* aff. *P. polygyrus* (sic) Agassiz 1839; Cicimurri: 7, figs 4G, H.
2006 *Ptychodus* cf. *P. latissimus* Agassiz 1843; Shimada and Fielitz: 194, fig. 2A.
2010 *Ptychodus*; Roghi: 59, fig. 3.
v2017 *Ptychodus*; Zorzin: 68, text fig., p. 60.
v2019a *Ptychodus*; Amadori et al.: 3, pl. I.
vp.2019a *Ptychodus* cf. *latissimus*; Amadori et al.: 16, pl. III, fig. C (non figs A-B¹).

Holotype. MSNUP I-17373 (Fig. 5-8), an articulated tooth set from Gallio (VI, northern Italy), represents the holotype of the species by monotypy (see Canavari 1916).

Emended diagnosis. A *Ptychodus* species with thick and transversally elongated ridges crossing the rectangular dental crown, without reaching the lateral tooth edges; ridges curving and tapering off at the lateral ends, never forming loops; surface of lower teeth bulging with an expanded marginal area compared to flat upper dental crowns; rare coarse granules characterizing the transition between crested and marginal areas; fine granulation covering the marginal areas without defined or diagnostic patterns; fine wrinkles covering the anterior occlusal surface; crown protruding on all the sides over a bilobate root; tooth size and ridge number decreasing mesio-distally within the dental plates, with the exception of the small upper symphyseals; distalmost teeth triangular in outline.

Referred material. Three articulated tooth sets (MCBG 4048, MPPSA IGVR 91031 and MSNUP I-17373), two of which also preserve remains of the skeleton. Six specimens (MCBG 4050, MGP-PD 6720, MGP-PD 13531, MGP-PD 13532 and MSNUP 274) including associated dental elements, not in natural position. A tooth set (MCSNV v.12508) with two detached teeth. Seventeen isolated

teeth (MCBL 677, MCSNV v.11791, MCSNV v.12507, MCSNV v.12528, MGP-PD 6717, MGP-PD 6718, MGP-PD 7345, MGP-PD 8494, MGP-PD 8497, MGP-PD 13533, MGP-PD 13534, MGP-PD 13535, MGP-PD 13536, MGP-PD 14040, MGP-PD 23539, MMC PTY01 and MMC PTY02) with different degrees of preservation.

Occurrence. All the specimens come from the Upper Cretaceous Scaglia Rossa Formation of northeastern Italy. Most of them were collected from the ‘Lastame’ lithozone of the Lessini Mountains (MCSNV v.11791, MCSNV v.12507, MCSNV v.12528, MGP-PD 6720, MGP-PD 7345, MGP-PD 8497, MGP-PD 13531, MGP-PD 13532, MGP-PD 13533, MGP-PD 13534, MGP-PD 13535, MGP-PD 13536, MGP-PD 14040, MSNUP 274 and MSNUP I-17373); other findings come from the ‘Pietra di Castellavazzo’ (MCBL 677, MGP-PD 6717, MGP-PD 6718 and MGP-PD 8494). The whitish hard limestone of the matrix of the holotype MSNUP I-17373 shows strong lithological affinities with some whitish beds of the Lessinian ‘Lastame’ (Giusberti L., pers. obs.) and possibly represents a unique record of this lithozone in the Asiago Plateau. The original localities of all the examined specimens are indicated in Fig. 1A. It was not possible to accurately define the sites of provenance of MCBG 4048, MCBG 4050, MCSNV v.12508, MMC PTY01, MMC PTY02 and MPPSA IGVR 91031. Nevertheless, based on the lithology of the sedimentary matrix and the degree of preservation, it is reasonable to hypothesize that MCSNV v.12508, MMC PTY01, MMC PTY02 and MPPSA IGVR 91031 come from the ‘Lastame’, whereas MCBG 4048 and 4050 from the ‘Brocchi collection’ probably come from the ‘Pietra di Castellavazzo’ near Belluno (see D’Erasmus 1922: p. 20; Amadori et al. 2019a). The calcareous nannofossil assemblage of the matrix indicates the UC8-UC9 zones of Burnett (1999) for MSNUP I-17373, suggesting a middle-late Turonian age for the holotype of *P. mediterraneus*. The calcareous nannofossil content of MGP-PD 13531 and MPPSA IGVR 91031 indicates the UC7-UC9 zones of Burnett (1999), corresponding to an early-late Turonian age (see Ogg and Hinnov 2012).

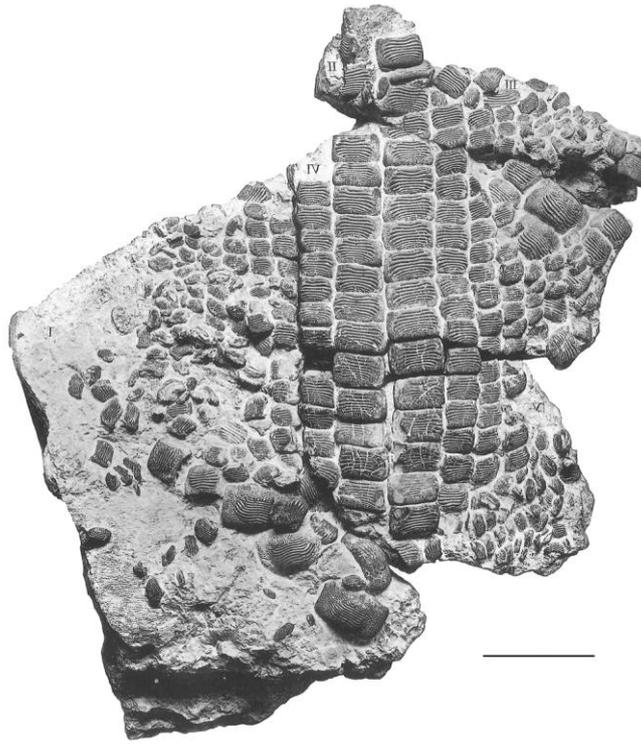


Fig. 5. The original state of preservation of the holotype of *Ptychodus mediterraneus* Canavari, 1916 (MSNUP I-17373). Canavari (1916) figured and described this articulated specimen after removal of several teeth from the slab. Photo after Canavari (1916). Scale bar equals 100 mm.



Fig. 6. Current condition of the holotype MSNUP I-17373 of *Ptychodus mediterraneus* Canavari, 1916. The specimen comes from Gallio (Vicenza, northeastern Italy). Scale bar equals 100 mm.

Description of the holotype. MSNUP I-17373 (Fig. 5-6) consists of five portions (I-V in Fig. 7) originally included in a single slab. This specimen exhibits over 370 associated teeth, of which about 220 are still articulated and arranged in antero-posterior parallel rows, forming two portions of dental plates partially overlapped to each other (see Fig. 7); other dental remains are probably still covered by the matrix. Dental morphologies vary within the dental plates and between them. In both upper and lower dentitions, worn teeth occur and the occlusal surfaces of several teeth exhibit different degrees of wear (Fig. 8A-B); in some cases, the entire dental surface is abraded (Fig. 8H). In the mesial rows of the upper dentition, abrasions are limited to the seven anterior teeth, where it is more extended and deeper on the mesial side of each occlusal surface (e.g., Fig. 8H). Mesio-distally, the number of worn teeth increases in the third and fourth distal rows, while the wear degree is minor on each tooth. In the distalmost portion of the plate the number of worn teeth decreases again and in the distalmost rows wear traces are almost absent. Starting from the markedly abraded anterior teeth, the wear gradually decreases antero-posteriorly, until they disappear completely into the posteriormost upper teeth (Fig. 8A-B). Similar wear patterns are present in the lower dentition (Fig. 8A). A portion of mineralized cartilage (Fig. 8G) and a calcified vertebral centrum impression (Fig. 8E-G) are also clearly recognizable on MSNUP I-17373. Conversely from what was reported by Diedrich (2013: p. 28), there is no evidence of shell fragments of inoceramids or other putative molluscs on the slab that preserves MSNUP I-17373 (Fig. 6). Measurements and other morphological details are provided in Tab. 2 (see also Tab. A.2, Appendices).

Tab. 2. Measurements of teeth of *Ptychodus mediterraneus* Canavari, 1916 belonging to the dental plates of the specimen MHNUP I-17373. **P**, placement within the dental plate (see interpretative line drawing in Fig. 19A-B); **CW**, Crown width; **CL**, Crown length; **nTR**, number of transverse ridges.

Upper dentition						
P	CW min.	CW max.	CL min.	CL max.	nTR min.	nTR max.
M	~ 12 mm	~ 14 mm	~ 20 mm	~ 21 mm	2	4
L1	~ 42 mm	~ 50 mm	~ 25 mm	~ 31 mm	8	10
L2	~ 31 mm	~ 34 mm	~ 24 mm	~ 27 mm	7	9
L3	~ 25 mm	~ 27 mm	~ 21 mm	~ 25 mm	7	8
L4	~ 22 mm	~ 25 mm	~ 18 mm	~ 21 mm	6	7
L5	~ 20 mm	~ 23 mm	~ 16 mm	~ 19 mm	5	7
L6	~ 20 mm	~ 23 mm	~ 14 mm	~ 16 mm	5	7
L7	~ 17 mm	~ 21 mm	~ 12 mm	~ 14 mm	5	6
L8	~ 16 mm	~ 18 mm	~ 11 mm	~ 12 mm	5	6
L9	~ 14 mm	~ 15 mm	~ 9 mm	~ 11 mm	4	4
Lower dentition						
P	CW min.	CW max.	CL min.	CL max.	nTR min.	nTR max.
m	~ 58 mm	~ 63 mm	~ 40 mm	~ 43 mm	8	10
l1	~ 33 mm	~ 38 mm	~ 28 mm	~ 33 mm	7	8
l2	~ 23 mm	~ 28 mm	~ 19 mm	~ 23 mm	7	7
l3	~ 21 mm	~ 23 mm	~ 17 mm	~ 19 mm	6	7
l4	~ 22 mm	~ 23 mm	~ 15 mm	~ 16 mm	6	7
l5	~ 19 mm	~ 20 mm	~ 12 mm	~ 14 mm	5	6
l6	~ 18 mm	~ 19 mm	~ 11 mm	~ 11 mm	5	6
l7	~ 16 mm	~ 19 mm	~ 9 mm	~ 10 mm	5	6
l8	~ 14 mm	~ 14 mm	~ 7 mm	~ 8 mm	5	5
l9	~ 10 mm	~ 12 mm	~ 5 mm	~ 6 mm	3	4

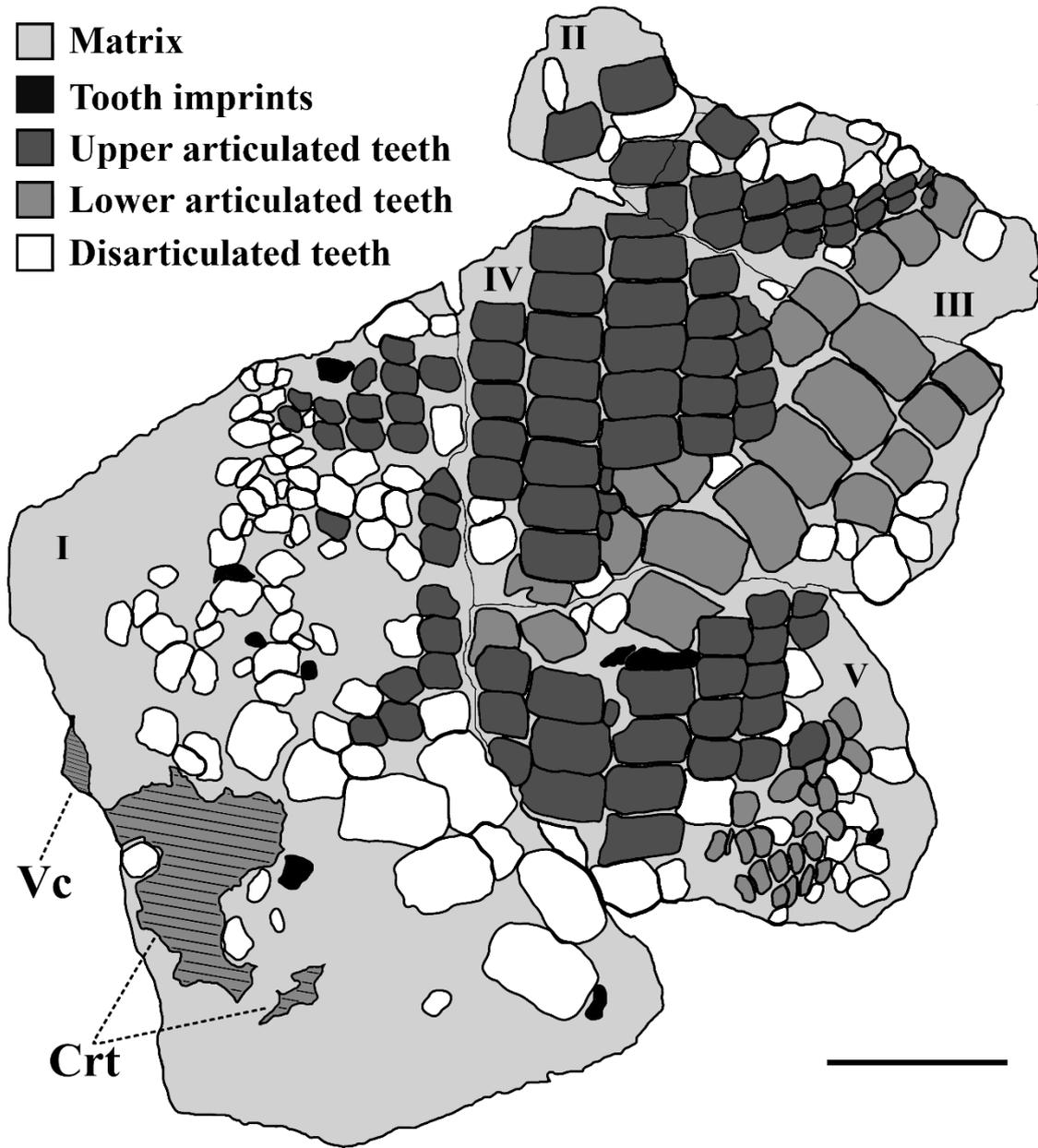


Fig. 7. Interpretative line drawing of MSNUP I-17373; the slab is composed of five portions (I-V) showing several articulated and disarticulated teeth of *Ptychodus mediterraneus* Canavari, 1916, a vertebral centrum (Vc) and tooth impressions and fragmentary mineralized cartilages (Crt). Scale bar equals 100 mm.

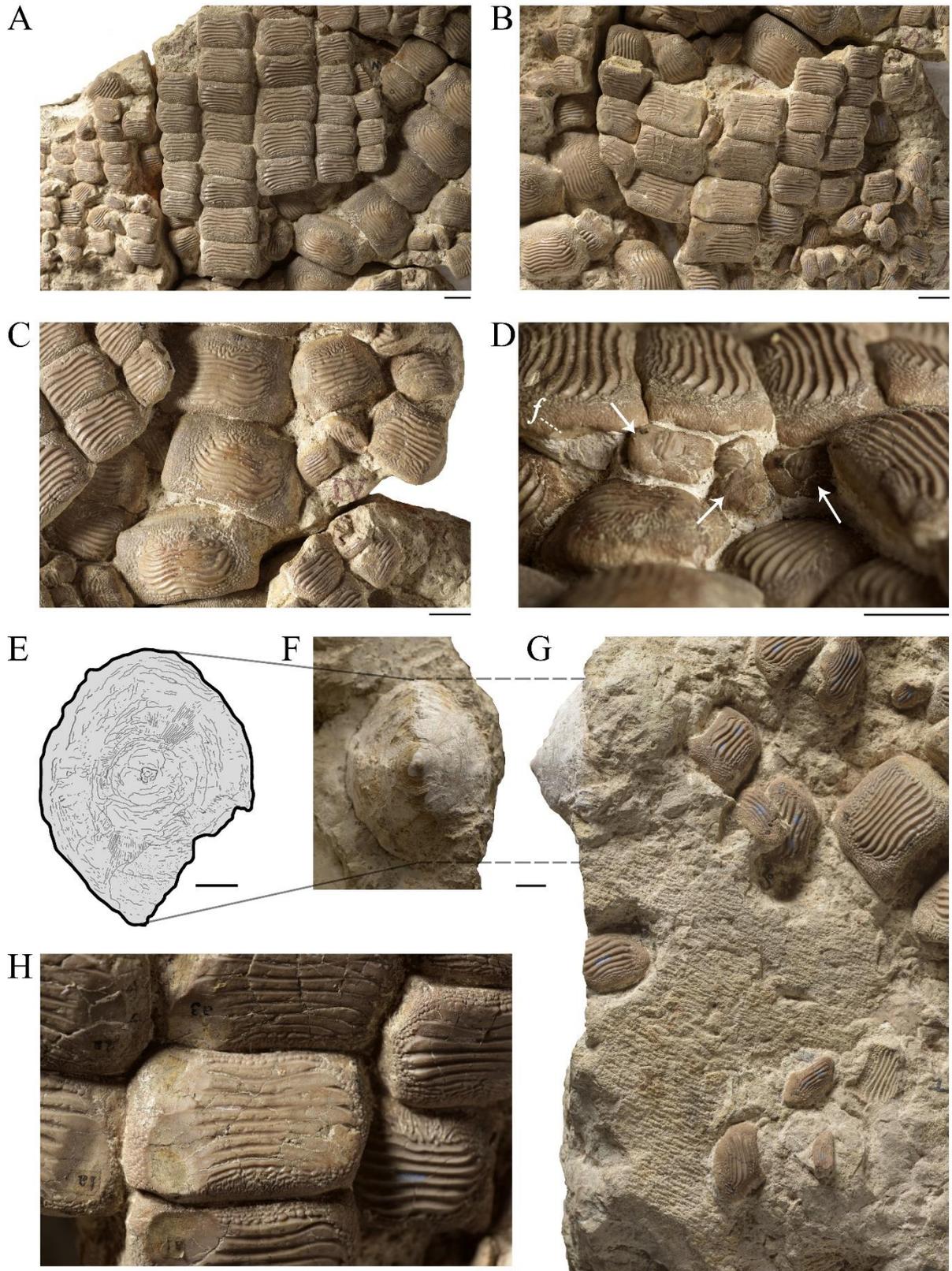


Fig. 8. Details of MSNUP I-17373 showing dental and skeletal remains of *Ptychodus mediterraneus* Canavari, 1916. **A–D, H.** articulated teeth (white arrows, upper symphyseal; *f*, articular facets); scale bars equal 10 mm. **E–F.** impression of vertebral centrum: **E.** interpretative line drawing; **F,** transversal view (scale bars equal 10 mm). **G.** impression of vertebral centrum (lateral view) and fragmentary mineralized cartilages (scale bar equals 10 mm).

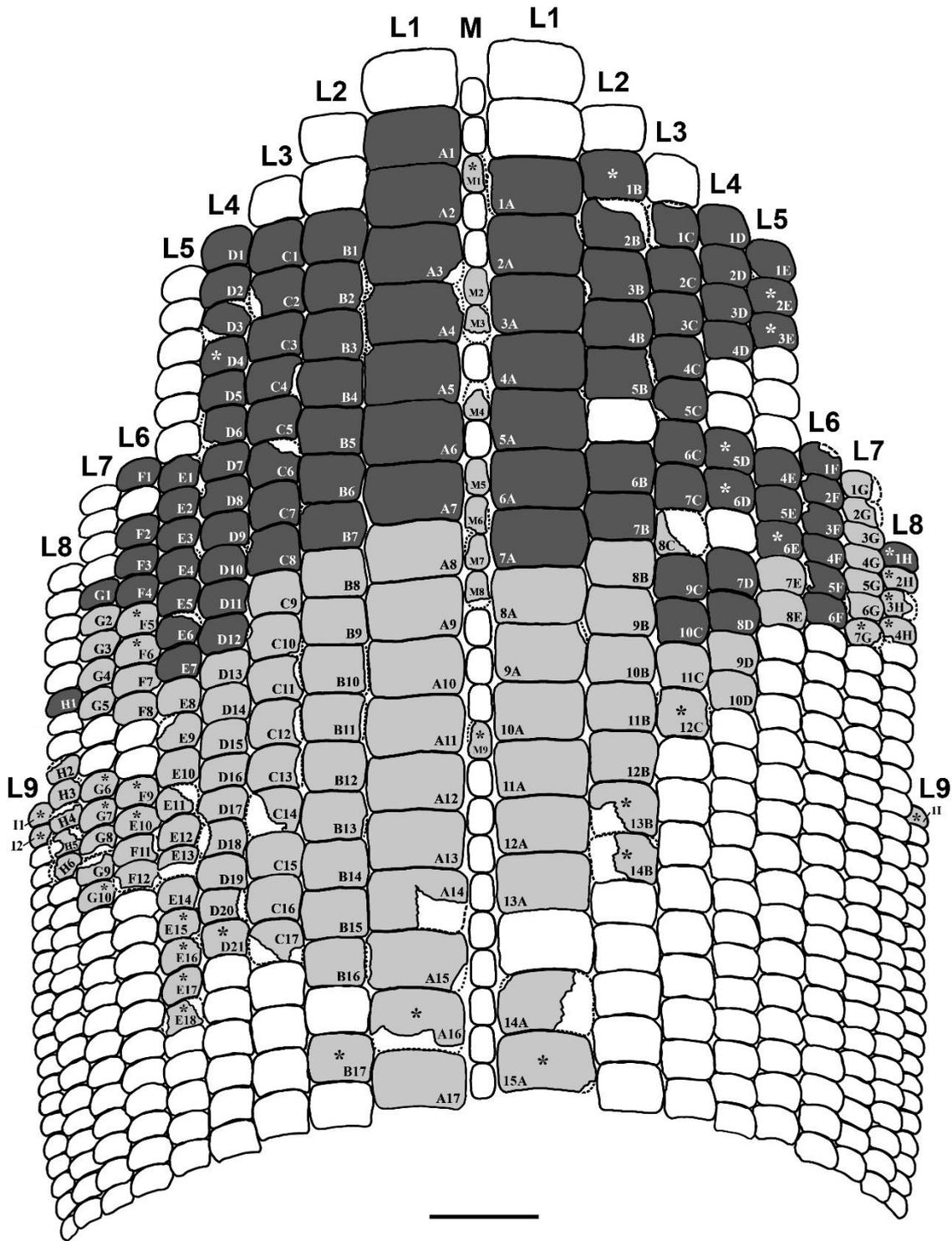


Fig. 9. Interpretative reconstruction of the upper dental plate of *Ptychodus mediterraneus* Canavari, 1916 based on the holotype MSNUP I-17373. White: missing teeth; light grey: preserved teeth; dark grey: preserved worn teeth. Asterisks indicate the disarticulated teeth whose position has been reinterpreted in this paper. The dotted lines indicate the missing parts of the teeth. A code (e.g., A1, A2, etc.) has been arbitrarily assigned to all the teeth preserved from anterior end of each tooth row. M, symphyseal row; L1-9, lateral rows. Scale bar equals 50 mm.

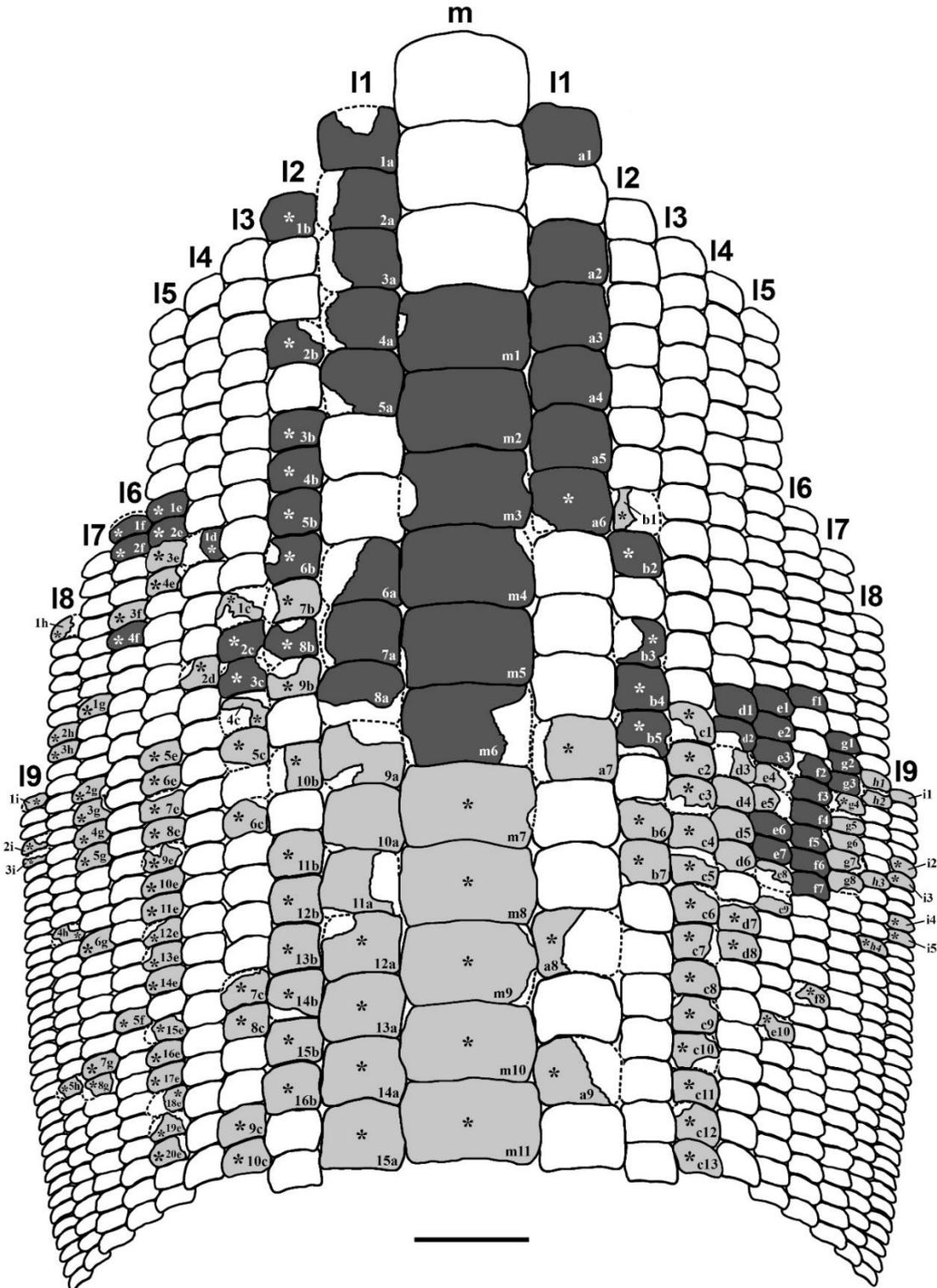


Fig. 10. Interpretative reconstruction of the lower dental plate of *Ptychodus mediterraneus* Canavari, 1916 based on the holotype MSNUP I-17373. White: missing teeth; light grey: preserved teeth; dark grey: preserved worn teeth. Asterisks indicate the disarticulated teeth whose position has been reinterpreted in this paper. The dotted lines indicate the missing parts of the teeth. A code (e.g., **a1**, **a2**, etc.) has been arbitrarily assigned to all the teeth preserved from anterior end of each tooth row. **m**, symphyseal row; **11–9**, lateral rows. Scale bar equals 50 mm.



Fig. 11. Side A of a partially articulated specimen herein assigned to *Ptychodus mediterraneus* Canavari, 1916 (MPPSA IGVR 91031) and presently housed at the Museo Paleontologico e Preistorico di Sant'Anna d'Alfaedo (Verona, northeastern Italy). Scale bar equals 100 mm.



Fig. 12. Side B of the partially articulated specimen MPPSA IGVR 91031 herein assigned to *Ptychodus mediterraneus* Canavari, 1916 and housed at the Museo Paleontologico e Preistorico di Sant'Anna d'Alfaedo (Verona, northeastern Italy). Scale bar equals 100 mm.

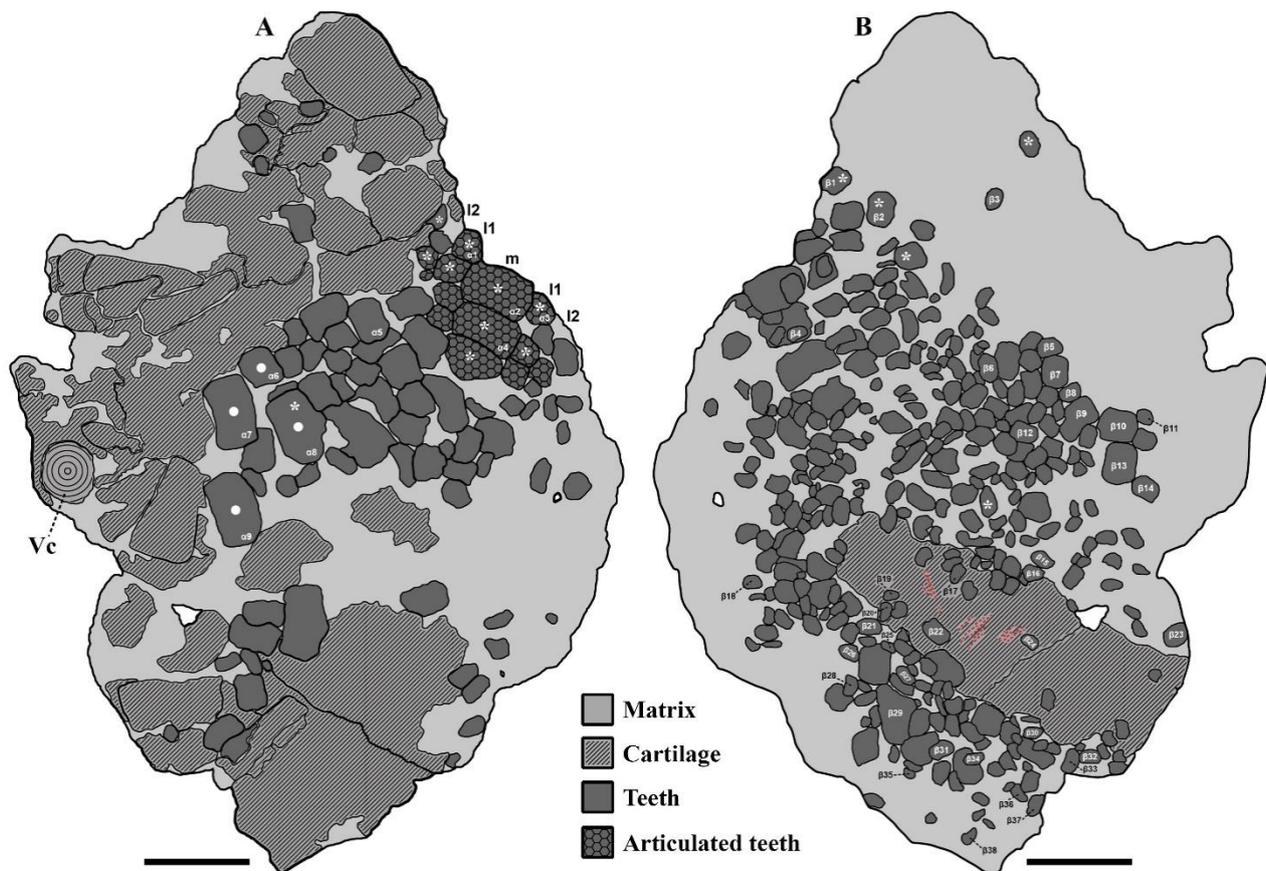


Fig. 13. Interpretative line drawing (side **A** and **B**) of MPPSA IGVR 91031 assigned to *Ptychodus mediterraneus* Canavari, 1916. **Vc**, vertebral centrum impression; **m**, symphyseal row; **I1–2**, lateral rows; white dot, re-attached teeth; asterisk, worn teeth; red dotted lines, scavenging traces. Scale bars equals 100 mm. A code (e.g. $\alpha/\beta 1, 2$, etc.) has been arbitrarily assigned as reference for measurements of table A.3 (see Appendices S.3.5).

Description of other articulated sets. Slab MPPSA IGVR 91031 contains more than 320 teeth, varying in size and morphology on both sides (labelled herein as ‘side A’ in Fig. 11 and ‘side B’ in Fig. 12). Some of these teeth also exhibit marked abrasions on the crested areas (see also Fig. 13). Side A shows about 60 teeth, with only twelve of these being articulated and forming a portion of the lower dental plate (Fig. 14A). On the same side, there is also an elliptical impression of a calcified vertebral centrum (Fig. 14C,F). About 260 disarticulated teeth are preserved on side B (Fig. 12,14G). In addition, both sides (A and B) show several portions of a tabular mineralized cartilage with rough surface (Fig A-D). Furrows varying in length and orientation mark one of the cartilages of side B (Fig. 18A-B). Whitish elements characterize the occlusal surface of a few scattered teeth on the same side (Fig. 18A,C,D). Measurements and other morphological details are provided in Tab. A.3 (Appendices). MCBG 4048 (Fig. 15G,H) includes five small teeth with irregular polygonal outline still associated in their natural position and two other small, disarticulated teeth. The dental plate portion preserved in MCBG 4048 consists of two tooth rows. Furthermore, the impressions of two

teeth belonging to a third mesial row (Fig. 15G) and ‘articular facets’ on the distal edge of the outermost teeth are also recognizable. The specimen exhibits asymmetrical dental crowns with damaged transversal ridges (Fig. 15H). The articulated teeth preserve also bilobate roots. The occlusal ridges are damaged, but none of the dental crowns shows wear traces (Fig. 15H). A more detailed description of dental features and skeletal remains is provided below (see ‘Anatomical description’). Measurements and other morphological details are provided in Tab. A.4 (Appendices).

