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UPPER CENOMANIAN FISHES FROM THE BONARELLI LEVEL (OAE2) OF NORTHEASTERN ITALY

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Abstract. The Bonarelli Level (BL) is a 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 documenting a rather diverse ichthyofauna. The assemblage was studied by Sorbini in 1976 based on material from a single locality, Cinto Euganeo. Subsequently, other localities yielding fish remains have been discovered. Our revision also includes fish remains from three new fish-bearing localities, the Carcoselle Quarry, the Valdagno-Schio tunnel and Quero other than those from Bomba Quarry near Cinto Euganeo. At least 27 taxa were identified, including nine previously not reported from the Bonarelli Level, namely: *Scapanorhynchus raphiodon*, *Cretalamna appendiculata*, *Archaeolamna kopingensis*, '*Nursallia*' *tethysensis*, *Belonostomus* sp., *Dixonanogmius dalmatius*, '*Protosphyraena*' *stebbingi* and the beryciform *Hoplopteryx* sp. The overall assemblage mostly consists of crossognathiforms, tselfatiiforms and aulopiforms. A comparison of the taxonomic diversity with coeval assemblages evidences a general similarity with nearby western Tethyan fish assemblages and especially with the Jbel Tselfat ichthyofauna, although some of the taxa are exclusively shared with the assemblages of the boreal realm (English Chalk, Westphalia and Saxony). However, additional information would be necessary to more properly define the main global ichthyogeographic patterns during the Cenomanian.

INTRODUCTION

The Bonarelli Level (BL) is a 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 & 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 micropaleontological studies (e.g. Bellanca et al. 1996; Salvini & Marcucci Passerini 1998; Luciani & Cobianchi 1999; Premoli Silva et al. 1999; Coccioni & 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 BL yielded one of the better-known Cenomanian ichthyofaunas (see Patterson 1993). The diverse fish assemblage of the BL from the locality of the Bomba Quarry near Cinto Euganeo (Padova) has been examined and discussed by several authors (Sorbini 1976, 1980; Astolfi & Colombara 1990, 2003; Biz-

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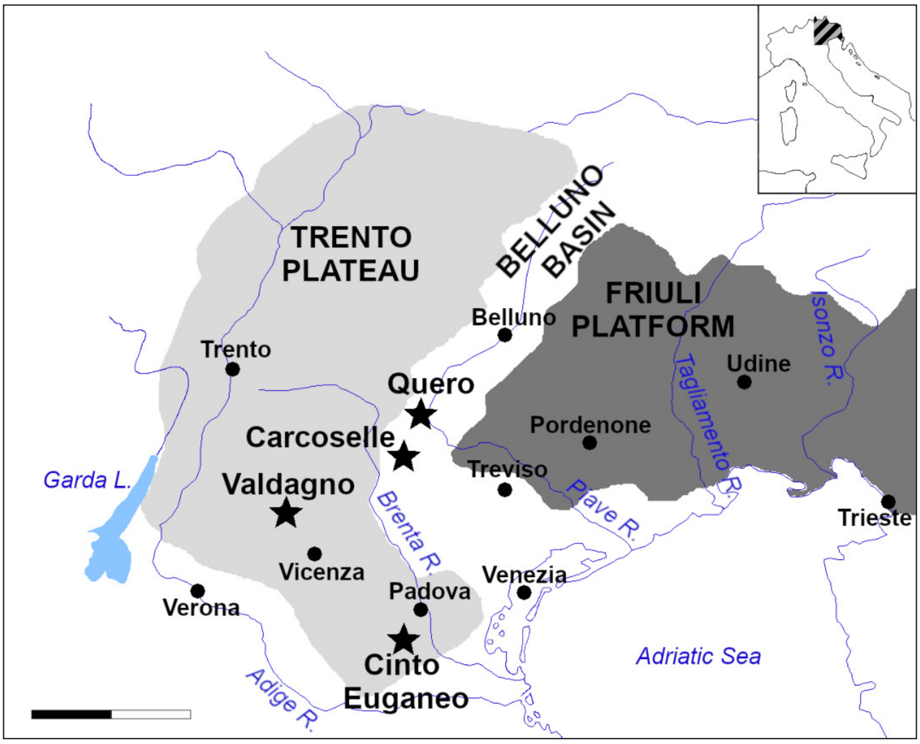

Fig. 1 - Sketch map of northeastern Italy with superimposed the main Cretaceous paleogeographic elements showing the position (black stars) of the fossiliferous localities examined in this study. Scale bar equals 50 km.

zarini & Coccioni 1990; Avanzini & Luciani 2002; Dalla Vecchia et al. 2005). However, recent discoveries from other localities (e.g. Bizzarini et al. 2018 and reference therein) and the urgent 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 properly interpreting the vertebrate disparity and diversity in the most important Upper Cretaceous vertebrate *Fossil-Lagerstätten* 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 performed 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 new and informative framework emerges from this study, which also includes a comparative paleobiogeographic analysis of the late Cenomanian (and early Turonian) Tethyan ichthyofaunas.

Geological context

The Southern Alpine domain (northeastern Italy) during the Cretaceous was characterized by three different depositional environments derived from a heterogeneous palaeogeographic setting, with a horst and graben trend inherited from the rifting associated with the opening of the central North Atlantic (Winterer & Bosellini 1981) (Fig. 1). A carbonate platform, the Friuli Platform, bordered eastwards a continental margin basin, the Belluno Basin, which was separated westwards from another basin (the Lombardian Basin) by a structural high, the Trento Plateau (Channell & Medizza 1981; Channell et al. 1992; Gomez et al. 2002, 2015; Fig. 1). 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 & Bosellini 1981). The western part of the basin was characterized by the pelagic limestones of 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 & Romano 2009; Fig. 2). The Trento Plateau (Trento-Vicenza-Verona-Padova provinces) is characterized by thinner successions of pelagic deposits, compared with the adjacent basins, comprising calcareous pelagic and hemipelagic oozes mostly consisting

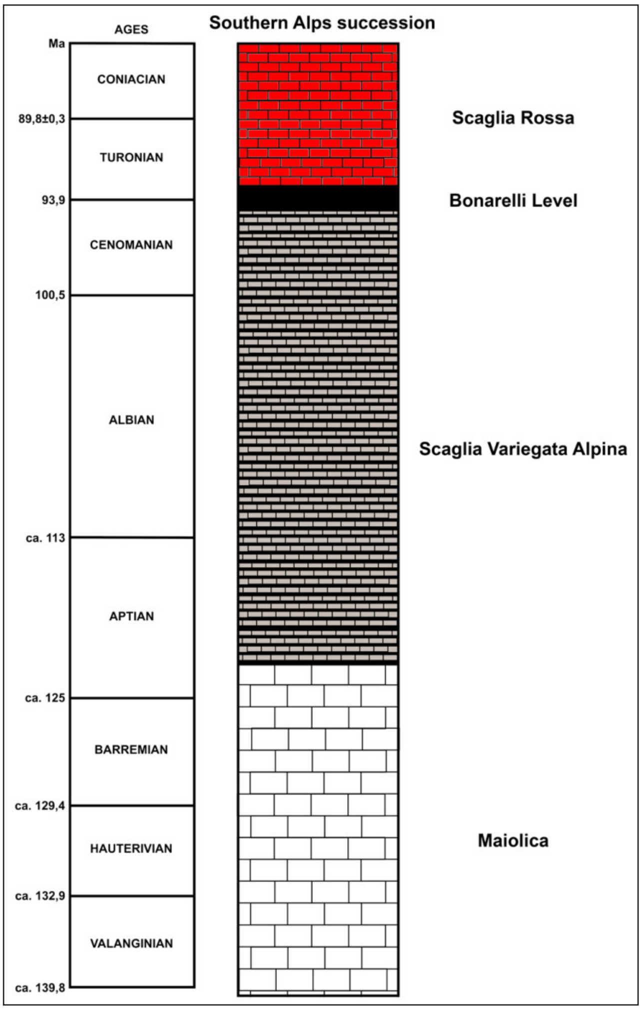

Fig. 2 - Lithostratigraphic framework of the Bonarelli Level in the Upper Cretaceous Southern Alps succession (modified from Salvini & Marcucci Passerini 1998).

of calcareous nannofossils, alternated with varicoloured marlstones of the Scaglia Variegata Alpina Formation and pinkish micrites and marlstones of the overlying Scaglia Rossa (Coccioni & Luciani 2005; Fig. 2). The black shales of the Bonarelli Level (close to the Cenomanian/Turonian boundary) usually 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; Fig. 2). This level is discontinuously present in the Southern Alps, ranging from 30 to 300 cm in thickness (Gomez et al. 2015; Amalfitano et al. 2017). We studied the ichthyofaunas from four main localities: Bomba Quarry near Cinto Euganeo (Euganei Hills, Padova Province), Carcoselle Quarry near Possagno (Venetian Prealps, Treviso Province), Schievenin Valley near Quero (Belluno Province), Schio-Valdagno tunnel (Vicenza Province). There are also minor outcrops that yielded fish remains near Crespano del Grappa (Treviso Province), and in the Sinigaglia Quarry near Villa di Teolo (Euganei Hills, Padova Province). The first paleoichthyological report from the BL of northeastern Italy was that of Bassani (1880, 1882) in which were described the fish remains from Crespano del Grappa.

