

## A REAPPRAISAL OF THE ITALIAN RECORD OF THE CRETACEOUS PACHYCORMID FISH *PROTOSPHYRAENA* LEIDY, 1857

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*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 & 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

& Fielitz 2006; Woodward 1908). *Protosphyraena* remains are primarily represented by fragments of scythe-like pectoral fins (but see Maltese & 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), erro-

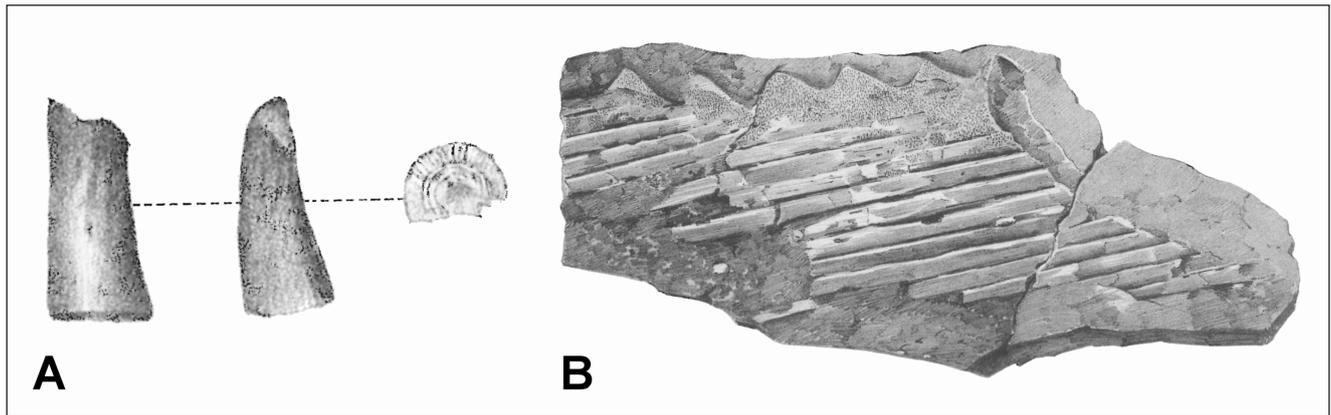


Fig. 1 - The original illustrations of *Protosphyraena* remains from the Scaglia Rossa Formation of northeastern Italy. A) Tooth from Castellavazzo (from Bassani 1886) and B) the fin fragment from Novale (from D'Erasmus 1922). The images do not reflect the original size.

neously 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 (*Cretoxyrhina mantelli*, *Ptychodus* spp., '*Lepidotus*' sp.; Bassani 1886), is 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 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 partic-

ularly, 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 lenticular 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 "isospindylous" fish.

The Bonarelli Level is an organic-rich marker bed accumulated during the late Cenomanian Oceanic Anoxic Event 2 (OEA2) (e.g., Coccioni & 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

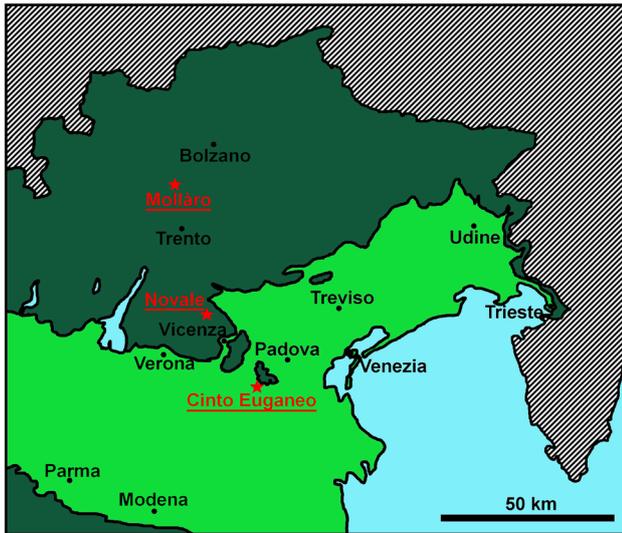


Fig. 2 - Location map of the sites in northeastern Italy that yielded remains of the pachycormid fish *Protosphyraena* described in this paper. The red stars indicate the fossiliferous sites.

ichthyofauna of the Bonarelli Level, currently under review, is quite diverse and includes bony fishes and less 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’, outcropping 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 & 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). Vertebrate remains also come from the ‘Pietra di Castellavazzo’ lithofacies (e.g., Bassani 1886, 1888), another condensed interval equivalent to the ‘lastame’ and outcropping in the surroundings of Longarone (Belluno).

## MATERIALS AND METHODS

The fossils described and figured herein consist of five specimens deposited in different 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 ImageJ (v. 1.47) using a Canon PowerShot SX720 HS and 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 Bengtson (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.