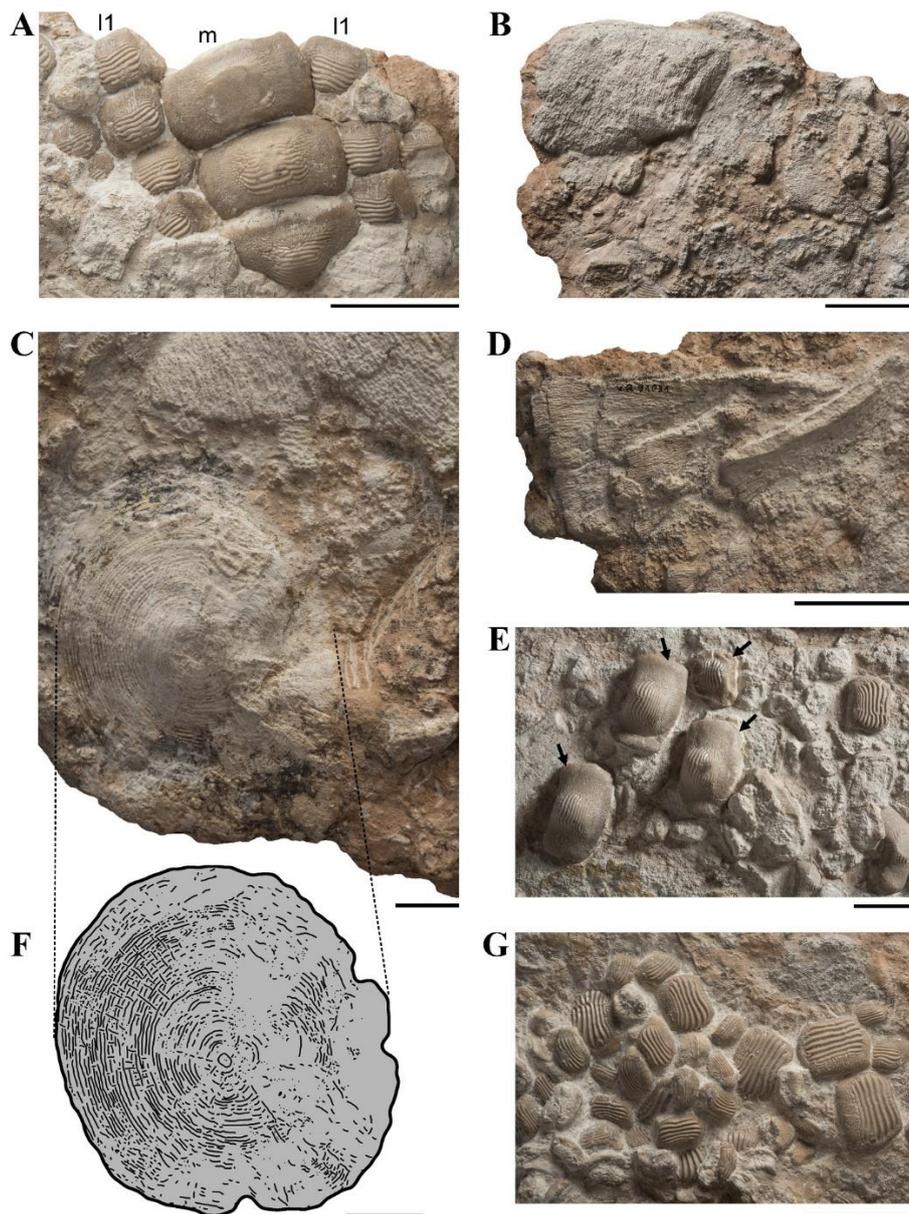


Fig. 14. Details of MPPSA IGVR 91031 showing dental and skeletal remains of *Ptychodus mediterraneus* Canavari, 1916. **A.** articulated teeth (**m**, symphyseal row, **l1**, lateral rows); scale bar equal 50 mm. **B, D.** fragmentary mineralized cartilages; scale bars equal 50 mm. **C, F.** vertebral centrum impression (**C.** transversal view; **F.** interpretative line drawing); scale bar equal 10 mm. **E, G.** disarticulated teeth of upper and lower dentitions (black arrows, re-attached teeth); scale bars equals 50 mm.

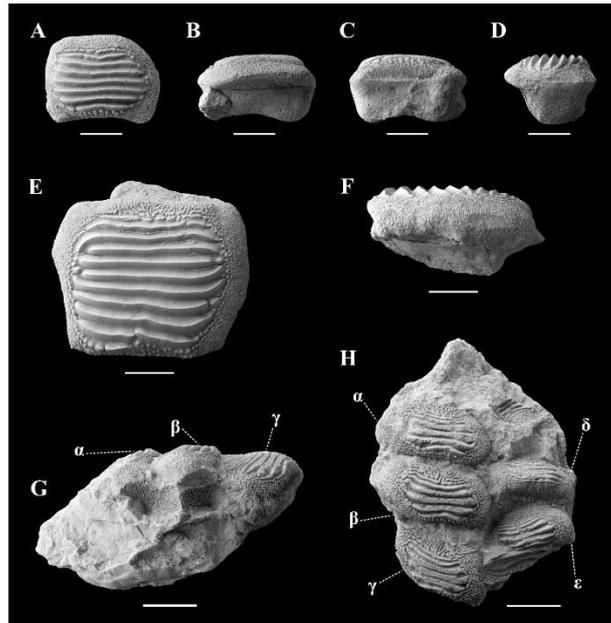


Fig. 15. Isolated (**A-F**) and articulated (**G-H**) teeth of *Ptychodus mediterraneus* Canavari, 1916 from the Scaglia Rossa Formation of Veneto region (northeastern Italy), after ‘smoking’ treatment (see ‘Methods’). **A-D**. isolated teeth MGP-PD 8497: **A**. occlusal view; **B**. anterior view; **C**. posterior view; **D**. lateral view. **E-F**. isolated teeth MGP-PD 13534: **E**. occlusal view; **F**. lateral view. **G-H**. articulated tooth set MCBG 4048: **G**. occlusal view; **H**. lateral view; α , MCBG 4048 α ; β , MCBG 4048 β ; γ , MCBG 4048 γ ; δ , MCBG 4048 δ ; ϵ , MCBG 4048 ϵ . All scale bars equal 10 mm.

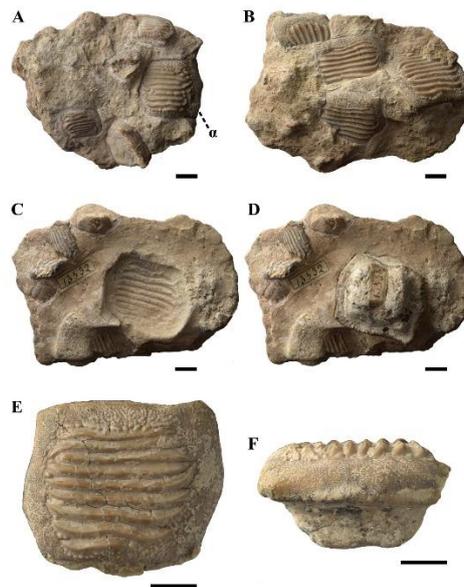


Fig. 16. Associated tooth sets of *Ptychodus mediterraneus* Canavari, 1916 from the Scaglia Rossa Formation of Veneto region (northeastern Italy). **A**. occlusal view of MGP-PD 13531; α , MGP-PD 13531 α . **B-C**. occlusal (**B**) and inferior (**C**) view of MGP-PD 13532. **D**. inferior view of MGP-PD 13536 re-attached to MGP-PD 13532. **E-F**. occlusal (**E**) and lateral (**F**) view of MGP-PD 13536. All scale bars equal 10 mm.

Description of associated and isolated teeth. MGP-PD 6720 consists of four poorly preserved teeth on a single portion of matrix; all of these teeth almost completely lack the marginal area. Eight to ten thick and transversally elongated ridges cross the dental crowns in MGP-PD 6720. In addition, the marginal area exhibits thin wrinkles anteriorly and coarse granulations posteriorly. MGP-PD 13531

(Fig. 16A) consists of a large, quadrangular and bulgy tooth (MGP-PD 13531 α) associated with four additional teeth with small, rectangular, flat crowns. MGP-PD 13532 (Fig. 16B-D) contains nine large and flat teeth with rectangular outline. The teeth preserved on these slabs (MGP-PD 13531 and MGP-PD 13532) exhibit slight variations in size and number of parallel ridges (six to nine). There are probably other dental fragments embedded in the matrix. Furthermore, several tooth impressions were also observed in the tooth sets MGP-PD 13531 and MGP-PD 13532. An impression in MGP-PD 13532 perfectly corresponds to the outline of MGP-PD 13536 (see Fig. 16C,D). The latter is a detached tooth, characterized by a squared and thick crown (see Fig. 16E,F). Its flat occlusal surface shows nine parallel ridges with slightly curved ends, while the marginal area is covered by coarse granulations. The crown of MGP-PD 13536 overhangs the root on all sides, which is squared and bilobate with an evident anterior-posterior sulcus (Fig. 16D). The associated set MSNUP 274 (Fig. 18F-I) consists of at least five small teeth characterized by rectangular (e.g., MSNUP 274 α) or triangular outlines (e.g., MSNUP 274 β). Parallel and sharp ridges cross the dental crowns of all these teeth. Several whitish traces are detectable on the occlusal surface of the largest tooth, indicating postmortem alterations (MSNUP 274 α ; see Fig. 18H). The tooth set MCBG 4050 includes two poorly preserved teeth. The first one is a large tooth (here labelled 'MCBG 4050 α ') with an asymmetrical and bulgy crown, associated with other tooth fragments and dental impressions. The second (here labelled 'MCBG 4050 β ', Fig. 17K,L) is an isolated tooth with a rectangular, flat crown crossed by eight transvers ridges. Specimen MCBG 4050 β exhibits a partial marginal area and a damaged quadratic root. MGP-PD 23539 is an isolated specimen almost identical to MCBG 4050 β , with the exception of the presence of five occlusal ridges and the lack of the root. Specimens MGP-PD 13534 (Fig. 15E,F), MGP-PD 13535 (Fig. 18E) and MMC PTY02 are isolated teeth with flat and rectangular crowns crossed by seven to nine thick and sharp ridges; some of them lack the root (e.g., MMC PTY02) and are characterized solely by a restricted small part of the marginal area (e.g., MGP-PD 13535). MGP-PD 13535 exhibits several irregular whitish traces on its crested area (see Fig. 18E). Specimens MGP-PD 6717, MGP-PD 6718, MGP-PD 7345, MGP-PD 8494 and MCBL 677 are very similar to MCBG 4050 β (Fig. 17K) in general shape, but they are smaller in size. All of them have flat dental crowns with just a small portion of marginal area still preserved and covered by lateral granulations and anterior wrinkles. In occlusal view, the isolated teeth exhibit six (MGP-PD 6717, MGP-PD 6718 and MCBL 677) or eight (MGP-PD 7345 and MGP-PD 8494) thick, parallel and sharp ridges. Only two of them have marked abraded ridges at their ends (MGP-PD 6718) or on the central portion of the dental crown (MGP-PD 7345). Specimen MCSNV v.12508 comprises two isolated teeth (labelled herein to as MCSNV v.12508 α and MCSNV v.12508 β) that have convex occlusal

surfaces, but only MCSNV v.12508 α displays a rectangular and symmetrical outline. Specimen MCSNV v.12508 β is morphologically consistent with MCSNV v.11791 (Fig. 17G,H) and MGP-PD 13533. These bulgy teeth have quadratic tooth crowns crossed by eight to nine ridges, of which the first and the last are thin and interrupted. The left edge of the three specimens (MCSNV v.12508 β , MCSNV v.11791 and MGP-PD 13533) is lowered and concave (see Fig. 17G). In lateral view (see Fig. 17H), their occlusal bulgy crowns have the posterior outline that is perpendicular to the tooth base, while the crown tilts anteriorly. Specimen MCSNV v.12528 (Fig. 17I,J) has a symmetrical and rectangular crown with 11 transverse ridges, which are slightly curved at their ends. An anterior protuberance and a posterior sulcus are well-developed. In occlusal view (Fig. 17I), the marginal area is covered with granulations, with exception of the anterior portion which is characterized by fine wrinkles. A similar morphology of the crown, as well as an identical pattern of ornamentation, is present in MCSNV v.12507 and MCSNV v.12508 α . However, these two specimens are characterized by eight and nine transversal ridges, respectively. MCSNV v.12508 α also has a rectangular dental root with an oblique anterior side. MMC PTY01 has only a small and symmetrical crested area, while the edges are badly damaged or completely missing. In occlusal view, the crown has six or seven sharp ridges markedly abraded at their lateral ends. In lateral view, the crown of MMC PTY01 appears thick and bulgy, while the root is lacking. MGP-PD 8497 (Fig. 15A-D) shows an asymmetrical occlusal surface with eight transversal ridges and marginal granulations. The tooth outline is rounded with a convex right edge and a straight left edge. In anterior view (Fig. 15B), the tooth root has a marked antero-posterior sulcus with the right lobe thicker than the left one, while in lateral view (Fig. 15D), the flat crown overhangs the root, which has a posterior side perpendicular to the crown base. Specimen MGP-PD 14040 is a squared tooth with an asymmetric and gently raised crown; five worn ridges characterize its occlusal surface; abrasion is much marked on the ridges ends. The marginal area is poorly preserved, but clearly discernable from the crested area and covered by granulations. The specimen also has a thick and bilobate root with a right side that is more developed than the left one. Measurements and other morphological details of the associated and detached teeth are provided in Tab. A.5 (Appendices).

Remarks. Among all examined specimens, the holotype MSNUP I-17373 (Fig. 5-7) shows the most complete dentition. Despite exhibiting slight taphonomic disarticulation, it has several articulated teeth belonging to both upper and lower dentitions in their natural position. The lower dental plate is more fragmentary than the upper one (see Fig. 9-10). MPPSA IGVR 91031 (Fig. 11, 13A, 14A) and MCBG 4048 (Fig. 15G,H) show only a little portion of an articulated dental plate. MPPSA IGVR 91031 also preserves skeletal remains (Fig. 13-14), representing rarities in *Ptychodus* findings

(Cappetta 2012). So far, no detailed anatomical description of MPPSA IGVR 91031 and MCBG 4048 has been published.

Originally, MSNUP I-17373 displayed 377 well-preserved teeth and 23 tooth fragments (see Fig. 5), many of which are still in their original position (see Fig. 6-7). These articulated remains represent two well-preserved dental plates (Fig. 9-10) and are interpreted as belonging to the same individual (see also Canavari 1916). Canavari (1916) removed some of the teeth originally preserved in order to expose the lower dentition that was originally hidden under the overlying teeth. Actually, the lower dental plate is not as well preserved as the upper one and several lower lateral teeth are disarticulated or missing (see Fig. 10). Additional small portions of the mandibular dentition still in their natural position are preserved in specimens MPPSA IGVR 91031 (Fig. 14A) and MCBG 4048 (Fig. 15G,H). The first specimen exclusively shows articulated mesial dental rows, while the second one consists of a few distal teeth belonging to the left side of the jaw.

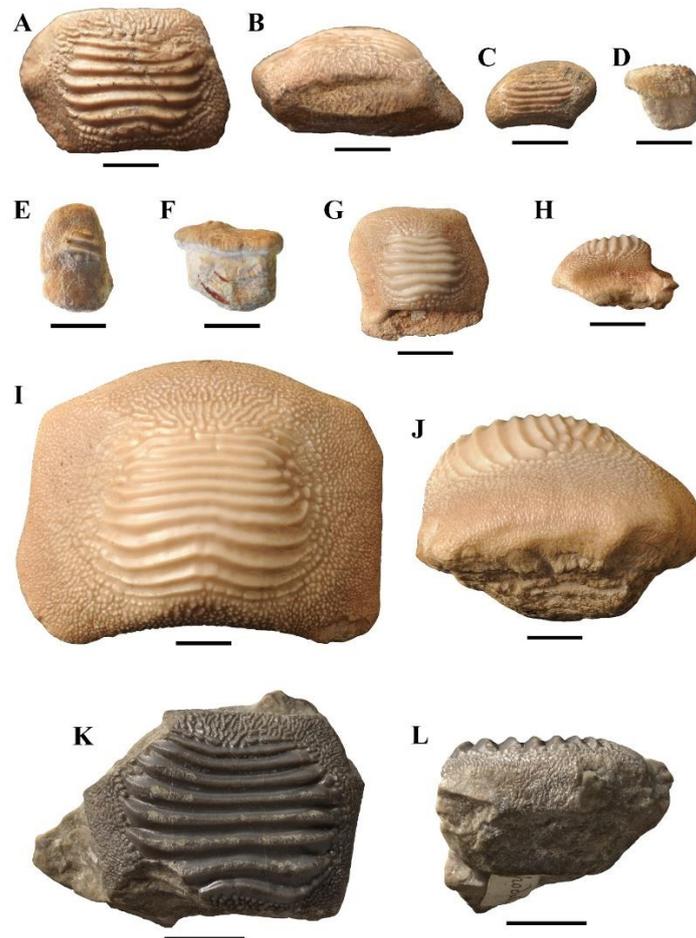


Fig. 17. Isolated teeth of *Ptychodus mediterraneus* Canavari, 1916 from the Scaglia Rossa Formation of Veneto region (northeastern Italy) in occlusal (A, C, E, G, I, K), anterior (B) and lateral (D, F, H, J, L) views. A–F, teeth ‘A1’ (A, B), ‘14e’ (C, D), ‘m5’ (E, F) detached from the holotype MSNUP I-17373 (see ‘A1’, ‘14e’, ‘m5’ in Supp. Fig. 1, 2 by Canavari, 1916). G–H. lateral tooth MCSNV v.11791. I–J. lower tooth MCSNV v.12528. K–L. upper tooth MCBG 4050β. All scale bars equal 10 mm.

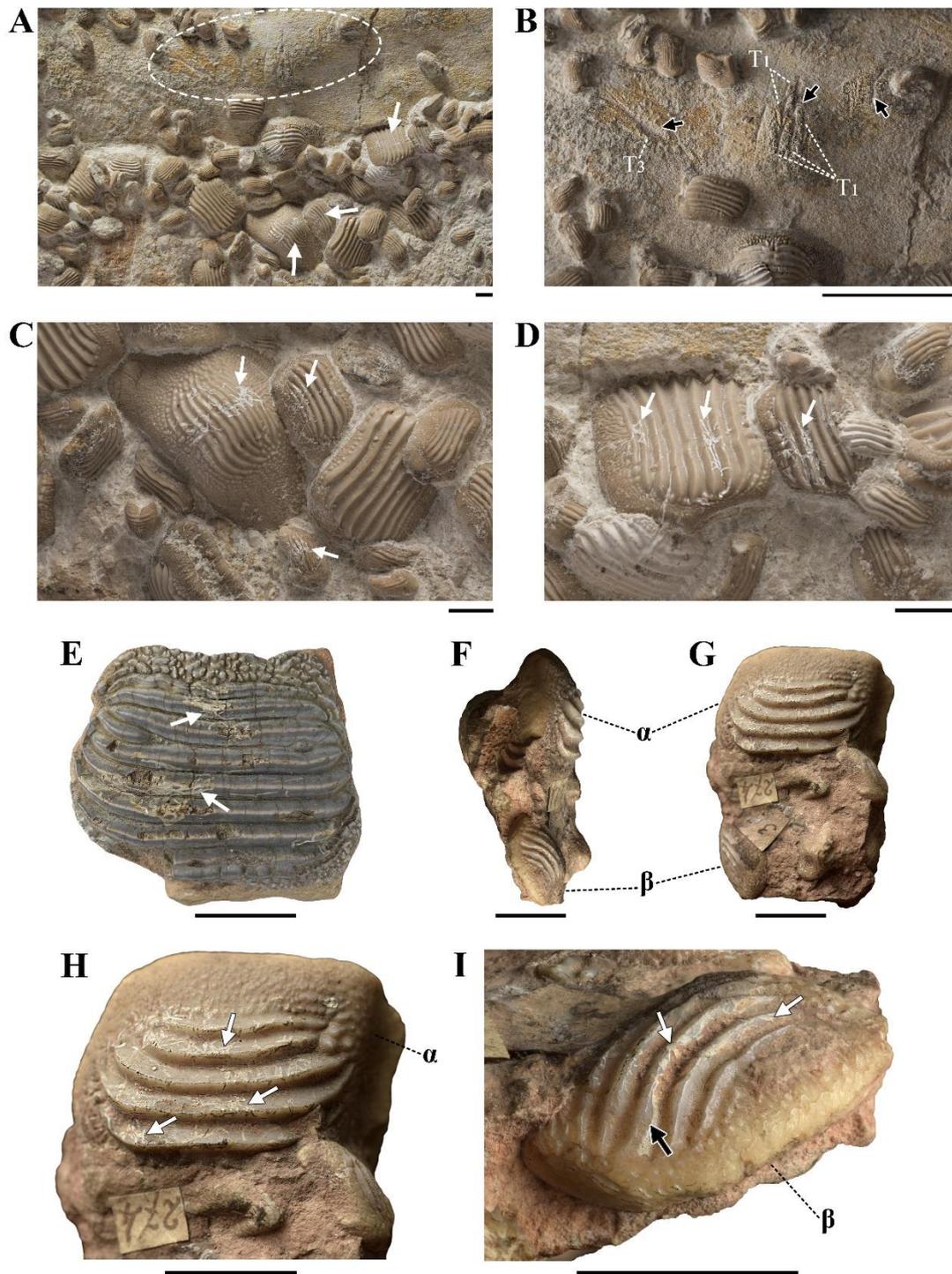


Fig. 18. Bioerosive traces in associated and isolated specimens of *Ptychodus mediterraneus* Canavari, 1916 from the Scaglia Rossa Formation of Veneto region (northeastern Italy). **A.** portion of cartilage and disarticulated teeth on MPPSA IGVR 91031 (dotted circle, traces of scavenging; white arrows, traces of bioerosion); **B.** detail of traces of scavenging (black arrows; T1, bite-marks type 1; T3, bite-marks type 3) on MPPSA IGVR 91031; **C-D.** details of bioerosion on MPPSA IGVR 91031. **E.** bioerosion of isolated tooth MGP-PD 13535 (white arrows, traces of bioerosion). **F-I.** associated specimens MSNUP 274 with details of bioerosion (white arrows in H-I) and traces of tooth wear (black arrow in I); α , MSNUP 274 α ; β , MSNUP 274 β . All scale bars equal 10 mm.

The partial dental rows disposed on both sides of the lower symphyseals of MPPSA IGVR 91031 (see 11 in Fig. 14A) seem to be interrupted anteriorly, suggesting that the preserved articulated teeth are not the rostralmost dental elements. Nevertheless, taking into account the very marked abrasions of the symphyseal teeth of MPPSA IGVR 91031 (see m in Fig. 14A), it could be excluded that they were placed well posteriorly in the series. Indeed, the most markedly worn teeth in MSNUP I-17373 are always placed anteriorly along symphyseal rows (see also Fig. 10). The slight differences in size and height of the bulged crowns of lower symphyseals in MPPSA IGVR 91031 (Fig. 14A) and MSNUP I-17373 (Fig. 8C) probably represent intraspecific variations or could be possibly due to ontogenetic or sexual dimorphisms (see also Tab. A.2 and A.3, Appendices).

The five articulated teeth of MCBG 4048 (Fig. 15G,H) and those belonging to distal lateral rows in MSNUP I-17373 are morphologically very similar to each other. Through the comparison with tooth sizes and proportions in MSNUP I-17373 (see also Tab. A.2 and A.4, Appendices), the small, articulated portions of the dental plate in MCBG 4048 can be referred herein to as the distal portion of the lower dental plate. Based on the impressions placed on the distal lateral surface of the teeth δ and ϵ (see Fig. 15H), its attribution to one of the distalmost rows can be excluded.

Within a single row, there is not much variation of size and morphology of the teeth (MCBG 4048, Fig. 15G,H, MPPSA IGVR 91031, Fig. 11,12 and MSNUP I-17373, Fig. 6), whereas the number of ridges varies mesio-distally and also within the same row (see also. Tab. A.2, Appendices). The thickness of the ridges changes depending on the position of the tooth within the plates and usually decreases mesio-distally (for example see Fig. 8A). Moreover, on the occlusal surface of the same tooth, the first anterior ridges are often thinner than the others (e.g., Fig. 17A-F). The species-specific patterns of the species are poorly recognizable in the distalmost teeth, in which the ridges are less thick and marked than those in mesialmost teeth. Actually, the lower symphyseal teeth exhibit the diagnostic characters of *Ptychodus mediterraneus*, as already evidenced for other *Ptychodus* species (e.g., *P. mammillaris* and *P. mortoni*; see Shimada 2012; Hamm 2017).

The original position within the dental plates occupied by the isolated and associated teeth described herein, has been interpreted based on the overall configuration of the articulated specimens and specific dental features (see ‘Anatomical description’ below) of *Ptychodus mediterraneus* (see also. Tab. A2-5, Appendices). MCBG 4050- β (Fig. 17K,L), MCBL 677, MCSNV v.12508 β , MGP-PD 6717, MGP-PD 6718, MGP-PD 6720, MGP-PD 7345, MGP-PD 8494, MGP-PD 13531 (excluding MGP-PD 13531 α , Fig. 16A), MGP-PD 13532 (Fig. 16B-D), MGP-PD 13534, MGP-PD 13535, MGP-PD 13536 (Fig. 16E,F), MGP-PD 14040, MGP-PD 23539, MMC PTY02 and MSNUP 274 (Fig. F-I) are upper teeth probably belonging to lateral rows, because of their flat crowns and

asymmetrical outline. The dental morphologies of MGP-PD 8497 (Fig. 15A-D) are consistent with those of the teeth belonging to the third row within the upper right side of the jaw (see Fig. 9). Other lateral teeth, originally placed in first lateral lower rows are MCBG 4050 α , MCSNV v.11791 (Fig. 17G,H), MGP-PD 13533 and MGP-PD 13531 α (Fig. 16A). MCSNV v.12507, MCSNV v.12508 α , MCSNV v.12528 (Fig. 17I,J) and MMC PTY01 are interpreted as lower symphyseal teeth. Slight morphological differences observed between articulated, associated and isolated teeth of *Ptychodus mediterraneus* are assumed to reflect intraspecific variability, ontogeny or sexual dimorphism (see also Hamm 2017).

The anatomy of *Ptychodus mediterraneus*

Dental features

Ptychodus mediterraneus exhibits a marked heterodonty, mainly consisting of mesio-distal variations in tooth shape. In addition, the dental morphology within the most mesial rows, including the symphyseal ones, strongly differs between upper and lower jaws (dignathic trend). Despite the mesio-distal heterodonty, a substantial morphological uniformity characterizes the teeth placed along the same row. As reported for other species (e.g., *P. mammillaris*; see Hamm 2017), the most diagnostic dental elements within the *P. mediterraneus* dentition are the lower symphyseal teeth, which have a polygonal outline, with weak anterior protuberance and shallow posterior sulcus (see also the ‘Emended diagnosis’ above). Thick, transversally elongated ridges cross the occlusal surface slightly and curve at their lateral ends. The ridges on the middle of the crown are the longest with the most anterior ridges being often interrupted. The ridges do not reach the lateral tooth edges and the marginal area is covered by a coarse granulation without a distinct pattern. Wrinkles are the only exception, starting perpendicularly from the anteriormost transverse ridge. The clear transition between crested and marginal areas is characterized by enamel bumps. The thick crown overhangs the anaulacorhizous dental root on all sides. An antero-posterior sulcus crosses the rectangular root separating two lobes. MSNUP I-17373, (Fig. 6), MPPSA IGVR 91031 (Fig. 11, 12) and MCBG 4048 (Fig. 16G,H) clearly exhibit the morphological variations and the natural configuration of the teeth within both the upper and lower dental plates of *Ptychodus mediterraneus*.

Upper dentition

Based on MSNUP I-17373 (Fig. 6), the upper dental plate originally contained 19 parallel rows of teeth, arranged with nine laterals rows (L1-9) on both sides of a very narrow symphyseal row (M =

medial; see interpretative illustrations in Fig. 9). MSNUP I-17373 shows four (three shown in Fig. 8D) upper symphyseal teeth arranged in a single central row (M) below the occlusal plane, together with five other scattered on the slab. The upper symphyseals do not exhibit wear traces. The upper symphyseal teeth (e.g., Fig. 17E,F) are very small and antero-posteriorly elongated with the posterior side usually being wider than the anterior one. The dental crown is flat, thin and protruding over the thick and unilobate root. The occlusal surface is crossed by two to four short and parallel ridges, which are placed anteriorly and do not reach the lateral edges of the tooth. Generally, small granules arranged in a single line precede and follow the ridges (Fig. 17E). The marginal area is more developed posteriorly and is covered by very slight and fine granulations. The root is higher than the crown and forms a right angle with the base of the crown both anteriorly and posteriorly (Fig. 17F). Furthermore, the root slightly narrows in correspondence of the crown base.

A first pair of lateral rows (L1) runs along both the flanks of the symphyseal row. It is possible to observe these rows in their natural position only in specimen MSNUP I-17373 (Fig. 8A,B). The teeth belonging to this first pair of lateral rows exhibit a rectangular outline (Fig. 8A), which are also the largest of the upper dentition. The dental crown is thick, flat and crossed by eight to ten transversal ridges with their antero-posterior thickness often decreasing anteriorly in the series. Coarse granules usually characterize the transition between crested and marginal areas. In some cases, the ends of the ridges continue with fine and concentric granulations. The ridges almost occupy the entire occlusal surface. The mesial marginal area is slightly wider than the distal one. The posterior ridges are wavy in their mid-part, but this undulation disappears in the anterior ridges (Fig. 8A). Towards the mesial and distal sides almost all the ridges tend to converge anteriorly, but not forming 'loops'. The anterior and the posterior ridges are often incomplete and interrupted. The marginal areas are covered by granulations that become finer towards the outer dental edges. The lateral surface of the medial dental side has articular facets (*f* in Fig. 8D). The dental edges have an irregular outline due to interlocking with adjacent teeth. The bilobate root is thicker than the crown and it is anteriorly and distally inclined, while it is perpendicular to the dental crown base posteriorly and mesially. The mesial lobe is always more developed than the distal one in all lateral teeth. The antero-posterior sulcus is around 2 mm deep. The second pair of lateral dental rows (L2) consists of teeth, which are less wide than those of the first pair (L1), with an approximately squared outline. The mesial and distal margins of the crown are irregular and the crowns also have a narrow lowered mesial edge to allow the imbrication with teeth of the adjacent row (L1). The occlusal surface is characterized by seven to nine ridges, the posteriormost of which is usually very short and interrupted. The ridges exhibit the same shape and pattern of those belonging to the first pair of lateral rows (L1), ending abruptly laterally

and curving anteriorly. The marginal area is very narrow and covered with fine granulations. Some of the teeth detached from row L2 also exhibit a complete bilobate root, in which the inclined side is the distal one, thus differing from the condition observed in the teeth in row L1 (see above). The teeth of the third pair of lateral rows (L3), although smaller, are similar in shape and ornamentation (ridges and marginal granulation) to the lateral teeth described above. Generally, their distal edge is angular (or gently convex) and the mesial one is straight (or gently concave) to allow the interlocking with teeth of the adjacent series (L2 and L4). These teeth are also identical to some disarticulated ones of the specimen MPPSA IGVR 91031 (Fig. 14G). The dental crown is more massive mesially and bears seven to eight ridges. The root is identical to those of the teeth of the second lateral rows (L2). Towards the distal extremities of the jaw, the lateral rows (L4 to L9) are increasingly incomplete with elements disarticulated or partly covered by teeth of other rows. The tooth crowns decrease in size mesio-distally and progressively become more asymmetrical in outline (see MSNUP I-17373, Fig. 8A). Irregular facets for articulation with teeth of the adjacent longitudinal rows are recognizable on the lateral sides of the dental crowns. Moreover, the crested area is less expanded proportionally to the entire occlusal surface and placed more distally than those of the most central pairs of dental rows (L1 to L3). The mesial side of the root is higher than the inclined, distal one. Many of these lateral teeth are also scattered on the surface of MPPSA IGVR 91031 (Fig. 14G). The dental crowns belonging to rows L4 are very similar in shape to those within rows L3 with six to seven transverse and parallel ridges; the first ridges are thin and often interrupted. The teeth of rows L5 have a subtriangular outline. Compared to the dental elements included in the previous lateral rows these teeth are slightly more elongated transversely and with a rounded distal edge. The flat tooth crowns show five to seven ridges, with the first ones being very thin and sometimes interrupted. The teeth of rows L6-8 have a subtriangular shape but they are much more transversely elongated compared than those of the row L5. Five to seven parallel ridges cross their occlusal surface. The anterior and posterior ridges are usually shorter than the middle ones. Moreover, the number of ridges gradually decreases mesio-distally (see also Tab. A.2, Appendices). The roots are lower with a shallow antero-posterior sulcus. All teeth of row L9 are preserved disarticulated in all of the examined specimens. These teeth are smaller and lower than those of the other rows. The dental crowns are similar in shape to those belonging to L8, except for being crossed by four curved ridges.