The BL of the 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 & 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 the Carcoselle Quarry was well exposed in the active front of the quarry, located near the village of Possagno, between Bassano del Grappa to the west and the Piave River to the east, about 50 km north of Padova. The lithology of the BL at the Carcoselle Quarry is very similar to that of the Bomba Quarry. As far as regards the Schio-Valdagno tunnel, the excavations took place in the mountains between the villages of Valdagno and Schio (about 20 km north-west of Vicenza) in the early 2000s; in this locality the BL mainly consists of greenish-grey to black mudstones and shales alternated with radiolarian-rich layers (Coccioni & Luciani 2005) containing an appreciable amount of $CaCO_3$. In the Schievenin Valley, near the village of Quero (ca. 30 km south-west of the city 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), observed in the Valdagno-Schio tunnel and the Carcoselle Quarry localities, are also present in the Quero outcrop. The atypical color of the Quero BL derives from intense weathering of the original black shales. The fossil remains are mainly concentrated in the laminites in the lower-middle part of the level and were all collected from the so-called exposure B of Gomez et al. (2002).

MATERIAL AND METHODS

The material comes from the collections of five museums in northeastern Italy and primarily consists of fragmentary fish debris embedded in blocks of rock coming from the BL of the localities mentioned above. Synonymy lists in the systematic analysis mostly refer to studies that directly figured and/or described material from northeastern Italy. 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). The majority of the images and interpretative drawings of the specimens were produced using the free software packages GIMP (v. 2.10.6) and Inkscape (v. 0.92). The synonymy lists and open nomenclature follow the standards proposed by Matthews (1973), Bengston (1988) and Sigovini et al. (2016).

Statistic analyses were performed using the software Past 3.26 (Hammer et al. 2001) in order to compare the BL assemblage with other coeval marine assemblages. The data set is presented in Tab. 1. The references used for the data set compilation are listed in Tab. S.1 (Supplementary information). Parameters of the PCA analyses are provided in Supplementary information.

Measurements abbreviations

BD: body depth, measured as the maximum depth of the body; **HL**: head length, measured as horizontal distance between tip of the premaxilla and posterior limit of the opercle; **PA**: preanal distance, measured as horizontal distance between tip of the premaxilla and the point of articulation between the first pterygiophore and first anal fin ray; **PD**: predorsal distance, measured as horizontal distance between tip of the premaxilla and the point of articulation between the first pterygiophore and first dorsal fin ray; **PV**: pelvic distance, measured as horizontal distance between the tip of the premaxilla and the point of articulation between outer pelvic fin ray and the pelvic girdle; **SL**: standard length, measured as horizontal distance between the tip of the premaxilla and the posterior-most limit of the hypurals; **TL**: total length, measured as maximum horizontal distance between the tip of the premaxilla and the posterior limit of the caudal fin lobes.

Institutional abbreviations

MCSNV: Museo Civico di Storia Naturale di Verona; **MCSNVE:** Museo Civico di Storia Naturale di Venezia; **MCR**: Museo Civico di Rovereto (Trento); **MCV:** Museo Civico di Valdagno (Vicenza); **MGCB:** Museo Geopaleontologico di Cava Bomba di Cinto Euganeo (Padova); **MGPPD:** Museo di Geologia e Paleontologia dell'Università degli Studi di Padova.

Anatomical abbreviations

aa: angulo-articular; **ang**: angular; **art**: articular; **cl**: cleithrum; **cor**: coracoid; **br**: branchiostegal rays; **bsph**: basisphenoid; **copr**: coronoid process; **den**: dentary; **df**: dorsal fin; **dhyo**: dermohyomandibula; **dsp**: dermosphenotic; **ecpt**: ectopterygoid; **enpt**: endopterygoid; **fr**: frontal; **h**: hypural; **hyph**: hypurapophysis; **hyo**: hyomandibula; **io**: infraorbital; **iop**: interopercle; **letm**: lateral ethmoid; **lpart**: left prearticular; **max**: maxilla; **met**: mesethmoid; **mtp**: metapterygoid; **mx**: maxilla; **op**: opercle; **pa**: parietal; **pal**: palatine bone; **par**: parasphenoid; **pch**: posterior ceratohyal; **pf**: pectoral fin; **ph**: parhypural; **pmx**: premaxilla; **ppr**: postparietal process; **pop**: preopercle; **pto**: pterotic; **pu**: preural vertebra; **q**: quadrate; **rart**: retroarticular; **rpart**: right prearticular; **scr**: sclerotic ring; **smx**: supramaxilla; **soc**: supraoccipital; **sop**: suborpercle; **sph**: sphenotic; **sym**: sympletic; **u**: ural vertebra; **un**: uroneural; **vert**: vertebra; **vo**: vomer.

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. 3A-C

1922 *Scapanorhynchus* sp. - D'Erasmo, p. 28, pl. 3, figs 18-20.
1994 *Scapanorhynchus* sp. - Sirna et al., p. 272.

Referred material: MGCB IG220945.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The mitsukurinid shark *Scapanorhynchus raphiodon* is represented by an isolated anterior tooth (Fig. 3A-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 and occupy the upper part of the cusp, becoming blunt where the cusp widens basally. The root is poorly preserved, especially the lobes. However, the lingual protuberance is very prominent and bears a short but deep nutritive groove.

Overall, these characters support the assignment to the genus *Scapanorhynchus* (see Hamm & Shimada 2002; Cappetta 2012). The species *S. raphiodon* is "the most frequently cited species" (Cappetta 1987: 93; Cappetta 2012: 187), but its morphological characterization is still uncertain (see Cappetta & Case 1975; Hamm & Shimada 2002; Welton & Farish 1993). However, the weak striations, the size and the stratigraphic position of the specimen are consistent with those of *S. raphiodon* (Hamm & Shimada 2002). *Scapanorhynchus raphiodon* is reported from the upper Cenomanian to the Santonian in pelagic sediments from several parts of the world (Hamm & Shimada 2002 and references therein). This is the first report of the genus and the species from the Bonarelli Level in Italy. *Scapanorhynchus* was previously reported in the Scaglia Rossa Formation of northeastern Italy by D'Erasmo (1922) and Sirna et al. (1994).

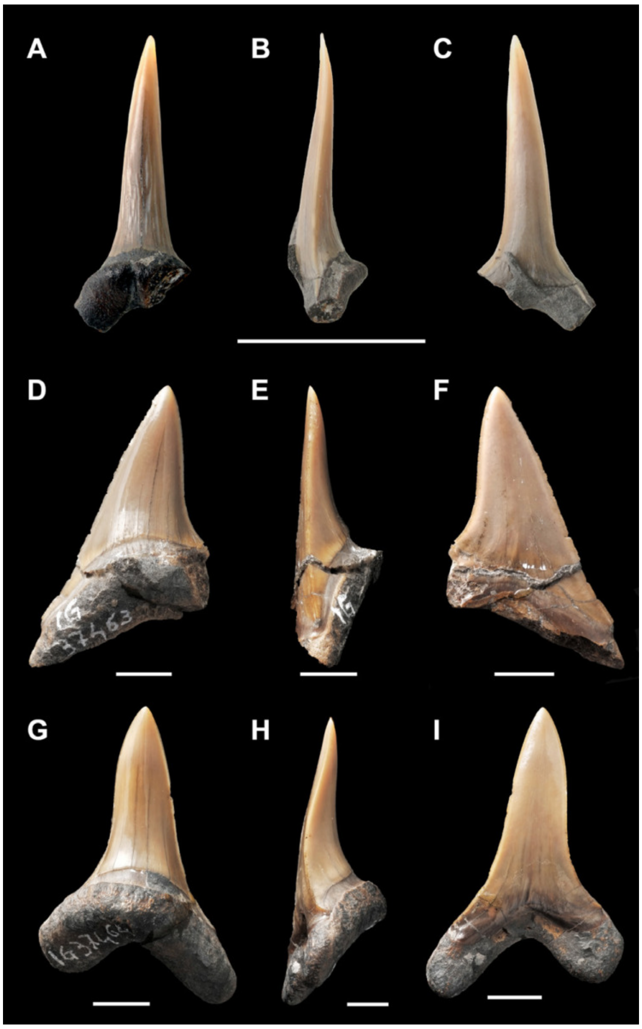

Fig. 3 - *Scapanorhynchus raphiodon* (Agassiz, 1835); Bomba Quarry (Cinto Euganeo); MGCB IG220945, A) lingual, B) lateral and C) labial view. *Cretoxyrhina mantelli* (Agassiz, 1835); Bomba Quarry (Cinto Euganeo); MGCB IG37463, D) lingual, E) lateral and F) labial view; MGCB IG37465, G) lingual, H) lateral and I) labial view.