1835-1844 *Saurocephalus lanciformis* (Harlan, 1824) - Agassiz (errore), vol. 5, p. 102, pl. 25c, figs 21-29.

1835-1844 *Saurocephalus lanceolatus* - Agassiz, vol. 5, p. 8 (misprint).

1850 *Saurocephalus lanciformis* (Harlan, 1824) - 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, 1857) - Cope, p. 823.

1877 *Erisichthe dixoni* (Leidy, 1857) - Davies, p. 260, pl. 8, fig. 3.

1878 *Protosphyraena ferox* (Leidy, 1857) - Newton, p. 789.

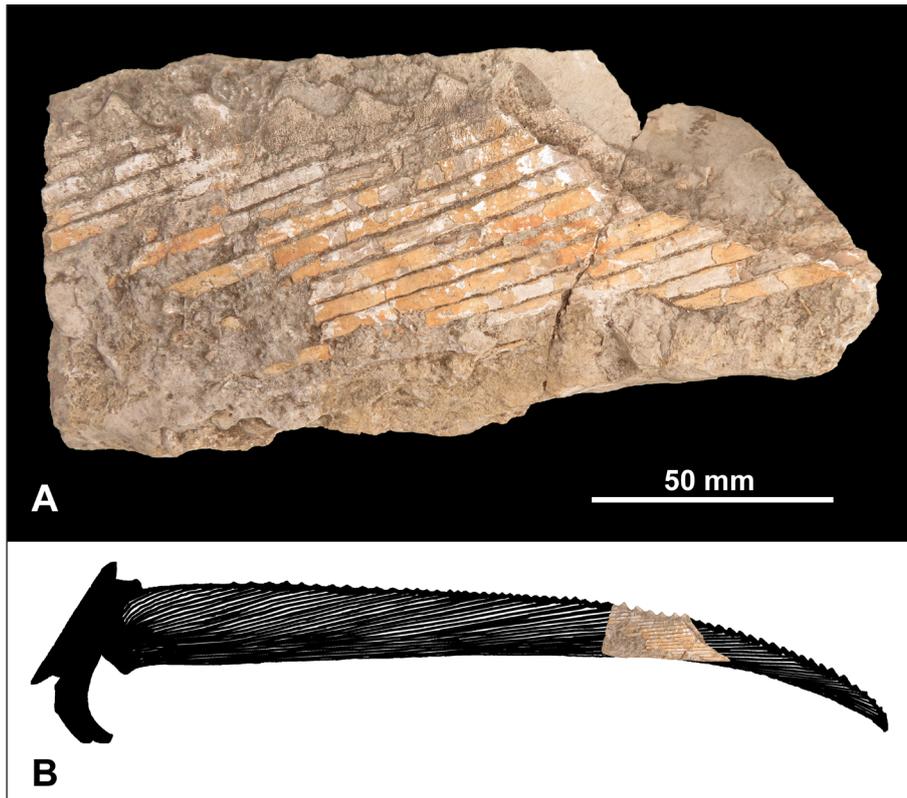


Fig. 3 - *Protosphyraena ferox* from the upper Turonian-Coniacian Scaglia Rossa Formation of Novale (VI), CDL 782. A) Photo of the specimen. Scale bar: 50 mm. B) Interpretative reconstruction of the original position of CDL 782 based on a complete pectoral fin of *Protosphyraena* figured by Woodward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

- 1886 *Saurocephalus lanciformis* (Harlan, 1824) - Bassani, p. 143; pl. 9, fig. 12.  
 1888 *Saurocephalus lanciformis* (Harlan, 1824) - Bassani, p. 5.  
 1888 *Protosphyraena ferox* (Leidy, 1857) - Woodward, p. 321.  
 1895a *Protosphyraena ferox* (Leidy, 1857) - Woodward, p. 211, woodc. fig. 3.  
 1895b *Protosphyraena ferox* (Leidy, 1857) - Woodward, p. 400, text-fig. 41, no. 3.  
 1903 *Protosphyraena* sp. - Dal Lago, p. 74.  
 1908 *Protosphyraena ferox* (Leidy, 1857) - Woodward, p. 147, text-fig. 45, pl. 31-32.  
 1922 *Protosphyraena* sp. - D'Erasmus, p. 62; pl. 6, fig. 17.  
 1976 *Protosphyraena ferox* (Leidy, 1857) - Sorbini, p. 485, pl. 9.  
 1978 *Protosphyraena ferox* (Leidy, 1857) - Mainwaring, p. 105.  
 1980 *Protosphyraena ferox* (Leidy, 1857) - 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 Supplementary material S1). 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.

**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 & 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 towards the distal end 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.