Lower dentition

Only MSNUP I-17373 (Fig. 8C) and MPPSA IGVR 91031 (Fig. 14A) show the central portions of the lower dental plate in its natural configuration. In addition, several teeth belonging to the lower

lateral series are preserved on both slabs. Based on these specimens and on lateral articulated teeth in MCBG 4048, it is possible to reconstruct the overall structure of the lower dental plate, which consists of a massive and bulgy symphyseal row (m = medial), flanked by nine lateral parallel rows (11-9) on both sides (see interpretative illustrations in Fig. 10). The teeth of the symphyseal row (m) have a large crown with rectangular outline (Fig. 8C and 14A). These teeth have a bulgy crested area that displays slight variations of height and transversal width. Nine to ten sharp ridges cross the occlusal surface curving slightly anteriorly at their lateral ends. The anterior and posterior ridges are usually interrupted, while the middle ones are the longest (see also Fig. 8I). The symphyseal teeth show coarse granules near the crested area and thin granulation towards the dental edges. The anterior marginal area is covered with little wrinkles perpendicular to the dental ridges. The bilobate root has a shallow antero-posterior sulcus and is slightly less thick than the crown. Its anterior side is posteriorly inclined, while the lateral ones slightly converge inwards. The crested areas are placed distally in lateral rows (11-9), while the marginal ornamentations are consistent with those of lower symphyseals (m, see above). Moreover, the bilobate root has anteriorly and mesially inclined sides, while the posterior and distal ones are perpendicular to the base of the crown. The first pair of lateral rows (11) consists of squared teeth with irregular outline (Fig. 8C and 14A) and slightly convex occlusal surfaces. Moreover, their mesial edge is depressed and inclined to allow the imbrication with the symphyseal teeth (see 11 in Fig. 14A) and the crown bears seven ridges, of which the last one is very short. Most of teeth belonging to successive lateral rows (12-9) are disarticulated and scattered over the surface of the slabs in both MSNUP I-17373 and MPPSA IGVR 91031. The teeth assigned to rows 12 and 13 have general features similar to the elements of the previous rows (11), but are slightly developed antero-posteriorly and crossed by five to six sharp ridges. The distal side of the crown is antero-posteriorly narrower than the mesial one. The right distal part of the dental plate is still articulated in MSNUP I-17373 (Fig. 6-7). The specimen exhibits four parallel rows (14-7) arranged antero-posteriorly with the same orientation of the symphyseal row (m). The teeth belonging to rows 14-6 are considerably wide and have a low crown. The mesial dental edge is concave, while the distal one is convex and rounded. Six parallel ridges cross the occlusal surfaces of the teeth of row 14. The teeth of rows 15-6 have five to six ridges, which are interrupted in some cases. The roots of the distal rows are bilobate, with a shallow antero-posterior sulcus. Five articulated teeth in specimen MCBG 4048 also exemplify the characteristic dental morphologies of rows 15-6 (Fig. 16G,H). The teeth composing rows 17 have a polygonal outline with convex edges on both mesial and distal sides, and five ridges traverse the crown, sometimes added by an additional interrupted anterior ridge. MSNUP I-17373 (Fig. 6) also had originally another partial row (18) arranged on the distal side of row 17 on

the right side (see also the reconstruction in Fig. 10). The teeth belonging to rows 17 and 18 show a very similar morphological outline but those in row 18 are smaller and show only four thin curved ridges on their occlusal surface. The existence of a further pair of external rows (19, see the reconstruction in Fig. 10) is very likely because additional small disarticulated teeth are preserved on slab MSNUP I-17373 (Fig. 6), which differ in size from those described above and they are extremely narrow antero-posteriorly although notably wide transversely (see. Tab. A.2, Appendices). The teeth likely pertaining to the row 19 have an elliptical dental crown crossed by three thin and curved ridges.

Cartilages

Remains of tessellated cartilage with irregular outline and rough, striated surfaces are identifiable in specimen MSNUP I-17373. These remains are markedly distinct from the surrounding matrix. The striated texture on the surface corresponds to the underlying polygonal prisms, well recognizable in the damaged areas (Fig. 8G). The same pattern is observed in a 3-5 mm thick rock layer placed under the central dental rows of both plates. It is reasonable to hypothesize that these remains are part of the cranial or jaw cartilages, because of their association with the dental plates.

Both sides (A and B) of the specimen MPPSA IGVR 91031 exhibit several portions of tabular tessellated cartilage (e.g., Fig. 14B,D) of different size and shape, with a striated and mosaic-like pattern composed by polygonal prisms. There are two larger portions, with an approximately rectangular outline, one visible on side A (Figs. 11) and another one visible on side B (Figs.12), which possibly are portions of the jaws. The portion on side A measures ca. 258 mm in length and ca. 136 mm in width, while that on the opposite side, measures ca. 339 mm in length and ca. 127 mm in width and exhibits a slightly arched shape.

Vertebral remains

MSNUP I-17373 (Fig.6-7) also exhibits an impression of a vertebral centrum (Fig. 8E-G). The elliptical outline, with a maximum diameter of about 57 mm, is probably due to taphonomic deformation. A depth of at least 19 mm can be estimated for the concavity of the articular face of the vertebral centrum, considering the conic shape of the impression (see Fig. 8G). An impression of a calcified vertebral centrum (Fig. 14C,F) is also preserved on side A of specimen MPPSA IGVR 91031 (Fig. 11,13A). It shows a circular shape with a diameter of about 50 mm. The vertebral impression in both MSNUP I-17373 (Fig. 8E,F) and MPPSA IGVR 91031 (Fig. 14C,F) locally exhibits the traces

of a calcification pattern consisting of concentric rings interrupted by several thin lines arranged in radial direction.

Discussion

Comparative remarks

Canavari (1916) considered *Ptychodus polygyrus* Agassiz, 1835 as a very heterogeneous ‘group’, which included the four varieties - *P. concentricus*, *P. sulcatus*, *P. polygyrus* ‘sensu stricto’ and *P. marginalis* - proposed by Agassiz (1839, 1843) in his original description of the species (see ‘Nomenclatural remarks’ of *P. polygyrus*). Based on his study of MSNUP I-17373, Canavari (1916) concluded that *Ptychodus mediterraneus* shares more morphological similarities with the *P. polygyrus* ‘group’ than with all the other known species. In addition, Canavari (1916: p. 101) pointed out the morphological affinity between the holotype of *Ptychodus mediterraneus* and some specimens previously examined, such as the teeth referred to *P. latissimus* described by Priem (1896) and the type material of *P. belluccii* (see Bonarelli 1899) and *P. martini* (see Williston 1900a,b). *Ptychodus latissimus*, *P. marginalis*, *P. martini* and *P. polygyrus* ‘sensu stricto’, are currently regarded as closely related to each other (see Hamm 2010a; Hamm and Harrell 2013).

NHMUK PV P4408 (Fig. 4A-D) and NHMUK PV P4410 (Fig. 4E-H), which are included in the type material of *Ptychodus polygyrus* ‘sensu stricto’ (see ‘Nomenclatural remarks’ above), show dental occlusal ornamentations that are different from that of *P. mediterraneus*, especially when compared to the first pair of upper lateral teeth (L1 in Fig. 9) of MSNUP I-17373 (see Fig. 8A). The dental ridges in MSNUP I-17373 do not taper and do not reach the lateral tooth margins, never forming lateral anastomoses, thus differing from those of the type material of *P. polygyrus*. The same differences are also clearly recognizable when comparing the lower symphyseals of *P. mediterraneus* (see MSNUP I-17373, Fig. 8C and MPPSA IGVR 91031, Fig. 14A) and *P. polygyrus* (see NHMUK PV P10771 α , Fig. 4I). In addition, in *P. polygyrus* the anterior ridges are usually the transversely longest in each tooth, whereas these ornamentations usually reduce their transverse extension anteriorly on the tooth crowns of *P. mediterraneus*.

Ptychodus polygyrus var. *marginalis* is the only variety proposed by Agassiz (1839, 1843; see above), which has been later considered as a separate species (e.g., Herman 1977; Hamm 2010a; Hamm and Harrell 2013). The ridges on the occlusal surface of the teeth of *P. marginalis* always form concentric loops in both the upper and lower dentitions (see Hamm 2010a; Hamm and Harrell 2013). Moreover, the marginal ornamentation is also concentric in the crested areas, with an

undefined transition between ridges and lateral granulations. These features are clearly distinguishable from the occlusal ridges pattern observed in *P. mediterraneus*, as well as in *P. polygyrus*, which also exhibit marginal granulation but not arranged with a recognizable pattern.

Bonarelli (1899) erected *Ptychodus belluccii* based on a single isolated tooth (Catalog number: N. 4257) from Umbria region, central Italy. Hermann (1977) considered *P. belluccii* as separate taxon, whereas Leriche (1902) suggested synonymizing it with *P. latissimus* Agassiz, 1835. Although Bonarelli (1899) solely figured a damaged tooth with rectangular outline, he provided a detailed description of dental features of the new species. The diagnostic characters of *P. belluccii* seem to be consistent with those of *P. polygyrus*. In particular, the specimen figured by Bonarelli (1899) is very similar to lower symphyseal teeth of *P. polygyrus* (see NHMUK PV P10771a, Fig. 4I). Therefore, *P. belluccii* Bonarelli, 1899 is interpreted herein as a junior synonym of *P. polygyrus* Agassiz 1835.

An associated tooth set from the Smoky Hill River, Kansas represents the type material of *Ptychodus martini* Williston, 1900a. Williston (1900a) arranged the teeth of the type specimen in order to restore a unique dental plate. Nevertheless, this interpretation may be incorrect, because the tooth set most probably includes both upper and lower jaw teeth (see Williston 1900a: p. 32). The putative lower symphyseal teeth of *P. martini* have very flat crowns that are transversely elongated, clearly different from the bulged lower symphyseals of *P. mediterraneus* (Fig. 8C). Moreover, the occlusal ridges are thin and often reach the lateral tooth edges (see also Hamm and Shimada 2004; Hamm and Harrell 2013). *P. martini* exhibits some general dental features similar to those described herein for *P. mediterraneus*. The comparison between the lower symphyseals, however, indicates that they are separate taxa. Nevertheless, a careful revision of *P. martini*, including a reevaluation of the interpretation of the original position of the teeth of the type material (see above), is desirable in order to clarify its limits and relationships with other species of the genus *Ptychodus*.

In a recent paper, Diedrich (2013) proposed to synonymize *Ptychodus mediterraneus* and *P. latissimus*, based on a comparison of the specimen MSNUP I-17373 originally described by Canavari (1916) with the teeth figured by Agassiz (1833-43) and Woodward (1912). In *P. latissimus* the transverse dental ridges of the lower symphyseal teeth (e.g., Fig. 3E-L) are thicker, higher and sharper than in all the other species and completely lack the loops at the ends of occlusal ridges. The crested area in the symphyseal teeth of *P. latissimus* is also transversally shorter than in teeth of *P. mediterraneus* (e.g., Fig. 17I,J) and *P. polygyrus* (Fig. 4I). The upper symphyseal teeth of *P. mediterraneus* (Fig. 17E,F) and *P. latissimus* (see Woodward 1887: pl.10, fig. 12; Woodward 1912: pl. 50, fig. 9) exhibit a similar general dental shape, but have different occlusal ornamentations. In *P. mediterraneus* these small teeth have thin, straight ridges and slight marginal granulations.

Conversely, the upper symphyseal teeth of *P. latissimus* have transverse ridges curved posteriorly and marked wrinkles on the marginal area, which radiate anteriorly from the crested area.

Isolated teeth of *Ptychodus latissimus* were commonly misinterpreted in the literature as *P. polygyrus* (Woodward, 1912). According to Agassiz (1843), these two taxa are morphologically related, but clearly differ from each other, based on features related to the tooth shape and the ridge patterns. In general, *P. polygyrus* has dental crowns that are more transversally elongated than those of *P. latissimus*, which has almost squared teeth. The occlusal ridges are longer and thinner in *P. polygyrus* and usually form loops, which completely are absent in *P. latissimus*. Moreover, differing from *P. latissimus* (see above), the upper symphyseal teeth of *P. polygyrus* have thin ridges placed centrally and additional fine granulation on the occlusal surface (see Woodward 1912: pl. 49, fig. 1o’).

Despite the thick and slightly bulging lower symphyseal teeth that characterize *Ptychodus latissimus* and *P. polygyrus*, both these taxa can be regarded as low-crowned, especially if compared with very high-cusped species, such as *P. altior*, *P. rugosus* and *P. mortoni* (see Hamm 2010b; Cappetta 2012; Shimada 2012; Amadori et al., 2019b). Summarizing this comparative discussion, *Ptychodus mediterraneus* Canavari, 1916 is reinterpreted herein as a valid, separate species that is morphologically close to (but still distinguishable from) other low-crowned taxa, such as *P. latissimus* Agassiz, 1835, *P. martini* Williston, 1900a and *P. polygyrus* Agassiz, 1835 (see also Tab. 3).

Tab. 3. Summary of main dental features of low-crowned species of *Ptychodus*.

Species	Dental ridges patterns	Transition between crested/marginal area	Marginal ornamentations
<i>Ptychodus latissimus</i> Agassiz, 1835	Very thick, short and sharp ridges not reach the tooth edges. No lateral anastomosis or loops.	Clear separation; very large granular bumps around ridges, which terminate abruptly.	Coarse granulations sometimes continuing anteriorly from ridges. No diagnostic patterns.
<i>Ptychodus polygyrus</i> Agassiz, 1835	Thick, transversally elongated ridges curved anteriorly until the lateral crown edges with several anastomoses and loops.	The ridges taper off at the ends sometimes merged with each other.	Coarse and fine granulations. No diagnostic patterns.
<i>Ptychodus marginalis</i> Agassiz, 1843	Thin ridges form concentric loops also reaching lateral crown edges.	Gradual transition between the concentric ornamentations.	Concentric, fine granulations arranged around the ridges.
<i>Ptychodus martini</i> Williston, 1900	Thick, transversally elongated ridges slightly curved anteriorly also extend to the tooth lateral margins.	Clear separation; the ridges terminate abruptly.	Coarse granulation. No diagnostic patterns.
<i>Ptychodus mediterraneus</i> Canavari, 1916	Thick, transversally elongated ridges without reach the tooth edges. No loops or lateral anastomosis.	Clear separation; the ridges curved anteriorly and terminate abruptly.	Coarse granules and anterior wrinkles. No diagnostic patterns.

Palaeobiology of *Ptychodus mediterraneus*

Reconstruction of dental plates

Woodward (1885: text fig. 83, p. 109) provided the first interpretative reconstruction of a *Ptychodus* dentition and subsequently defined the structures of both the upper and lower dental plates, primarily based on a single articulated specimen of *P. decurrens* (Woodward 1887, 1904). Woodward (1887, 1904) suggested that the upper symphyseal teeth of *Ptychodus* are small in size, while the lower symphyseal ones are large (see also Shimada et al. 2009). Later, several authors followed this interpretation (e.g., Williston 1900a,b; Dibley 1911; Malecki 1980; Everhart and Caggiano 2004; Shimada 2012; Hamm 2017), while others (e.g., Canavari 1916; Fossa-Mancini 1921; MacLeod 1982; Welton and Farish 1993) erroneously interpreted this reconstruction by inverting the position of the dental plates.

Although the articulated specimens of *Ptychodus mediterraneus* (MCBG 4048, MPPSA IGVR 91031 and MSNUP I-17373) exhibit evidences of post-mortem disturbance (biotic and abiotic; e.g., Fig. 18A), they can be used to obtain a reliable reconstruction of both dental plates almost in their original configuration ('composite dentition', see Shimada 2005). In this context, the original positions of teeth scattered on the slab of MSNUP I-17373 (see Fig. 6,7) have been established comparing their size, crown shape and number of ridges with those of still articulated dental elements. In occlusal view, both the dental plates are semi-elliptic in shape and longer than wide (Fig. 19A,B). Considering sizes and arrangement of articulated and associated teeth preserved in MSNUP I-17373, it is possible to estimate a length of about 55 cm for both plates, and a width of about 37 cm. However, a correct interpretation of the original size of the dental plates can be actually problematic, mostly because of the commonly insufficient preservation of their outer margins (see Fig. 9,10), but also because it is not possible to exclude that upper and lower plates may differ in size from each other, like in certain batoids (e.g., *Myliobatis*, *Aetobatus*; Canavari 1916; Kolmann et al. 2015). The anterior margins of the tooth plates of *Ptychodus mediterraneus* seem to be convex, while the posterior margins are concave exhibiting a pattern similar to that of other congeners (e.g., *P. decurrens*, *P. mortoni*; see Woodward 1904, 1912; Shimada 2012).

Canavari (1916) estimated that the specimen from Gallio could have had more than 520 teeth in the upper dental plate and about 570 in the lower one, resulting in about 1090 teeth, not considering the 'replacement teeth' (*sensu* Shimada 2012) that are not preserved in MSNUP I-17373. The reconstruction of the dental plates of *Ptychodus mediterraneus* proposed herein (Fig. 19A,B) hypothesizes the presence of about 490 'functional teeth' (*sensu* Shimada 2012) for the lower

dentition and about 450 for the upper one. In both the jaws the teeth were probably arranged in nine lateral rows on each side of a central symphyseal row. Therefore, each grinding plate had 19 antero-posterior rows. Shimada (2012) suggested that the ‘replacement teeth’ represent at least 12% of the entire lower dentition and 15% of the upper one in *Ptychodus mortoni*. If a similar proportion is applied to *P. mediterraneus*, the complete mandibular plate would consist of about 556 teeth, while the upper should include about 529 teeth. Therefore, the entire dentition of *P. mediterraneus* could include at least 1085 teeth.

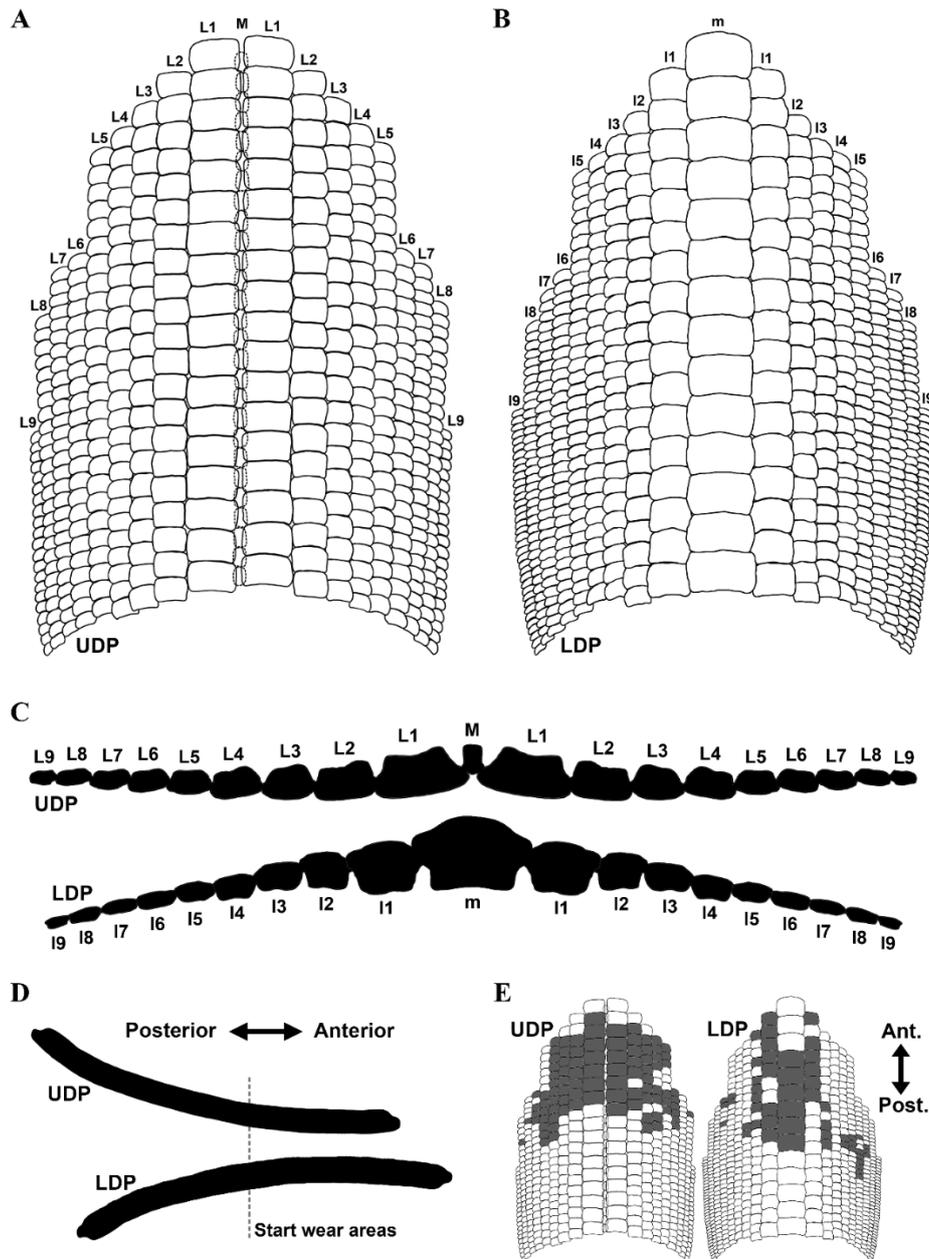


Fig. 19. Interpretative reconstruction of tooth plates of *Ptychodus mediterraneus* Canavari, 1916 in occlusal (A-B), anterior (C) and lateral (D) views. E. worn teeth on both reconstructed dentitions based on wear traces in articulated specimen MSNUP I-17373 (see also Supp. Fig. 1, 2). **UDP**, upper dental plate; **LDP**, lower dental plate; **M**, **m**, upper and lower symphyseal rows; **L1-9**, **I1-9**, upper and lower lateral rows.

Williston (1900a,b) suggested that the complete dental plates of *Ptychodus mortoni* were originally composed of 17 rows, based on a reassembled specimen. More recently, Shimada (2012) examined several articulated findings of *P. mortoni* and established that this cusped species had 19 rows in both the upper and lower dental plates. *P. decurrens* would be characterized by 13-15 antero-posterior rows, as reported by Woodward (1887, 1904, 1912). The associated tooth set rearranged by Hamm (2017) indicates that the *P. mammillaris* lower plate could have at least eight dental rows on each side of the symphyseal row. Hamm (2010a) described an associated specimen of *P. marginalis* with an artificially restored lower dentition containing 15 rows and the upper dentition represented by eight rows of the right side. Several partially articulated and associated dental remains of *P. rugosus* described by Hamm (2010b) clearly show eight to ten lateral rows. Therefore, both known dental plates of *P. rugosus* could be characterized by 17 to 21 antero-posterior rows. This variation of row numbers could be ontogenetically related (see Hamm 2010b). Shimada et al. (2009) suggested that *P. occidentalis* could have 13-15 dental rows, based on small, articulated specimens. In summary, the number of dental rows is variable among the species of *Ptychodus*, with the number of antero-posterior tooth rows probably depending on the ontogenetic stage or sexual dimorphism as verified in some extant elasmobranch (e.g., *Heterodontus*; Reif 1976; Powter et al. 2010).

The teeth of *Ptychodus mediterraneus* are characterized by morphological variations according to their position within dentitions (heterodonty; *sensu* Cappetta 2012). Indeed, mesio-distally along the same plate, the teeth differ in crown shape, number of ridges, root features, morphometric proportions and overall thickness (see also Tab. 2). The *P. mediterraneus* heterodonty is clearly exemplified by the considerable morphological diversity between the symphyseal and lateral teeth. The various degree of distal shift of occlusal ridges in lateral teeth provides another compelling evidence of morphological variations within a dental plate. A gradual mesio-distal variation is also observed in other species, such as *P. decurrens*, *P. mortoni*, *P. occidentalis* (Woodward 1887, 1904; Shimada et al. 2009; Shimada 2012). Moreover, Welton and Farish (1993: p. 56) suggested that *Ptychodus* dentitions could also have a slight dignathic heterodonty excluding the upper and lower symphyseal row teeth. The articulated specimens of *P. mediterraneus* described herein also exhibit a certain degree of dignathic heterodonty (see description above). In general, lower dental crowns have a bulgier occlusal surface than upper ones. Marked differences in shape and ridge patterns also are observable between the upper and lower symphyseal teeth. Specimen MSNUP I-17373 has nine upper symphyseal teeth, some of them are still articulated or just slightly displaced (Fig. 8D). Only one of these was initially exhibited (see Fig. 8B) and Canavari (1916) removed several teeth of the adjacent rows to expose the others. In addition, Canavari (1916) detached some upper symphyseals for

pursuing more detailed observations (for example see Fig. 17E,F). Differing from all the other teeth, the upper symphyseal teeth (see Fig. 17E) are more developed in their antero-posterior length (Canavari, 1916). To date, upper symphyseals of *Ptychodus* were reported from associated and articulated specimens of *P. mortoni*, *P. rugosus*, *P. latissimus*, *P. polygyrus*, *P. mammillaris* and *P. marginalis* (Woodward 1887, 1912; Canavari 1916; Hamm 2010a, b; Shimada 2012; Amadori et al. 2019a,b). In *P. mediterraneus* (e.g., MSNUP I-17373; see Fig. 8D) the upper symphyseal row (M in Fig. 19A) is placed below the plane of the first pair of lateral teeth (L1, see Fig. 19A) resulting in an antero-posterior groove along the upper dentition (see also Fig. 19C). This condition is also present in other taxa, such as *P. decurrens* (Woodward 1904), *P. mortoni* (Shimada 2012) and *P. occidentalis* (Shimada et al. 2009). Moreover, according to Woodward (1912) the morphology of the upper symphyseal teeth is subject to intraspecific and ontogenic variability (see also Dibley 1911). The lower symphyseal teeth of *P. mediterraneus* preserved in MPPSA IGVR 91031 (Fig. 14A) and MSNUP I-17373 (Fig. 8C) are the largest teeth of the dentition (see Tab. A.2-3, Appendices). Such teeth gradually increase in transversal width antero-posteriorly, while the anterior-posterior length is almost unaltered. The bulgy crested area also can vary in extension. In all the articulated *Ptychodus* specimens so far known, the lower symphyseals are the largest teeth of the dentition (Williston 1900a,b; Woodward 1904, 1912; Shimada 2012), which is also observable in some reconstructed dentitions based on associated teeth (e.g., Hamm 2010a, b).

The lateral teeth (rows L1), as well as the lower symphyseal teeth (row m), have both lateral root surfaces tilted and converging inwards, while all the other lateral teeth (rows L2-9 and rows I1-9) have the mesial root side perpendicular to the dental crown and the distal one inclined mesially. This inclination of lateral surfaces of the roots suggests a convex shape of both the plates in anterior view (Fig. 19C; see also Canavari 1916). Moving mesio-distally, the distal edge of each tooth of *P. mediterraneus* overlaps the mesial marginal area of the adjacent one (e.g., Fig. 8A). Additionally, the lateral teeth (articulated and isolated) often exhibit lowered the mesial edges forming a sort of groove or imprint (see Fig. 17G,H) that allows the imbrication with their adjacent teeth. This feature is not marked in the most upper central rows (e.g., Fig. 8A). This imbrication probably accentuated the mesio-distal convexity in the lateral portion in both the dental plates (see Fig. 19C).

All the tooth roots of *Ptychodus mediterraneus* have the anterior side inclined posteriorly, while the posterior one is usually almost perpendicular to the dental crown (e.g., Fig. 16D). Considering the antero-posterior tooth interlocking together with the inclination of the root sides (see above), both plates were probably also longitudinally convex (Fig. 19D; see also Canavari 1916). Moreover, this rostro-caudal curvature could be greater in the posteriormost part of the *P. mediterraneus* plates, as

already proposed for other *Ptychodus* taxa. Indeed, in the articulated specimens of *P. occidentalis* and *P. mortoni* the posterior ends of the upper plate curves dorsally, while that of the lower one is folded ventrally (Shimada et al. 2009; Shimada 2012). This folding is, at least, partly due to the inclination of the ‘replacement teeth’ (see Shimada 2012: fig. 1E). Nevertheless, the interpretation of rostro-caudal convexity proposed herein (Fig. 19D) does not consider the upper and lower ‘replacement teeth’, because they are not preserved in the examined specimens of *P. mediterraneus*.

Although some batoids exhibit upper and lower dental plates of different size (see above), the upper and lower ‘start wear areas’ (posteriormost ones) are always antero-posteriorly overlapped (Kolmann et al. 2015: fig. 1). The anterior-posterior alignment of the major abraded areas of both MSNUP I-17373 dentitions may suggest their incomplete overlap during occlusion, with the lower plate protruding anteriorly (Fig. 19D, E). Such mandibular prognathism is also observed in some extant neoselachians, such as *Aetobatus* (Kolmann et al. 2015). However, the lower dental plate of *Ptychodus mediterraneus* probably occupied the anterior part of the Meckel’s cartilage, as shown by other species of *Ptychodus* described by Woodward (1904) and Shimada et al. (2009).

Functional dental specialization

Although recent studies questioned the existence of a close relation between dental features and ecological role in sharks (e.g., Whitenack and Motta 2010) certain their morphological features can be easily associated with durophagy, including molariform teeth forming a ‘pavement-like’ dentition and rigid, robust jaws with large adductor muscles, which generate bite forces necessary to fracture hard shells (Moss 1977; Summers 2000; Compagno 2002; Dean et al. 2007; Cappetta 2012; Motta and Huber 2012; Kolmann et al. 2014, 2015). Tooth wear can be also an important indicator of diet preferences in Mesozoic cartilaginous fishes (e.g., durophagous stingrays; Claeson et al. 2010). In their complex evolutionary history, cartilaginous fishes have adapted to durophagy multiple times adopting several solutions to the ‘cracking hard prey problem’ (see Summers et al. 2004). Different durophagous specializations are indeed largely known among chondrichthyans, both in batoids and, more rarely, in selachians (Wilga and Motta 2000; Summers et al. 2004; Cappetta 2012; Kolmann et al. 2015). Their feeding habit can be revealed by worn teeth commonly observed in durophagous dentitions of extinct and extant chondrichthyans (e.g., Woodward 1912; Summers 2000; Claeson et al. 2010; Cappetta 1987; Kolmann et al. 2015). The occlusal abrasion on dental crowns is usually considered as the result of processing shell-covered prey (see Canavari 1916; Summers et al. 2004; Cappetta 2012; Underwood et al. 2015; Adnet et al. 2018). *Ptychodus* is commonly regarded as a

durophagous shark, because of its molariform teeth arranged to form dental plates suited for crushing hard prey (MacLoed 1982; Everhart and Darnell 2004; Everhart and Caggiano 2004; Shimada et al. 2009, 2010; Cappetta 2012; Shimada 2012; Diedrich 2013; Amadori et al. 2019b). Moreover, worn teeth are quite common in different species of *Ptychodus* (e.g., Agassiz 1837, 1839; Dixon 1850; Woodward 1887, 1912; Williston 1900a,b; Shimada 2012; Amadori et al. 2019a,b), thereby suggesting that a durophagous diet was widespread within this genus.

Among the anatomical features associated to durophagy, a stiff jaw contributes to increase the bite-force during the food processing (Summers 2000; Motta and Huber 2012). For example, durophagous stingrays (e.g., *Rhinoptera bonasus*, *Myliobatis californicus*, *Aetobatus narinari*) have far more robust jaws than the other batoids, because of their fused symphysis and calcified struts concentrated under the central area of dental plates where prey is crushed (Summers 2000). The stiffest jaw regions in the hard-prey specialist *Aetobatus narinari* (spotted eagle ray) correspond to the dentition areas affected by the major bite-induced load (Summers et al. 2004). Probably, these are also the only dental regions engaged in prey grinding, as suggested by worn tooth positions within the upper dental plate (Summers et al. 2004: fig. 7A). The stiffest and thickest region is located in the center of the jaw also in other stingrays, such as *Rhinoptera bonasus* and *Myliobatis californicus*, and it corresponds to the most markedly abraded portion of the dental plates (see Summers 2000: fig. 4,5). Contrarily, *Heterodontus* (horn shark) lacks a fused symphysis and uses its lateral molariform teeth to process hard prey items (see Summers et al. 2004). Shimada et al. (2009) described both jaws of *Ptychodus occidentalis* that clearly show the fused symphyses. The occlusal abrasions in partially articulated upper dentition of *P. mortoni* are concentrated on the medial region of the upper plate (see Shimada 2012: fig. 3B). Moreover, Summers (2000) suggested that the multiple layers of tesserae represent a plesiomorphic condition in cartilaginous fishes. Ptychodontid sharks probably also had massive jaws formed by multi-layered cartilage. For this reason, detailed histological analyses on cartilaginous remains of *Ptychodus* are desirable to evaluate the presence of calcified struts and their concentration under the dental plates.

Durophagous chondrichthyans are usually characterized by having molariform teeth arranged labio-lingually over the jaws (e.g., horn sharks and hybodonts; Reif 1976, Summers et al. 2004; Shimada et al. 2009) or upper and lower pavement-like dentitions arranged in antero-posterior rows (e.g., stingrays and ptychodontids; Woodward 1912; Cappetta 2012; Kolmann et al. 2015). In both conditions the teeth are often closely interlocked to each other. Among durophagous chondrichthyans, several taxa (e.g., *Rhinoptera*, *Myliobatis* and *Heterodontus*) solely show juxtaposed dental crowns, while some others (e.g., *Chiloscyllium plagiosum*, *Pastinachus* sp.) are instead characterized by

slightly imbricated dentitions (see Ramsay and Wilga 2007; Cappetta 2012; Kolmann et al. 2015). The interlocked condition (juxtaposition or imbrication) in *Ptychodus* can vary according to the different species. For examples, both low-crowned *P. decurrens* and high-crowned *P. occidentalis* seem to have had juxtaposed dentition (see Woodward 1887; Shimada et al. 2009). Conversely, Shimada (2012) described the imbricated dentition of the sharp-tipped *P. mortoni* and also hypothesized that the tooth imbrication improved the distribution of bite-induced load on dental plates, allowing this species to apply heavy biomechanical strength during the food processing (Shimada 2012).

Based on the morphological features of the teeth and the position of the dental morphotype within the jaws, Cappetta (2012) distinguished different ‘adaptive dental types’. For examples, he associated the ‘grinding type’ to the dentition of *Ptychodus*, considering the latter as a hybodont shark. The same dental type is also widespread in batoids, such as *Myliobatis* (eagle rays) and *Rhinoptera* (cownose rays), because of their flat and transversally elongated teeth arranged in several antero-posterior rows to form consolidated dental plates. Cappetta (2012) also described the intermediate ‘crushing-grinding type’ as a combination of flat and bulgy teeth narrowly imbricated with the contact between the two dentitions occurring only in the symphyseal region, characterized by an upper labio-lingual groove. This ‘adaptive type’ had been previously reported only for batoids (e.g., *Pastinachus*; Cappetta 2012; Adnet et al. 2018).