Family Cretoxyrhinidae Glickman, 1958
Genus *Cretoxyrhina* Glickman, 1958

Cretoxyrhina mantelli (Agassiz, 1835)
Fig. 3D-I

1922 *Oxyrhina Mantelli* Ag. - D'Erasmo, p.36, pl. 3, figs 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 & Colombara, p. 144, fig. 205.
1994 *Isurus mantelli* (Agassiz) - Colombara & Astolfi, p. 33.
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); Schio-Valdagno Tunnel.

Description and remarks. Five isolated teeth can be assigned to *Cretoxyrhina mantelli* (Fig. 3D-I). The triangular crown is slender and asymmetrical in the 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 exhibit rounded extremities. The lateral teeth bear 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 are of 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 examined specimens is fully consistent with those of *Cretoxyrhina mantelli* reported by various authors (e.g. Shimada 1997; Cappetta 2012; Amalfitano et al. 2019a). *Cretoxyrhina* is so far the most common lamniform shark in the Upper Cretaceous of Italy (Amalfitano et al. 2019a).

Genus *Cretalamna* Glickman, 1958

Cretalamna appendiculata (Agassiz, 1835)
Fig. 4A-C

1922 *Lamna appendiculata* (Ag.) - D'Erasmo, p. 38, pl. 4, fig. 8.
p. 1976 *Lamna serrata* (Agassiz) 1838-1843 - Sorbini, p. 481, pl. 3 (IG 37467).
p. 1994 *Lamna serrata* (Agassiz) - Colombara & Astolfi, p. 34.
1994 "*Lamna*" *serrata* (Agassiz, 1833-1843) - Sirna et al., p. 271.

Referred material: MCSNV IG37467.

Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The available material consists of a single isolated tooth (a lateral one, 9 mm high and 8 mm wide; Fig. 4A-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* (Cappetta

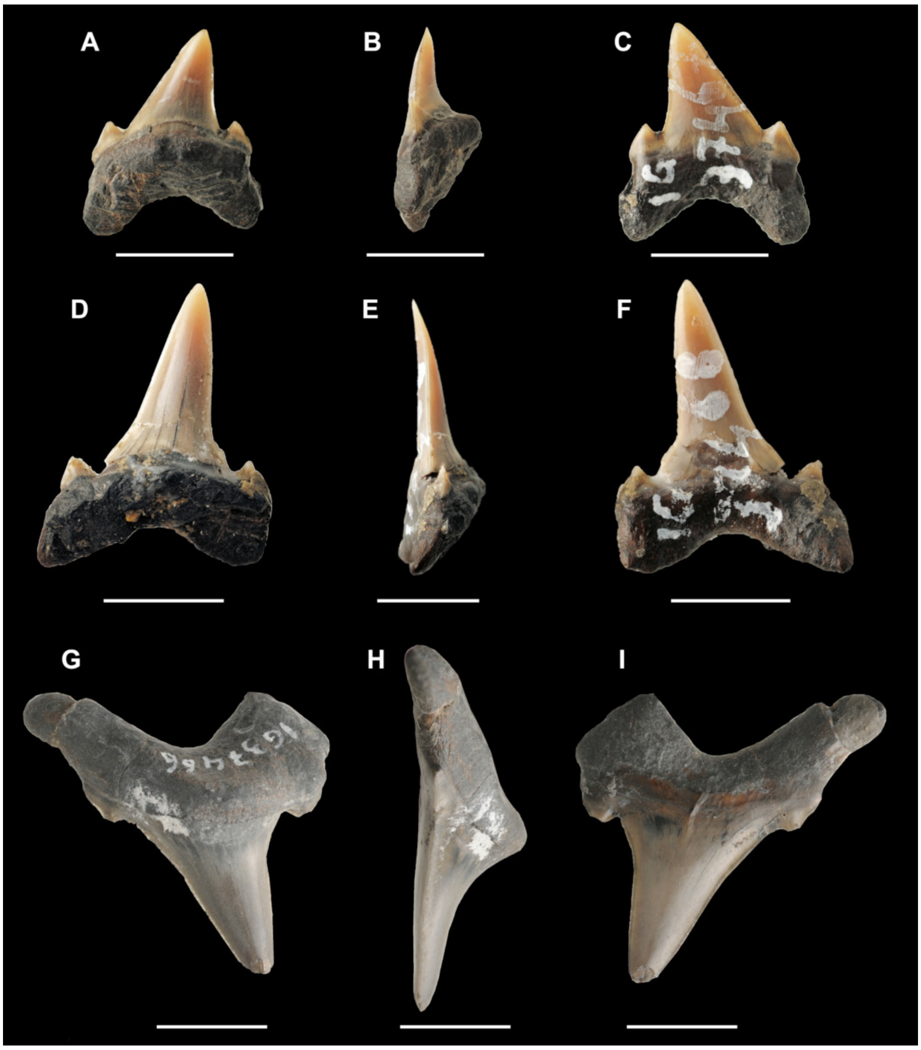

Fig. 4 - *Cretalamna appendiculata* (Agassiz, 1835); Bomba Quarry (Cinto Euganeo); MCSNV IG37467, A) lingual, B) lateral and C) labial view. *Archaeolamna kopingensis* (Davis, 1890); Bomba Quarry (Cinto Euganeo); MGCB IG37466, D) lingual, E) lateral and F) labial view; MCSNV IG37468, G) lingual, H) lateral and I) labial view.

2012; Siversson et al. 2015). The taxon is rather common in Cretaceous and Cenozoic pelagic deposits worldwide from the Albian to the Ypresian (Cappetta 1987, 2012; Siversson et al. 2015). In Italy *C. appendiculata* was reported by D'Erasmo (1922) from the 'Senonian' red-purple chalk (Scaglia Rossa Veneta) of Feltre (Belluno).

Family Archaeolamnidae Underwood & Cumbaa, 2010

Genus *Archaeolamna* Siversson, 1992

Archaeolamna kopingensis (Davis, 1890)

Fig. 4D-I

p. 1976 *Lamna serrata* (Agassiz) 1838-1843 - Sorbini, p. 481, pl. 2 (IG 37466), pl. 3 (IG 37468).
p. 1994 *Lamna serrata* (Agassiz) - Colombara & Astolfi, p. 34.
1994 "*Lamna*" *serrata* (Agassiz, 1833-1843) - Sirna et al., p. 271.

Referred material: MGCB IG37466; MCSNV IG37468.

Locality: Bomba Quarry (Cinto Euganeo).

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. 4D-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.

Family Anacoracidae Casier, 1947

Genus *Squalicorax* Whitley, 1939

Squalicorax falcatus (Agassiz, 1843)

Fig. 5

1976 *Corax* cfr. *falcatus* Agassiz 1843 - Sorbini, p. 482, plate 4.
1994 *Corax* cfr. *falcatus* Agassiz - Colombara & Astolfi, p. 34.
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.
2018 *Squalicorax falcatus* - Bizzarini et al., p. 226, fig. 4.

Referred material: MGCB IG 37469; MGCB U3S1/3; MCSNVE 12430.

Locality: Bomba Quarry (Cinto Euganeo); Carcoselle Quarry (Possagno).

Description and remarks. All the three examined teeth have a triangular crown with serrated cutting edges (see Fig. 5). 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; MCSNVE 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 MCSNVE 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 midlenght, more evident in MGCB U3S1/3 and in MCSNVE 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 agree with the definition of *Squalicorax falcatus* provided by Cappetta (2012). The taxon occurs from the Cenomanian to the Santonian (Cappetta 2012; Shimada & Cicimurri 2005). Sorbini (1976) tentatively referred a single tooth from the Bomba Quarry (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, but outside Veneto Region, 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). The teeth from the Carcoselle Quarry were preliminarily reported by Dalla Vecchia et al. (2005).

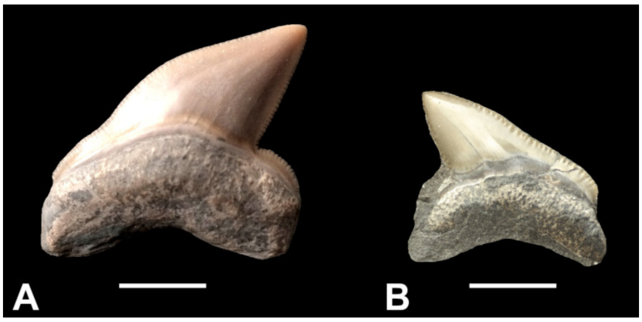

Fig. 5 - *Squalicorax falcatus* (Agassiz, 1843). A) MGCB U3S1/3, Bomba Quarry (Cinto Euganeo), lingual view. B) MCSNVE 12430, Carcoselle Quarry (Possagno), lingual view. Scale bars equal 5 mm.