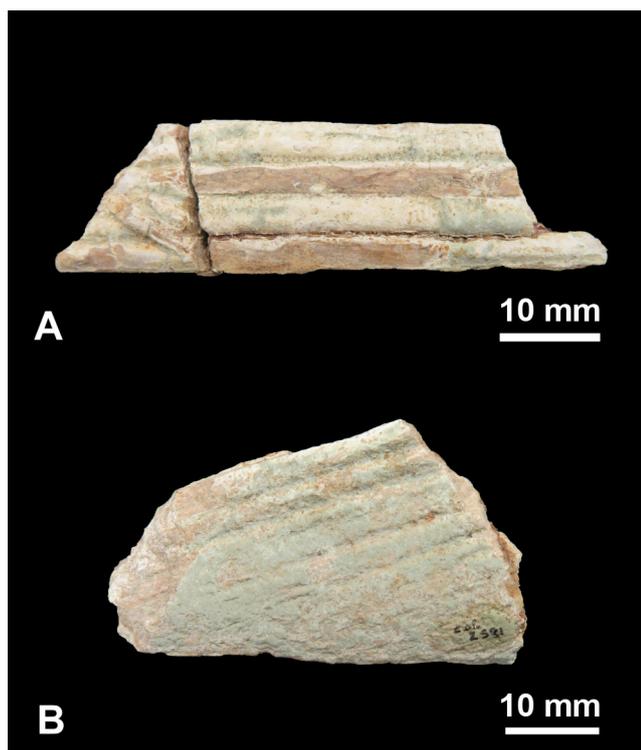


Fig. 4 - Fragments of a fin of *Protosphyraena ferox* from the Scaglia Rossa Formation of Novale (VI), CDL 2580-2581. A) Photo of specimen CDL 2580. B) Photo of specimen CDL 2581. Scale bars: 10 mm.

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 & Liston 2014, Liston & 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 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).

**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 & 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 congenics, *P. pernicioso* 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 & Maltese, 2016). The fin characters of *Protosphyraena tenuis* are not easily distinguishable from those of *P. pernicioso*, so that some authors (e.g., Everhart 2012) consider them as conspecific. The pectoral fin serrations of *Protosphyraena pernicioso* 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 & 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 congenics primarily inhabited the American Western Interior Seaway (Everhart 2005; Loomis 1900; Shimada & Fielitz 2006). The genus *Protosphyraena* had a worldwide distribution, and was reported from Belgium (Friedman 2012), Canada

(Manitoba, Bardack 1968; Saskatchewan, Cum-baa 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 & Metcalf 1999) to the Maastrichtian (Friedman 2012). Therefore, the stratigraphic position 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.

#### 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).

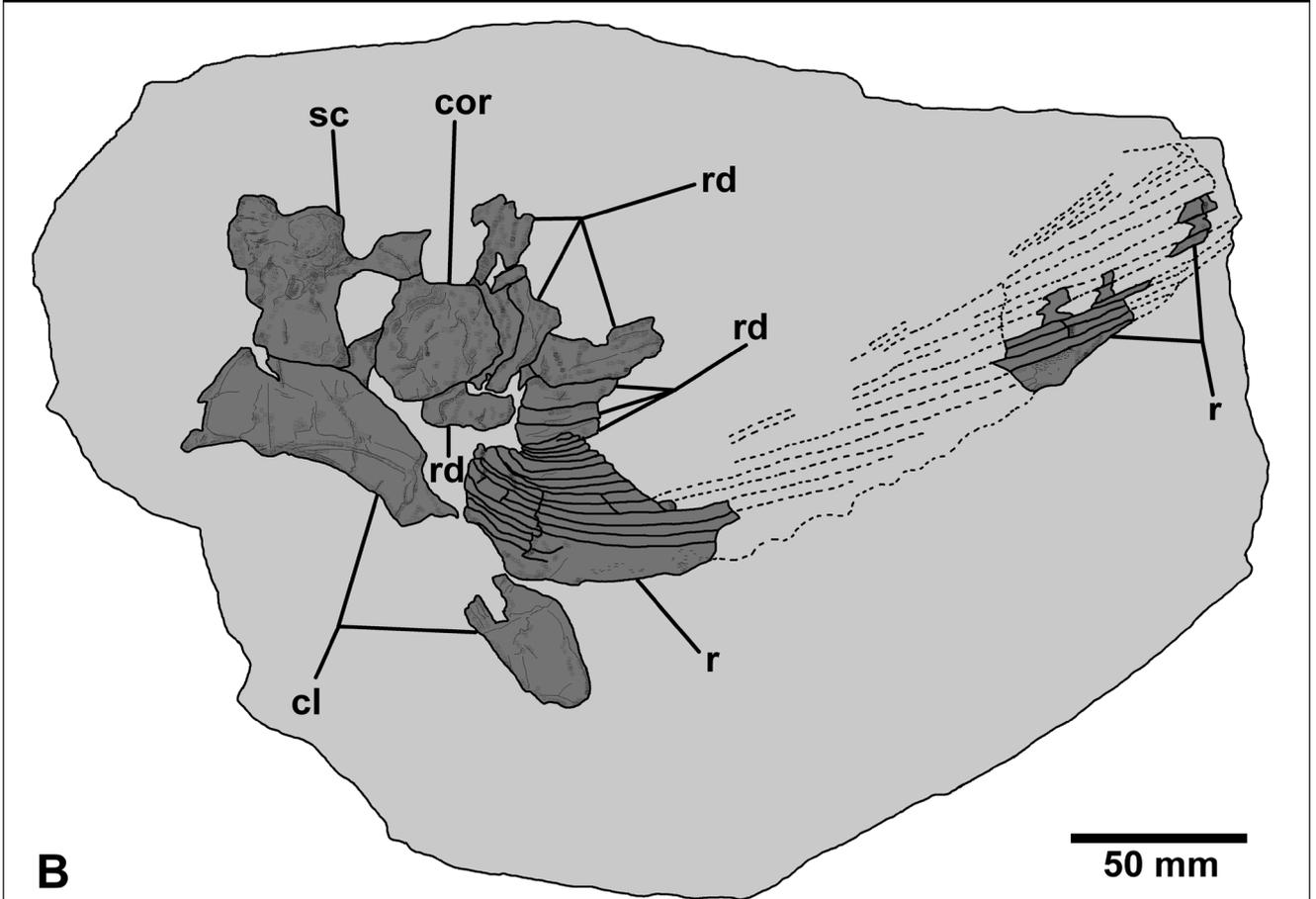
**Description.** The specimen MUSE 6822 (Fig. 6) is figured herein for the first time and consists of the impression of what appears to be a partial fin. The fin consists of the impression of seven rays plus three additional ray fragments. The impression of the fin is ca. 126 mm long. The impression 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 tselfatiiform 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.