In *Ptychodus mediterraneus*, closely imbricated teeth form upper and lower pavement-like dentitions. The flat upper dental plate is opposed to the embossed surfaces of the lower ones (Fig. 19C). In particular, the antero-posterior groove along the upper symphyseal row (M in Fig. 19C) provides the space for the occlusion with the large opposite lower symphyseal row (m, Fig. 19C). Consequently, the occlusion in *P. mediterraneus* was not ‘cusp-to-cusp’, but rather each crested area (cusp in other species) occluded the lateral marginal area of two adjacent teeth within the opposite dentition (see Fig. 19C). Moreover, the upper symphyseal teeth of *P. mediterraneus* (Fig. 17E,F), as those of other *Ptychodus* species (e.g., *P. rugosus*, see Amadori et al. 2019b), strongly differ from the other functional teeth (see ‘Anatomical description’ above). This morphological variation is due to a loss of the primary function (crushing hard preys) of the upper symphyseals, because of their position under the occlusion plane (Fig. 19C). However, the features of occlusion and imbrication in the dentition of *P. mediterraneus* (see Fig. 19A-C) seem to be consistent with the ‘crushing-grinding type’ dental characters illustrated by Cappetta (2012). In particular, the contact between the upper, flat teeth and the lower, embossed ones could occur only in small areas of the dental crowns during food processing. Therefore, considerable voids remained between the dental plates. Considering that

fine grinding requires an extensive contact between quite large surfaces (Fossa-Mancini 1921), as it occurs in very flat ‘grinding type’ dentition of *Myliobatis* and *Rhinoptera* (see Cappetta 2012), the ‘uncompleted occlusion’ of *P. mediterraneus* probably allowed just a coarse crushing of shell-covered prey.

Based on all the considerations above, *Ptychodus mediterraneus* was probably highly specialized for durophagy, because it has low-crowned and crested teeth imbricated to each other. Assuming that both the fused symphyses and calcified struts are plesiomorphic conditions in *Ptychodus*, *P. mediterraneus* might have had very rigid jaws, especially in their medial regions. This central area is interpreted herein as the portion of the jaws mainly engaged in hard prey processing, also considering the mesial concentration of the most markedly abraded teeth in *P. mediterraneus* (Fig. 19E). Although performance tests on complete dentitions are necessary to corroborate any interpretation on bite-induced load and force (e.g., Whitenack and Motta 2010), the centremost rows of the dental plates of *P. mediterraneus* seemingly were able to impress enough strength to break even the thickest and most resistant shells.

Tooth replacement

Sharks and batoids are polyphyodonts, which means that their teeth are continuously replaced through lifetime (see Cappetta 2012; Kolmann et al. 2015; Underwood et al. 2015; Smith et al. 2018). Teeth in each lingual-to-labial series pass through several stages (Underwood et al. 2015): tooth germ (development stage); tooth with not fully formed roots (pre-functional stage); completely formed tooth, but not taking part in food processing (non-functional stage); tooth positioned in the jaw portion where food processing takes place (functional stage); tooth no longer involved in food processing but to be lost yet (post-functional stage). The replacement rate is species-specific, also depending on the age of the animal, diet, seasonal changes and water temperature (Moss 1967; Cappetta 2012; Belleggia et al. 2014; Underwood et al. 2015). In particular, younger teeth of durophagous rays are mineralized and are conveyed to the anterior edge of the dental plates to replace the older, worn teeth (Kolmann et al. 2015). For examples, in *Myliobatis* and *Aetobatus*, the flat teeth move anteriorly to the ‘grinding zone’ becoming mature (functional stage). *Aetobatus narinari* (spotted eagle ray) has an unusual condition compared to other myliobatids, because after reaching the edge of the plate the lower functional teeth stay attached, forming an anterior appendage used to dig up prey items (Summers, 2000; Motta and Huber 2012). However, the exact replacement process is still poorly

known in batoids and sharks with closely interlocked dentition, including the extinct *Ptychodus* (see Cappetta 2012; Belleggia et al. 2014; Underwood et al. 2015).

Nowadays, the genus *Ptychodus* is generally included within the elasmobranchs (= neoselachians), because of the enameloid structure, tooth morphology, tessellate texture of cartilages, and presence of calcified vertebral centra (Shimada et al. 2009; Cappetta 2012, Shimada 2012, Hoffman et al. 2016). Considering the widespread dental replacement in neoselachians, it is most likely that *Ptychodus* also continuously renewed its teeth during its life-cycle. This hypothesis is supported by the presence of ‘replacement teeth’ (pre-functional stage) observed in the articulated dentitions of *P. mortoni* and *P. occidentalis* (Shimada et al. 2009; Shimada 2012). Like in other chondrichthyans, pre-functional teeth of *Ptychodus* have cancellous and incompletely mineralized roots (see Reif 1976; Schwimmer et al. 1997; Cappetta 2012; Shimada 2012; Underwood et al. 2015). These incompletely formed teeth are placed at the back of the jaws, forming the tilted basal side of the dental plates of *Ptychodus* (see Shimada et al. 2009; Shimada 2012). The rare ‘replacement teeth’ placed anteriorly in dentition of *P. mortoni* and *P. occidentalis* therefore could represent taphonomic artifacts. Supporting our interpretation, a similar posterior position has also been described in some stingray taxa (e.g., *Rhinoptera*, *Pastinachus*; Summers 2000; Adnet et al. 2018). In addition, the detailed examination of dental wear traces can also provide new insights about the modalities or rates of tooth renewal in extinct chondrichthyans (see Botella et al. 2009; Cicimurri 2010; Belleggia et al. 2014). For example, marked differences between the extent of tooth wear in functional and newly formed teeth can indicate slow rate of tooth replacement (Botella et al. 2009). Shimada (2012) reports slight abrasions present on a partially articulated upper dentition of *P. mortoni*. The specimen described by Shimada (2012) shows anterior occlusal abrasions on the mesial dental rows, while no traces of wear are indicated on the posterior teeth and in the entire lower dentition (see Shimada 2012: fig. 3A,B). Unexpectedly, in the semi-articulated cusped dentition of *P. rugosus* described by Macleod (1982), which is clearly suitable for crushing shell-covered prey, worn teeth are completely absent. In some neoselachian genera (e.g., *Heterodontus*, *Myliobatis*), juveniles might prefer to feed on relatively soft prey (e.g., small clams and decapods) compared to adults (e.g., Gray et al., 1997; Powter et al. 2010). Nevertheless, artificially assembled dental plates representing different ontogenetic stage have been examined by Hamm (2010b) without any occurrence of tooth wear.

The worn tooth position was mapped on the articulated dental plates of *Ptychodus mediterraneus* preserved in MSNUP I-17373 (see Fig. 19E). In addition, four different degrees of tooth wear are present along the crushing dental plates (see Fig. A-D,H), which form a posterior-to-anterior (lingual-to-labial in other selachians; see Underwood et al. 2015) pattern in both dentitions with the anterior

teeth being much worn. Starting from the posteriormost portion, the tooth plates exhibit occlusal abrasions (1) limited to the ends of the ridges, (2) focused in the central part of the crown, (3) marked on all the crested area or (4) extended over almost the entire occlusal surface. Similar occlusal tooth wear patterns are also observed in associated and isolated teeth (e.g., Fig. 18I). No replacement teeth were observed, but their original position at the back edge of the plates is hypothesized herein (see above). The posteriormost teeth preserved in MSNUP I-17373 (Fig. 8A) are interpreted as non-functional teeth, because they are completely formed and do not have wear traces. In posterior-to-anterior direction along the dentitions, the first degree of wear (abrasions limited at the ends of the ridges) characterizes the functional teeth placed in the central portion of the dental plates (Fig. 8A). The teeth displaying abrasions on the complete crested area, as well as the completely worn crowns, represent the anteriormost teeth of the dentition (Fig. 8H). This anterior portion was probably engaged in processing hard prey items. As documented above, the anterior margins of the dental plates are not preserved in MSNUP I-17373 (see also Fig. 9, 10). The teeth belonging to this portion of the dental plates probably illustrate the post-functional stage. The comparison between upper and lower dentition of MSNUP I-17373 highlights that the lower dental plate is relatively less abraded than the upper one (19E). Indeed, the most worn lower teeth preserved in MSNUP I-17373, placed anteriorly within the lower dental plate, display marked abrasions only on the centre of the crested areas; none of them exhibits traces of occlusal wear on the entire crown (Fig. 8C). Moreover, a further wear degree has been observed in the articulated portion of lower dental plate of MPPSA IGVR 91031. In this specimen, the lower symphyseal teeth actually have completely worn crested areas (see Fig. 14A). A similar marked abrasion degree was likely present also in the lower teeth of MSNUP I-17373; unfortunately, the anterior portion in this specimen is poorly preserved (see Fig. 10).

Generally speaking, *Ptychodus* probably had a tooth renewal pattern characterized by posterior-to-anterior direction (lingual-to-labial in other neoselachians), as suggested by wear patterns described herein for *P. mediterraneus* and the posterior position of the ‘replacement teeth’ in other species (Shimada et al. 2009; Shimada 2012). Therefore, the non-fully formed teeth were probably conveyed from the basal side to the anterior dental region becoming functional teeth in *Ptychodus* dentitions. Whitenack et al. (2011) speculated that tooth renewal may depend on tooth wear rather than on tooth failure. Considering the close interlocking between the polygonal *Ptychodus* teeth, the independent advancement of the sole antero-posterior rows in which worn teeth occur is highly unlikely. Rather, the teeth arranged mesio-distally would be forced to move forward in posterior-to-anterior direction as a single element. The widespread presence of both worn and complete teeth among isolated findings of *Ptychodus* seems to further support this hypothesis.

The marked differences between wear degrees in functional and non-functional teeth in the upper dentition of *Ptychodus mediterraneus* indicate a slow tooth replacement rate. In addition, the slight extent of abrasion in the lower dentition may suggest a faster replacement rate than in the opposite dental plate, similarly to the hypothesized elasmobranch condition (see also Moss 1967; Belleggia et al. 2014). However, the poor preservation of the anterior part of the lower dentition in MSNUP I-17373 makes it difficult to correctly evaluate the dental renewal in the lower dental plate. In a different way from the condition observed in *P. mediterraneus*, the lack of tooth wear in the *P. rugosus* semi-articulated specimen (see MacLeod 1982), together with several isolated worn teeth of *P. rugosus* housed in Natural History Museum, London, suggest a faster tooth renewal rate for this cusped species.

Here, we only presented a preliminary evaluation of dental abrasion pattern, as further careful analyses on the wear traces in well-preserved *Ptychodus* specimens is mandatory to clarify the patterns and rates of dental renewal in the genus *Ptychodus* and, more particularly in the species *P. mediterraneus*.

Skeletal remains and body morphology

The anatomy and morphology of the jaws can vary considerably among durophagous chondrichthyans (e.g., Dean et al. 2007; Underwood et al. 2015). For example, several myliobatids (e.g., *Myliobatis*, *Rhinoptera*) have a rectangular mouth formed by rigid ‘bar-like’ jaws, very different from the ‘V-shaped’ jaws of heterodontid sharks (e.g., *Heterodontus francisci*; see Reif 1976; Summers 2000; Motta and Huber 2012). Woodward (1904) described and figured an interpretative reconstruction of the lower jaw of the low-crowned *Ptychodus decurrens*, which was characterized by an acute symphyseal angle (‘V-shaped’) (see also Woodward 1912). Later, Shimada et al. (2009) described both jaws of the high-crowned *P. occidentalis* showing a general shape that is very similar to that of the specimen figured by Woodward (1904, 1912). Among stingrays, *Aetobatus narinari* has an antero-posteriorly elongated and anteriorly narrowed lower jaw (see Summers 2000: fig. 3), which recalls the ‘V-shaped’ morphology of *Ptychodus* and *Heterodontus*.

The preserved portion of the jaw on side A of MPPSA IGVR 91031 (Fig. 11) is wider than that of the opposite side, suggesting that the portion on side A could be interpreted as the Meckel’s cartilage, whereas the other could be interpreted as the palatoquadrate. In the only known specimen with preserved jaws, BMB 008524 (*Ptychodus decurrens*; see also Woodward 1904), the Meckel’s cartilage is 117% wider than the palatoquadrate (without considering the width in correspondence of

the mandibular ramus). In MPPSA IGVR 91031 the purported Meckel's cartilage is 107% wider than the purported palatoquadrate. The values are readily comparable, and the arcuated shape of the portion of palatoquadrate of MPPSA IGVR 91031 is similar to that of BMB 008524, supporting the tentative identification of the larger portions of cartilage in the specimen described herein. The fragments in Fig. 14B could be tentatively interpreted as the remains of the nasal capsules. The original position of other fragments of tessellated cartilage could not be interpreted.

The material described herein is fragmentary but offers the opportunity to briefly discuss the body of literature focused on the anatomy of *Ptychodus*, although the exact body form of this taxon remains largely speculative, a complete and articulated specimen of this genus being missing so far (see also Shimada et al. 2010). Casier (1953) firstly acknowledged that the morphology of the mineralized cartilage of the jaws of *Ptychodus* reminds more the morphology observed in the heterodontid sharks (V-shaped) rather than of batoids (bar-like). Based on jaw, vertebral and placoid scale morphology, Shimada et al. (2009, 2010) also suggested that *Ptychodus* possibly had a body form similar to the extant benthic sharks with a stout, streamlined body, such as orectolobiforms (e.g., the nurse shark, *Ginglymostoma*) and heterodontids (such as *Heterodontus*). In particular, vertebral centra of *Ptychodus* were reported in several papers; the shape of the centra is clearly circular and the calcification pattern consists of several concentric rings, sometimes interrupted by thin lines radially arranged (e.g., Stewart 1980; Macleod 1982; Woodward 1912; Everhart and Caggiano 2004; Hamm 2010b; Shimada et al. 2009, 2010; Hamm 2019). The specimens described herein (I-17373 and MPPSA IGVR 91031) solely exhibit the impressions of a vertebral centrum, and the overall shape and calcification pattern are recognizable, appearing consistent with those of vertebral centra previously illustrated for other species of *Ptychodus* (e.g., Everhart and Caggiano 2004: fig. 6; Hamm 2019: fig. 7). According to Shimada et al. (2009), even though the relationship between the vertebral shape and body form in sharks has never been adequately surveyed, some benthic sharks (e.g., squatiniforms) have dorsoventrally compressed centra (Applegate 1967: pl. 2-3.2) that reflect a dorsoventrally flattened body, similar to those of certain batoids. In the light of this consideration, *Ptychodus* could not have had a dorsoventrally flattened body form. However, it should be noted that other chondrichthyans also have circular vertebral centra despite having a dorsoventrally flattened body (e.g., pristids, sclerorhynchiforms and orectolobiforms; see Cappetta 1980; De Carvalho et al. 2008; Wueringer et al. 2009; Amalfitano et al. 2017b; Sternes and Shimada 2018). As far as the calcification pattern is concerned, Applegate (1967) discussed the threefold classification for designating different cross-sectional mineralization patterns (i.e. asterospondylic, tectospondylic and cyclospondylic). These patterns can be recognized through a cross-section of vertebral centra, while

they are difficult to recognize on the surface of the vertebral discs (Applegate 1967; Cappetta 1980). The impressions of the articular surface of the vertebral centrum presented herein do not allow a clear assignment to one of the mineralization patterns designated by Applegate (1967). Indeed, despite the concentric rings recognizable in I-17373 (Fig. 8E,F) and MPPSA IGVR 91031 (Fig. 14C,F) are similar to those described by Applegate (1967) and Cappetta (1987) based on vertebrae of the genera *Squatina* and *Narcine*, the arrangement of the radial lines appears quite different from all the pattern illustrated by both these authors, including those of squatinoids and torpediniforms sharks. In addition, Hamm (2019: p. 8) defined as ‘diagnostic feature of *Ptychodus*’ the ‘parallel bands’ observed by him on the articular surface of the vertebral centra of different species of *Ptychodus* (e.g., *P. anonymus*, *P. rugosus*; see also Hamm 2010b: p. 52). Hamm (2019) probably referred to the fine lines radially directed that interrupt the concentric rings (see Hamm 2019: fig. 7; see present work, above). However, detailed analyses (e.g., CT-scan investigation) on the vertebrae of *Ptychodus*, specially focused on their inner structure, are desirable to confirm any interpretation on the cross-sectional mineralization patterns.

Taphonomic remarks

A fast post-mortem degradation characterizes the fate of the soft-tissues of chondrichthyans, which are mainly represented by isolated teeth, and rarely articulated remains, in the fossil record (Schäfer 1972; Shimada 2005; Cabrera et al. 2012; Cappetta 2012). In addition, fossil preservation on the seafloor in open sea environments is regulated by biological processes, such as scavenging and microbial decay (e.g., Allison et al. 1991; Behrensmeyer et al. 2000). The sedimentation rate and bottom-water oxygen concentration also affect the degree of fossil preservation (see Allison et al. 1991; Canfield 1994; Behrensmeyer et al. 2000). Anoxic conditions and quick burial certainly improve the degree of preservation of the associated or articulated skeletons of vertebrates (see Brett and Baird 1986; Canfield 1994). Therefore, relatively low sedimentation rates characterizing the ‘Lastame’ (i.e. a nodular condensed lithozone; see Trevisani and Cestari 2007, Amalfitano et al. 2017a, 2019) could have prevented a rapid burial of the fossils described herein, leaving them exposed to possible bioturbations. Recently, Amalfitano et al. (2019) have reported several large deadfalls of *Cretoxyrhina mantelli* from the ‘Lastame’. All the specimens are preserved within the limestone beds or on their bedding surfaces, sometimes draped with calcareous marly sediments and can be interpreted as examples of various degrees of disarticulation of slowly decaying deadfall exposed for more or less long-lasting periods on the seafloor under low energy conditions (Amalfitano et al.,

2019). The *Ptychodus* specimens exhibit a similar condition, despite including mainly cranial remains.

In particular, the articulated specimen of *Ptychodus mediterraneus* MSNUP I-17373 (Fig. 6) showing the upper and lower dentitions with several teeth still in their original position exhibits clear evidence of post-mortem disturbances (see Fig. 7). Both the dental plates probably lack the teeth that originally occurred on the anterior edge of the plates. Moreover, the distal rows that contained the smallest teeth of the plates are rarely or poorly preserved (see Fig. 9,10). Canavari (1916) suggested that the lateralmost teeth might be detached more easily because of their distal position. The relatively easy detachment and dispersal of distal dental elements seems to be confirmed by other articulated *Ptychodus* specimens, which often lack the distal portions of the plates (e.g., Woodward 1887, 1904; Shimada et al. 2009; Shimada 2012). Additionally, the upper dentition symphyseal teeth (see Fig. 8D) are imbricated between first pair of lateral rows (see also Shimada et al. 2009; Cappetta 2012; Shimada 2012). The two upper rows L1 of MSNUP I-17373 are in contact with each other (Fig. 8A), completely hiding some symphyseal teeth. The same imbrication also was observed in articulated specimens of *P. mortoni* (Shimada 2012: fig. 2). Nevertheless, the upper symphyseal teeth of *P. mediterraneus* were originally partially covered by lateral teeth (rows L1), as well as in the upper dentition of *P. occidentalis* (Shimada et al. 2009: fig. 3A,B). This can be easily demonstrated by comparing the measurements of the upper dentition of MSNUP I-17373: in lateral teeth (rows L1), the ‘articular facets’ (*f* in Fig. 8D) on the mesial edges have a ‘transverse depth’ (Td-*f* in Fig. 20) of about 4 mm from the tooth margin, while the symphyseal width is around 12-14 mm. Therefore, the mesial edges of the upper lateral teeth are not wide enough to entirely hide the symphyseal teeth (see Fig. 20). According to Canavari (1916), taphonomic processes (e.g., soft tissue degradation) probably triggered the collapse of the two jaw halves, bringing in contact the first pair of lateral rows (L1) in the *P. mediterraneus* specimen. Conversely, the offset alignment of adjacent antero-posterior rows (see Fig. 19A), already described in other *Ptychodus* specimens (e.g., *P. mortoni*, see Shimada 2012), is interpreted as the original tooth position. This arrangement is also confirmed by the irregular morphology of mesial and distal edges of the teeth (e.g., Fig. 8A).

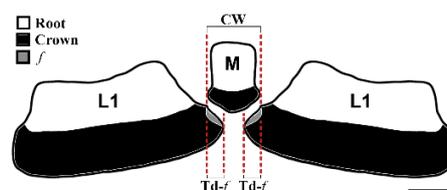


Fig. 20. Interpretative drawing of arrangement between the most medial rows of upper dentition in *Ptychodus mediterraneus* Canavari, 1916 based on articulated specimen MSNUP I-17373. **M**, upper symphyseal row; **L1**, first upper lateral rows; **f**, articular facets; **CW**, Crown width; **Td-f**, ‘transverse depth’ of articular facets. Scale bar equals 10 mm.

Although most of the teeth in MSNUP I-17373 (Fig. 6) are still articulated, the two dental plates are rotated and exhibit antero-posterior directions that are opposite to each other. The upper dentition, vertically oriented in Fig. 7, has the anterior margin close to the posterior side of the lower plate (bottom of the figure). The lower dentition conversely is rotated rightward of about 40° with respect to the antero-posterior axis of the upper plate (see Fig. 7). Considering the life position, with frontal edges overlapping, this plate arrangement is clearly unnatural. In addition, MSNUP I-17373 (Fig. 6) shows the occlusal surfaces of both dental plates on the same side of the slab (see also Fig. 8A), contrarily to the expected original jaw occlusion. This placement is very unusual in articulated specimens, and it is difficult to interpret. MSNUP I-17373 was deposited under low energy conditions and post-cranial skeletal elements occurrence (e.g., the vertebral centrum impression) nearby indicates reduced post-mortem disturbance (see also Shimada 1997). Considering this taphonomic evidence, it is unlikely that such a degree of disarticulation depends on sea floor conditions. However, it is possible that the *Ptychodus* carcass was dismembered and disarticulated during a prolonged floatation before sinking at the seafloor, as already hypothesised for fossil cetaceans (e.g., *Chilcacetus*) based on several accumulation occurrences (e.g., Bianucci et al. 2018). These remains have undergone biogenic and physical processes of partial destruction, including scavenging by sharks. Instead, oxygen-deficient bottom conditions inhibited the scavenging action of benthic organisms (Bianucci et al. 2018). Schäfer (1972) described this phenomenon as ‘bloat and float’, where the lower jaw and skull are usually among the first parts of a decomposing carcass to disintegrate, also assuming quite unusual orientations during the deposition (see also Lyman 1994). On the largest mineralized cartilage portion of MPPSA IGVR 91031 there are at least eight furrows arranged in three small groups and concentrated in a relatively small area. These 1-2 mm deep marks vary from 3 to 12 mm in length and measure 1-2 mm in width (see Fig. 18A,B). Such straight and marked traces with serration grooves are interpreted herein as bite-marks, resulting from scavenging by large predators. Cigala Fulgosi (1990) evidenced different types of bite-marks based on skeletal remains of a Pliocene bottlenosed dolphin; this classification has been modified and improved by Bianucci et al. (2010) and Collareta et al. (2017), with the recognition of five peculiar types of bite-marks. In particular, the classification summarized by Collareta et al. (2017) includes sub-rectilinear or weakly curved incisions (type 1) and scrapes composed by several parallel, more or less rectilinear marks (type 3); both types of bite traces seem to be very similar to some of the serrated furrows observed in MPPSA IGVR 91031 (see Fig. 18B). However, the bite patterns present in MPPSA IGVR 91031 seem to be more complex if examined in detail and require further careful investigation. As

far as regards the serrated margins of the marks in MPPSA IGVR 91031, similar bite traces have been described on bones of turtles, and interpreted as the result of predation/scavenging by *Squalicorax* by Schwimmer et al. (1997: fig. 2G, 3E) and Ehret and Harrell Jr (2018: fig 3B). The teeth of *Squalicorax* produced very distinctive bite-marks on skeletal remains, consisting of grooves left by their serrations. *Squalicorax* was characterized by an opportunistic diet, being commonly considered as a scavenger (Shimada 1997; Walker and Brett 2002; Everhart and Caggiano 2004; Bice et al. 2013; Nelms et al. 2014; Ehret and Harrell Jr 2018). In addition, other direct and indirect evidence of scavenging by *S. falcatus* are already reported on other species of *Ptychodus* (e.g., *P. mortoni*, *P. anonimus*; see Stewart 1980; Everhart and Caggiano 2004). Other possible predators that could have left the bite marks described above might have been the lamniform shark *Cretodus*. In fact, a *Cretodus* specimen from the 'Lastame' was found in association with marine turtle remains interpreted as stomach content. Currently, this finding represents the only direct evidence of predation/scavenging by *Cretodus* (see Amalfitano et al. 2017a). The scavenging by *Cretoxyrhina* and *Cretodus* on cartilage of MPPSA IGVR 91031 is regarded herein as largely unlikely, considering the unserrated tooth marks typically left by these two lamniform sharks on marine vertebrate remains (North America; see Everhart 2004, 2005). *Squalicorax* remains have never been found so far from the Cretaceous Scaglia Rossa Formation. Nevertheless, Cenomanian-Turonian rocks (e.g., 'Bonarelli Level') from Veneto region (Italy; see Sorbini 1976 and Sirna et al. 1994) have yielded both *Squalicorax* and *Ptychodus* specimens; *Squalicorax* is also known from Coniacian-Santonian blocks within the Vernasso megabed of Friuli-Venezia Giulia region (Italy; see Dalla Vecchia 2003).

Moreover, whitish irregular signs characterize the occlusal surface of few large teeth in MPPSA IGVR 91031 (e.g., Fig. 18A,C,D). Very similar traces were observed in MGP-PD 13535 (Fig. 18E) and MSNUP 274 (Fig. 18H,I). These microborings, mainly concentrated on the enameloid ridges, have rounded extremities and unbranched patterns. Similar traces have been considered as the product of bioerosion by endolithic organisms (Underwood et al. 1999). Underwood et al. (1999) recognized different endolithic ichnotaxa, based on microborings occurring in isolated shark teeth from the mid-Cretaceous of Eastern England. The whitish traces seem to be morphologically close to the examples of *Mycelites ossifragus* Roux, 1887 figured by Underwood et al. (1999: fig. 1b-h) and the author consider this ichnospecies to be a senior synonym of *M. enameloides* described by Martill (1989), based on fungal borings on shark teeth coming from the Middle Jurassic of England (see also Cappetta 2012).

All bioerosional (scavenging and microboring) traces are restricted to one of the sides (B) on MPPSA IGVR 91031 (Fig. 11), while the opposite side (side A, Fig. 12) does not show furrows or whitish

traces. This suggests that this side was exposed at the sediment-water interface, providing a suitable substrate for endolithic organisms (e.g., *Mycelites*) and being vulnerable to scavenging by other sharks (e.g., *Squalicorax*).

Concluding remarks

Ptychodus latissimus, *P. mediterraneus* and *P. polygyrus* are considered herein as clearly separated species, even if morphologically close to each other. In addition, the main diagnostic dental features of these species are discussed, also extending the comparative analysis to other similar low crowned taxa. We recognized ridge patterns, transition between crested/marginal area and marginal ornamentations as the most distinctive features useful for identification purposes (see Tab. 3).

The articulated specimens MSNUP I-17373, MPPSA IGVR 91031 and MCBG 4048 well document the digynathic dental heterodonty characterizing *Ptychodus mediterraneus*. The most relevant morphological differences occur between upper and lower symphyseal rows (M in Fig. 19A and m in Fig. 19B), while a gradual mesio-distal variation characterizes lateral teeth (L1-9 and 11-9). Furthermore, comparing the monognathic heterodont dentition of *P. mortoni* (see Shimada 2012) with that described herein for *P. mediterraneus*, different degrees of heterodonty emerge among *Ptychodus* taxa. *P. mediterraneus* and *P. decurrens* are currently the only low-crowned taxa known also from articulated specimens (see also Woodward 1904). Other tooth sets assigned to not-cusped species (e.g., *P. latissimus*, *P. marginalis*, *P. martini*) were artificially re-arranged to form dental plates (see Williston 1900a,b; Leriche 1902; Hamm 2010a). Based on the non-overlapping dentition of the oldest known species *Ptychodus decurrens*, Shimada (2012) assumed that the tooth juxtaposition represents the plesiomorphic condition within *Ptychodus* and considered the imbricated tooth rows of the cusped *P. mortoni* as apomorphic. Currently, the known stratigraphic range of *P. decurrens* spans from the Albian to the Turonian and the Turonian imbricated dentition of *P. mediterraneus* described herein does not disagree with Shimada's hypothesis. In addition, no relationship between interlocking type and dental shape seems to occur, but imbrications occur in both cusped *P. mortoni* and low-crowned *P. mediterraneus*, while cusped *P. occidentalis* and low-crowned *P. decurrens* have juxtaposed teeth. Nevertheless, until the relationships among the various species of *Ptychodus* are not clarified, it will be difficult to trace back the evolutionary history of the dentition of these Cretaceous sharks.

The imbricated, low-crowned teeth of *Ptychodus mediterraneus* with occlusal transverse ridges are indicative of a very high specialization to a durophagous life style. Large molluscs (e.g., inoceramids,

rudists, oysters), which probably formed a large part of the diet of *P. mediterraneus*, developed strong anti-predatory skeletal adaptations during the Cretaceous, such as thick, heavy shells, in response to predation by durophagous vertebrates (Fossa-Mancini 1921; Vermeij 1977; Walker and Brett 2002). The close tooth interlocking system occurring in *P. mediterraneus* probably also acquired a further functional significance, including the protection of the oral mucosa, leaving no spaces between the teeth (see also Fossa-Mancini 1921). In general, *Ptychodus* was common in deep and shallow seas and these hard prey specialists were able to feed near the bottom and scooped up mouthfuls of mud containing hard-shelled prey (Fossa-Mancini 1921; Everhart 2017). Nevertheless, opportunistic feeding was probably common among *Ptychodus* species, as other durophagous groups (see also Walker and Brett 2002); for example, high-cuspidate taxa (e.g., *P. altior*, *P. occidentalis*) could also feed on soft-bodied molluscs, crustaceans and small fishes and even preyed in the water column (Fossa-Mancini 1921; Shimada et al. 2009; Everhart 2017; Amadori et al. 2019b).

As already observed for Devonian sharks (e.g., *Leonodus carlsi*), the markedly worn teeth described in *Ptychodus mediterraneus* could indicate a slow tooth renewal (see Radinsky 1961; Williams 1992, 2001; Botella et al., 2009), whereas the generalist high-crowned species possibly had a faster replacement, as suggested for living sharks that feed on crustaceans (Belleggia et al. 2014).

Ptychodus has dental plates morphologically similar to those commonly observed in batoids. Instead, the ‘V-shaped’ jaws in *Ptychodus* might indicate a body shape similar to that of extant fusiform sharks (e.g., galeomorphs). Despite *Ptychodus* exhibits features of both groups of elasmobranchs (sharks and rays), it is unlikely that it represents a transitional form between them.

Considering the fragmentary record and the heterodont dentition of chondrichthyans, the careful examination of articulated remains still positioned in natural placement is crucial for a correct evaluation of interspecific variations and polymorphisms in extinct sharks and, in particular, in *Ptychodus*. The comparison between articulated and associated (or isolated) teeth could be also useful to evaluate their intraspecific variability (see also Welton and Farish 1993; Shimada et al. 2009; Cappetta 2012). Moreover, further analyses, such as dental wear pattern examinations and tomographic analyses conducted on well-preserved specimens of *Ptychodus* (e.g., articulated tooth sets, mineralized cartilaginous remains) is highly desirable to confirm hypotheses and interpretations proposed herein.

Acknowledgements

This paper is dedicated to Magda Biasiolo (curator of the Natural Sciences section of the Museo Civico di Bassano del Grappa), taken from us too soon. The authors deeply thank Chiara Sorbini (Museo di Storia Naturale dell’Università di

Pisa), Elisa Marchesini (Associazione Culturale Officina 3; Museo Paleontologico e Preistorico di S. Anna d'Alfaedo), Mariagabriella Fornasiero (Museo di Geologia e Paleontologia dell'Università di Padova), Roberto Zorzin (Museo Civico di Storia Naturale di Verona), Denis Ton (Museo Civico di Belluno), Valentina Carpanese (Museo 'Menin' di Chiampo), Emma Bernard (Natural History Museum of London, NHMUK) and Ursula Göhlich (Naturhistorisches Museum, Wien) for permissions to examine the specimens in their care. Thanks are also due to Stefano Castelli (Department of Geosciences of University of Padova) for his valuable help with photographs and figures preparation and Kevin Webb (NHMUK) for the accurate photos of the English Chalk specimens housed in the NHMUK. The photograph of NHMUK PV P75453 was made available thanks to Arnaud Brignon. The copyright of the NHMUK photos is reserved to the NHMUK ('NHM') and Kevin Webb. Special thanks are due to Patrick Jambura (University of Vienna) for useful suggestions. We thank Alberto Collareta, an anonymous reviewer and the editor for helpful comments and suggestions. Funding for this research was provided by University of Padova (Progetto di Ateneo CPDA159701/2015 titled 'Reappraisal of two key Fossil-Lagerstätten in Scaglia deposits of northeastern Italy in the context of Late Cretaceous climatic variability: a multidisciplinary approach', to Eliana Fornaciari) and by OeAD-GmbH/ICM through the Ernst Mach grant - worldwide (Reference number ICM-2019-13192; Project titled 'The durophagous Cretaceous shark *Ptychodus* (Chondrichthyes, Elasmobranchii): Taxonomy, dental evolution and palaeobiological implications', to Manuel Amadori) on behalf of the Austrian Federal Ministry of Education, Science and Research (BMBWF).