Order *incertae sedis*
Family Ptychodontidae Jaekel, 1898
Genus *Ptychodus* Agassiz, 1934a

Ptychodus decurrens Agassiz, 1838

Fig. 6

1904 *Ptychodus latissimus* Ag. - Squinabol: p. 8; pl. 1, fig. 1.
1921 *P. decurrens* - Fossa-Mancini: p. 194.
1922 *Ptychodus decurrens* Ag. - D'Erasmo: p. 17; pl. 2, figs 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 & Colombara, p. 145, fig. 206.
1990 *Ptychodus polygyrus* Agassiz - Astolfi & Colomabara, p. 146.
1994 *Ptychodus decurrens* Agassiz - Colombara & Astolfi, p. 34 and unnumbered fig. (p. 34, 35).
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); Carcoselle Quarry (Possagno); Schio-Valdagno Tunnel.

Description and remarks. The available material consists of 17 isolated teeth (Fig. 6). One of these teeth (MGCB IG37483) was erroneously referred to *Ptychodus polygyrus* by Sorbini (1976). 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 across the occlusal plane, laterally extending and bifurcat-

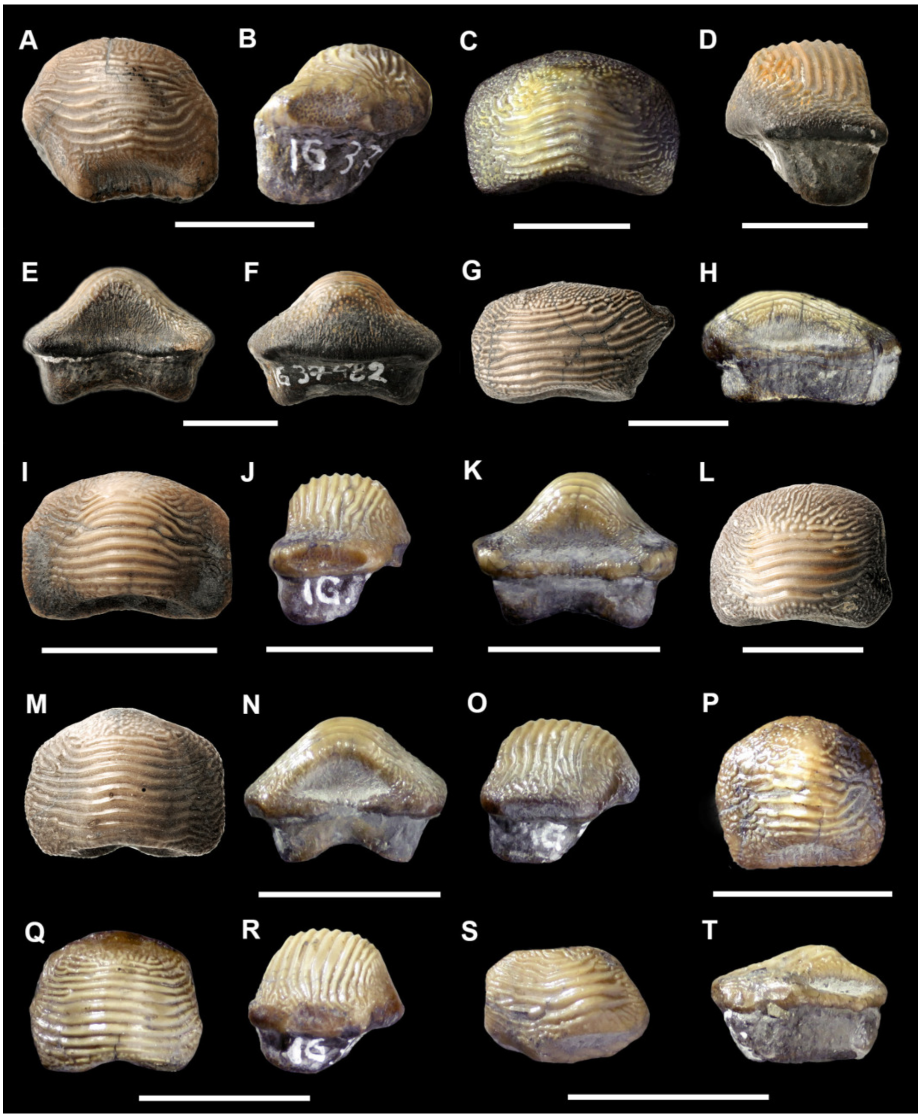

Fig. 6 - *Ptychodus decurrens* Agassiz, 1938; Bomba Quarry (Cinto Euganeo). MGCB IG37483, A) occlusal and B) lateral view; MGCB IG37482, C) occlusal, D) lateral, E) posterior view and F) anterior view; MGCB IG37481, G) occlusal and H) posterior view; MGCB IG37479, I) occlusal, J) lateral and K) posterior view; MGCB 446, L) occlusal view; MGCB IG37478, M) occlusal, N) posterior and O) lateral view; MGCB IG37477, P) occlusal view; MGCB IG37476, Q) occlusal and R) lateral view; MGCB IG37475, S) occlusal and T) posterior view. Scale bars equal 5 mm.

ing into the marginal area; fine and dense wrinkles perpendicular to the transverse ridges extending on anterior and posterior marginal areas. 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 BL of Colli Euganei by Squinabol (1904) and has been recently reported from the Cenomanian of Trentino-Alto Adige by Amadori et al. (2019).

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 the 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 & 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-

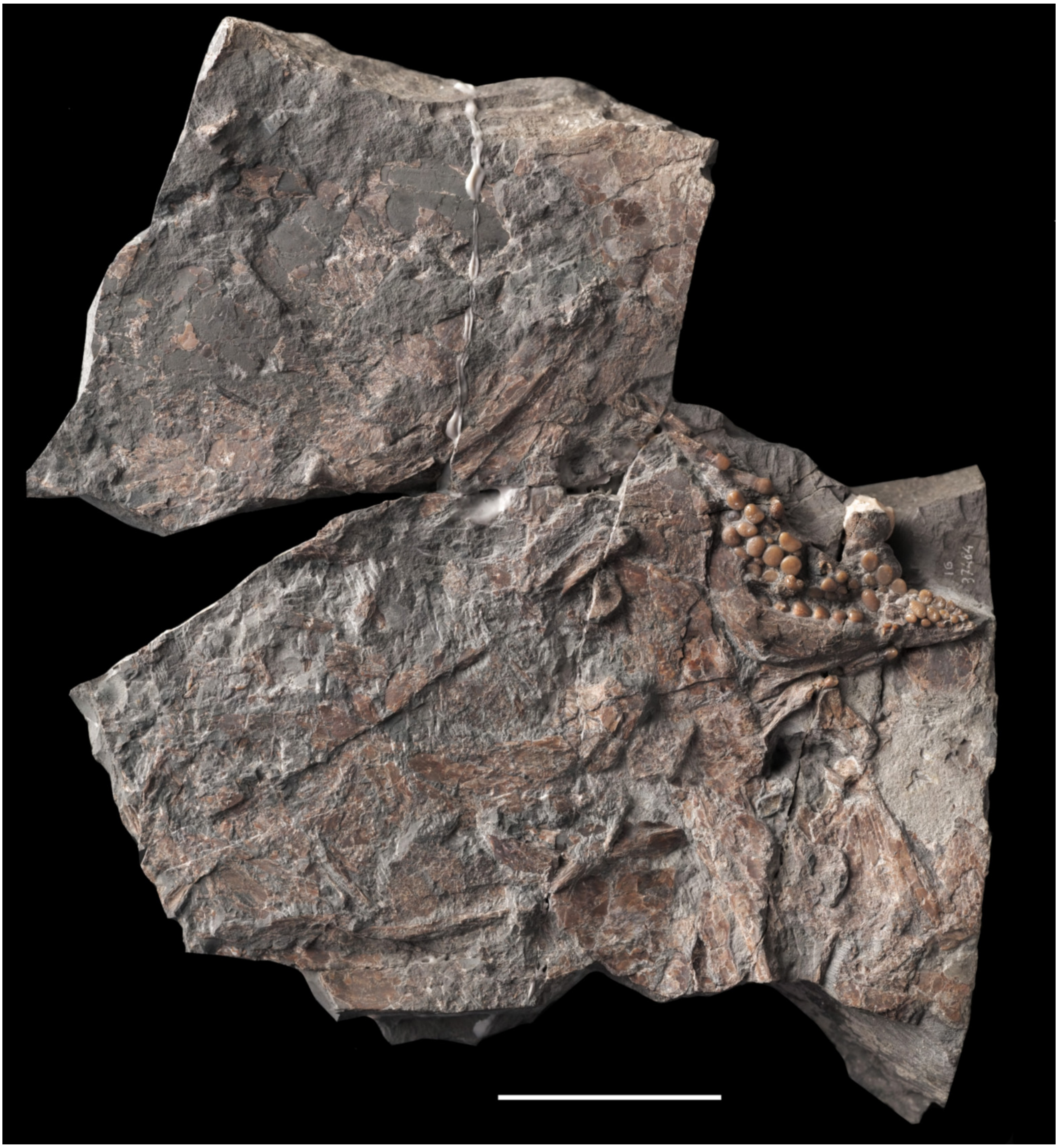

Fig. 7 - *Paranursallia gutturosa* (Arambourg, 1954); Bomba Quarry (Cinto Euganeo), MGCB IG37484. Scale bar equals 50 mm.

preserved Cenomanian pycnodont taxa have been described from the Middle East (e.g. Marramà et al. 2016; Cawley & 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 BL 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 the BL of Veneto exhibit a few autapomorphic characters but preserve partial or complete dentitions, which are therefore very helpful for supporting their identification.