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.



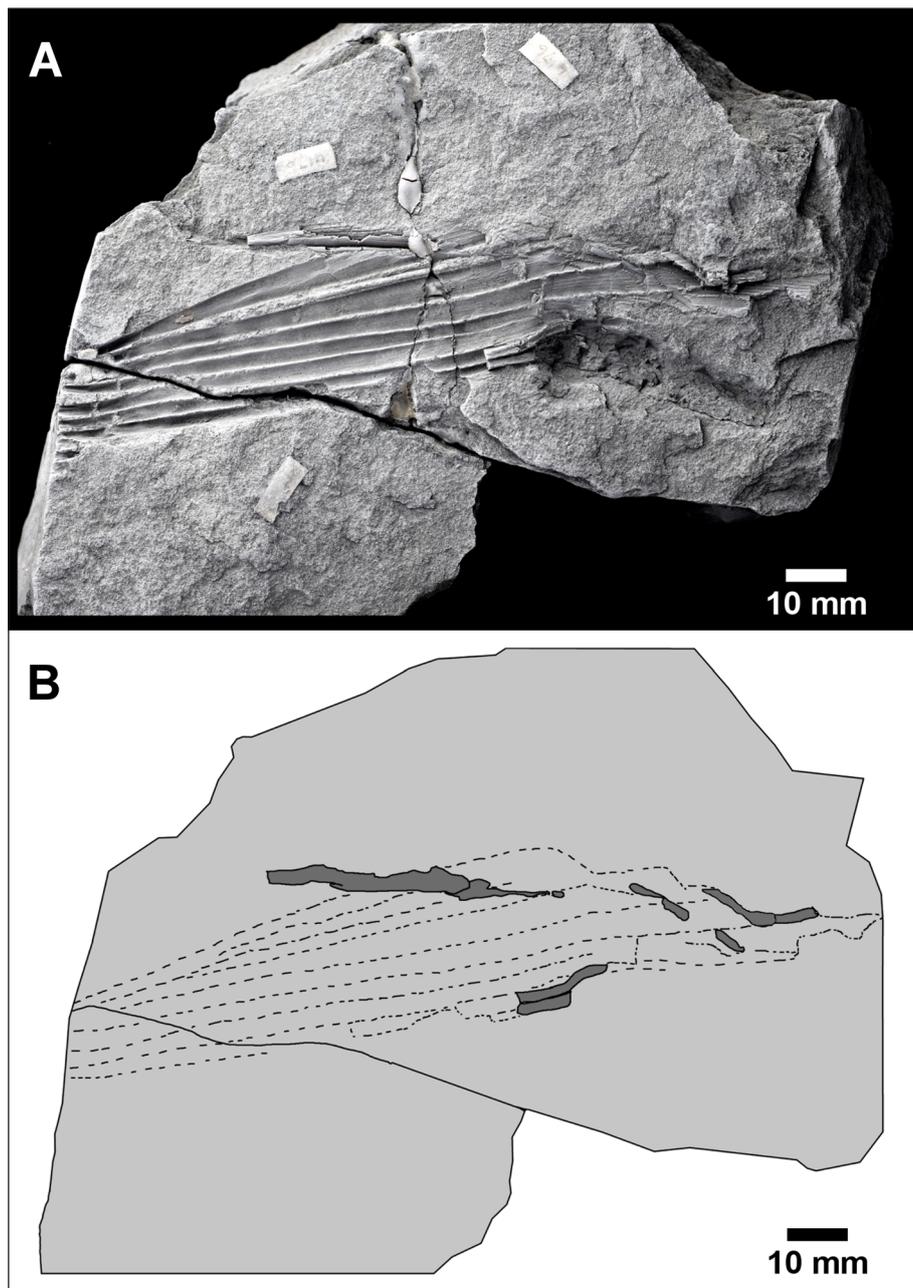


Fig. 6 - Actinopterygii indet. from the black-shales of Mollàro (TN), MUSE 6822, originally ascribed by D'Erasmus (1927) to *Protosphyraena*. A) Photo of the specimen coated with ammonium chloride. B) Interpretative drawing of the specimen. The bones are colored in dark grey, the matrix in light grey.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