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4.

Concluding remarks

The Cenomanian-Turonian ichthyofaunas of northeastern Italy depict a precise scenario in the context of the Tethyan domain. As discussed in the Section 2.3, the BL ichthyofauna apparently reveals many similarities with western Tethyan assemblages, especially Jbel Tselfat and the German assemblages. The English Chalk ichthyofauna has been repeatedly addressed for its peculiarity (e.g., Forey et al., 2003; Cavin et al., 2007; Friedman et al., 2016). All of the Cenomanian Tethyan fish assemblages share a large part of their taxa compared to the more endemic boreal Chalk fish; these assemblages share numerous taxa restricted to the Tethyan localities, especially the three Lebanese Cenomanian localities, Hakel, Hajula and Namoura, but also in Israel, Adriatic region and Morocco (Cavin et al., 2007; Guinot and Cavin, 2016). The analysis of BL ichthyofauna of northeastern Italy and its comparison with coeval ichthyofauna support the strong endemism characterizing the Late Cretaceous marine biota. This trend may be in some ways related to brief interval of invasion of boreal faunas induced by the oceanic circulation perturbations related to the OAE2. However, additional information would be necessary to more properly define the main global ichthyogeographic patterns during the CTB.

The Turonian ‘lastame’ ichthyofauna, on the other hand, exhibit some differences. The occurrence of large lamniform shark *Cretodus* (S. 3.2) is confirmed in northern areas by isolated teeth and a partial skeleton with vertebral centra associated with a partial tooth set coming from the English Chalk and housed at the Booth Museum in Brighton (Woodward, 1911). Another partial skeleton was reported from the Western Interior Seaway (Shimada et al., 2011). The same happens with *Cretoxyrhina mantelli* (see Woodward, 1911 and Shimada, 1997; S. 3.4) and the *Ptychodus* species (S. 3.3, 3.5), except for *Ptychodus altior* (S. 3.3.), a taxon apparently very similar to *P. whipplei* from the Western Interior Seaway. The sclerorhynchid *Onchosaurus* (S. 3.1) is the only taxon that apparently does not occur in the English Chalk and seems to be restricted to the Tethys. As regards the bony fishes, the ‘lastame’ is apparently poor in actinopterygians, with only some fragmentary remains of *Protosphyraena ferox* (S. 2.1) and scattered bones of a large plethodid? fish (*Dixonanogmius?*). The dearth of actinopterygians remains is likely due to a preservation/sampling bias. The quarrying activity is not supervised by experts, therefore there is no effective control on what emerges from the

rocks, and a large part of the specimens currently in the museum collections represents historical findings or were collected during the 1970s. Overall, the Turonian ichthyofauna of Scaglia Rossa is represented by taxa with a worldwide distribution. These widespread taxa may be related to the Turonian global transgressive trend. The $\delta^{13}\text{C}$ record of the 'lastame' suggests that the 'lastame' probably was deposited during the major perturbations inducted by the Europe-wide trend of stepped cooling that accompanied long-term sea-level fall, beginning in the late-middle Turonian and culminating in the mid-late Turonian - the "Late Turonian Cool Phase" (Wiese and Voigt, 2002; Jarvis et al., 2015) and the occurrence of fossils within the strata may be in some ways correlated with these events (Eliana Fornaciari, pers. com.). However, further investigations are certainly required, integrating the data from the different faunal groups (calcareous nannoplankton, planktic forams, fishes and reptiles).

In conclusion, the BL ichthyofauna was completely revised by updating the previous identifications by Sorbini (1976) and by including the new findings occurred after that study from the same locality and from other new sites. The revision evidenced the occurrence of some taxa never reported before, such as the goblin shark *Scapanorhynchus raphiodon*, the lamniform sharks *Cretalamna appendiculata* and *Archaeolamna kopingensis*, the pycnodontiform fish '*Nursallia*' *tethysensis*, at least two species of the aspidorhynchid *Belonostomus*, the tselfatiiforms *Dixonagmius dalmatius* and '*Protosphyraena*' *stebbingi* and the beryciform *Hoplopteryx* (S. 2.3). The ichthyofauna from the 'lastame' was for the first time deeply studied, evidencing some large-sized skeletal remains of the lamniform sharks *Cretoxyrhina mantelli* (S. 3.4) and the most complete skeletal remains of the genus *Creodus* (S. 3.2), associated with the remains of a chelonioid turtle that were interpreted as a gastric pellet. The study also reported the first skeletal remains of the sawfish *Onchosaurus* (S. 3.1), the first associated tooth set of the durophagous shark *Ptychodus altior* (S. 3.2), and the revision of the most complete remains of the species *P. mediterraneus* (S. 3.5) after a century since the last study. These two fish assemblages are particularly significant for the interpretation of the Tethyan fish diversity during the mid-Cretaceous and for the understanding of the influence of the extrinsic factors affecting its dynamics, especially the climatic disruptions of the greenhouse regime and the correlated factors, such as tectonic forcing and general oceanic circulation.

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Appendix S. 2.1.

Appendix A.1

Calcareous nannofossil analysis of sample CDL 782

The sample was prepared from unprocessed material as smear slides and examined using a light microscope at 1250x magnification. A count of the calcareous nannofossil assemblage was carried out in a predetermined area of about 7-9 mm² (four vertical transects; modified after Gardin and Monechi, 1998). The results of the analysis are reported below.

The sample contains a few common calcareous nannofossils in a poor state of preservation, showing marked dissolution. The genus *Watznaueria* (a dissolution resistant taxon) is dominant in the calcareous nannofossil assemblage. In particular, the genus *Watznaueria* is represented by 91 specimens. The rest of the assemblage includes: *Braarudosphaera bigelowii* (1), *Cribrosphaerella ehrenbergii* (1), *Diloma galei* (1), *Discorhabdus* sp. (2), *Eiffellithus eximius* (2), *Eiffellithus turriseiffelii* (1), *Eiffellithus* sp. (1), ***Lithastrinus septenarius*** (1), *Lithraphidites carniolensis* (1), *Lucianorhabdus quadrifidus* (1+3cf.), *Quadrum gartneri* (3), *Prediscosphaera* sp. (4), *Retecapsa angustiforata* (8), *Tranolithus orionatus* (1+ 2cf.), *Zeugrhabdotus embergeri* (1), *Zeugrhabdotus* sp.(1).

Biozone and Age of Sample

The presence of *Lithastrinus septenarius* indicates the calcareous nannofossil Zones UC9-UC11 of Burnett (1999). The absence of *Micula staurophora* would permit us to further constrain the specimen to the UC9 Zone, however paleoenvironmental controls could have excluded *Micula staurophora*. Therefore, we prefer to assign the sample to Zones UC9-UC11 of Burnett (1999). On this basis, the age of CDL 782 corresponds to the late Turonian-Coniacian, and ranges from 76.82 Ma to 85.56 Ma according to Gradstein et al. (2012).

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Appendix S. 2.2.

Appendix A.1

Estimated length of the rostrum MGP-PD 6716Z

We present herein a simplified method to tentatively estimate the length of the rostrum MGPD 6716Z despite its incompleteness. The rostrum shape can be roughly approximated to an isosceles triangle with a very acute vertex (see Fig.1 below).

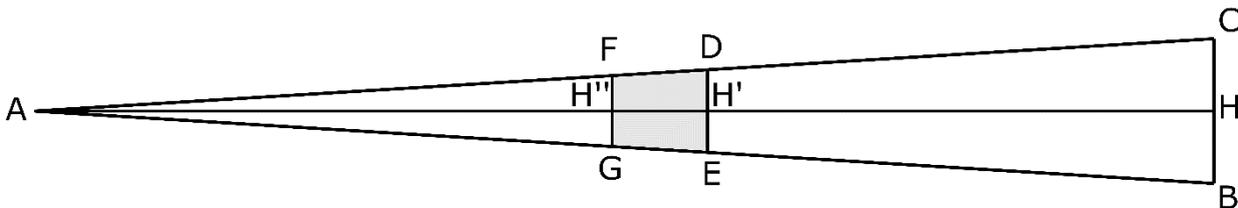


Fig. 1. Simplified line drawing of the rostrum shape for rough length estimate. The light grey area represents the missing portion between the two remaining portions of the rostrum.

The estimate is based on similitude criteria of the rectangle triangles and proportions. Considering the rectangle triangles AH''F and AH'F, they are similar for having the three angles equiangular (AAA similarity). For this reason, we can deduce the following proportions:

$$\frac{AD}{AF} = \frac{DH'}{FH''} = \frac{AH'}{AH''}$$

From this proportions we obtained the following equation:

$$AH' = \frac{DH'}{FH''} * AH''$$

Knowing the width of the rostrum in correspondence of DE (ca. 25 mm) and FG (ca. 22 mm), we obtained the values of DH' and FH'', respectively 12,5 and 11 mm. The length of the distalmost portion (corresponding to AH'') equals 191 mm. AH' results 217 mm long, which, summed to the length of the most proximal portion of the rostrum (ca. 217 mm), provide a minimum rough length estimate of the rostrum of 434 mm. The missing portion of the rostrum between the remaining portions here considered (DEFG) was at least 26 mm long. The rough estimate we provide is consistent with the estimate provided by Woodward (1912), which estimated a total length of 450 mm, combining the type specimen housed in the NHMUK and the specimen from the Hull Museum collection.

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Appendix S. 3.1.

Tab. A.1. List of taxa from selected marine Cenomanian/Turonian locality. Abbreviations: Fm., formation; Tur., Turonian; WIS, Western Interior Seaway

Taxonomy	Italy (Bonarelli Level)		Morocco				Dinarids	Portugal	England	France	Germany	Middle East				North America	Mexico								
	NE Italy (this study)	Umbria-Marche	Sicily	Jbel Tsefat	Agout	Goulmina (Tur)	OT1	Komen-Krais	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Haïke (Lebanon)	Hajoula (Lebanon)	Narnoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.		
Chondrichthyes																									
Elasmobranchii																									
<i>Cretomanta canadensis</i>																									
Selacimorpha																									
<i>Polyacrodus polyptychus</i>																									
<i>Hybodus</i> sp.																									
Squalomorpii																									
<i>Hexanchus microdon</i>																									
<i>Gladioserratus aptiensis</i>																									
<i>Protosqualus barringtonensis</i>																									
<i>Squatina (Cretascyllium) cranei</i>																									
Galeomorpii																									
<i>Heterodontus polydictyos</i>																									
<i>Heterodontus canaliculatus</i>																									
<i>Heterodontus</i> sp. 1																									
<i>Mesiteia emiliae</i>																									
<i>Chiloscyllium greenei</i>																									
<i>Chiloscyllium</i> sp. 2																									
<i>Chiloscyllium</i> sp.																									
<i>Pseudospinax pusillus</i>																									
<i>Pararhynchodon lehmani</i>																									
<i>Pararhynchodon</i> ? sp.																									
<i>Cantioscyllium decipiens</i>																									
<i>Cantioscyllium</i> sp.																									
<i>Paranomotodon angustidens</i>																									
<i>Squalicorax falcatus</i>																									
<i>Squalicorax primolus</i>																									
<i>Squalicorax curvatus</i>																									
<i>Squalicorax baharijensis</i>																									
<i>Squalicorax</i> sp.																									
<i>Nanacorax</i> sp.																									
<i>Palaeoanacorax</i> aff. <i>pawpawensis</i>																									
<i>Microcorax crassus</i>																									
<i>Cardabiodon venator</i>																									
<i>Archaeolamna kopingsensis</i>																									
<i>Archaeolamna</i> sp.																									
<i>Cretoxyrhina mantelli</i>																									
<i>Cretoxyrhina denticulata</i>																									
<i>Cretoxyrhina agassizensis</i>																									
<i>Dallasiella owstoni</i>																									
<i>Dwardius woodwardi</i>																									
<i>Cretalamna appendiculata</i>																									
<i>Pseudoscapanorhynchus compressidens</i>																									
<i>Cretodus semiplicatus</i>																									
<i>Cretodus "longiplicatus"</i>																									
<i>Cretodus crassidens</i>																									
<i>Leptostyrax</i> sp.																									
<i>Protalamna acuta</i>																									
<i>Protalamna sokolovi</i>																									
<i>Protalamna compressidens</i>																									
<i>Protalamna</i> sp.																									
<i>Haimirichia amonensis</i>																									
<i>Scapanorhynchus raphiodon</i>																									
<i>Scapanorhynchus minimus</i>																									
<i>Anomotodon</i> sp.																									
<i>Anomotodon</i> cf. <i>principalis</i>																									
<i>Carcharias</i> sp.																									

Taxonomy		Italy (Bonarelli Level)		Morocco				Dinarids	Portugal	England	France	Germany	Middle East			North America	Mexico									
		NE Italy (this study)	Umbria-Marche	Sicily	Jbel Tselfat	Agout	Goulmina (Tur)	OTI	komen-kraas	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoule (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.		
	<i>Tomognathus mordax</i>									X																
	<i>Pachyamia latimaxillaris</i>													X												
	<i>Paleamia cenomaniensis</i>								X																	
	Caturidae indet.																		X							
	<i>Spathiurus dorsalis</i>									X					X											
	<i>Neorhombolepis excelsus</i>									X																
	<i>Neorhombolepis ? punctatus</i>									X																
	<i>Aphanepygus dorsalis</i>														X											
	<i>Petalopteryx syriacus</i>														X											
	Pycnodontiformes indet.																X	X				X	X			
	<i>Coccodus armatus</i>														X											
	<i>Coccodus insignis</i>															X										
	<i>Ichthyoceros spinosus</i>														X											
	<i>Hensodon spinosus</i>														X											
	<i>Rhinopycnodus gabriellae</i>														X											
	<i>Corusichthys megacephalus</i>														X											
	<i>Paracoccodus woodwardi</i>														X											
	<i>Cosmodus carentonensis</i>										X															
	<i>Trewavasias carinatus</i>														X											
	<i>Akromystax tilmachiton</i>														X		X									
	<i>Ocleodus costai</i>							X																		
	<i>Coelodus saturnus</i>							X																		
	<i>Anomoedus angustus</i>											X														
	<i>Anomoedus willetti</i>									X																
	<i>Anomoedus muensteri</i>											X														
	"Nursallia" goedeli														X	X	X									
	<i>Paranursallia gutturosa</i>	X	X	X	X							X									X					
	"Nursallia" thetyensis	X																			X					
	"Coeldus" fimbriatus																		X							
	"Pycnodus" scrobiculatus											X														
	<i>Palaeobalistum</i> sp.							X																		
	<i>Proscinetes</i> sp.																X									
	<i>Scalacurvichthys naishi</i>												X													
	<i>Haquelpycnodus picteti</i>													X												
	<i>Flagellipinna rhomboides</i>													X												
	<i>Sygmmapycnodus giganteus</i>													X												
	<i>Corusichthys magacephalus</i>													X												
	<i>Micropycnodon kansasensis</i>																		X							
	<i>Gladiopycnodus karami</i>													X												
	<i>Gladiopycnodus byrnei</i>															X										
	<i>Monocerichthys scheuchzeri</i>															X	X									
	<i>Rostropycnodus gayeti</i>													X												
	<i>Joinvillichthys lindstroemi</i>													X												
	<i>Joinvillichthys kriweti</i>													X	X											
	<i>Pankowskichthys libanicus</i>													X			X									
	<i>Hayolperichthys pectospinus</i>													X												
	<i>Ducrotayichthys cornutus</i>													X												
	<i>Tricertichthys wenzii</i>													X												
	<i>Ichthyoceros spinosus</i>													X												
	<i>Stenoprotome hamata</i>													X												
	<i>Gebayelichthys uyenoii</i>													X												
	<i>Gebayelichthys vexillarius</i>													X												
	<i>Maraldichthys verticalis</i>													X												
	<i>Acrorhinichthys payatoi</i>													X		X										
non-teleostean(?) Actinopterygii	non-teleostean(?) Actinopterygii																									X
Teleostei incertae sedis	? <i>Carsotrissops delorenzi</i>							X																		
	<i>Idrissia jubae</i>			X	X																					
	Teleostei indet. (sp. A)																									X
	Teleostei indet. (sp. B)																									X
	Teleostei indet. (sp. C)																									X
	Teleostei indet. (sp. D)																									X
	? <i>Protosphyraena</i> sp.									X																
	<i>Protosphyraena</i> sp.											X	X													
	<i>Protosphyraena ferox</i>	X								X																
	<i>Protosphyraena minor</i>									X																
	<i>Rhinchonichthys taylora</i>									X																
	<i>Belonostomus</i> sp. 1																								X	
	<i>Belonostomus</i> sp. 2	X																							X	
	<i>Belonostomus cinctus</i>	X								X			X													
	<i>Belonostomus</i> indet.	X																								

Taxonomy		Italy (Bonarelli Level)		Morocco				Dinarids	Portugal	England	France	Germany	Middle East			North America	Mexico							
		NE Italy (this study)	Umbria-Marche	Sicily	Jbel Tselfat	Agout	Goulmina (Tur)	OTI	komen-kraas	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoule (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
	<i>Barcarenichthys joneti</i>								X															
	<i>Paravinciguerra praecursor</i>	X		X																				
	<i>Protostomia maroccanus</i>	X	X		X							X												
	<i>Rharbichthys ferox</i>	X		X	X							X												
	<i>Apateodus striatus</i>									X		X												
	<i>Yabrudichthys striatus</i>													X										
	<i>Exocoetoides minor</i>														X									
	<i>Telepholis tenuis</i>														X	X								
	<i>Chirothrix libanicus</i>														X	X								
	<i>Ichthyotringa delicata</i>														X	X								
	<i>Ichthyotringa africana</i>	X	X		X							X												
	<i>Ichthyotringa mexicana</i>																					X		
	<i>Apatepopholis laniatus</i>														X	X	X							
	<i>Apatepopholis lanceolatus</i>									X														
	<i>Apatepopholis</i> nov. sp.																X							
	nov. gen, nov. sp.														X									
	<i>Cimolichthys lewesiensis</i>								X			X												
	<i>Cymolichthys nepaholica</i>																	X						
	<i>Cimolichthys</i> sp.											X												
	<i>Dercetis elongatus</i>								X															
	<i>Dercetoides venator</i>													X										
	<i>Hastichthys gracilis</i>													X	X		X							
	<i>Hastichthys</i> sp.													X	X		X							
	<i>Rhynchodercetis</i> sp.	X	X									X									X			
	<i>Rhynchodercetis hakelensis</i>														X	X								
	<i>Rhynchodercetis serpentinus</i>															X								
	<i>Rhynchodercetis yovanovitchi</i>			X	X																			
	<i>Rhynchodercetis gortani</i>							X																
	<i>Rhynchodercetis regio</i>																			X				
	<i>Leptotrachelus</i> sp.											X												
	nov. gen., nov. sp.												X											
	<i>Prionolepis cataphractus</i>														X	X								
	<i>Prionolepis angustus</i>									X														
	<i>Aspidopleurus kickapoo</i>																							X
	<i>Enchodus lewesiensis</i>								X			X												
	<i>Enchodus marchesetti</i>														X	X								
	<i>Enchodus mecoanalis</i>																X							
	<i>Enchodus</i> cf. <i>major</i>							X																
	<i>Enchodus dentex</i>							X																
	<i>Enchodus lycodon</i>							X																
	<i>Enchodus venator</i>	X		X	X							X												
	<i>Enchodus shumardi</i>																			X				
	<i>Enchodus brevis</i>												X											
	<i>Enchodus zimapanensis</i>																				X			
	<i>Enchodus</i> sp.																		X					X
	<i>Enchodus gladiolus</i>																		X					
	<i>Enchodus</i> sp. 1														X									
	<i>Enchodus</i> sp. 2																X							
	<i>Parenchodus longipterygius</i>													X										
	<i>Eurypholis boissieri</i>														X	X	X							
	<i>Eurypholis pulchellus</i>									X														
	<i>Saurorhamphus freyeri</i>							X																
	<i>Saurorhamphus judeaensis</i>													X										
	<i>Saurorhamphus giorgiae</i>																							
	nov. gen., nov. sp.																							
	<i>Phylactcephalus microlepis</i>														X	X								
	<i>Hemisaurida hakelensis</i>														X									
	<i>Hemisaurida neocomiensis</i>							X																
	<i>Serrilepis longidens</i>													X										
	<i>Serrilepis prymnostrigos</i>																					X		
	<i>Serrilepis minor</i>																					X		
	<i>Halec eurypterygius</i>										X													
	<i>Halec haueri</i>							X																
	<i>Nematonotus bottae</i>							X							X		X							
	<i>Nematonotus longispinus</i>																X							
	<i>Aulolepis typus</i>												X											
	<i>Hakelia laticauda</i>									X					X	X								
	<i>Sardionioides minimus</i>														X	X								
	<i>Sardionioides attenuatus</i>														X	X								
	<i>Sardionioides pontivagus</i>														X	X								

Taxonomy		Italy (Bonarelli Level)		Morocco			Dnairids	Portugal	England	France	Germany	Middle East			North America	Mexico								
		NE Italy (this study)	Umbria-Marche	Sicily	Jbel Tselfat	Agout	Goulmina (Tur)	OTI	komen-kraas	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoule (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
	<i>Sardiniooides guestphoicus</i>						X																	
	" <i>Sardiniooides</i> " <i>illustrans</i>							X																
	<i>Acrognathus boops</i>								X															
	<i>Acrognathus dodgei</i>									X					X	X								
	<i>Volcichthys</i> sp.									X					X									
Acanthomorpha	<i>Ctenothrissa vexillifer</i>														X									
	<i>Ctenothrissa protodorsalis</i>														X									
	<i>Ctenothrissa signifer</i>															X								
	<i>Ctenothrissa radians</i>								X															
	<i>Ctenothrissa microcephala</i>								X															
	<i>Heterothrissa signeuxae</i>															X								
	<i>Pateroperca libanica</i>															X								
	<i>Pteroperca robusta</i>									X						X								
	<i>Pattersonichthys delicatus</i>															X								
	<i>Phoenicolepis arcuatus</i>															X								
	<i>Humlichthys orientalis</i>															X								
Acanthomorpha	<i>Gigapteryx thetyestris</i>																X							
	<i>Pratriacanthus gortani</i>						X																	
	<i>Dalgoichthys tropicalis</i>																					X		
	<i>Muhichthys cordobai</i>																					X		
	<i>Spinocaudichthys oumtkoutensis</i>				X																			
	" <i>Aipichthys</i> " <i>nuchalis</i>								X															
	gen. indet. 1														X									
	nov. gen., nov. sp.																X							
	Polymixiiformes indet.	X																						
	<i>Omosoma tselfatensis</i>				X																			
	<i>Omosoma</i> /gen. nov, sp. nov.																X							
	<i>Omosomopsis simum</i>		X	X																				
	<i>Berycopsis elegans</i>								X															
	<i>Berycopsis pulcher</i>															X								
	? <i>Cylindracanthus libanicus</i>														X	X								
	<i>Pharmacichthys venenifer</i>														X									
	<i>Pharmacichthys numismalis</i>														X									
	<i>Pharmacichthys judensis</i>												X											
	<i>Errachidia pentaspinosa</i>				X																			
	<i>Homalopagus multispinosus</i>				X																			
	<i>Fregichthys elleipsis</i>															X								
	<i>Aipichthys minor</i>														X	X								
	<i>Aipichthys velifer</i>														X									
	<i>Aipichthys oblungus</i>														X									
	<i>Aipichthys pretiosus</i>						X																	
	<i>Aipichthyoides galeatus</i>												X											
	<i>Aipichthyoides formosus</i>											X												
	<i>Aipichthyoides</i> sp. nov.																X							
	<i>Paraipichthys lusitanicus</i>							X																
	<i>Pycnosteroides levispinus</i>															X								
	<i>Homonotichthys dorsalis</i>									X														
	<i>Homonotichthys rotundus</i>									X														
	<i>Homonotichthys pulchellus</i>									X														
	<i>Maghrebichthys nelsoni</i>				X																			
Acanthopterygii	? <i>Beryciformes</i> indet.	X																						
Acanthopterygii	<i>Plesioberyx maximus</i>														X									
	<i>Plesioberyx discoides</i>														X									
	<i>Cryptoberyx minimus</i>															X								
	<i>Cryptoberyx brevis</i>							X					X											
	<i>Pattersonoberyx pharsus</i>													X										
	<i>Stichocentrus liratus</i>															X								
	<i>Stichocentrus elegans</i>															X								
	<i>Stichocentrus spinulosus</i>															X								
	<i>Stichocentrus</i> nov. sp.															X								
	<i>Paracentrus lebanonensis</i>																X							
	<i>Paracentrus</i> sp. nov.																X							
	<i>Trachichthyoides ornatus</i>								X															
	<i>Stychoberyx lewisi</i>														X	X								
	<i>Stychoberyx polydesmus</i>				X																			
	<i>Lissoberyx daiyi</i>															X								
	<i>Lissoberyx arambourgi</i>															X								
	<i>Lissoberyx denticulatus</i>															X								
	<i>Lissoberyx anceps</i>			X																				
	<i>Beryx dalmaticus</i>						X																	

Tab. A.2. List of selected references used to compile table A.1 divided per locality.

Italy (Bonarelli Level)	Umbria-Marche	Capasso (2007)
	Sicily	Rindone (2008), Carnevale and Rindone (2011) and references therein
Morocco	Jbel Tselfat	Vullo et al. (2016), Khalloufi et al. (2017) and references therein
	Agoult	
	Goulmima	
	OT1	
Dinarids	Komen-Kras	Forey et al. (2003) and references therein
Portugal	Portugal	Forey et al. (2003) and references therein
England	Chalk	Guinot et al. (2012a,b), Guinot et al. (2013); Friedman et al. (2016) and references therein
France	Chalk and other localities	Vullo et al. (2007), Vullo et al. (2018) and references therein
Germany	Westphalia	Diedrich (2012)
	Saxony	Müller and Diedrich (1991); Licht et al.(2016), Fischer et al., (2017); Stumpf et al. (2019)
Middle East	Israel (Ein Yabrud, etc.)	Forey et al., (2003), Cawley and Kriwet (2018)
	Hakel	Forey et al. (2003), Bannikov and Bacchia (2005), Gayet et al., (2012), Bannikov (2015), Cawley and Kriwet (2019) and references therein
	Hajoula	
	Nammoura	
North America	Western Interior Seaway (Greenhorn, etc.)	Williamson et al., (1993), Shimada et al. (2006), Cumbaa et al. (2010), Underwood and Cumbaa (2010), Gallardo et al. (2012), Nagrodsky et al. (2012), Bice et al. (2013) and references therein
Mexico	Agua Nueva Fm.	Bannikov (2015), Gonzalez-Rodriguez et al. (2016), Alvarado-Ortega et al. (2019) and references therein
	Boquillas Fm.	
	El Doctor Fm.	
	Cintalapa Fm.	
	Eagle Ford Fm.	

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Appendix. A.3. Results neighbor joining cluster analyses and parameters PCAs

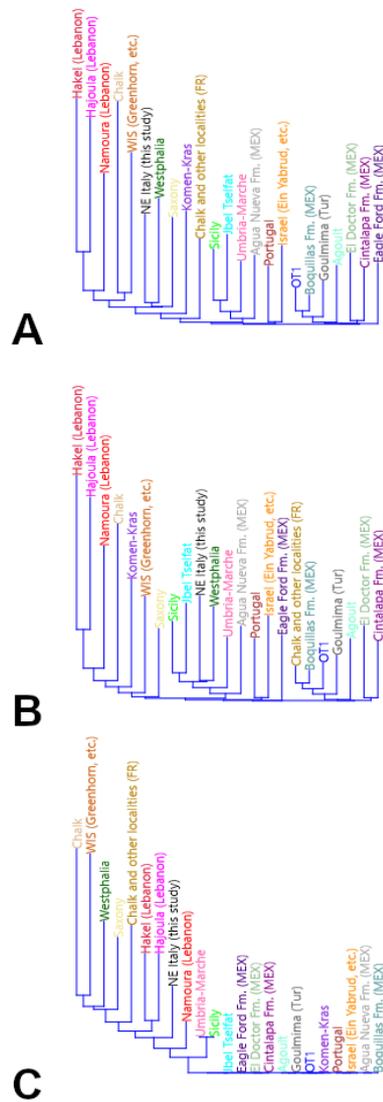


Fig. A.3. Neighbor joining clustering of the CTB assemblages. **A.** ‘Fish’ data set output. **B.** Bony fishes data set output. **C.** Chondrichthyan data set output.

- **PCA ‘Fish’ (Bony fishes+chondrichthyans)**

Summary

PC	Eigenvalue	% variance
1	5.5824	20.033
2	4.23472	15.197
3	2.67353	9.5944

4	2.45279	8.8022
5	2.08842	7.4946
6	1.7435	6.2568
7	1.29138	4.6343
8	1.12601	4.0408
9	1.11033	3.9846
10	0.773031	2.7741
11	0.72237	2.5923
12	0.690964	2.4796
13	0.602364	2.1617
14	0.476014	1.7082
15	0.459444	1.6488
16	0.427453	1.534
17	0.377928	1.3563
18	0.356453	1.2792
19	0.294358	1.0563
20	0.233387	0.83754
21	0.123435	0.44296
22	0.0253363	0.090923

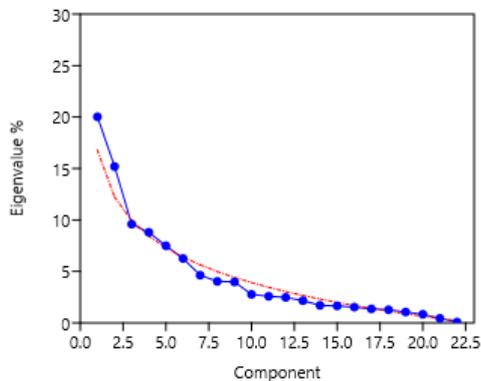
Scores PCA 'Fish'

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11	PC 12	PC 13
13	PC 14	PC 15	PC 16	PC 17	PC 18	PC 19	PC 20	PC 21	PC 22				
NE Italy (this study)			-1.1788	-0.18887		-0.34794		0.061194		1.6917	2.3679	0.42395	
	2.6725	-1.7107	-0.14031		1.9581	-0.44988		0.41951	-0.39924		0.038684		
	0.062852		-0.10567		0.34232	0.32918	-0.094922		-0.019859		-0.0047338		
Umbria-Marche	-0.75273			-0.81236		-0.36453		0.023028		0.74925	0.43313	-0.19391	
	0.88358	-0.12975		0.23968	-0.236	-0.25962		-0.57217		0.43222	-0.51354		-
0.20448	0.80255	-0.62565		-2.0621	0.33016	0.066582		0.018973					
Sicily	-0.61415		-0.96125		-0.81738		0.010374		1.1047	0.7259	0.11638	0.86093	
	0.82846	-0.040751		-1.2309	0.63296	0.018452		-0.076424		-0.1415	-1.4092	1.2624	-
0.96555	1.0994	-0.043061		0.019476		0.008878							

Jbel Tselfat	-0.74086	-1.173	-1.1022	0.051278	1.39	1.1209	0.23641	1.298	1.4163	-	
0.33946	-1.9682	1.2847	0.45871	0.036504	0.25082	1.1046	-0.95015	0.70457	-0.17693		
	0.086808	0.027134	0.0091637								
Agoult	-0.44708	-0.78252	-0.28829	0.012189		-0.35746		-1.0129	-0.42059		
	0.015582	0.23343	0.31909	-0.080652	-0.72095	-0.70585		-0.65468		-	
2.234	1.193	0.53511	0.41806	0.60766	0.34606	0.11953	0.03634				
Goulmima (Tur)	-0.37205	-0.80824	-0.35865	0.013944		-0.31507		-0.82285			
	-0.32212	-0.090149	0.093593	0.089005		-0.0025438		-0.21405			
	0.03498	-0.39496	-0.058408	-0.032989	-0.22829	-0.14716		-0.23565			
	-1.8229	0.76661	0.11056								
OT1	-0.36589	-0.79051	-0.34603	0.013408		-0.30073		-0.77759		-	
0.29773	-0.082232	0.085247	0.077143	-0.0021776	-0.18162	0.028762				-	
0.30173	-0.044	-0.024078	-0.15599	-0.096783	-0.13035	-0.65977		-1.3761			
	0.26385										
Komen-Kras	0.098206	-0.96492	-0.61068	0.039585		0.2671	-1.0654	4.8545		-	
0.97622	-0.88226	-0.065471	-0.049894	0.05347	-0.10808	0.22477	0.036099				
	0.1147	0.024015	-0.037536	0.0080544	0.056265	0.026011		0.0095828			
Portugal	-0.29483	-0.83412	-0.43027	-0.0094375		-0.21956		-0.89878		-	
0.28522	-0.42451	-0.024943	0.33745	-0.0199	0.17836	0.017244	-1.0009	-0.23432		-	
1.9481	-0.5989	1.5007	-0.31235	0.4793	0.13418	0.038794					
Chalk	-3.4479	8.6151	-0.82295	0.059194	-0.83802	-0.66669	0.35075	0.51371			
	0.36748	0.14922	-0.17543	0.077155	0.030122	0.017815	-0.0070872			-	
0.044517	-0.014159	-0.011167	-0.027142	0.0035227	0.0013546	0.00064491					
Chalk and other localities (FR)	-0.56814	-0.31586	0.31452	-0.045263		-0.32633				-	
1.1745	-0.66138	-0.28626	-0.072418	-3.7536	0.63496	0.51299	-0.08954	0.35122		-	
0.01248	-0.016655	0.15051	0.019096	-0.0062101	0.16583	0.062495	0.020717				
Saxony	-1.0587	0.37465	0.58644	-0.017559	0.43942	0.49804	-1.3499	-1.3462	-3.8714	0.26995	-1.4718
	0.49415	-0.060393	0.30475	0.10607	0.20331	-0.061579	-0.032879	0.19195	0.050669		
	0.026635	0.0096147									
Westphalia	-1.4477	0.66752	-0.98535	0.021309	2.4947	2.9031	-0.32864	-3.2556			
	1.3363	-0.024806	0.84067	-0.42843	-0.037644	-0.037891	-0.011399				
	0.10951	-0.023196	-0.010429	-0.012841	-0.0082196	-0.0014618	0.00010028				
Israel (Ein Yabrud, etc.)	-0.33266	-0.92523	-0.45963	0.16315	-0.58215		-1.1723			-	
0.64343	-0.26756	0.2432	1.3561	1.7963	2.7637	-0.083205	0.63624	0.10077	0.32384	0.1995	-
0.11874	0.095785	0.14361	0.062865	0.021735							
Hakel (Lebanon)	7.803	2.1353	0.52406	4.4187	1.3548	-0.34069	-0.22513	0.090856			
	0.019512	0.0099181	-0.012287	-0.043559	0.016994	0.001415					
	0.0016176	0.016813	-0.0072551	-0.0029415	-0.0050514	0.003794					
	0.0020012	0.00089045									
Hajoula (Lebanon)	6.2008	1.537	-0.012096	-5.7565	0.025269	0.33654	-0.096733				
	0.070878	0.029531	0.039253	0.021046	0.031441	0.003562					