Fig. 8 - *Paranursallia gutturosa* (Arambourg, 1954); Bomba Quarry (Cinto Euganeo), MGCB IG37484. Details of the A) oral region and B) vomerine and prearticular dentition. Scale bars equal (A) 50 and (B) 20 mm.

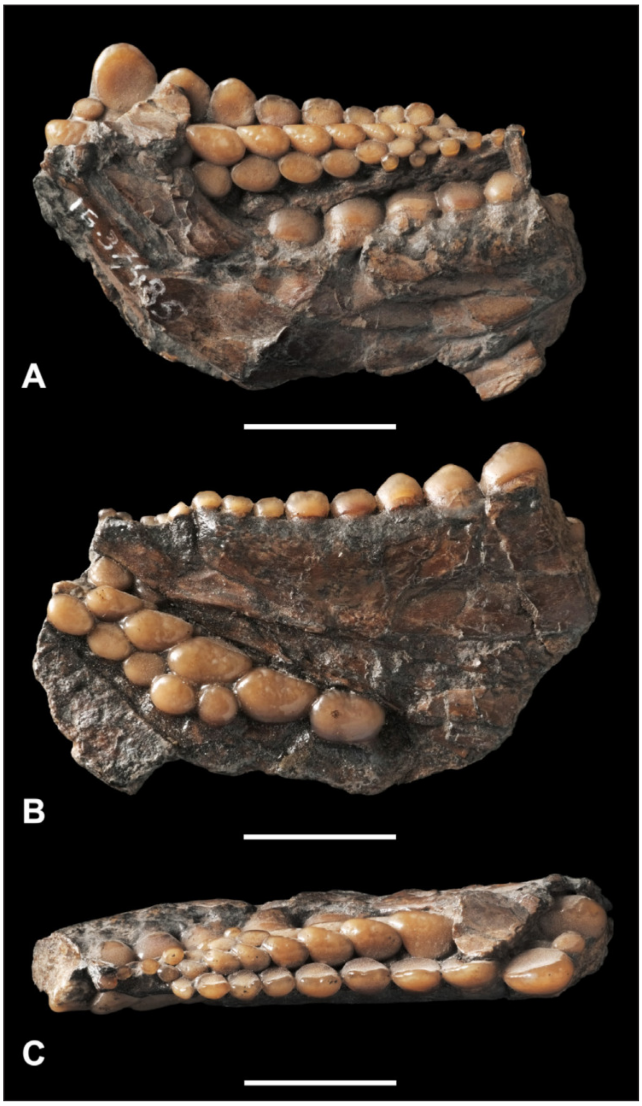

Fig. 9 - *Paranursallia gutturosa* (Arambourg, 1954); Bomba Quarry (Cinto Euganeo), MGCB IG37485. A) Right and B) left prearticular; C) occlusal view of the prearticular dentition. Scale bars equal 10 mm.

Family Pycnodontidae Agassiz, 1833 (sensu Nursall 1996a)
Subfamily Nursalliinae Poyato-Ariza & Wenz, 2002
Genus *Paranursallia* Taverne et al., 2015

Paranursallia gutturosa (Arambourg, 1954)

Figs 7-10

1976 *Paleobalistum* cfr. *gutturosum* Arambourg, 1954 - Sorbini, p. 484, pl. 7-8.
1980 *Paleobalistum* cfr. *gutturosum* - Sorbini, p. 119 and unnumbered fig.
1987 *Nursallia gutturosum* - Blot, p. 200.
1990 *Paleobalistum* cfr. *gutturosum* Arambourg - Astolfi & Colombara, p. 146, fig. 209.
1990 *Paleobalistum* - Bizzarini & Coccioni, p. 79.
1994 *Paleobalistum* cfr. *gutturosum* Arambourg - Colombara & Astolfi, p. 34.
1994 *Paleobalistum* cf. *gutturosum* - Sirna et al., p. 271.
2005 *Nursallia*? *guttorosum* - Dalla Vecchia et al., p. 106.
2007 *Nursallia gutturosum* (Arambourg 1954) - Capasso, p. 190, fig. 2.
2010 *Nursallia gutturosum* - Khalloufi, p. 48.
2015 *Paranursallia gutturosa* - Taverne et al., p. 226.

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

Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. Specimen MGCB IG37484 (Figs 7-8) 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. 8A for details). The recognizable bones include mostly elements of the right side of

Fig. 10 - *Paranursallia gutturosa* (Arambourg, 1954); Carcoselle Quarry (Possagno), MCSN-VE 24556. Scale bar equals 50 mm.

the head, including a thin (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, and the vomerine and prearticular teeth arranged in rows justify the attribution of the specimen to the Pycnodontiformes (see Poyato-Ariza & Wenz 2002). The presence of a dermohyomandibular supports its inclusion within the Pycnodontoidea (sensu Poyato-Ariza & Wenz 2002). The combination of characters listed herein support the attribution of the specimen to *Paranursallia gutturosa* (see Poyato-Ariza & Wenz 2002), including: two premaxillary and dentary teeth respectively, 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 forming a series of regularly increasing size posteriorly, 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 in the main prearticular tooth row; coronoid process of the prearticular with high and straight dorsal border.

The vomerine and prearticular teeth are weakly ornamented (Fig. 8B). 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 in addition to the serrated edges.

MGCB IG37485 (Fig. 9) comprises two prearticulars (left and right) pertaining to a single individual. The bones are slightly disarticulated. The prearticular dentition exhibits the same characters of the other specimens (prearticular teeth with oval contour and arranged in three regular rows, 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 contours arranged in two partial rows. This specimen is tentatively referred to *Paranursallia gutturosa* based on its 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 cross-like 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 & Wenz 2002: 179). Adjacent arcocentra have hyper-complex contacts. This character is typical of *Nursallia* and *Paranursallia* (see Poyato-Ariza & 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 the largest pycnodontiform taxon reported from BL of northeastern Italy so far.

Genus *Nursallia* Blot, 1987

'Nursallia' tethysensis Capasso, Abi Saad & Taverne 2009

Figs 11-12

1976 *Coelodus* cfr. *saturnus* Heckel, 1856 - Sorbini, p. 483, pls 6, 12.
1980 *Coelodus* cfr. *saturnus* - Sorbini, p. 119.
1990 *Coelodus* cfr. *saturnus* Heckel - Astolfi & Colombara, p. 146, fig. 208.
1994 *Coelodus* cfr. *saturnus* Heckel - Colombara & Astolfi, p. 34.
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), Schievenin Valley (Quero).

Description and remarks. Two specimens are referred herein to *'Nursallia' tethysensis*. Specimen MGP-PD 32093 (Fig. 11) was collected from the Schievenin Valley (Quero) and is described herein for the first time. It consists of a nearly complete skeleton, lacking the caudal portion of the body. The specimen is moderately well-preserved and a series of characters are clearly recognizable (Fig. 11A), including: peltate squamation; head relatively large, with a wide orbit and a short snout; frontal (=parietal of Kriwet 2005 and Cawley et al. 2018) broad and curved, forming a round profile to the upper surface of the head in lateral view, apparently not covering the mesethmoid (possibly representing a taphonomic artifact); crescent-shaped maxilla preserved as impression only in front of the vomer; mesethmoid large located antero-dorsally to the narrow and long parasphenoid. The vomer (Fig. 11C) bears five molariform teeth, while the left prearticular bears six molariform teeth (like *'Nursallia' tethysensis*; Capasso et al. 2009). The right prearticular (Fig. 11C) 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 number of tooth rows cannot be determined due to inadequate preservation. The dentary is small, posteriorly elongate and bears three incisiform teeth with a shallow 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) although it may also represent the possible product of taphonomic processes. The opercle is well-preserved and reduced, as in other pycnodontiforms (Poyato-Ariza & Wenz 2002). The neural and haemal arcocentra contact each other surrounding the notochord as in *Paranursallia gutturosa* and other Nursallinae (see Poyato-Ariza & Wenz 2002: 179). Furthermore, adjacent arcocentra have hyper-complex contacts (apparently with at least two prezygapophyses and postzygapophyses, see Fig. 11D). This character is typical of *Nursallia* and *Paranursallia* (see Poyato-Ariza & Wenz 2002; Capasso et al. 2009; Taverne et al. 2015). Anterior sagittal flanges are preserved on some neural spines.