## 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.

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## REFERENCES

- Agassiz L. (1833-1843) - Recherches sur les poissons fossiles. Petitpierre, Neuchâtel.
- Agnini C., Fornaciari E., Giusberti L., Grandesso P., Lanci L., Luciani V., Muttoni G., Pälke H., Rio D., Spofforth D.J.A. & Stefani C. (2011) - Integrated bio-magnetostratigraphy of the Alano section (NE Italy): A proposal for defining the Middle-Late Eocene boundary. *GSA Bull.*, 123(5/6): 841-872.
- Amalfitano J., Carnevale G., Fornaciari E. & Giusberti L. (2017a) - A revision of the fishes from the Bonarelli Level (uppermost Cenomanian) of northeastern Italy. In: Sames B. (Ed.) - 10th International Symposium on the Cretaceous-Abstracts, 21-26 August 2017, Vienna. *Ber. geol. Bundesanst.*, 120: 11.
- Amalfitano J., Dalla Vecchia F.M., Giusberti L., Fornaciari E., Luciani V. & Roghi G. (2017b) - Direct evidence of trophic interaction between a large lamniform shark, *Cretodus* sp., and a marine turtle from the Cretaceous of northeastern Italy. *Palaeogeogr., Palaeoclimatol. Palaeoecol.*, 469: 104-121.
- Amalfitano J., Giusberti L., Dalla Vecchia F.M. & Kriwet J. (2017c) - First skeletal remains of the giant sawfish *Onchosaurus* (Neoselachii, Sclerorhynchiformes) from the Upper Cretaceous of northeastern Italy. *Cret. Res.*, 69: 124-135.
- Applegate S. P. (1970) - The vertebrate fauna of the Selma Formation of Alabama. *Fieldiana: Geol. Mem.*, 3(8): 385-433.
- Avanzini M., Tomasoni R. & Rinaudo M. (2012) - Stratigrafia delle successioni sedimentarie e vulcaniche permo-meso-cenozoiche. In: Avanzini M., Bargossi G.M., Borsato A., Cucato M., Morelli C., Picotti V. & Selli L. (Eds) - Note illustrative della Carta Geologica d'Italia alla scala 1: 50.000. Foglio 043 Mezzolombardo: 43-99. Provincia Autonoma di Trento-Provincia Autonoma di Bolzano, LTS Land Technology & Services-Padova e Treviso.
- Avnimelech M. (1949) - On vertebrate remains in Senonian phosphate beds in Transjordan. *Eclogae geol. Helv.*, 42(2): 486-490.
- Bardack D. (1968) - Fossil vertebrates from the marine Cretaceous of Manitoba. *Can. J. Earth Sci.*, 5: 145-153.
- Bassani F. (1880) - Su due giacimenti ittiolitici nei dintorni di Crespano. *Boll. Soc. veneto-trentina Sci. nat.*, 1(4): 147-154.
- Bassani F. (1882) - Descrizione dei pesci fossili di Lesina accompagnata da appunti su alcune altre ittiofaune cretacee (Pietrarroia, Voirons, Comen, Grodischitz, Crespano, Hakel, Sahel-Alma e Vestfalia). *Denkschr. (kais.) Akad. Wiss. Wien*, 45: 1-96.
- Bassani F. (1886) - Sull'età degli strati a pesci di Castellavazzo nel Bellunese. *Boll. Soc. geol. ital.*, 4: 143-148.
- Bassani F. (1888) - Colonna vertebrale di *Oxyrhina Mantelli*, Agassiz, scoperta nel calcare senoniano di Castellavazzo, nel Bellunese. *Mem. Soc. ital. Sci.* (detta dei XL), 7 (III,1): 1-5.