	0.029824	0.0055149	0.03236	0.0016924	-0.0043461	-0.0054879	0.01228	
	0.0058925	0.0023088						
Namoura (Lebanon)	1.163	-0.62965	-0.11362	1.0874	-5.3521	3.3003	0.38822	-0.14079
	0.14313	-0.13988	-0.13129	0.055284	-0.12923	0.038868		-0.0043391
	-0.026555	0.057863	0.036349	-0.01144	0.024622		0.013358	
	0.005299							
WIS (Greenhorn, etc.)	-1.473	0.06994	7.2524	-0.26598	0.36818	0.28622	0.43011	0.095845
	0.77069	0.28015	-0.059008	0.095654	-0.06615	-0.076052	0.048825	-
	0.016825	-0.02888	0.033682	0.020201	-0.019457	-0.0034305		-0.00034865
Agua Nueva Fm. (MEX)	-0.55913	-0.88412	-0.4779	0.022909		0.087121		-0.50476
	-0.46708	0.60964	0.44745	0.40909	0.025472	-1.2654	-2.0108	1.8731
	-0.67652	0.26635	0.51101	0.070085	0.049449		0.018218	
Boquillas Fm. (MEX)	-0.35993	-0.77354	-0.33426		0.012911		-0.28764	-
	0.73704	-0.27677	-0.075593	0.078267	0.068071	-0.0019035		-0.15773
	0.024422	-0.2441	-0.035294	-0.018957	-0.11846	-0.072099		-0.090093
	-0.40278	-0.3626	-0.68287					
El Doctor Fm. (MEX)	-0.42243	-0.9159	-0.12059		0.031425		-0.55489	-0.99246
	-0.45172	-0.15169	0.32238	0.43808	-0.021475	-1.2246	2.7013	1.3233
	0.081607	0.55446	0.4332	0.067041	0.17685	0.078251		0.026398
Cintalapa Fm. (MEX)	-0.40166	-0.86575	-0.25563		0.035046		-0.44967	-
	0.76782	-0.34652	0.035969	0.087496	0.17717	0.21745	-0.54452	0.61863
	-0.074379	-0.054983	-1.6131	-1.7728	0.11708	0.69132	0.17341	0.047566
Eagle Ford Fm. (MEX)	-0.42735	-0.7736	-0.42938		0.017715		-0.38855	-1.0383
	0.43342	-0.05072	0.189	0.2449	-0.030584	-0.68943	-0.50956	-1.4088
	0.82168	0.9941	0.14375	0.028251	0.40992	0.1282	0.03831	2.0778

Scree plot



- **PCA Bony fishes**

Summary

PC	Eigenvalue	% variance
1	4.82918	22.837
2	2.52591	11.945
3	2.14182	10.129
4	1.94524	9.199
5	1.53675	7.2672
6	1.27935	6.05
7	1.00534	4.7542
8	0.755539	3.5729
9	0.686459	3.2462
10	0.600893	2.8416
11	0.586849	2.7752
12	0.548881	2.5956
13	0.459867	2.1747
14	0.428381	2.0258
15	0.40237	1.9028
16	0.363204	1.7176
17	0.332256	1.5712
18	0.263383	1.2455
19	0.242404	1.1463
20	0.132728	0.62767
21	0.0649803	0.30729
22	0.0144656	0.068408

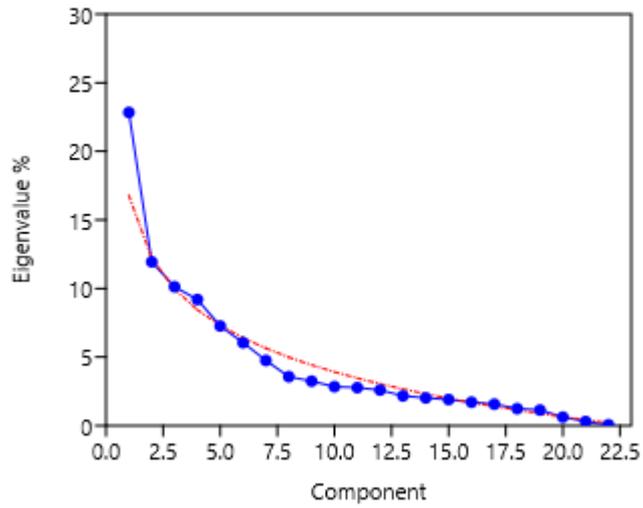
Scores

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11	PC 12	PC
13	PC 14	PC 15	PC 16	PC 17	PC 18	PC 19	PC 20	PC 21	PC 22				

NE Italy (this study)	-1.0151	-0.38713	-0.18396	-1.4046	2.575	-0.12941	0.91733	-
2.8849	0.42242	-0.25421	0.80388	0.12529	-0.55636	-0.22042	-0.22104	0.1973
	0.30232	0.43092	-0.12463	-0.020307	-0.0047803	-0.0013743		
Umbria-Marche	-0.90577	-0.45375	-0.078775	-0.68873	0.63692	-0.41359		
	0.34192	-0.57615	-0.20906	0.54648	-0.12123	-0.32698	0.64725	-0.020776
	0.352	0.37742	-0.49626	-2.0568	0.29951	0.051324	0.016176	0.0060256
Sicily	-0.79967	-0.68383	-0.15674	-1.0668	1.3739	-0.19457	-0.27818	
	1.1508	-0.14767	0.37402	0.30354	-0.55968	0.14246	-0.22131	-1.2433
1.7812	0.57423	0.047187	0.038631	0.013215	0.0050602			0.66676
Jbel Tselfat	-1.0488	-0.82765	-0.16703	-1.4707	2.2891	-0.31671	-0.13624	
	1.9429	0.010878	0.53684	0.96855	-1.1858	-0.078548	0.31762	0.66748
	1.1801	0.077076	0.057674	0.021562	0.007332	0.002853		-0.49969
Agoult	-0.65836	-0.20615	0.017909	0.11471	-0.8746	-0.30676	-0.37315	-
0.062523	-0.57104	0.5634	-0.2212	0.036003	0.086003	-1.9667	1.4116	0.95712
	0.093054	0.57213	0.51652	0.15656	0.046376	0.016419		
Goulmima (Tur)	-0.58791	-0.30066	0.022223	0.10205	-0.693	-0.18856	-0.49773	
	-0.021701	-0.26934	-0.09159	-0.071785	-0.11255	-0.25739		-
0.28594	0.029421	-0.21807	-0.023805	-0.17519	-1.6834	0.99269	0.15327	0.043315
OT1	-0.57663	-0.28943	0.021238	0.097047	-0.64942	-0.17414		-
0.44824	-0.018732	-0.22823	-0.075263	-0.058626	-0.09021	-0.19397		-
0.20891	0.020834	-0.14527	-0.014839	-0.08285	-0.67321	-1.1653	0.69066	
	0.094826							
Komen-Kras	-0.10689	-0.70077	-0.07344	-0.67924	-0.49262	5.0845		
	0.26148	0.026942	0.024869	0.12785	0.0072547	0.069142	0.1397	0.11972
	0.11355	-0.035729	-0.019852	0.00059134	0.061024	0.02708	0.0095574	
	0.0037556							
Portugal	-0.51144	-0.35623	-0.023699	0.0086616	-0.7944	-0.060602	-0.76499	
	0.1142	0.089281	-0.53461	-0.78372	-0.40777	-0.019288	-0.63759	
	-1.9404	0.53797	1.3654	-0.27915	0.46683	0.13533	0.040912	0.014661
Chalk	-1.3598	7.119	-0.27417	0.57781	0.34539	0.31693	0.043478	0.14891
	0.15215	0.25183	-0.12543	0.040584	-0.0015971	-0.085994	-0.0054583	0.033759
	0.001184	-0.021985	0.014512	0.0087991	0.0035134	0.0014785		
Chalk and other localities (FR)	-0.57115	-0.28413	0.020778	0.094725	-0.62963			
	-0.16772	-0.42702	-0.017533	-0.21205	-0.069104	-0.053704		-
0.082065	-0.1727	-0.18412	0.01818	-0.12449	-0.012487	-0.06557	-0.51784	
	-0.55837	-0.91715	0.23392					
Saxony	-0.74084	-0.093563	-0.0043119	0.011503	-0.74225	-0.40971		
	0.11396	-0.94274	-0.14124	-0.93004	-1.42	-1.9572	1.0474	1.0136
0.20296	-0.20677	0.59583	0.21575	0.09142	0.02927	0.010804	0.53611	-
Westphalia	-0.9532	0.062726	-0.22944	-1.2237	1.8898	-0.23635	0.29476	1.0327
	0.49753	-1.4826	-1.8659	1.7669	-0.058251	0.0088989	0.44167	-0.12006
	-0.012985	0.020159	0.010349	0.0041389	0.0017528			-0.078779

Israel (Ein Yabrud, etc.)	-0.57576	-0.40235	0.21984	0.274	-1.0976	-0.3769	-1.557	-0.12257
	3.2855	0.47228	0.49225	0.34095	0.2633	0.32693	0.25078	0.034741
	0.16373	0.070272	0.023769	0.0090576			-0.14944	0.058811
Hakel (Lebanon)	7.6574	0.8535	3.6982	-2.0194	-0.26788	-0.3109	0.061242	-0.007022
	0.045195	-0.0045225	0.018386	-0.0052006	-0.0010409	0.005525	0.015201	
	-0.00946	0.004452	-0.0032686	0.0058458	0.0029356	0.0011591		
	0.00049181							
Hajoula (Lebanon)	5.8936	-0.12053	-5.3158	1.0372	0.28606	-0.16345	0.086579	
	0.0062364	0.061274	0.031558	0.039213	-0.00012128	0.019414		
	0.027158	0.030165	-0.0061655	0.0022851	-0.0040068	0.018109		
	0.0085663	0.0031434	0.0012679					
Namoura (Lebanon)	1.0051	-0.91317	2.2087	5.3936	2.1732	0.34674	0.19662	0.0905
	0.07045	-0.11574	-0.016202	0.045817	0.033383	-0.010069	0.06345	-0.0038477
	0.0076234	-0.0034094	0.024543	0.01465	0.005577	0.0022816		
WIS (Greenhorn, etc.)	-0.84189	-0.41708	0.10862	0.32062	-1.87	-0.65652	4.0176	
	0.69704	0.73555	0.41924	0.063603	0.028229	-0.29151	0.027385	-0.21076
	0.063785	0.07373	0.10237	-0.030242	0.0083371	0.004853	0.002294	
Agua Nueva Fm. (MEX)	-0.80416	-0.34346	-0.031254	-0.29202	-0.15257			
	0.56704	-0.28021	-0.47244	-1.0545	2.1039	-0.41959	1.4438	1.2742
	-0.53175	0.34284	0.4568	0.065832	0.051723	0.018345	0.0071294	-0.40672
Boquillas Fm. (MEX)	-0.56577	-0.27902	0.020337	0.092512	-0.61101			
	0.16176	-0.40771	-0.016479	-0.19801	-0.063877	-0.049544	-0.075269	
	0.15563	-0.16458	0.016127	-0.10891	-0.010779	-0.054254	-0.42073	
	0.36715	-0.27559	-0.50111					
El Doctor Fm. (MEX)	-0.65866	-0.41398	0.10158	0.34373	-1.1032	-0.38202	-0.11727	
	0.26688	-0.90837	-1.8581	2.0663	0.90426	0.96393	0.62275	0.12024
	0.031213	0.19055	0.084006	0.027989	0.010537	0.56619	0.086128	
Cintalapa Fm. (MEX)	-0.62722	-0.37075	0.081625	0.24752	-0.73163	-0.26676		
	-0.28357	-0.24408	-0.38644	-0.47266	0.4436	0.032554	-0.66725	
	-0.76381	-0.20991	-2.1571	-0.5664	-0.11186	0.81868	0.19398	0.054842
	0.018972							
Eagle Ford Fm. (MEX)	-0.64704	-0.19156	0.017588	0.12944	-0.85954	-0.26469		
	-0.76371	-0.09022	-0.78615	0.43844	-0.27739	0.1973	-2.2181	1.4615
	0.30488	0.70038	-0.098586	-0.028638	0.46354	0.14288	0.043419	0.015582

Scree Plot



- **PCA chondrichthysans**

Summary

PC	Eigenvalue	% variance
1	2.07033	30.811
2	1.51108	22.488
3	0.773511	11.512
4	0.656503	9.7703
5	0.572213	8.5159
6	0.484817	7.2152
7	0.317177	4.7203
8	0.156253	2.3254
9	0.0841546	1.2524
10	0.0533278	0.79364
11	0.0400078	0.59541
12	6.3753E-32	9.488E-31
13	4.52332E-32	6.7318E-31
14	9.37266E-33	1.3949E-31

15	7.08337E-33	1.0542E-31
16	3.92995E-33	5.8487E-32
17	3.15694E-34	4.6983E-33
18	1.22053E-34	1.8164E-33
19	6.36937E-61	9.4791E-60
20	3.4312E-96	5.1064E-95
21	5.85167E-129	8.7087E-128
22	9.47109E-160	1.4095E-158

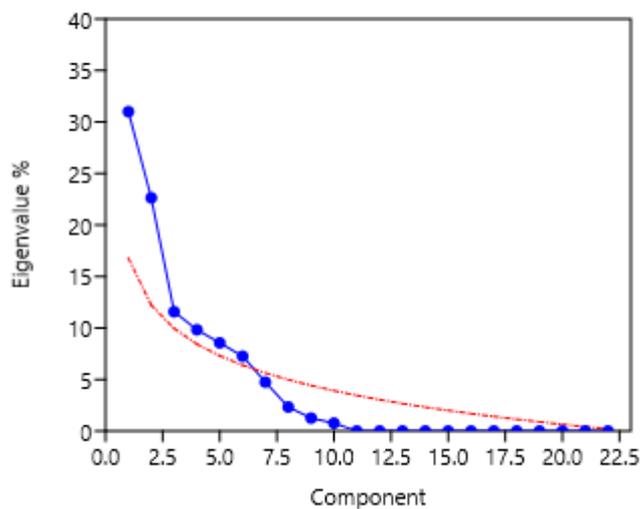
Scores

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11	PC 12	PC
13	PC 14	PC 15	PC 16	PC 17	PC 18	PC 19	PC 20	PC 21	PC 22				
NE Italy (this study)			0.51673	0.063981		-0.43857		0.032809		-0.30663		-1.0526	
	0.028353		-1.5741	0.0066748		0.3423	-0.078688		-7.893E-17		-5.4514E-16		
	1.0061E-16		-8.7842E-16	-1.7174E-16		-4.1026E-16		7.8058E-16		1.2409E-15		-	
5.9588E-16		-3.7947E-16		-4.6653E-16									
Umbria-Marche	-0.49044		-0.047748		-0.2666	0.0095392		-0.34241		-0.039387			
	0.0021357		-0.22976		-0.57769	-0.49939		0.16071	2.4026E-16		1.4181E-16		
	3.8164E-17		-4.5515E-16		-2.6194E-16	3.6689E-16		-1.0449E-17		2.0697E-16			
	3.2006E-16		2.2985E-17		2.0654E-16								
Sicily	-0.49044		-0.047748		-0.2666	0.0095392		-0.34241		-0.039387		0.0021357	
	-0.22976		-0.57769		-0.49939		0.16071	2.4026E-16		1.4181E-16		3.8164E-17	
	-4.5515E-16		-2.6194E-16		3.6689E-16		-1.0449E-17		2.0697E-16		3.2006E-16		
	2.2985E-17		2.0654E-16										
Jbel Tselfat	-0.71218		-0.065563		-0.039562		0.042928		-0.38025		0.072678		
	0.0024167		0.14745	0.013019		0.065433		-0.11061		1.8215E-17		-5.2475E-17	
	-3.7817E-16		-2.1229E-16		9.0206E-17		1.8648E-16		-2.9494E-16		-2.4405E-16		
	3.2353E-16		-8.1098E-17		3.4803E-17								
Agoult	-0.72817		-0.067596		-0.042032		0.046121		-0.41307		0.080197		
	0.002821		0.20793	0.028311		0.44319	0.81243	3.5128E-16		-3.5779E-16		-2.6715E-16	
	-5.0372E-16		1.1102E-16		-6.7394E-16		-3.1229E-16		-3.9671E-16		4.623E-16		-
2.5587E-17		1.8052E-16											
Goulmima (Tur)	-0.71218		-0.065563		-0.039562		0.042928		-0.38025		0.072678		
	0.0024167		0.14745	0.013019		0.065433		-0.11061		1.8215E-17		-5.2475E-17	
	-3.7817E-16		-2.1229E-16		9.0206E-17		1.8648E-16		-2.9494E-16		-2.4405E-16		
	3.2353E-16		-8.1098E-17		3.4803E-17								
OT1	-0.71218		-0.065563		-0.039562		0.042928		-0.38025		0.072678		
	0.0024167		0.14745	0.013019		0.065433		-0.11061		1.8215E-17		-5.2475E-17	

	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-2.4405E-16		
	3.2353E-16	-8.1098E-17	3.4803E-17					
Komen-Kras	-0.71218	-0.065563	-0.039562	0.042928	-0.38025	0.072678		
	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17	-5.2475E-17	
	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-2.4405E-16		
	3.2353E-16	-8.1098E-17	3.4803E-17					
Portugal	-0.71218	-0.065563	-0.039562	0.042928	-0.38025	0.072678		
	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17	-5.2475E-17	
	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-2.4405E-16		
	3.2353E-16	-8.1098E-17	3.4803E-17					
Chalk	4.9631	-2.8475	1.0604	0.85819	-0.74673	0.19851	0.082507	0.13657
	-0.017306	0.0025801	6.245E-16	1.1102E-16	1.0686E-15	2.897E-15	4.996E-16	-
	-1.2629E-15	2.5587E-17	9.4022E-16	-2.04E-15	7.0083E-16	-8.5695E-16		
Chalk and other localities (FR)	0.37592	0.3768	2.4612	-2.8644	0.52702	-0.043209	-0.02367	-
	0.084075	0.0087138	-0.025231	0.011522	-7.4853E-16	2.7322E-17	2.9837E-16	
	1.8063E-16	5.0654E-16	-5.0741E-16	3.2119E-18	-2.0242E-16	-8.4134E-16		
	1.0625E-16	-5.6021E-16						
Saxony	1.2662	-0.25499	-1.343	-0.50111	1.1727	-2.4502	-0.075067	0.64881
	-0.022357	0.0010141	-2.1771E-16	6.8305E-16	9.9573E-16	3.2895E-16	-	
	3.0531E-16	-4.519E-16	7.8752E-16	2.0597E-15	-1.0122E-15	2.6585E-16	-2.3755E-16	
Westphalia	1.2513	-1.129	-2.431	-1.3321	1.1876	1.7547	-0.037741	-0.16678
	0.033948	-0.0061997	2.6411E-15	-8.1922E-16	1.8215E-15	6.3426E-16	-	
	1.1293E-15	6.3057E-16	1.6649E-16	-1.9548E-16	-2.3159E-16	-2.4069E-16	-1.0224E-16	
Israel (Ein Yabrud, etc.)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025			
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17	
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-	
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17				
Hakel (Lebanon)	-0.74589	-0.027454	0.8773	1.1973	1.9157	0.2422	1.8602	-0.079724
	0.083057	0.038451	-0.0057003	-4.5016E-16	2.8927E-16	4.9266E-16	-9.7426E-16	-
	5.5858E-16	-4.2414E-16	-1.7351E-16	-1.339E-16	4.4582E-16	6.0498E-16		
	2.4384E-16							
Hajoula (Lebanon)	-0.61713	-0.13596	0.98316	1.3126	1.7821	0.29636	-1.8714	-0.11806
	-0.080812	0.041421	-0.0061219	-9.541E-18	1.0942E-15	6.5226E-16	-	
	2.3852E-18	-8.8471E-17	8.6649E-16	1.7029E-16	-2.4405E-16	4.3368E-18	2.1727E-16	
	5.0708E-16							
Namoura (Lebanon)	-0.55047	-0.016843	0.019166	0.31832	-0.10534	-0.17972		
	0.0074605	-0.25133	1.0773	-0.55494	0.16573	1.2924E-16	2.1294E-16	-
	5.1348E-16	-2.4525E-16	9.194E-17	-6.6006E-16	-1.316E-17	8.9013E-17	2.0817E-16	
	-8.8037E-17	2.0697E-16						
WIS (Greenhorn, etc.)	3.0833	4.8553	-0.17826	0.44094	-0.14568	0.43316	-0.0042849	
	0.11831	0.0025627	-0.00046353	-0.0013185	-1.1336E-15	3.6039E-16	-4.1633E-17	
	1.78E-15	-7.9797E-17	-8.5435E-16	1.6471E-15	-1.1045E-15	-7.7108E-16		
	9.528E-16	1.4843E-16						

Agua Nueva Fm. (MEX)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025		
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17			
Boquillas Fm. (MEX)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025		
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17			
El Doctor Fm. (MEX)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025		
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17			
Cintalapa Fm. (MEX)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025		
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17			
Eagle Ford Fm. (MEX)	-0.71218	-0.065563	-0.039562	0.042928	-0.38025		
	0.072678	0.0024167	0.14745	0.013019	0.065433	-0.11061	1.8215E-17
	-5.2475E-17	-3.7817E-16	-2.1229E-16	9.0206E-17	1.8648E-16	-2.9494E-16	-
	2.4405E-16	3.2353E-16	-8.1098E-17	3.4803E-17			

Scree plot



• **PCA ‘fish’ (bony fishes+chondrichthyans) without Lebanon and Chalk**

Summary

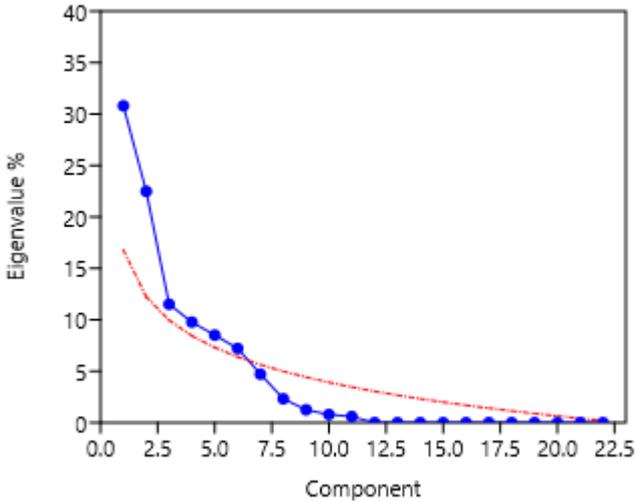
PC	Eigenvalue	% variance
1	3.30781	19.559
2	2.374	14.037
3	1.60866	9.5118
4	1.43292	8.4727
5	1.36396	8.0649
6	0.951918	5.6286
7	0.892115	5.275
8	0.846367	5.0045
9	0.738673	4.3677
10	0.582668	3.4452
11	0.561583	3.3206
12	0.524153	3.0992
13	0.462848	2.7368
14	0.436068	2.5784
15	0.360403	2.131
16	0.285785	1.6898
17	0.151149	0.89372
18	0.0311973	0.18447

Scores

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11	PC 12	PC 13
13	PC 14	PC 15	PC 16	PC 17	PC 18								
NE Italy (this study)			-0.12721		2.9003	0.63892	-1.5918	-2.7851	0.30387	1.9995	-0.29334		
	0.41436	-0.39049		0.036313		0.047574		-0.094303		0.3462	0.32232	-0.091296	
	-0.018373		-0.004209										
Umbria-Marche	-0.3657		0.71126	-0.0089838		-0.87303		-0.4911	-0.23719		-0.2259	-0.27017	
	-0.58781		0.44241	-0.51592		-0.20843		0.78864	-0.645	-2.0645	0.32253	0.064823	
	0.018599												
Sicily	-0.84202		1.0806	0.44821	-1.3027	0.37294	-0.032343		-1.2748	0.53141	0.013476		-
	0.083842		-0.1487	-1.3947	1.2433	-0.99117		1.109	-0.039675		0.02021	0.0090998	
Jbel Tselfat		-1.1218	1.5208	0.70493	-2.0116	0.6951	0.21127	-2.0414	1.1102	0.47034	0.023321		
	0.26198	1.1229	-0.93234		0.72785	-0.17245		0.085089		0.026507		0.0089788	

Agoult	-0.38889	-1.0455	-0.43245	-0.14118	0.22199	-0.2732	0.002388	-0.73242
	-0.7258	-0.64802	-2.2253	1.2128	0.55084	0.40965	0.59997	0.35095
	0.1206	0.036808						
Goulmima (Tur)	-0.46203	-0.89126	-0.34017	-0.0008743	0.14233	-0.083927		
	0.012371	-0.21312	0.032496	-0.39347	-0.058918	-0.034353	-	
	0.23115	-0.14261	-0.23119	-1.8177	0.77348	0.11175		
OT1	-0.44597	-0.8475	-0.31493	-0.00080081	0.12971	-0.072836	0.010611	-
	0.18092	0.026742	-0.30076	-0.044386	-0.025112	-0.15813	-0.09385	-
	0.12815	-0.66145	-1.373	0.26712				
Komen-Kras	-0.83484	-0.97018	4.6487	1.9621	-0.44944	0.058011	-0.055902	
	0.044346	-0.10959	0.23223	0.038648	0.12586	0.023976	-0.037855	
	0.0061892	0.059929	0.027722	0.010272				
Portugal	-0.54769	-0.90453	-0.31702	0.32527	0.20277	-0.35593	-0.053843	
	0.18479	0.006005	-0.99436	-0.2481	-1.9497	-0.5543	1.5181	-0.31559
	0.13547	0.039364					0.48397	
Chalk and other localities (FR)	0.2853	-1.0278	-0.79363	0.42082	0.087581	3.7878	0.29799	
	0.63156	-0.054655	0.36383	-0.014771	-0.028394	0.14466	0.011288	-0.016093
	0.16842	0.063404	0.021154					
Saxony	0.80596	0.99301	-1.8023	2.6751	-2.752	-0.51613	-1.6372	0.41703
	0.10615	0.1944	-0.066269	-0.034079	0.18391	0.053598	0.02774	0.010087
Westphalia	-0.54633	4.2304	-0.45208	2.1153	2.691	-0.017141	0.79689	-0.33315
	-0.015925	-0.028902	-0.014403	0.088104	-0.031989	-0.016	-0.024722	
	-0.0072668	-0.0011459	0.00026781					
Israel (Ein Yabrud, etc.)	-0.60194	-1.3252	-0.67971	0.03127	0.36577	-1.2854	1.6417	2.8868
	0.11394	0.64354	0.1032	0.32541	0.20283	-0.1189	0.093624	0.14699
	0.064315	0.022339						
WIS (Greenhorn, etc.)	7.3148	-0.0033436	0.64242	-0.51509	0.64934	-0.28607	-0.049981	
	0.088055	-0.068564	-0.076252	0.048452	-0.018916	-0.027731		
	0.034466	0.018979	-0.018815	-0.0030396	-0.0001772			
Agua Nueva Fm. (MEX)	-0.55357	-0.40824	-0.34177	-0.82243	0.14691	-0.32358		
	0.14118	-1.2575	-2.038	1.8704	0.58594	-0.2715	-0.67892	0.27842
	0.049846	0.01841						0.51306
								0.071801
Boquillas Fm. (MEX)	-0.43099	-0.80783	-0.29318	-0.00073871	0.11914	-0.064334		
	0.0092894	-0.15717	0.02272	-0.24341	-0.035604	-0.019789	-0.12017	
	-0.069937	-0.08864	-0.40428	-0.36371	-0.68425			
El Doctor Fm. (MEX)	-0.24484	-1.193	-0.4745	-0.091762	0.37172	-0.44551	0.10554	-
	1.2295	2.6773	1.3449	0.11691	0.078524	0.57852	0.42939	0.065376
	0.027011					0.17994	0.079695	
Cintalapa Fm. (MEX)	-0.36318	-0.94484	-0.3666	-0.12464	0.070145	-0.1675		
	0.27354	-0.52929	0.62785	-0.67309	-0.075043	-0.055424	-1.6443	-1.7317
	0.11129	0.70377	0.1764	0.048614				
Eagle Ford Fm. (MEX)	-0.52916	-1.0671	-0.46587	-0.053283	0.21111	-0.19986		
	0.047928	-0.69763	-0.52666	-1.3983	2.0836	0.81063	1.0068	0.12578
	0.4135	0.12909	0.038759					0.017641

Scree plot



Appendix S. 3.1.

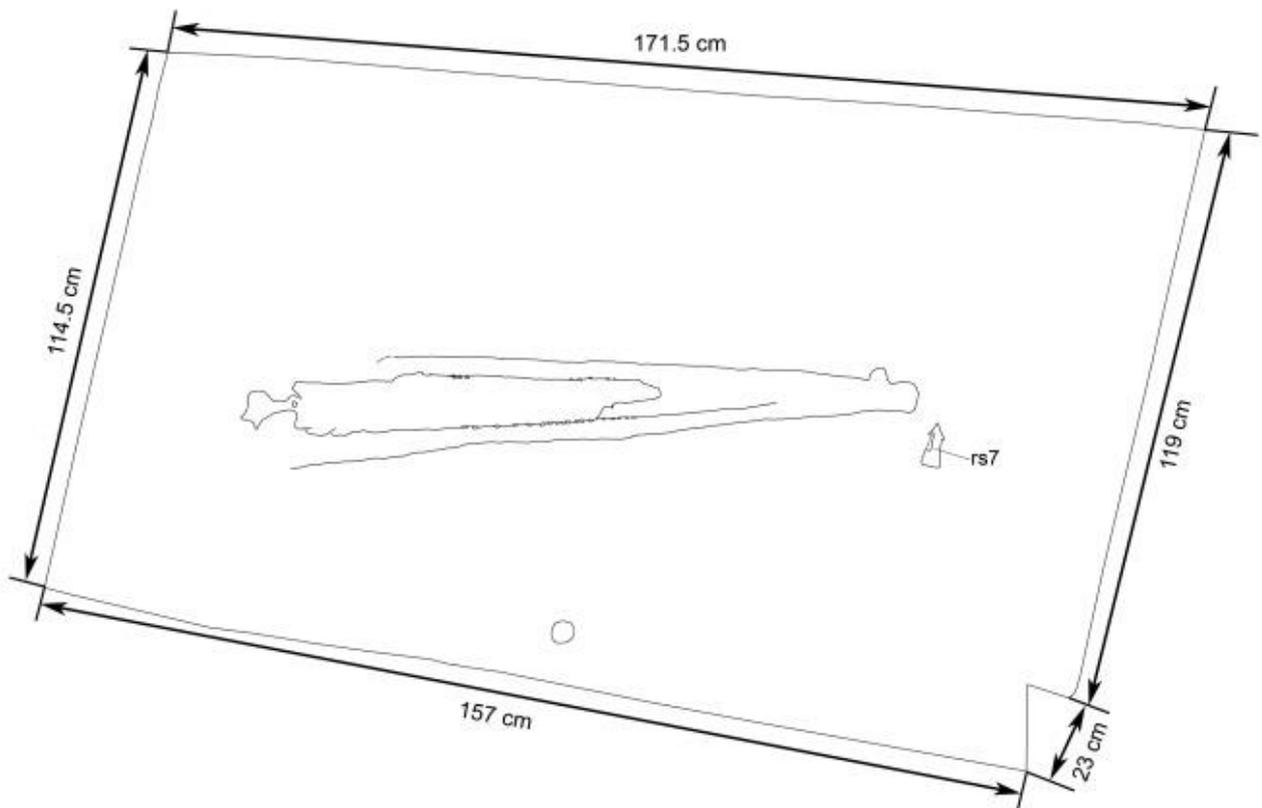
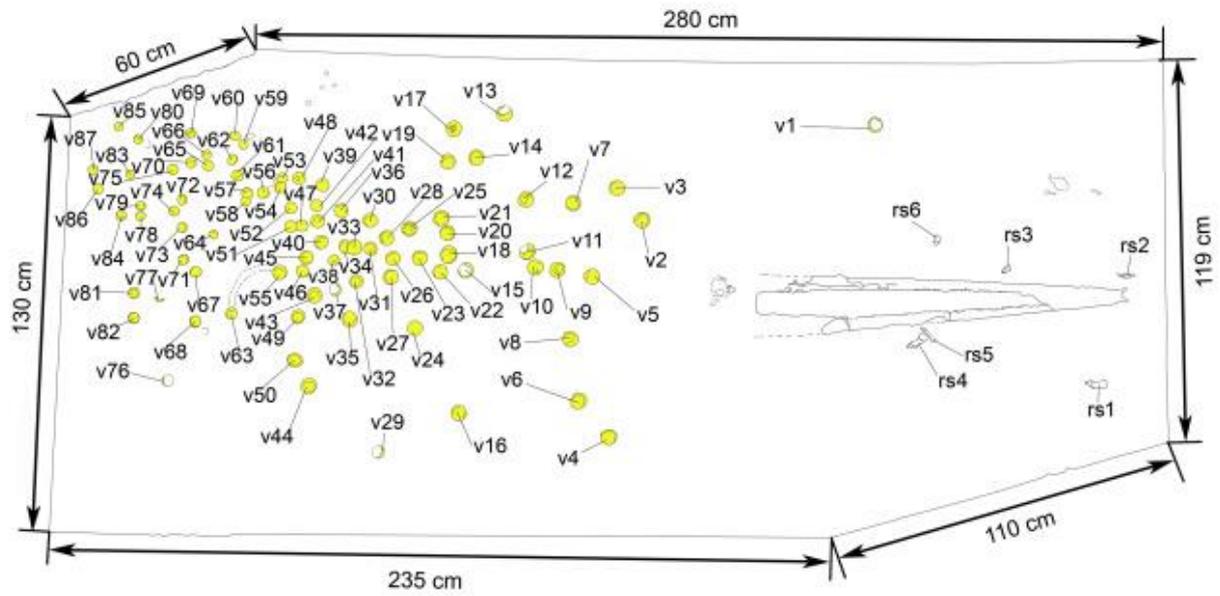


Fig. S1. *Onchosaurus pharao*. Interpretative drawing of IGVR 45303 (above) and 45304 (counterslab; below) with rostral spines and vertebral centra location and the measurements of the two slabs. Vertebral centra are highlighted in yellow. Abbreviations: rs = rostral spine; v = vertebral centrum.