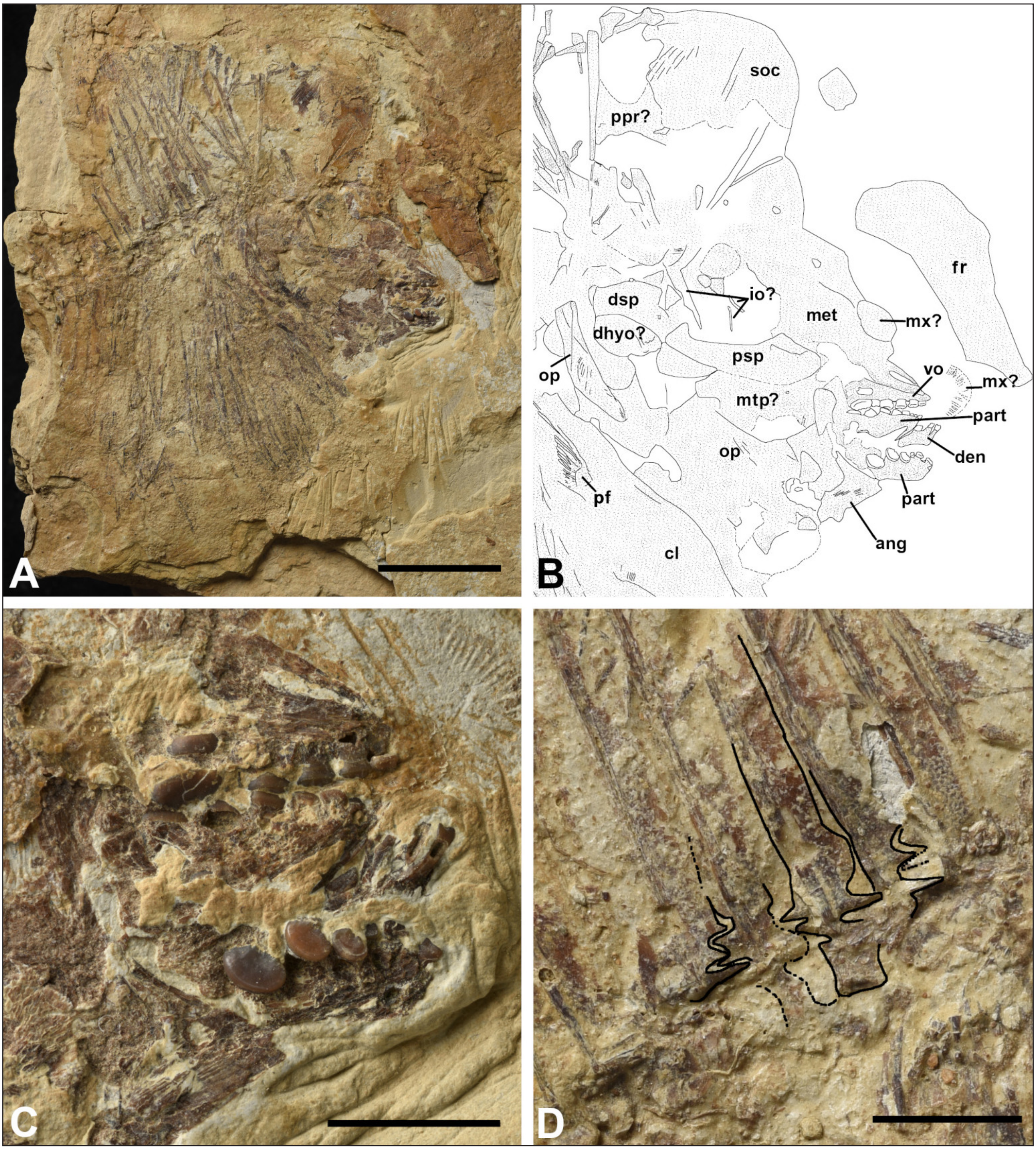

Fig. 11 - '*Nursallia*' *tethysensis* Capasso, Abi Saad & Taverne, 2009; Schievenin Valley (Quero). A) MGPPD 32093, B) interpretative drawing, C) dentition and D) detail of the vertebral column showing the hyper-complex contact between adjacent arcocentra. Scale bars equal (A) 10 mm and (C and D) 5 mm.

All the described characters allow to refer the specimen to '*Nursallia*' *tethysensis*.

Specimen MGCB IG37470 comes from the Bomba Quarry (Cinto Euganeo) and includes mainly disarticulated or partially articulated and fragmentary cranial and postcranial elements of a single individual (see Fig. 12A-D for details). The squamation is peltate. A portion of the 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

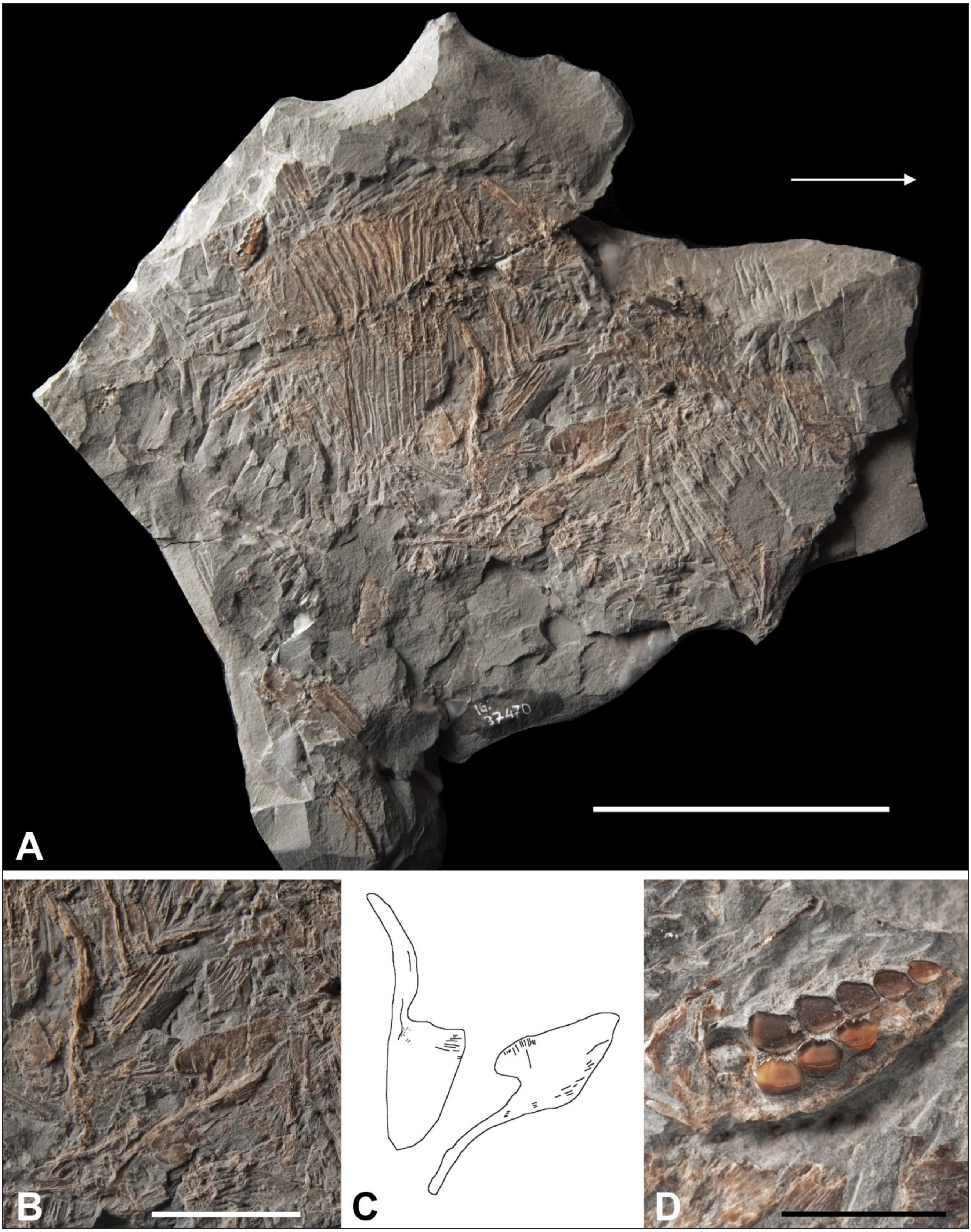

Fig. 12 - *'Nursallia' tethysensis*. Capasso, Abi Saad & Taverne, 2009; Bomba Quarry (Cinto Euganeo). A) MGCB IG37470 (the arrow indicates the alleged anterior part of the specimen); B) detail of the specimen showing the cleithra; C) interpretative reconstruction of the cleithra; D) prearticular dentition. Scale bars equal (A) 50 mm, (B) 20 mm and (C) 5 mm.