- Bazzi M., Einarsson E. & Kear B. P. (2016) - Late Cretaceous (Campanian) actinopterygian fishes from the Kristiansstad Basin of southern Sweden. *Geol. Soc. London spec. Publ.*, 434(1): 277-292.
- Bengston P. (1988) - Open nomenclature. *Palaeontology*, 31(1): 223-227.
- Berg L. S. (1940) - Classification of fishes both recent and fossil. *Trudy zool. Inst. Akad. Nauk S.S.S.R.*, Leningrad, 5: 346-517.
- Bosellini A., Broglio Loriga C. & Busetto C. (1978) - I bacini cretacei del Trentino. *Riv. ital. Paleontol. Stratigr.*, 84(4): 897-946.
- Burnett J.A. 1999 - Upper Cretaceous. In: Bown P.R. (Ed.) - *Calcareous Nannofossil Biostratigraphy*. Springer Science+Business media, LLC, pp. 132-199 (reprint with corrections).
- Capellini G. (1884) - Il chelonio veronese (*Protosphargis veronensis*, Cap.) scoperto nel 1852 nel Cretaceo superiore presso S. Anna di Alfaedo in Valpolicella. *Mem. Accad. Lincei Roma s. 3*, 18: 291-320.
- Cavin L., Forey P.L. & Giersch S. (2013) - Osteology of *Eubiodectes libanicus* (Pictet & Humbert, 1866) and some other ichthyodectiformes (Teleostei): phylogenetic implications. *J. Syst. Palaeontol.*, 11(2), 115-177.
- Cestari R., Trevisani E. & Roghi G. (2013) - Record of a rudist from pelagic basinal limestones (Upper Cretaceous, Lessini Mountains, Northern Italy). *Riv. ital. Paleont. Stratigr.*, 119 (1): 31-39.
- Coccioni R. & Luciani V. (2005) - Planktonic foraminifers across the Bonarelli Event (OAE2, latest Cenomanian): the Italian record. *Palaeogeogr., Palaeoclimatol. Palaeoecol.*, 224(1): 167-185.
- Cope E.D. (1877) - On the genus *Erisichthe*. *Bull. U.S. geol. Surv. Territ.*, 3: 821-823.
- Cumbaa S.L. (1997) - A Cenomanian age bone bed of marine origin, Saskatchewan, Canada. In: Fifty-seventh annual meeting, Society of Vertebrate Paleontology, Abstracts of papers. *J. Vert. Paleontol.*, 17(3 Suppl.): 40A.
- Dal Lago D. (1903) - Note illustrative alla carta geologica della provincia di Vicenza. Giovanni Galla Editore, Vicenza, 140 pp.
- Dalla Vecchia F.M., Barbera C., Bizzarini F., Bravi S., Delfino M., Giusberti L., Guidotti G., Mietto P., Papazzoni C., Roghi G., Signore M. & Simone O. (2005) - Il Cretaceo marino. In: Bonfiglio L. (Ed.) - *Paleontologia dei Vertebrati in Italia*. *Mem. Mus. civ. Storia nat. Verona, Sez. Sci. Terra*, 6: 101-116.
- Davies W. (1877) - On the nomenclature of *Sauropscephalus lanciformis* of the British Cretaceous deposits: with description of a new species (*S. woodwardi*). *Geol. Mag. n. Ser.*, 5(6): 254-261.
- D'Erasmo G. (1922) - Catalogo dei pesci fossili delle Tre Venezie. *Mem. Ist. Geol. R. Univ. Padova*, 6: 1-181.
- D'Erasmo G. (1927) - Su alcuni ittioliti del Museo di Storia Naturale di Trento. *Arti Grafiche A. Scotoni*, Trento, 12 pp.
- De Zigno A. (1883) - Sui vertebrati fossili dei terreni mesozoici delle Alpi Venete. *Mem. r. Accad. Sci., Lett. Arti Padova*, 9: 1-12.