AGE (Ma)	Epoch/Age		Polarity Chron	Planktonic foraminifera	
85	Late Cretaceous	Santonian	C34	<i>Dicarinella asymetrica</i>	
86.3					
		Coniacian			<i>Dicarinella concavata</i>
89.8					
90		Turonian		<i>Marginotruncana schneegansi</i>	
				<i>H. helvetica</i>	
				<i>W. archaeocretacea</i>	
		93.9			

Fig. S2. Dating of IGVR 45303-4. Turonian-Santonian biostratigraphy of planktonic foraminifera after Ogg and Hinnov (2012) and the stratigraphic position of IGVR 45303-4, which is indicated by the grey band.



Fig. S3. *Onchosaurus pharao*. Rostral spines (large size image). **A**, spine no. 1; **B**, spine no. 2; **C**, spine no. 3; **D**, spine no. 4; **E**, spine no. 5; **F**, spine no. 6; **G**, spine no. 7. Abbreviations: as, anterior side; ps, posterior side; cr, crown; p, peduncle; bo, boss; ba, barb.

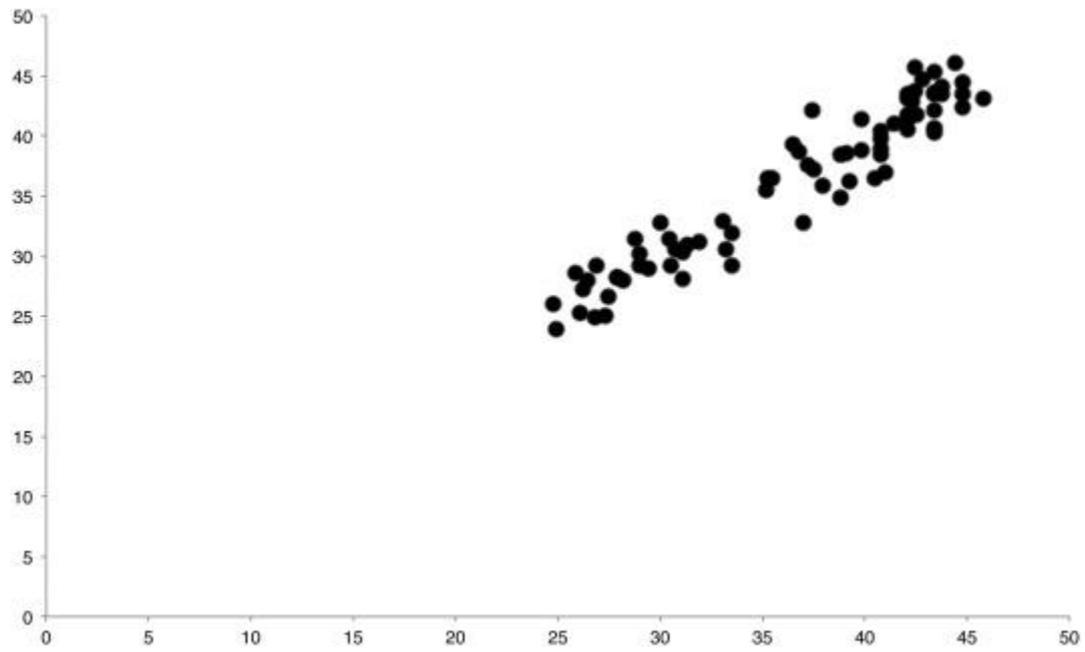


Fig. S4. Linear regression model extrapolated by vertebral measurements in Table 1. The vertebral width (in mm) is on the y-axis: the vertebral height (in mm) is on the x-axis.

Appendix S. 3.2.

Appendix A. Shark teeth measurements (in millimetres). The numbers of the teeth are those reported in Fig.5. Abbreviations: (abn), deformed or abnormal tooth (*sensu* Becker et al. 2000); ant, anterior tooth; CH, crown height; CT, crown thickness (labiolingual); CW, crown width; DCL, distal cutting edge length; lat, lateral tooth; imp, impression only (tooth split away); indet, indeterminate; interm, intermediate tooth; LCH, cusplet height; MCL, mesial cutting edge length; PCH, central cusp height; PCW, central cusp width; TH, tooth height; TW, tooth width; TT, tooth thickness (labiolingual). *Tooth preserved within the turtle remains.

Tooth	Position	TH	TW	TT	CH	CW	CT	LCH	PCH	PCW	MCL	DCL
1	ant	36	-	-	34	37	11	9	29	21	33	33
2	ant (abn)	~50	49	11	-	41	-	9	-	21	-	-
3	ant	69	52	22	51	46	16	16	39	27	42	41
4	ant?	-	-	-	36	-	-	-	31	19	36	36
5	ant?	-	-	-	34	-	-	-	31	20	35	35
6	ant	41	-	21	33	-	10	-	-	-	-	-
7	ant(abn)	60	51	17	-	48	14	16	28	31	34	29
8	lat	60	62	22	-	52	18	-	-	-	-	-
9	ant (abn)	~58	52	19	~48	42	14	16	~32	28	-	-
10	ant (abn)	56	55	18	~49	48	10	12	31	15	30	30
11	ant	66	52	21	-	-	17	-	31	26	38	31
12	ant	-	46	21	-	41	15	14	-	24	-	-
13	ant	61	47		53	43	-	17	39	22	41	40
14	ant	57	42	23	49	39	-	14	36	21	39	36
15	ant	~67	-	16	~53	-	12	13	~35	28	~39	~33
16	interm	~48	36	10	34	25	6	11	22	11	26	24
17	imp	-	-	-	-	-	-	-	-	-	-	-
18	imp	-	-	-	-	-	-	-	-	-	-	-
19	ant	-	-	-	-	-	-	-	29	-	-	-
20	lat	55	39	17	31	37	9	10	27	24	30	24
21	lat?	-	44	21	-	39	11	11	-	22	-	-
22	ant (abn)	54	38	19	42	35	10	9	29	22	31	31
23	ant	-	-	-	45	45	-	16	42	25	37	35
24	lat (abn)	51	50	14	48	46	10	14	29	20	37	31
25	lat?	-	44	18	-	-	-	16	-	-	-	-
26	ant	-	-	-	-	-	-	-	30	20	31	28
27	ant	-	-	-	-	-	-	-	23	19	25	22
28	ant	-	-	-	52	48	-	16	39	26	43	41
29	ant	49	40	-	42	38	-	13	29	16	32	31
30	ant	-	40	25	-	38	16	12	-	22	-	-
31	ant	-	-	-	-	-	-	-	38	-	-	-
32	ant (abn)	-	40	15		37	11	13	-	24	-	-
33	lat (abn)	54	39	15	43	37	11	12	26	22	29	26
34	lat	-	-	-	-	-	-	-	~29	-	-	-
35	ant (abn)	-	42	21	-	39	12	15	-	-	-	-

36	ant	-	-	-	-	-	-	-	37	-	35	34
37	lat	51	-	-	43	-	-	14	30	20	36	36
38	lat	-	-	-	-	-	-	-	32	~22	36	30
39	lat	-	-	-	-	-	-	-	31	-	-	-
40	ant?	46	38	-	-	-	-	-	-	-	-	-
41	ant	-	-	-	45	-	12	13	33	24	35	34
42	lat	-	47	20	-	42	11	17	-	-	-	-
43	lat	-	-	-	38	36	8	12	27	19	31	24
44	lat?	-	-	-	-	-	-	10	-	-	-	-
45	ant?	-	-	-	-	-	-	-	-	-	-	-
46	ant	50	49	-	47	41	12	14	31	-	36	36
47	indet (abn)	-	-	-	-	-	-	-	-	-	-	-
48	lat	50	42	16	39	40	10	13	29	20	37	31
49	indet	-	-	-	-	-	-	-	-	-	-	-
50	ant	-	-	-	46	44	9	16	32	20	30	29
51	lat	49	-	-	40	45	7	12	26	21	28	28
52	ant	48	-	-	-	-	10	-	32	-	35	35
53	ant	~46	45	15	~42	42	9	15	30	25	~36	~32
54	lat	53	48	19	-	-	12	-	-	-	36	-
55	indet	-	-	-	-	-	-	-	-	-	-	-
56	lat	-	-	-	-	-	7	-	37	-	-	-
57	ant	-	-	-	-	~35	-	16	30	-	33	-
58	lat (abn)	-	-	-	25	-	8	10	22	20	33	23
59	lat	54	44	-	47	38	-	14	30	18	33	31
60	lat	58	41	14	49	38	9	14	28	20	33	27
61	lat	-	-	-	42	45	-	12	26	25	37	28
62	lat	53	50	-	47	45	-	12	28	20	35	29
63	ant	-	-	-	-	-	-	-	27	-	-	-
64	ant	-	-	-	38	38	9	16	30	18	30	29
65	indet	-	-	-	-	-	-	-	-	-	-	-
66	indet (abn)	-	-	-	-	-	-	-	-	-	-	-
67	lat	-	-	-	-	-	-	-	25	-	-	-
68	indet	-	-	-	-	-	-	-	-	-	-	-
69	ant?	-	-	-	-	-	-	-	-	-	-	-
70	lat	50	-	18	37	-	11	9	22	25	30	21
71	lat	40	-	15	34	-	-	-	29	23	30	28
72	lat	44	-	-	39	-	-	12	25	19	33	25
73	lat	50	44	~17	43	42	-	12	24	19	31	21
74	lat	53	~40	15	47	-	10	13	28	21	33	30
75	indet	-	-	-	-	-	-	-	-	-	-	-
76	ant	-	-	17	37	-	-	13	29	23	30	30
77	lat	-	-	-	-	-	-	-	22	-	29	24
78	ant	-	-	-	-	-	9	-	30	-	37	37
79	indet	-	-	-	-	-	-	-	-	-	-	-

80	ant	-	-	-	-	-	12	-	-	-	-	-
81	lat	32	34	12	30	30	8	9	18	17	22	17
82	lat	-	42	13	-	38	9	12	-	18	-	-
83	lat?	38	-	16	24	-	8	-	20	-	23	23
84	lat	40	-	18	-	-	11	-	20	20	28	20
85	lat	54	-	16	45	-	12	-	31	23	34	26
86	indet	-	-	-	-	-	-	-	-	-	-	-
87	indet	-	-	-	-	-	-	-	-	-	-	-
88	lat	41	43	15	-	-	11	-	23	17	25	22
89	lat	38	44	10	33	39	8	14	23	18	25	22
90	lat	46	39	13	25	36	8	12	19	24	26	18
91	ant	-	-	-	-	-	-	-	~23	-	~24	~24
92	post	-	-	13	22	21	6	9	15	-	13	12
93	lat	-	-	-	-	-	8	-	17	15	22	18
94	lat	32	35	7	22	32	-	10	17	14	20	14
95	lat	-	40	11	36	34	9	11	26	18	30	25
96	lat	-	-	-	36	-	9	-	32	23	34	25
97	post	19	18	-	12	18	-	6	9	10	12	8
98	post	34	35	-	-	-	-	-	17	13	28	17
99	post	-	-	-	-	-	-	5	8	10	11	9
100	post	-	-	-	-	-	-	3	4	7	6	5
101	lat	-	-	-	-	-	-	9	17	19	26	22
102	lat	-	-	-	-	-	4	-	20	15	22	19
103	lat	36	39	20	34	32	9	10	18	18	25	16
104	post	16	23	-	11	21	-	6	6	10	10	7
105	post?	30	26	14	24	24	6	8	16	14	14	14
106	lat	-	33	19	-	-	~9	-	-	-	-	-
107	post	-	-	-	17	-	8	9	12	10	13	11
108	ant	49	37	14	41	35	10	-	28	19	38	38
109	lat?	-	-	-	-	-	6	-	27	-	30	25
110	ant	-	-	-	-	-	-	-	29	20	32	32
111	lat *	55	-	19	-	-	10	12	26	27	36	23
112	lat	-	-	-	-	-	-	-	32	20	33	28
113	lat	-	-	-	-	-	11	-	-	-	30	28
114	lat	-	-	-	-	-	-	-	21	19	29	20
115	lat	-	-	-	-	-	-	-	-	-	-	-
116	lat	-	-	-	-	-	9	-	22	18	25	20
117	ant	-	-	15	-	-	-	-	34	22	35	29
118	ant?	-	-	-	-	-	-	-	-	-	-	-
119	ant	-	-	-	-	-	10	-	35	18	39	34
120	lat	-	-	-	-	-	-	-	19	17	23	19

Becker, M. A., Chamberlain, J. A., Stoffer, P. W. (2000). Pathologic tooth deformities in modern and fossil chondrichthians: a consequence of feeding-related injury. *Lethaia*, 33(2), 103-118.

Appendix B. Measurements of the vertebral centra (in millimetres). Centra A are from slab A, while centra B are from slab B (numbers are progressive; see Fig. 10).

Centrum	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11
Diameter	53	58	64	~80	~80	86	85	86	87	90	88
Thickness	-	-	-	34	-	38	-	-	-	40	-
	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22
	94	94	86	-	~139	-	~134	~125	~127	~129	~113
	-	-	-	36	38	37	37	35	34	38	34
	A23	A24	A25	A26	A27	A28	A29	A30	A31	A32	A33
	~119	~126	~120	~122	~129	94	~113	~113	98	~103	~112
	~35	~30	~35	~32	~32	-	-	-	-	-	~30
	A34	A35	A36	A37	A38	A39	A40	A41	A42	A43	A44
	~130	~110	~110	~102	112	~100	~92	~106	-	112	~106
	~30	34	~30	~33	28	-	-	-	-	-	-
	A45	A46	A47	A48	A49	A50	A51	B1	B2	B3	B4
	108	115	109	111	~102	101	93	79	78	-	77
	-	-	-	-	-	-	-	-	-	-	-
	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
	~75	~80	~74	~73	~74	74	75	~71	76	75	75
	-	-	-	-	-	-	-	-	-	-	-
	B16	B17	B18	B19	B20	B21	B22	B23	B24	B25	B26
	~75	~74	73	73	71	-	48	50	47	39	-
	-	-	-	-	-	-	-	-	-	-	24
	B27	B28	B29	B30	B31	B32	B33	B34	B35		
	-	-	44	36	35	34	28	28	28		
	23	24	-	-	-	-	-	15	18		

Appendix S. 3.3.

Table A.1. Main calcareous plankton taxa and biostratigraphic classification.

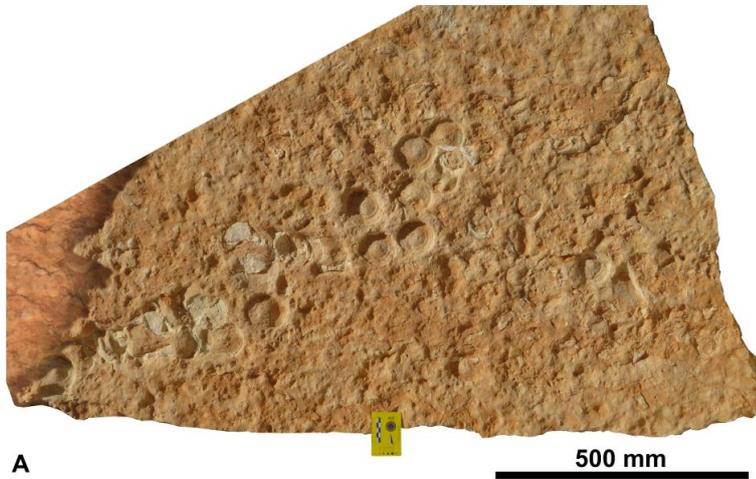
SAMPLE	TAXON	LOCALITY	LITHOZONE	PLANKTON BIOSTRATIGRAPHY			
				Calcareous nannofossil assemblage	NANNOS (Burnett, 1998).	Planktic foraminiferal assemblage	FORAMS (Coccioni & Premoli Silva, 2015)
MCSNV V. 3995	Associated tooth set of <i>Ptychodus</i> <i>altior</i>	Monte Loffa (S. Anna d'Alfaedo, Verona)	Lastame (Scaglia Rossa Fm.)	<i>Watznaueria</i> spp. (A); <i>Zeugrhabdotus</i> <i>birescenticus</i> (F); <i>Chiastrzygus</i> spp. (R); <i>Cribrosphaerella</i> <i>ehrenbergii</i> (R); <i>Eprolithus floralis</i> (RR); <i>Eprolithus moratus</i> (R); <i>Eiffelithus eximius</i> (R) ; <i>Quadrum gartneri</i> (R); <i>Prediscosphaera</i> spp. (R)	UC8-UC9 Zone. Concomitant presence of <i>E.</i> <i>eximius</i> and absence of <i>Micula</i> <i>staurophora</i> . The vacancy of <i>Lithastrinus</i> <i>septenarius</i> could be an ecological exclusion. Hence, its stratigraphical absence cannot be confirmed.	<i>Marinotruncana sigali</i> (F); <i>M. schneegansi</i> (R); <i>M. renzi</i> (F); <i>M. pseudoinneiana</i> (R); <i>Dicarinella algeriana</i> (F); <i>D. canaliculata</i> (F); <i>Whitella aprica</i> (R) <i>Heterohelix</i> spp. (C); <i>Muricohedbergella</i> <i>planispira</i> (C); <i>M. delrioensis</i> (C); <i>Macroglobigerinelloides</i> spp. (F)	<i>Dicarinella primitiva</i> / <i>Marginotruncana</i> <i>sigali</i> Zone: occurrence of marginotruncanids and dicarinellids in absence of <i>Helvetoglobotruncana</i> <i>helvetica</i> and <i>Dicarinella</i> <i>concovata</i> , markers of the total range zones underlying and overlying.

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

Appendix S. 3.4.

Supplementary material

Fig. A.1 α - λ : Specimens described and not figured in the main text



MGC:

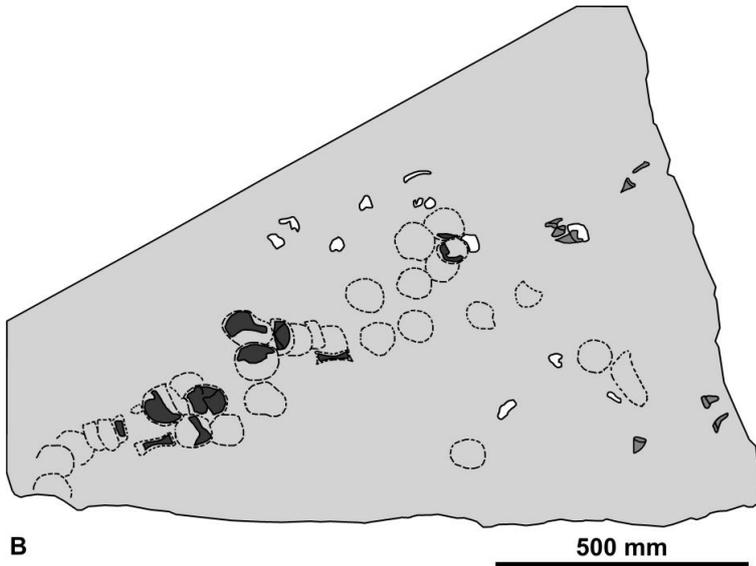


Fig. A.1 α . *Cretoxyrhina mantelli* (Agassiz 1835). MGC-IGVR 81376. A. Photo of MGC-IGVR 81375. B. Line drawing of MGC-IGVR 81376. Colors map: dark gray = vertebral centra; gray = teeth; light gray = rocky matrix; white = fragments of tessellated cartilage. Dashed lines delimit imprints of teeth and vertebrae. Scale bars = 500 mm.

MPPSA:

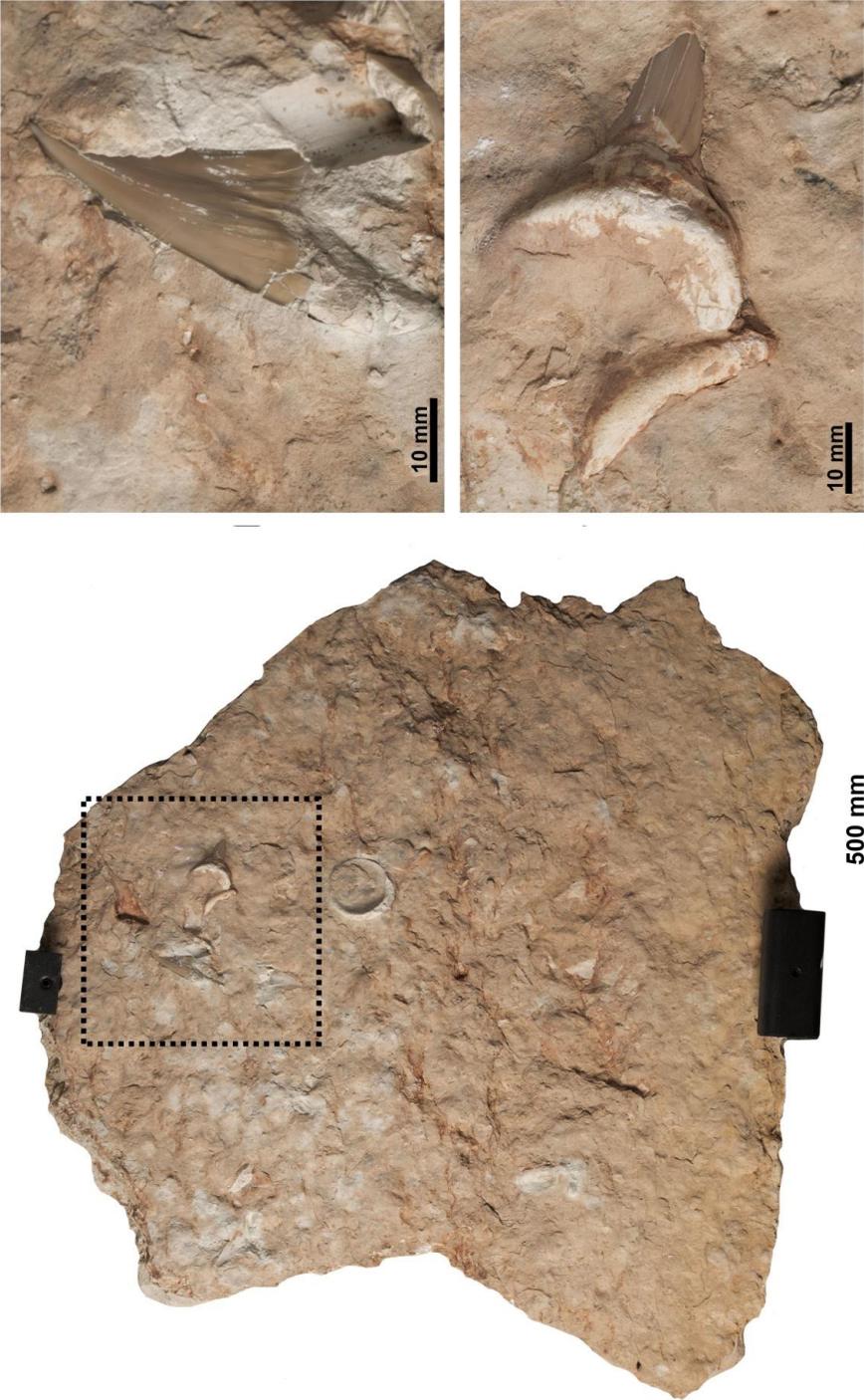


Fig. A.1β. *Cretoxyrhina mantelli* (Agassiz, 1835). MSNVR IGVR 45324. Dashed lines indicate the areas where teeth are located.

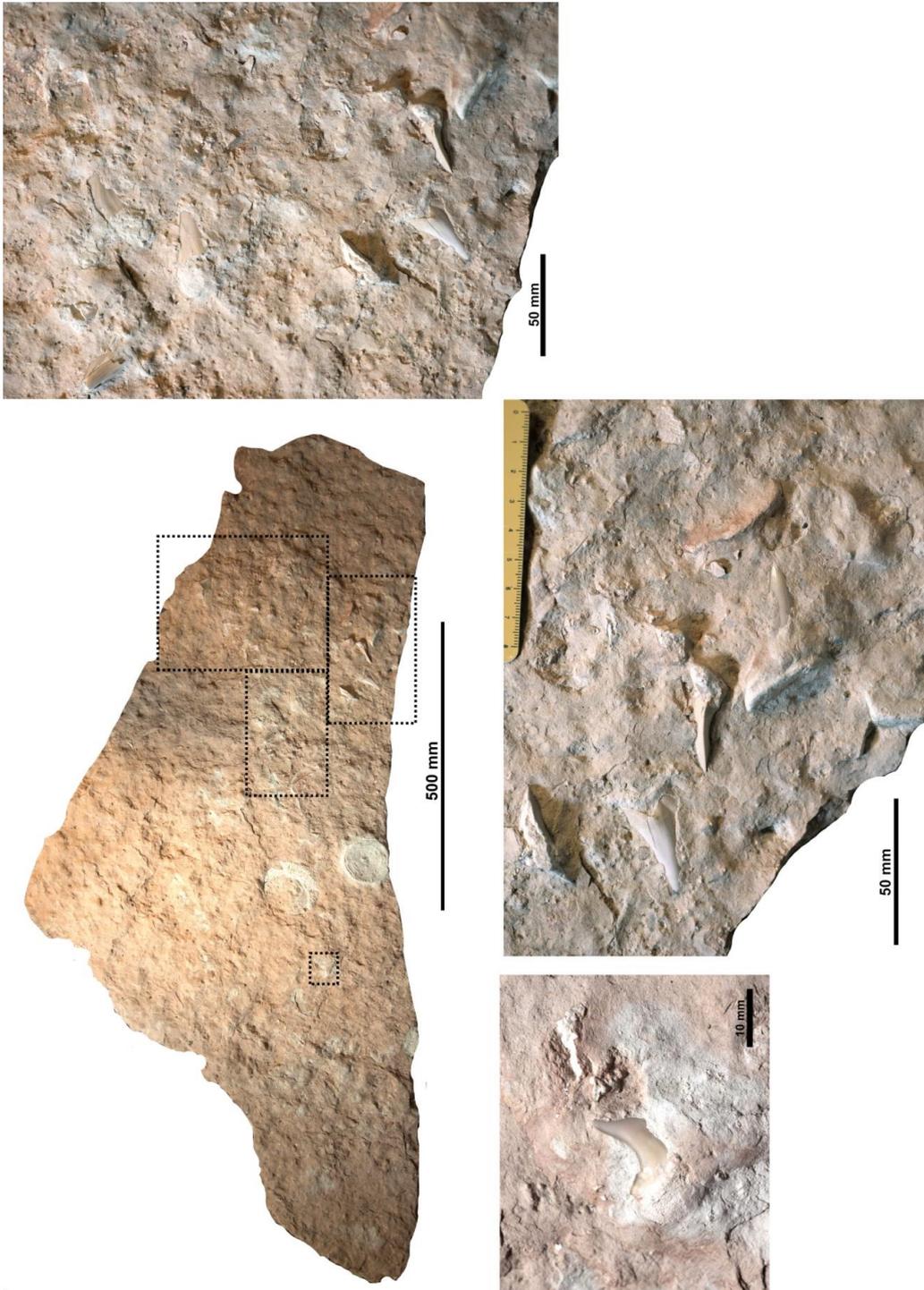


Fig. A.1γ. *Cretoxyrhina mantelli* (Agassiz, 1835). MSNVR IGVR 45326. Dashed lines indicate the areas where teeth are located.

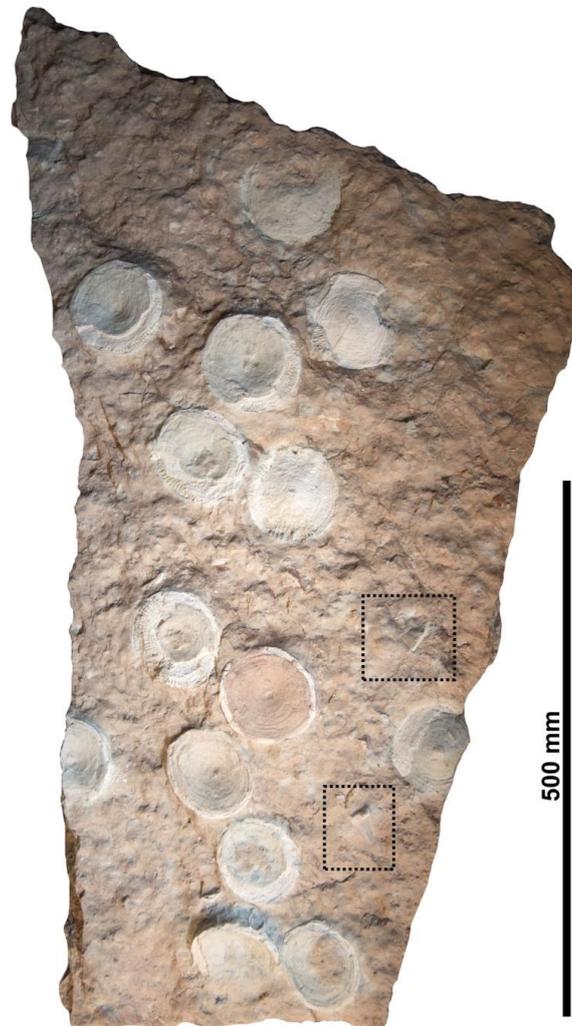


Fig. A.1δ. *Cretoxyrhina mantelli* (Agassiz, 1835). MSNVR IGVR 45334. Dashed lines indicate the areas where teeth are located.

Fig. A.1ε. ?*Cretoxyrhina* sp. MSNVR IGVR 45321.

Below.



Fig. A.1ζ. ?*Cretoxyrhina* sp. MSNVR IGVR 45322.

Below.



Fig. A.1η. ?*Cretoxyrhina* sp. MSNVR IGVR 45337. Dashed lines indicate the areas where vertebrae are located.



MGP-PD:



Some of the isolated teeth from historical collections:

**Fig. A.10. *Cretoxyrhina mantelli* (Agassiz, 1835).
MGP-PD 3805.**



Fig. A.1ι. *Cretoxyrhina mantelli* (Agassiz, 1835). MGP-PD 7343 C.



Fig. A.1κ. *Cretoxyrhina mantelli* (Agassiz, 1835). MGP-PD 8889.

Fig. A.1λ. *Cretoxyrhina mantelli* (Agassiz, 1835). MGP-PD 14020.



Table A.1. Tooth measurements MPPSA IGVR 36371. Abbreviations: **ID**: tooth position identification; **TH**: total height; **CH**: crown height; **TW**: total width; **CW**: crown width; **ML**: mesial cutting edge length; **DL**: distal cutting edge length. Abbreviations follow Shimada (1997a). The slash (/) indicates alternative identification in tooth position. Measurements are in millimetres. Hyphen (-) indicates a missing or no measurable datum.

Teeth N.	ID	TH	CH	TW	CW	ML	DL	Notes
1	Ind.	-	-	-	25	35	30	crown only, broken apex, purported measurements
2	Ind.	-	-	-	22	-	-	crown only, broken
3	A2	37	30	28	24	32	32	not functional tooth, distal cusplet?
4	L2	48	41	43	39	50	41	complete, not functional
5	Ind.	-	-	-	-	-	-	crown only, broken
6	L/1	42	-	42	-	-	-	imprint
7	Ind.	-	-	-	-	-	-	partial imprint
8	Ind.	34	-	-	-	-	-	imprint
9	Ind.	39	33	18	-	31	27	imprint with enamel remains
10	Ind.	-	21	-	-	-	-	imprint
11	I1	30	26	17	14	28	24	complete, not functional
12	L1	49	42	41	38	51	38	complete, not functional
13	Ind.	-	-	-	-	-	-	partial imprint
14	L/1?	54	45	42	38	51	39	complete, functional
15	1	32	24	30	25	30	25	functional?
16	A1	49	44	45	41	47	35	root + crown imprint, functional?
17	L3/13		49		39	51	38	crown only
18	Ind.	26	17	25	16	19	12	broken apex, lacking distal root lobe
19	Ind.	-	-	-	-	-	-	broken crown, no root
20	Ind.	-	39	-	37	45	32	crown only, broken apex
21	A1	64	52	39	31	53	52	complete, functional
22	a2	64	50	43	39	55	45	complete, functional
23	A/a	55	50	25	22	52	48	imprinta
24	a1	67	52	35	28	57	53	complete, functional

Tooth N.	ID	TH	CH	TW	CW	ML	DL	Notes
25	Ind.	-	-	-	-	-	-	crown fragment + imprint
26	L/1	-	-	40	-	-	-	imprint
27	A1/A2	51	44	-	-	41	-	imprint
28	L/1	-	-	30	28	-	-	imprint
29	A2	-	57?	-	-	-	-	imprint with enamel remains
30	A1	48	44	34	30	47	41	crown complete, root poorly preserved
31	Ind.	-	-	41	-	-	-	root imprint
32	l3	-	-	35	-	-	-	root imprint
33	Ind.	-	-	33	-	-	-	root imprint
34	i?/a3?	51	44	39	36	47	38	complete, functional
35	Ind.	-	-	38	35	-	-	broken crown, well-developed root
36	Ind.	-	-	-	-	-	-	imprint
37	A1/a1	44	37	-	25	39	36	complete, not functionale, root poorly preserved

Table A.2. Tooth measurements IGVR 45305. Abbreviations: **Tooth N.:** tooth number; **ID:** tooth position identification; **TH:** total height; **CH:** crown height; **TW:** total width; **CW:** crown width; **ML:** mesial cutting edge length; **DL:** distal edge length. Abbreviations follow Shimada (1997a). The slash (/) indicates alternative identification in tooth position. Measurements are in millimetres. Hyphen (-) indicates a missing or no measurable datum.