Fig. 13 - *Protosphyraena ferox* Leidy, 1857; Bomba Quarry (Cinto Euganeo), MGCB IG37527.

and the reduced opercle allow to refer the specimen to the Pycnodontiformes (see Poyato-Ariza & 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 in the inner main row and five teeth in the outer row (Fig. 12D). The occlusal surface of the teeth has a trapezoidal to subtriangular profile in the main inner row and a subcircular profile in the first lateral row. The occlusal surface also exhibits intense wear, with a blunt ridge characterizing 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 become larger than those of the inner row. Sorbini (1976) referred these remains from the Bomba Quarry to *Coelodus* cfr. *saturnus* based on dental characters. However, *Coelodus* teeth are completely different, being extremely elongated in transversal direction (Poyato-Ariza 2002: 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. 12D), similarly to '*N.*' *tethysensis* (six teeth) and *Paranursallia gutturosa* (seven teeth) (see Capasso et al. 2009; Poyato-Ariza & Wenz 2002). We tentatively refer the specimen to '*N.*' *tethysensis* based on the almost identical prearticular dentition.

'*Nursallia*' *tethysensis* is currently known only from the Cenomanian of Lebanon (Capasso et al. 2009).

Subdivision **Teleostei** Müller, 1846 (sensu Patterson & Rosen 1977)
Order **Pachycormiformes** Berg, 1940
Family Pachycormidae Woodward, 1895
Genus *Protosphyraena* Leidy, 1857

Protosphyraena ferox Leidy, 1857

Fig. 13

1922 *Protosphyraena* sp. - D'Erasmo, p. 62; pl. 6, fig. 17.
1976 *Protosphyraena ferox* Leidy 1856 - Sorbini, p. 485, pl. 9.
1980 *Protosphyraena ferox* - Sorbini, p. 119 and unnumbered fig. (p. 121).
1990 *Protosphyraena ferox* Leidy - Astolfi & Colombara, p. 146.
1994 *Protosphyraena ferox* Leidy - Colombara & Astolfi, p. 35.
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*), figs 3-6.

Referred material: MGCB IG37527.
Locality: Bomba Quarry (Cinto Euganeo).

Remarks. A single specimen was found and referred to this taxon (Fig. 13). 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).

Order **Aspidorhynchiformes** Bleeker, 1859
Family Aspidorhynchidae Nicholson & Lydekker, 1889
Genus *Belonostomus* Agassiz, 1834b

Remarks. The greatly elongated body with a long snout and very deep lateral-line scales unquestionably supports the assignment of the aspidorhynchiforms of the BL to the genus *Belonostomus* (see Brito 1997; Forey et al. 2003: tab. 2). The specimens described herein consist of a few fragmentary remains of problematic taxonomic placement. Due to their fragmentary nature, we prefer to assign all of these three specimens to a single indeterminate species of *Belonostomus* until much complete and better preserved material will be available. Remains of the genus *Belonostomus* were originally reported from the BL by Bassani (1880, 1882), who described material collected from outcrops in the vicinity of the village of Crespano del Grappa, about 2,5 km from the Carcoselle Quarry.

***Belonostomus* sp.**

Fig. 14

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

Referred material: MCSNVE 25515a-b; 24519a-b; MCV 10/25-10/26.

Provenance locality: Carcoselle Quarry (Possagno); Schio-Valdagno Tunnel (Valdagno).

Description and remarks. Specimen 25515a-b (Fig. 14A) is a largely incomplete specimen, in part and counterpart, consisting 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 of the dorsal scutes immediately anterior to the tail that terminates into a spiny portion (see close-up in Fig. 14A). According to Forey et al. (2003), this character should be regarded as diagnostic of a still unnamed species-level taxon (*Belonostomus* sp. 2; Forey et al. 2003: 243, figs 13-15) from Namoura (Lebanon). Dorsal scutes characterized by a similar morphology have also been reported in a single specimen from Komen (Slovenia) referred to *Belonostomus lesinaensis* by D'Erasmo (1946: fig. 9). *Belonostomus lesinaensis* has been considered as a junior synonym of *B. crassirostris* by Brito (1997) and Forey et al. (2003).

Specimen 24519a-b, in part and counterpart (Fig. 14B-C), is largely incomplete and consists of the head and anterior portion of the trunk. The head lacks the distal portion of predentaries and premaxillae. The predentary has needle-like teeth

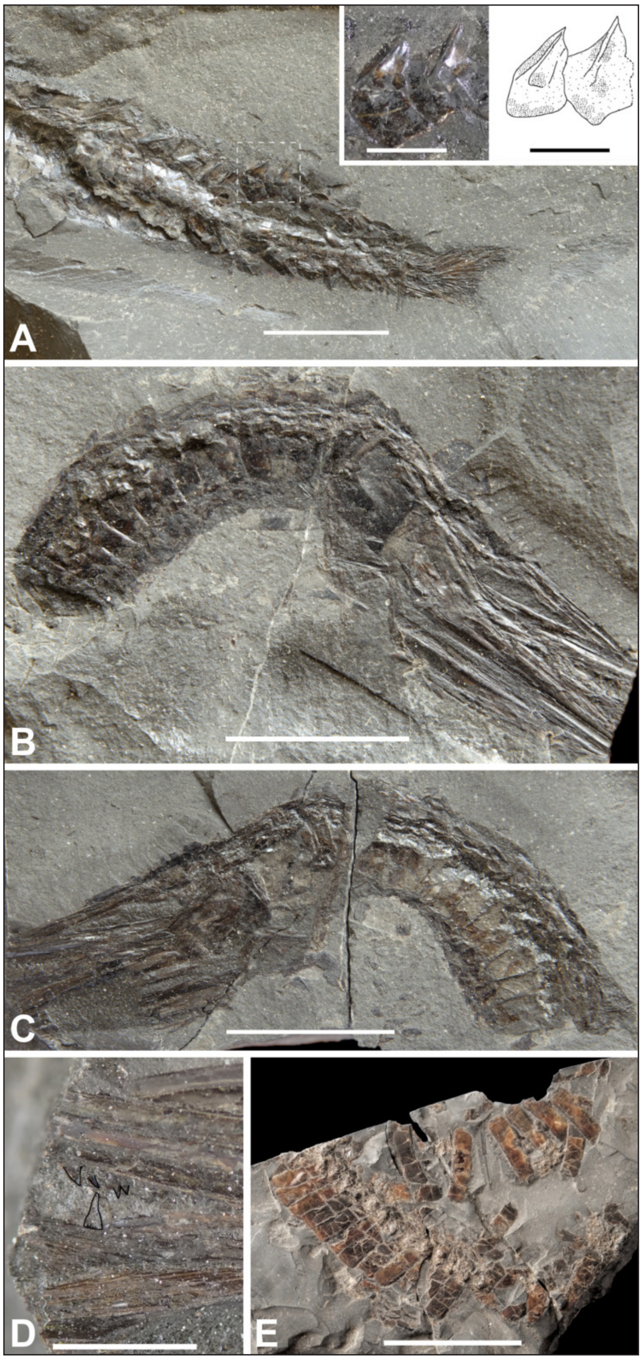

Fig. 14 - *Belonostomus* sp. A) MCSNVE 25515, Carcoselle Quarry (Possagno); close up with detail of the dorsal scales from the dashed area and interpretative drawing. B) MCSNVE 24519, Carcoselle Quarry (Possagno); C) counterpart of specimen in B; D) detail of the dentition showing the different size of the teeth and teh fluted base of the larger teeth. E) MCV 10/25, Schio-Valdagno Tunnel. Scale bars equal (A,B and C) 20 mm, (close-ups in A and D) 5 mm and (E) 50 mm.

Fig. 15 - *Heckelichthys vexillifer* (Heckel, 1856); Bomba Quarry (Cinto Euganeo). A) MCSNV IG37486; B) MGCB IG37487, counterpart of specimen in A. Scale bars equal 20 mm.

marked by fine striations and fluted bases (Fig. 17); predentary teeth are much longer than premaxillary teeth. The morphology of the predentary teeth is very similar to that characteristic of the species *B. cinctus*, to date exclusively known from the Turonian of England (see Forey et al. 2003).

Specimens MCV 10/25 (Fig. 14E) and specimen MCV 10/26 are 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*.

Order **Ichthyodectiformes** Bardack & Sprinkle, 1969
Suborder **Ichthyodectoidei** Romer, 1966
Family Saurodontidae Cope, 1871
Genus *Heckelichthys* Taverne, 2008

Heckelichthys vexillifer (Heckel, 1856)
Figs 15-16

1976 *Thrissops microdon* (Heckel) 1850 - Sorbini, p. 486, fig. 1, pl. 5.
1980 *Thrissops microdon* - Sorbini, p. 119.
1990 *Thrissops microdon* (Heckel) - Astolfi & Colombara, p. 146.
1976 *Thrissops microdon* (Heckel) - Colombara & Astolfi, p. 35.
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.