- Diedrich C. (2001) - Ein Pectoralflossenrest von *Protosphyraena* sp. (Pachycormidae, Actinopterygii) aus dem Ober-Cenoman von Halle/Westf. (Teutoberger Wald, NW-Deutschland). *Ber. natw. Ver. Bielefeld Umgegend*, 41: 31-44.
- Dineley D.L. & Metcalf S.J. (1999) - Fossil fishes of Great Britain. Joint Nature Conservation Committee, Peterborough, xxi + 675 pp.
- Dixon F. (1850) - The geology and fossils of the Tertiary and Cretaceous formations of Sussex. Longman, Brown, Green and Longmans, London, 422 pp.
- Everhart M.J. (2005) - Oceans of Kansas. Indiana University Press, Bloomington, 322 pp.
- Everhart M.J. (2012) - *Protosphyraena*: A Late Cretaceous pachycormid "Swordfish". <http://oceansofkansas.com/Protosphyra.html> (accessed 07.06.2017).
- Fabiani R. (1923) - Giacitura ed età degli scisti bituminosi di Mollaro in Val di Non (Trentino). *Natura. Riv. Sci. nat.*, 14: 33-41.
- Friedman M. (2012) - Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium. In: Jagt J.W.M., Donovan S.K. & Jagt-Yazykova E.A. (Eds) - Fossils of the type Maastrichtian (Part 1). *Scr. Geol. spec. Issue*, 8: 113-142.
- Friedman M., Beckett H.T., Close R.A. & Johanson Z. (2016) - The English Chalk and London Clay: two remarkable British bony fish Lagerstätten. In: Johanson Z., Barrett P. M., Richter M. & Smith M. (Eds) - Arthur Smith Woodward: His Life and Influence on Modern Vertebrate Palaeontology: 165-200. *Geol. Soc. London spec. Publ.*, London, 430 pp.
- Friedman M., Shimada K., Everhart M.J., Irwin K.J., Grandstaff B.S. & Stewart J.D. (2013) - Geographic and stratigraphic distribution of the Late Cretaceous suspension-feeding bony fish *Bonnerichthys gladius* (Teleostei, Pachycormiformes). *J. Vert. Paleontol.*, 33(1): 35-47.
- Friedman M., Shimada K., Martin L.D., Everhart M.J., Liston J., Maltese A. & Triebold M. (2010) - 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science*, 327(5968): 990-993.
- Fuganti A. (1964) - La geologia dei dintorni di Mollaro (Trentino occidentale). *Studi trent. Sci. nat.*, anno XLI, 1: 73-110.
- Giusberti L., Boscolo Galazzo F. & Thomas E. (2016) - Variability in climate and productivity during the Paleocene-Eocene Thermal Maximum in the western Tethys (Forada section). *Clim. Past*, 12(2): 213-240.
- Gomez B., Thévenard F., Fantin M. & Giusberti L. (2002) - Late Cretaceous fossil plants from the Bonarelli Level of the Venetian Alps, northeastern Italy. *Cret. Res.*, 23: 671-685.
- Gomez B., Giusberti L., Roghi G., Chiari M., Daviero-Gomez V. & Ewin T.A. (2015) - Cretaceous conifers and angiosperms from the Bonarelli Level; Reassessment of Masalongo's plant fossil collections of "Monte Colle", Lessini Mountains, northern Italy. *Cret. Res.*, 52: 179-193.
- Harlan R. (1824) - On a new fossil genus, of the order Enalio Sauri (of Conybeare). *J. Acad. nat. Sci. Philadelphia*, 3: 331-337.
- Hill R. T. (1901) - Geography and geology of the Black and Grand Prairies, Texas. *Ann. Rep. Dir. U.S. geol. Surv.*, 21(7): 1-666.
- Kear B.P. (2007) - First record of a pachycormid fish (Actinopterygii: Pachycormiformes) from the Lower Cretaceous of Australia. *J. Vert. Paleontol.*, 27(4), 1033-1038.
- Kear B.P., Rich T.H., Ali M.A., Al-Mufarrih Y.A., Matiri A.H., Al-Masary A.M. & Attia Y. (2009) - An Upper Cretaceous (Campanian-Maastrichtian) actinopterygian fish assemblage from the marginal marine Adaffa Formation of Saudi Arabia. *Cret. Res.*, 30(5): 1164-1168.
- Leidy J. (1857) - Remarks on *Saurocephalus* and its allies. *Trans. Amer. Phil. Soc.*, 11: 91-95.
- Liston J.J. (2015) - A collection without a catalogue: Captain John Laskey and the missing vertebrate fossils from the collection of William Hunter. In: Hancock E.G., Pearce N. & Campbell M. (Eds) - William Hunter's World: The Art and Science of Eighteenth-Century Collecting. Chapter 12: 199-222. Ashgate Publishing, Farnham.
- Liston J.J. & Maltese A.G. (2016) - Daggers, swords, scythes and sickles: Pachycormid fins as ecological predictors. *PeerJ Preprints*, 4:e2550v1.
- Liston J., Newbrey M., Challands T. & Adams C. (2013) - Growth, age and size of the Jurassic pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii). In: Arratia G., Schultze H. & Wilson M. (Eds) - Mesozoic Fishes 5 – Global Diversity and Evolution: 145-175. Verlag Dr. Friedrich Pfeil, München, Germany.
- Loomis F. B. (1900) - Die Anatomic und die Verwandtschaft der Ganoid- und Knochen-Fische. *Palaeontographica*, 46: 213-283.
- Lozar F. & Grosso F. (1997) - Biostratigrafia della successione cretacea del margine dei Lessini occidentali (Provincia di Verona, Italia). *Boll. Mus. reg. Sci. nat. Torino*, 15(1): 111-136.
- Mainwaring A.J. (1978) - Anatomical and systematic review of the Pachycormidae, a family of mesozoic fossil fishes. PhD thesis. Westfield College, University of London. 162 pp.
- Maltese A.G. & Liston J.J. (2014) - Daggers, Swords, Scythes and Sickles: Pachycormid Fins As Ecological Predictors: 176. *J. Vert. Paleont., Program and Abstracts*, 2014.
- Mantell G.A. (1822) - The Fossils of the South Downs, or Illustrations of the Geology of Sussex. Lupton Relfe, London, 442 pp.
- Massari F., Medizza F. & Channell J.E.T. (1983) - Santonian to Maastrichtian stratigraphy of some pelagic limestone sections of the Venetian Alps (Northern Italy). *Nouv. Stratigr.*, 12: 18-28.
- McClung C.E. (1908) - Ichthyological notes on the Kansas Cretaceous, I. *Kansas Univ. Sci. Bull.*, IV: 235-246.
- Nagrodski M., Shimada K. & Schumacher B.A. (2012) - Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. *Cret. Res.*, 37: 76-88.
- Newton E.T. (1878) - Remarks on *Saurocephalus*, and on the species which have been referred to that genus. *Quart. J. geol. Soc. London*, 34: 786-796.