Teeth N.	ID	TH	CH	TW	CW	ML	DL	Notes
1	Ind.	-	44	-	36	52	43	crown only
2	L/I	-	-	-	25	-	-	crown only, broken
3	Ind.	-	-	30	25	-	-	nearly complete, crown apex broken
4	Ind.	25	20	17	14	20	19	crown only
5	L/I	-	37	-	28	41	33	crown only
6	L/I	38	31	-	26	38	30	crown only
7	L/I	-	29?	-	30	-	-	crown only, broken
8	Ind.	-	31	-	-	-	-	crown only
9	L2	45	37	29	24	43	36	nearly complete
10	I2	17	6	12	9	9	7	complete, functional
11	Ind.	11	-	-	-	-	-	crown only
12	I1	33	29	33	27	34	26	complete
13	L/I dist.	15	9	20	17	15	10	complete
14	L/I dist.	17	15	20	18	23	13	complete
15	L/I	-	29	-	24	-	27	crown only
16	L/I	-	31	-	-	-	29	crown only
17	L1/I1	-	36	-	32	46	33	crown only
18	L/I dist.	23	15	22	20	23	15	complete
19	L/I dist.	25	20	23	20	28	18	complete, not funzionale
20	L/I dist.	15	11	17	16	19	11	complete, not functional
21	Ind.	-	32	-	20	34	31	crown only
22	L/I dist.	-	14	-	19	20	14	crown only
23	L1	52	36	34	24	38	37	complete, functional
24	L2/I2	-	-	37	34	-	-	broken crown, functional

Tooth N.	ID	TH	CH	TW	CW	ML	DL	Notes
25	L2/I2	44	33	32	25	37	32	complete, broken apex
26	I2/L dist.	24	19	18	13	21	18	complete
27	I2	10	6	11	8	9	6	complete, functional
28	I2	-	11	-	11	11	8	crown only
29	L/I dist.	-	4	-	6	6	4	crown only
30	Ind.	39	29	-	16	29	28	broken root
31	L/I dist.	-	13	-	18	20	11	crown only
32	L/I	-	38	-	30	51	40	crown only
33	L/I dist.	-	24	-	19	32	20	crown imprint
34	L2/I2	-	21	-	12	21	20	crown only
35	L1/I1	58	42	46	32	47	35	complete, functional
36	Ind.	-	-	-	21	-	-	crown only, broken
37	L/I dist.	8	5	7	5	5	4	complete
38	L1/I1	-	-	37	30	-	-	broken crown, functional
39	Ind.	-	39	-	-	-	-	crown only
40	L1/I1	-	-	28	26	-	-	broken crown, functional
41	Ind.	-	-	-	-	-	-	crown only, broken
42	Ind.	-	-	-	-	-	-	crown only, broken
43	L/I dist.	21	12	22	18	22	10	complete, functional
44	L/I dist.	37	26	32	27	35	25	complete, functional
45	L/I	39	28	31	28	32	30	complete, functional
46	A2/a2	44	32	36	30	41	30	complete, functional
47	Ind.	-	-	-	-	-	-	crow only, damaged
48	Ind.	-	-	-	-	-	-	crown only, damaged
49	Ind.	-	-	-	-	-	-	crown only, damaged

Tooth N.	ID	TH	CH	TW	CW	ML	DL	Notes
50	L dist.	13	11	17	15	20	9	complete, functional
51	L dist.	-	10	-	11	11	11	crown only
52	a3	45	36	40	34	35	45	imprint, functional
53	Ind.	-	41	-	-	-	-	crown only, broken base
54	L/l	50	37	41	34	40	40	imprint
55	a3/11	-	35	-	23	38	38	crown only

Appendix S. 3.5.

Table A.1. Examined specimens of *Ptychodus*, housed in several museums in Northern Italy and in the Natural History Museum, London; some of these belong to different historical collections (B, ‘Brocchi collection’; C, ‘Catullo collection’; M, ‘Mantell collection’; Z, ‘De Zigno Collection’).

Catalogue number	Description	Previous determination	Provenance	Worn teeth
MCBG 4048	Five articulated and two associated teeth	<i>Ptychodus</i> sp.	Possibly Castellavazzo (Belluno)	
MCBG 4050-Br	Detached tooth and four associated teeth	<i>Ptychodus</i>	Possibly Castellavazzo (Belluno)	✓
MCBL 677	Badly preserved tooth with matrix	Undetermined	Possibly Castellavazzo (Belluno)	✓
MCSNV v.11791	Tooth with matrix	<i>Ptychodus</i> ?	Mt. Loffa (Verona)	
MCSNV v.12507	Detached tooth	<i>Ptychodus polygyrus</i>	Mazzurega (Verona)	
MCSNV v.12508	Two detached teeth	<i>Ptychodus polygyrus</i>	Possibly Lessini Mountains	
MCSNV v.12528	Well-preserved tooth	<i>Ptychodus polygyrus</i>	S. Anna d’Alfaedo (Verona)	
MGP-PD 6717-Z	Tooth with matrix	<i>Ptychodus latissimus</i>	Castellavazzo (Belluno)	✓
MGP-PD 6718-Z	Tooth with matrix	<i>Ptychodus latissimus</i>	Castellavazzo (Belluno)	✓
MGP-PD 6720-Z	Four associated teeth	<i>Ptychodus polygyrus</i>	Breonio (Verona)	
MGP-PD 7345-C	Tooth with matrix	<i>Ptychodus latissimus</i>	Breonio (Verona)	✓
MGP-PD 8494-C	Tooth with matrix	<i>Ptychodus</i> sp.	Castellavazzo (Belluno)	
MGP-PD 8497-C	Tooth with matrix	<i>Ptychodus latissimus</i>	Breonio (Verona)	
MGP-PD 13531	Several associated teeth	<i>Ptychodus polygyrus</i>	Mazzan sopra Negrar (Verona)	
MGP-PD 13532	Several associated teeth	<i>Ptychodus polygyrus</i>	Mazzan sopra Negrar (Verona)	

MGP-PD 13533	Badly preserved tooth with matrix	<i>Ptychodus polygyrus</i>	Mazzan sopra Negrar (Verona)	
MGP-PD 13534	Tooth with matrix	<i>Ptychodus polygyrus</i>	Negrar (Verona)	
MGP-PD 13535	Tooth with matrix	<i>Ptychodus polygyrus</i>	Mazzan sopra Negrar (Verona)	
MGP-PD 13536	Tooth with matrix	<i>Ptychodus polygyrus</i>	Mazzan sopra Negrar (Verona)	
MGP-PD 14040	Badly preserved tooth with matrix	<i>Ptychodus latissimus</i>	Val Cismon (Belluno/Trento)	✓
MMC PTY01	Detached tooth	<i>Ptychodus mediterraneus</i>	Chiampo (Vicenza)	✓
MMC PTY02	Detached tooth	<i>Ptychodus mediterraneus</i>	Chiampo (Vicenza)	✓
MPPSA IGVR 91031	Articulated and associated teeth with skeletal remains	<i>Ptychodus cf. latissimus</i>	S. Anna d'Alfaedo (Verona)	✓
MSNPS 274	Several associated teeth and tooth fragment	<i>Ptychodus latissimus</i>	Mazzan sopra Negrar (Verona)	
MSNPS I-17373	Articulated and associated teeth with skeletal remains	<i>Ptychodus mediterraneus</i>	Gallio (Vicenza)	✓
NHMUK PV OR P4369-M	Detached tooth	<i>Ptychodus latissimus</i>	Lewes, Sussex (UK)	
NHMUK PV OR P4372-M	Detached tooth	<i>Ptychodus latissimus</i>	Lewes, Sussex (UK)	✓
NHMUK PV P75453-M	Detached tooth	<i>Ptychodus latissimus</i>	Lewes, Sussex (UK)	
NHMUK PV P4408-M	Detached tooth	<i>Ptychodus polygyrus</i>	Lewes, Sussex (UK)	
NHMUK PV P4410-M	Detached tooth	<i>Ptychodus polygyrus</i>	Lewes, Sussex (UK)	✓

Table A.2. Measurements of teeth of *Ptychodus mediterraneus* belonging to upper and lower dental plates of the specimen MHNUP-I-17373. P = placement within the dental plate (see interpretative line drawing in Fig. 9,10); CW, Crown width; CL, Crown length; CH, Crown height; RW, root width; RL, root length; RH, root height; nTR, number of transverse ridges. Except for nTR, all measurements in millimetres. Estimated values are indicated in parentheses.

Upper dentition							
Row M							
P	CW	CL	CH	RW	RL	RH	nTR
M1	(12)	20	4	10	-	11	2
M2	13	20	-	-	-	-	2
M3	(13)	-	7	12	-	11	3
M4	(13)	-	-	-	-	-	2
M5	13	20	6	11	16	-	2
M6	(13)	(21)	-	-	-	-	4
M7	14	(20)	-	-	-	-	2
M8	(13)	-	-	-	-	-	3
M9	(13)	(21)	-	-	-	-	3
Row L1							
P	CW	CL	CH	RW	RL	RH	nTR
A1	47	29	-	-	-	-	8
A2	47	29	-	-	-	-	8
A3	46	27	-	-	-	-	8
A4	-	29	-	-	-	-	8
A5	47	30	-	-	-	-	8
A6	50	30	10	42	24	13	10
A7	49	29	-	-	-	-	8
A8	48	29	-	-	-	-	8
A9	47	29	-	-	-	-	8
A10	47	(28)	-	-	-	-	9
A11	49	(28)	-	-	-	-	9
A12	47	-	-	-	-	-	8
A13	46	27	-	-	-	-	9
A14	-	-	-	-	-	-	8
A15	-	-	-	-	-	-	10
A16	-	-	-	-	-	-	8
A17	46	31	-	-	-	-	10
1A	46	28	-	-	-	-	9
2A	46	31	-	-	-	-	8
3A	45	-	-	-	-	-	8
4A	45	29	-	-	-	-	8

5A	48	31	10	37	27	12	9
6A	48	31	-	-	-	-	9
7A	-	28	-	-	-	-	10
8A	(47)	-	-	-	-	-	8
9A	(44)	(25)	-	-	-	-	8
10A	42	-	-	-	-	-	8
11A	45	27	-	-	-	-	8
12A	44	25	-	-	-	-	8
13A	44	-	-	-	-	-	8
14A	-	29	-	-	-	-	8
15A	44	31	-	-	-	-	8
Row L2							
P	CW	CL	CH	RW	RL	RH	nTR
B1	33	26	-	-	-	-	8
B2	-	26	-	-	-	-	8
B3	31	25	-	-	-	-	9
B4	34	-	-	-	-	-	9
B5	34	25	10	27	19	11	9
B6	32	-	-	-	-	-	7
B7	32	25	-	-	-	-	8
B8	32	24	12	26	18	9	8
B9	33	24	-	-	-	-	8
B10	33	-	-	-	-	-	8
B11	-	-	-	-	-	-	8
B12	32	-	-	-	-	-	7
B13	31	24	-	-	-	-	7
B14	-	-	-	-	-	-	7
B15	32	25	-	-	-	-	8
B16	31	25	-	-	-	-	9
B17	32	25	-	-	-	-	-
1B	33	24	-	-	-	-	7
2B	-	-	-	-	-	-	-
3B	31	27	-	-	-	-	9
4B	32	-	-	-	-	-	7
5B	-	26	11	29	24	10	9
6B	34	26	-	-	-	-	7
7B	34	24	-	-	-	-	7
8B	33	25	-	-	-	-	7
9B	33	-	-	-	-	-	7
10B	33	-	-	-	-	-	7
11B	33	-	-	-	-	-	7
12B	32	-	-	-	-	-	7
13B	32	27	-	-	-	-	-

14B	32	25	-	-	-	-	-
Row L3							
P	CW	CL	CH	RW	RL	RH	nTR
C1	-	24	-	-	-	-	7
C2	-	23	-	-	-	-	8
C3	-	23	-	-	-	-	8
C4	-	-	-	-	-	-	8
C5	26	23	-	-	-	-	8
C6	26	-	-	-	-	-	7
C7	26	24	11	22	20	8	7
C8	27	25	-	-	-	-	8
C9	27	24	-	-	-	-	7
C10	-	24	-	-	-	-	7
C11	-	-	-	-	-	-	8
C12	-	23	-	-	-	-	-
C13	-	-	-	-	-	-	-
C14	-	24	8	-	21	9	-
C15	-	22	-	-	-	-	8
C16	-	-	-	-	-	-	8
C17	-	-	-	-	-	-	-
1C	-	-	-	-	-	-	-
2C	25	24	-	-	-	-	7
3C	26	24	-	-	-	-	8
4C	26	22	-	-	-	-	7
5C	26	21	-	-	-	-	-
6C	-	23	-	-	-	-	8
7C	-	-	-	-	-	-	8
8C	-	-	-	-	-	-	-
9C	-	23	-	-	-	-	8
10C	27	23	10	24	18	7	7
11C	26	22	-	-	-	-	7
12C	25	24	-	-	-	-	8
Row L4							
P	CW	CL	CH	RW	RL	RH	nTR
D1	25	21	-	-	-	-	7
D2	25	20	-	-	-	-	6
D3	-	18	-	-	-	-	7
D4	23	19	-	-	-	-	7
D5	23	20	-	-	-	-	7
D6	-	-	-	-	-	-	-
D7	24	19	-	-	-	-	6
D8	-	-	-	-	-	-	6
D9	23	19	-	-	-	-	7

D10	-	17	-	-	-	-	6
D11	23	19	-	-	-	-	7
D12	24	20	-	-	-	-	6
D13	23	20	-	-	-	-	-
D14	23	19	-	-	-	-	7
D15	23	20	7	20	15	8	6
D16	25	20	7	22	15	9	6
D17	25	18	7	23	14	7	7
D18	-	18	-	-	-	-	7
D19	23	-	-	-	-	-	7
D20	-	-	-	-	-	-	6
D21	-	20	-	-	-	-	7
1D	-	20	-	-	-	-	7
2D	-	-	-	-	-	-	7
3D	22	19	-	-	-	-	7
4D	23	20	-	-	-	-	6
5D	22	19	-	-	-	-	-
6D	24	21	9	21	16	7	7
7D	-	18	-	-	-	-	7
8D	23	19	-	-	-	-	7
9D	-	-	-	-	-	-	7
10D	22	18	-	-	-	-	7
Row L5							
P	CW	CL	CH	RW	RL	RH	nTR
E1	20	17	-	-	-	-	-
E2	21	16	-	-	-	-	5
E3	20	17	-	-	-	-	6
E4	-	-	-	-	-	-	-
E5	22	16	7	19	14	7	6
E6	21	-	-	-	-	-	-
E7	20	18	-	-	-	-	6
E8	22	18	6	18	14	7	6
E9	21	19	-	-	-	-	6
E10	23	18	-	-	-	-	7
E11	-	-	-	-	-	-	-
E12	21	16	-	-	-	-	7
E13	-	-	-	-	-	-	-
E14	20	16	-	-	-	-	6
E15	21	17	-	-	-	-	6
E16	21	18	-	-	-	-	6
E17	21	17	6	19	13	6	6
E18	21	16	-	-	-	-	6
1E	22	17	-	-	-	-	6

2E	22	19	-	-	-	-	-
3E	21	18	-	-	-	-	-
4E	21	18	-	-	-	-	6
5E	21	18	-	-	-	-	7
6E	22	19	7	19	17	7	6
7E	24	19	-	-	-	-	7
8E	22	18	-	-	-	-	7
Row L6							
P	CW	CL	CH	RW	RL	RH	nTR
F1	22	15	-	-	-	-	7
F2	22	16	-	-	-	-	6
F3	22	15	-	-	-	-	6
F4	23	15	6	21	12	6	6
F5	22	15	7	20	12	7	5
F6	22	16	5	20	14	6	6
F7	23	15	-	-	-	-	6
F8	23	-	-	-	-	-	6
F9	22	15	-	-	-	-	6
F10	22	16	-	-	-	-	6
F11	23	-	-	-	-	-	6
F12	23	15	-	-	-	-	6
1F	20	14	-	-	-	-	7
2F	-	15	-	-	-	-	6
3F	21	15	-	19	11	-	6
4F	22	15	6	20	11	6	7
5F	21	16	-	-	-	-	7
6F	20	15	-	-	-	-	7
Row L7							
P	CW	CL	CH	RW	RL	RH	nTR
G1	21	13	5	19	10	6	6
G2	21	13	5	18	10	5	5
G3	20	14	-	-	-	-	-
G4	20	13	-	-	-	-	6
G5	20	14	-	-	-	-	6
G6	21	13	5	19	10	6	6
G7	19	-	-	-	-	-	5
G8	19	13	-	-	-	-	6
G9	20	-	-	-	-	-	5
G10	20	12	-	-	-	-	5
1G	-	13	-	-	-	-	5
2G	18	-	-	-	-	-	5
3G	19	12	-	-	-	-	5
4G	18	-	-	-	-	-	-

5G	18	13	-	-	-	-	5
6G	16	13	-	-	-	-	5
7G	17	12	-	13	8	-	5
Row L8							
P	CW	CL	CH	RW	RL	RH	nTR
H1	18	11	-	-	-	-	6
H2	18	11	-	-	-	-	5
H3	18	12	4	17	10	4	5
H4	18	11	-	-	-	-	5
H5	-	-	-	-	-	-	-
H6	-	-	-	-	-	-	-
1H	16	12	5	15	10	4	5
2H	17	11	-	-	-	-	-
3H	17	12	-	-	-	-	-
4H	16	12	-	-	-	-	-
Row L9							
P	CW	CL	CH	RW	RL	RH	nTR
I1	14	10	4	13	8	3	4
I2	14	11	-	-	-	-	4
II	15	9	-	-	-	-	4
Lower dentition							
Row m							
P	CW	CL	CH	RW	RL	RH	nTR
m1	58	41	35	-	-	-	9
m2	60	40	-	-	-	-	8
m3	-	41	-	-	-	-	9
m4	61	40	-	-	-	-	8
m5	61	40	25	46	-	13	9
m6	(61)	40	-	-	-	-	9
m7	62	(41)	25	46	-	9	8
m8	63	43	-	-	-	-	8
m9	-	-	-	-	-	-	10
m10	(60)	(41)	(23)	-	-	-	10
m11	63	41	-	-	-	-	9
Row I1							
P	CW	CL	CH	RW	RL	RH	nTR
a1	38	28	17	-	-	-	7
a2	(36)	(30)	-	-	-	-	8
a3	(36)	30	-	-	-	-	7
a4	-	31	-	-	-	-	7
a5	37	33	-	-	-	-	8
a6	(37)	31	-	-	-	-	8

2a	(33)	(30)	-	-	-	-	8
3a	(33)	31	-	-	-	-	7
4a	(36)	(30)	-	-	-	-	8
5a	(36)	(32)	-	-	-	-	7
12a	(34)	31	-	-	-	-	8
15a	(35)	(32)	13	29	25	11	7
Row l2							
P	CW	CL	CH	RW	RL	RH	nTR
b2	24	22	-	-	-	-	7
b4	(24)	19	-	-	-	-	7
b6	(24)	21	-	-	-	-	7
1b	(28)	21	-	-	-	-	7
2b	(25)	(22)	-	-	-	-	7
13b	23	23	9	20	18	9	7
Row l3							
P	CW	CL	CH	RW	RL	RH	nTR
c1	21	18	-	-	-	-	6
c2	22	17	-	-	-	-	6
c3	(22)	(17)	-	-	-	-	7
c5	-	18	-	-	-	-	7
c12	(21)	(19)	-	-	-	-	6
c13	23	17	-	-	-	-	6
2c	-	(17)	-	-	-	-	7
3c	(22)	(19)	-	-	-	-	6
5c	(22)	(17)	-	-	-	-	6
9c	21	17	6	19	16	8	7
Row l4							
P	CW	CL	CH	RW	RL	RH	nTR
d1	(22)	(16)	-	-	-	-	7
d2	(23)	(15)	-	-	-	-	6
d4	23	15	-	-	-	-	6
d5	23	15	7	21	12	8	7
d6	(23)	(15)	-	-	-	-	6
1d	-	(15)	-	-	-	-	6
Row l5							
P	CW	CL	CH	RW	RL	RH	nTR
e1	20	12	-	-	-	-	5
e2	19	12	-	-	-	-	5
e3	19	12	-	-	-	-	6
e6	(20)	(13)	-	-	-	-	6
e7	20	12	-	-	-	-	5
1e	20	12	-	-	-	-	6

2e	20	14	6	19	12	5	6
3e	20	13	-	-	-	-	6
5e	19	13	6	17	(10)	5	6
7e	19	(12)	-	-	-	-	5
14e	19	12	5	18	10	6	6
Row 16							
P	CW	CL	CH	RW	RL	RH	nTR
f1	18	11	5	17	-	4	5
f2	(19)	(11)	-	-	-	-	6
f3	18	11	-	-	-	-	6
f4	(18)	(11)	-	-	-	-	5
f5	(18)	(11)	-	-	-	-	6
f6	(19)	11	-	-	-	-	6
f8	(18)	(11)	-	-	-	-	(6)
4f	19	11	-	-	-	-	5
5f	18	11	6	17	8	5	6
Row 17							
P	CW	CL	CH	RW	RL	RH	nTR
g1	16	9	3	15	8	4	5
g2	17	9	-	-	-	-	6
g3	18	9	-	-	-	-	6
g6	19	9	-	-	-	-	6
1g	19	10	-	-	-	-	6
2g	16	10	5	17	-	5	5
3g	(16)	10	-	-	-	-	5
Row 18							
P	CW	CL	CH	RW	RL	RH	nTR
h1	14	8	4	13	5	3	5
h2	14	7	-	-	-	-	(5)
h3	-	7	-	-	-	-	5
h4	14	7	-	-	-	-	5
Row 19							
P	CW	CL	CH	RW	RL	RH	nTR
i1	11	6	-	-	-	-	(3)
i2	12	6	-	-	-	-	4
i4	(10)	6	-	-	-	-	(3)
i5	(12)	5	4	9	4	2	(3)
3i	12	(5)	-	-	-	-	(3)

Table A.3. Measurements of articulated and associated teeth of *Ptychodus mediterraneus*, preserved in MPPSA IGVR 91031; the findings are housed in Museo Preistorico e Paleontologico di Sant’Anna d’Alfaedo (Verona). α 1- α 9, teeth preserved in side A (see Fig. 13A); β 1- β 38, teeth preserved in side B (see Fig. 13B); CW, Crown width; CL, Crown length; CH, Crown height; RW, root width; RL, root length; RH, root height; nTR, number of transverse ridges. Except for nTR, all measurements in millimetres. Estimated values are indicated in parentheses.

MPPSA IGVR 91031 - Side A							
P	CW	CL	CH	RW	RL	RH	nTR
α 1	~ (30)	~ 26	~ 22	-	-	~ 12	7
α 2	~ 64	~ 40	~ 23	~ (48)	-	~ 14	-
α 3	~ (30)	~ (24)	-	-	-	-	6
α 4	~ 63	~ (37)	-	-	-	-	10
α 5	~ 39	~ 30	-	-	-	-	8
α 6	~ (38)	~ 32	-	-	-	-	7
α 7	~ 65	~ 42	~ (25)	-	-	-	11
α 8	~ (66)	~ (40)	-	-	-	-	11
α 9	~ 67	~ (41)	~ (27)	-	-	-	11
MPPSA IGVR 91031 - Side B							
P	CW	CL	CH	RW	RL	RH	nTR
β 1	~ 28	~ 21	-	-	-	-	7
β 2	~ 32	~ 24	-	-	-	-	7
β 3	~ 22	~ 14	-	-	-	-	6
β 4	~ 22	~ 14	-	-	-	-	6
β 5	~ 23	~ 17	-	-	-	-	7
β 6	~ 26	~ 17	-	-	-	-	8
β 7	~ 31	~ 24	-	-	-	-	8
β 8	~ 20	~ 14	-	-	-	-	5
β 9	~ (39)	~ (28)	-	-	-	-	8
β 10	~ 37	~ 29	-	-	-	-	8
β 11	~ (16)	~ 12	-	-	-	-	6
β 12	~ 27	~ 19	-	-	-	-	7
β 13	~ 39	~ 29	-	-	-	-	7
β 14	~ 26	~ 18	-	-	-	-	7
β 15	~ 21	~ 12	-	-	-	-	5
β 16	~ 20	~ 13	-	-	-	-	5
β 17	~ 18	~ 11	-	-	-	-	4
β 18	~ 17	~ 13	-	-	-	-	6
β 19	~ 15	~ 8	-	-	-	-	4
β 20	~ 16	~ (11)	-	-	-	-	4
β 21	~ 23	~ 14	-	-	-	-	6
β 22	~ 24	~ 17	-	-	-	-	7
β 23	~ (25)	~ (19)	-	-	-	-	7

β_{24}	~ 17	~ 11	-	-	-	-	4
β_{25}	~ 14	~ 11	-	-	-	-	4
β_{26}	~ 19	~ 10	-	-	-	-	4
β_{27}	~ 20	~ 10	-	-	-	-	5
β_{28}	~ 19	~ 13	-	-	-	-	6
β_{29}	~ (57)	~ (36)	-	-	-	-	9
β_{30}	~ 17	~ 11	-	-	-	-	4
β_{31}	~ 22	~ 14	-	-	-	-	6
β_{32}	~ 20	~ 11	-	-	-	-	5
β_{33}	~ 22	~ (14)	-	-	-	-	6
β_{34}	~ 18	~ 10	-	-	-	-	4
β_{35}	~ 12	~ 6	-	-	-	-	3
β_{36}	~ 16	~ 10	-	-	-	-	4
β_{37}	~ 19	~ (11)	-	-	-	-	4
β_{38}	~ 16	~ 10	-	-	-	-	3

Table A.4. Measurements of articulated and associated teeth of *Ptychodus mediterraneus*, preserved in MCBG 4048; the findings are housed in Museo Civico di Bassano del Grappa (Vicenza). The letters following the catalogue number indicate the position of the teeth with in the tooth set (see Fig. 16G,H); CW, Crown width; CL, Crown length; CH, Crown height; RW, root width; RL, root length; RH, root height; nTR, number of transverse ridges. Except for nTR, all measurements in millimetres. Estimated values are indicated in parentheses

Catalogue Number	CW	CL	CH	RW	RL	RH	nTR
MCBG 4048 α	~ 21	~ 11	~ 5	-	-	-	6
MCBG 4048 β	~ 22	~ 11	~ 7	-	-	-	6
MCBG 4048 γ	~ 21	~ 12	~ 8	~ 11	~ 7	~ 4	6
MCBG 4048 δ	~ 17	~ 8	~ 6	-	-	-	5
MCBG 4048 ϵ	~ 19	~ 9	~ 5	~ 15	~ 5	~ 5	6

Table A.5. Measurements of teeth of associated and isolated specimen of *Ptychodus mediterraneus* housed in several museums in Northern Italy. CW, Crown width; CL, Crown length; CH, Crown height; RW, root width; RL, root length; RH, root height; nTR, number of transverse ridges. Except for nTR, all measurements in millimetres. Estimated values are indicated in parentheses.

Catalogue number	CW	CL	CH	RW	RL	RH	nTR
MCBG 4050- α	~ 27	~ 25	~ 8	-	-	-	8
MCBG 4050- β	~ 34	~ 23	~ 9	~ 21	~ 18	~ 8	9
MCSNV v.11791	~ 25	~ 22	~ 20	-	-	-	8
MCSNV v.12507	~ 38	~ 27	-	-	-	-	8
MCSNV v.12508 α	~ (46)	~ 40	~ 22	-	-	~ (11)	8
MCSNV v.12508 β	~ (36)	~ 33	-	-	-	-	8
MCSNV v.12528	~ 66	~ 43	~ 24	-	-	-	11
MGP-PD 8494-C	~ (29)	~ 24	~ (7)	-	-	-	8
MGP-PD 8497-C	~ 28	~ 21	~ 9	~ 27	~ 17	~ 9	8
MGP-PD 13531 α	~ (32)	~ (30)	~	-	-	-	9
MGP-PD 13533	~ 41	-	~	-	-	-	8
MGP-PD 13534	~ 41	~ 34	~ 14	-	-	-	10
MGP-PD 13536	~ 44	~ 36	~ 15	~ 32	~ 31	~ 10	9
MGP-PD 14040	~ (38)	~ 32	~ 14	~29	~ 24	~ (8)	5
MMC PTY01	-	~ (16)	~ (13)	-	-	-	6
MMC PTY02	~ 31	~ 27	~ 11	-	-	-	7
MSNPS 274 α	~ 25	~ (17)	~	-	-	-	(6)
MSNPS 274 β	~ 12	~ (9)	-	-	-	-	(6)

Ringraziamenti

Vorrei ringraziare tutti coloro che mi hanno sostenuto e aiutato in questi tre anni di lavoro, *in primis* i miei relatori Proff. Luca Giusberti, Eliana Fornaciari e Giorgio Carnevale. I risultati e le soddisfazioni sono stati tanti e li ringrazio molto per avermi trasmesso molto a livello professionale e umano e per la fiducia riposta nelle mie capacità. Un ringraziamento particolare è sicuramente dovuto anche al Dott. Guido Roghi e al Dott. Fabio Dalla Vecchia, senza i quali non avrei potuto intraprendere lo studio dei reperti del ‘lastame’ e poi tutto quello che ne è conseguito, anche questa tesi. Ringrazio inoltre tutte le persone con cui ho avuto modo di lavorare nel corso della mia esperienza, tutti i curatori e il personale dei musei che ho visitato, i Dott.ri Roberto Zorzin, Franco Colombara, Mariagabriella Fornasiero, Barbara Favaretto, Bernardetta Pallozzi, Fabiana Zandonai, Fabrizio Bizzarini, Massimo Bernardi, Luca Simonetto, Chiara Sorbini, Emma Bernard. Sono grato inoltre alle persone che nel corso degli anni mi hanno garantito l’accesso a musei come quelli di Sant’Anna d’Alfaedo e Camposilvano, da Elisa Marchesini a Marta Castagna e tanti altri. Ringrazio anche molto anche due persone che purtroppo ci hanno lasciato troppo presto, Anna Vaccari e Magda Biasiolo. Ringrazio anche tutti coloro che hanno collaborato alla stesura degli articoli che compongono questa tesi, il Prof. Jürgen Kriwet, la Prof. Valeria Luciani, e Manuel Amadori, che ha fatto un gran lavoro sul materiale di *Ptychodus*. Si ringrazia inoltre Stefano Castelli, senza il quale non ci sarebbero molte delle stupende foto presenti in questa tesi. Un ringraziamento va anche al resto del Dipartimento e ai coordinatori del Dottorato, che si sono dimostrati sempre disponibili nei miei confronti.

Ringrazio infine (*last but not least*) i miei cari, la mia famiglia e la mia fidanzata Anita e la sua famiglia, tutti i miei parenti in generale e gli amici, per il sostegno e l’affetto che mi hanno sempre dedicato.

Spero di non aver dimenticato nessuno, in caso ringrazio sentitamente chiunque abbia in qualche modo contribuito, anche nel minimo aspetto, durante questi tre anni.

Acknowledgment

I would like to thank all the people who supported and helped me during these three years, *in primis* the Prof. Luca Giusberti, Eliana Fornaciari and Giorgio Carnevale. Results and satisfaction from our works were many, and I thank them very much for transmitting me so much from the professional and personal perspectives, and for their trust in my competence. A special thank goes also to Dott. Guido Roghi and Dott. Fabio Dalla Vecchia, who helped me starting this experience with the ‘lastame’ fossils. I am grateful also for all the people and staff of the museums I have visited during these three years, Roberto Zorzin, Franco Colombara, Mariagabriella Fornasiero, Barbara Favaretto, Bernardetta Pallozzi, Fabiana Zandonai, Fabrizio Bizzarini, Massimo Bernardi, Luca Simonetto, Chiara Sorbini, Emma Bernard. I would also thank all the staff that helped me accessing the collection of the museums in Sant’Anna d’Alfaedo, Camposilvano and Cinto Euganeo, from Elisa Marchesini to Marta Castagna and many others. I am grateful for two persons that were taken from us too soon, Anna Vaccari and Magda Biasiolo. I thank very much all the coauthors that contributed to the articles in this dissertation, Prof. Jürgen Kriwet, Prof. Valeria Luciani and Manuel Amadori, who did a hard work with *Ptychodus*. I thank also Stefano Castelli, for his beautiful photographs. I thank all the Departement staff and the PhD coordinators, who have always been kind to me during these three years.

I thank very much also (last but not least) my family, my girlfriend Anita and her family, all my relatives and friends, for their support and love.

I hope not to have forgotten anybody, thank anyways for your support.