- Palci A., Caldwell M.W. & Papazzoni C.A. (2013) - A new genus and subfamily of mosasaurs from the Upper Cretaceous of northern Italy. *J. Vert. Paleontol.*, 33(3): 599-612.
- Schumacher B.A. (2007) - A new polycotyloid plesiosaur (Reptilia; Sauropterygia) from the Greenhorn Limestone (Upper Cretaceous; lower upper Cenomanian), Black Hills, South Dakota. *Geol. Soc. Amer. spec. Pap.*, 427: 133-146.
- Schumacher B.A., Shimada K., Liston J. & Maltese A. (2016) - Highly specialized suspension-feeding bony fish *Rhinconichthys* (Actinopterygii: Pachycormiformes) from the mid-Cretaceous of the United States, England, and Japan. *Cret. Res.*, 61: 71-85.
- Shimada K. & Fielitz C. (2006) - Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas. *Bull. New Mex. Mus. nat. Hist.*, 35: 193-213.
- Shimada K., Schumacher B.A., Parkin J.A. & Palermo J.M. (2006) - Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. *J. Paleontol.*, 80(63): 1-45.
- Sirna G., Dalla Vecchia F. M., Muscio G. & Piccoli G. (1994) - Catalogue of Paleozoic and Mesozoic vertebrates and vertebrates localities of the Tre Venezie area (northeastern Italy). *Mem. Sci. Geol.*, 46: 255-281.
- Sorbini L. (1976) - L'ittiofauna cretacea di Cinto Euganeo (Padova - Nord Italia). *Boll. Mus. Civ. St. nat. Verona*, 3: 479-567.
- Sorbini L. (1980) - Il giacimento di Cinto Euganeo. In: I vertebrati fossili italiani. Catalogo della mostra: 119-122. Verona.
- Stewart J.D. (1988) - The stratigraphic distribution of Late Cretaceous *Protosphyraena* in Kansas and Alabama. *Fort Hays Stud.*, 10: 80-94.
- Varol O. (1992) - Taxonomic revision of the Ploycyclolithaceae and its contribution to Cretaceous biostratigraphy. *Newsl. Stratigr.*, 27: 93-127.
- Vullo R., Bernardez E. & Buscalioni A.D. (2009) - Vertebrates from the middle?-late Cenomanian La Cabana Formation (Asturias, northern Spain): Palaeoenvironmental and palaeobiogeographic implications. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 276: 120-129.
- Vullo R., Néraudeau D. & Videt B. (2003) - Un faciès de type falun dans le Cénomanién basal de Charente-Maritime (France). *Ann. Paléontol.*, 89(3): 171-189.
- Woodward A.S. (1895a) - A Contribution to Knowledge of the Fossil Fish Fauna of the English Purbeck Beds. *Geol. Mag. (Decade IV)*, 2(04): 145-152.
- Woodward A.S. (1895b) - Catalogue of the Fossil Fishes in the British Museum. Part 3. British Museum of Natural History, London, 728 pp.
- Woodward A.S. (1888) - A synopsis of the vertebrate fossils of the English Chalk. *Proc. geol. Ass. London*, 10: 273-338.
- Woodward A.S. (1908) - The Fossil Fishes of the English Chalk. Part IV. Palaeontogr. Soc., London, 62: 129-152. London.
- Woodward A.S. (1909) - The Fossil Fishes of the English Chalk. Part V. Palaeontogr. Soc., London, 63: 153-184. London,
- Zangerl R. (1953) - The vertebrate fauna of the Selma Formation of Alabama. Part III. The turtles of the family Protostegidae. *Fieldiana: Geol. Mem.*, 3(3): 63-133.