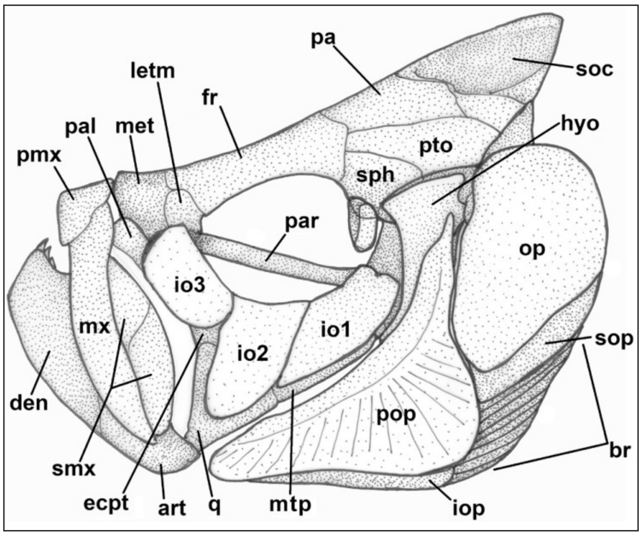

Fig. 16 - *Heckelichthys vexillifer* (Heckel, 1856). Interpretative reconstruction of the head primarily based on MCSNV IG37486 and MGCB IG37487.

Referred material: MCSNV IG37486-MGCB IG37487; MCSNV IG37488-37489, 37551.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The specimens were formerly described by Sorbini (1976, 1980) and referred to *Thrissops microdon* but subsequently assigned to *Heckelichthys* by Taverne (2008). The genus *Heckelichthys* was recently included in the ichthyodectoid family Saurodontidae by Cavin & Berrel (2019). MCSNV IG37486-MGCB IG37487 (Fig. 15-16) is represented by the head, pectoral girdle and fins of a single individual, in part and counterpart (HL 39 mm; HD 30 mm). The head is longer than deep, with a slightly concave dorsal profile. The frontals are broad. The supraoccipital crest is considerably developed. The second infraorbital is the largerst element of the series. The premaxilla is compact, almot triangular in outline. The maxilla is slightly curved. The lower jaw is short, with a moderately deep symphyseal border. The lower jaw joint is located just in front of the anterior border of the orbit. The mandibular sensory canal is not located in a groove. A few conical teeth with recurved tips can be observed in the symphyseal region of the dentary. There are two oblong supramaxillae. 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 & 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, including the possession of a broad second infraorbital bone, 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).

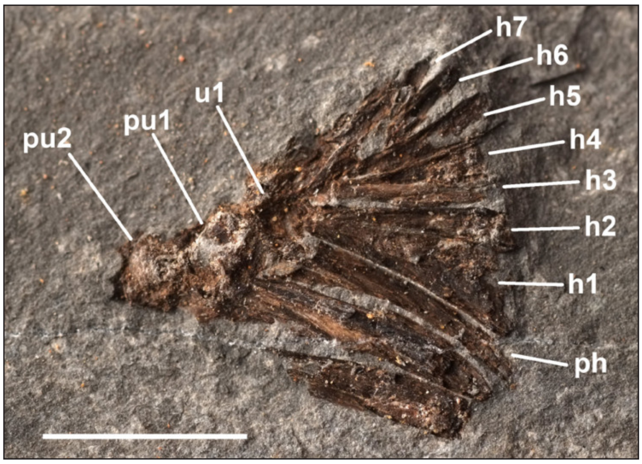

Fig. 17 - Ichthyodectoidei indet., Bomba Quarry (Cinto Euganeo), MGCB U3/5. Scale bar equals 5 mm.

Specimen MCSNV IG37488-37489, also in part and counterpart, is represented by scattered bones and scales. The morphology of the preopercle (ventral and dorsal arms ratio) and the paddle-like first pectoral-fin ray concur to support its attribution to *Heckelichthys vexillifer*.

Specimen MCSNV IG37551 consists of an isolated preopercular that exhibits the same morphology of the specimen above mentioned and, for this reason, is tentatively referred to the same taxon.

Ichthyodectoidei indet.

Fig. 17

Referred material: MGCB U3/5.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The specimen referred herein to an indeterminate ichthyodectoid is solely represented by an isolated ural skeleton in part and counterpart (Fig. 17). The first hypural articulates with the ural centrum through a ball-and-socket joint (see Patterson & Rosen 1977 and Cavin et al. 2013) and the second hypural is smaller compared to the first one. The ball-and-socket articula-

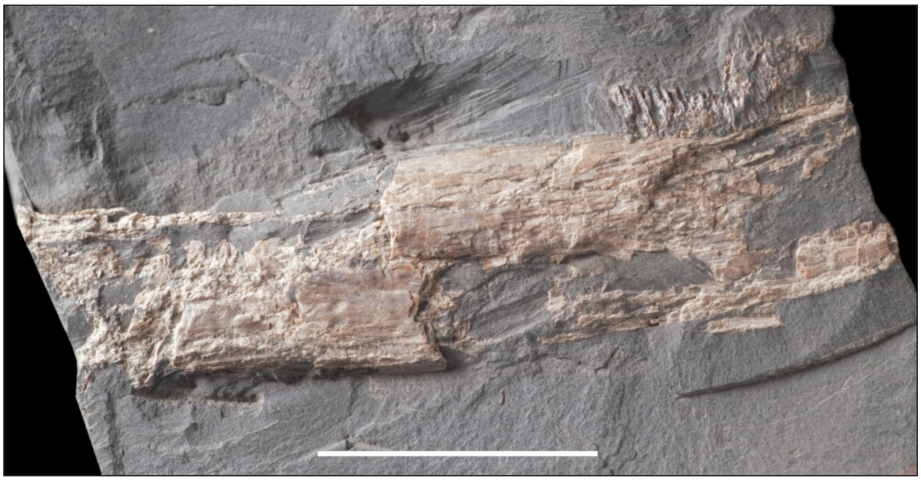

Fig. 18 - ?Elopiformes indet., Bomba Quarry (Cinto Euganeo), MCSNV IG37502. Scale bar equals 20 mm.

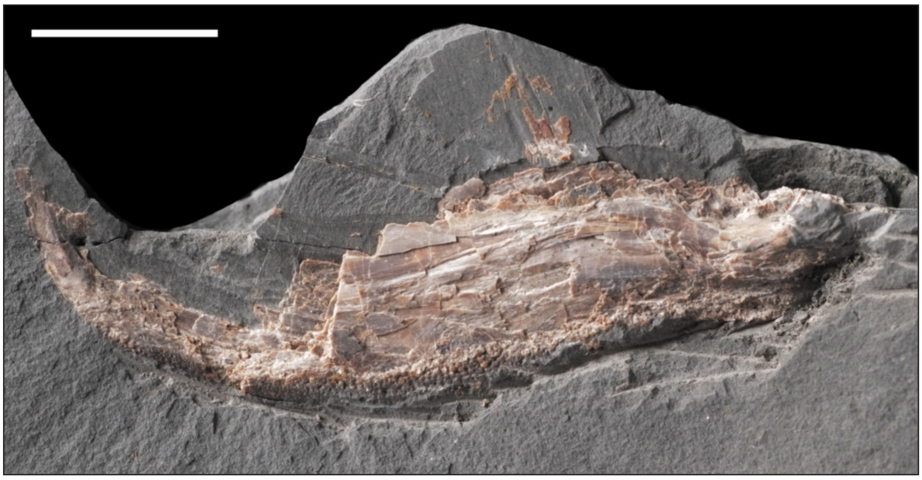

Fig. 19 - *Davichthys lacostei* (Arambourg, 1954); Bomba Quarry (Cinto Euganeo), MGCB IG37491. Scale bar equals 10 mm.

tion 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.

Superorder **Elopomorpha** Greenwood et al., 1966
Order **Elopiformes** Greenwood et al., 1966
?Elopiformes indet.

Fig. 18

1976 *Protelops* sp. - Sorbini, p. 493, fig. 5, pl. 13.
1980 *Protelops* sp. - Sorbini, p. 119.
1990 *Protelops* sp. - Astolfi & Colombara, p. 147.
1994 *Protelops* sp. - Colombara & Astolfi, p. 35.
1994 *Protelops* sp. - Sirna et al., p. 271.
2005 *Protelops* sp. - Dalla Vecchia, p. 106.
2010 *Protelops* sp. - Khalloufi, p. 48.

Referred material: MCSNV IG37502.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The specimen is represented by an isolated robust lower jaw with dentition restricted to its anterior portion (Fig. 18). 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 elopiforms, to which the specimen is provisionally referred (see Forey 1973).

Genus *Davichthys* Forey, 1973

Davichthys lacostei (Arambourg, 1954)

Fig. 19

1976 *Holcolepis* sp. - Sorbini, p. 502, fig. 11, pl. 19.
1980 *Holcolepis* sp. - Sorbini, p. 119.
1990 *Holcolepis* sp. - Astolfi & Colombara, p. 148.
1994 *Holcolepis* sp. - Colombara & Astolfi, p. 37.
1994 *Holcolepis* sp. - Sirna et al., p. 271.
2010 ?*Davichthys* sp. - Khalloufi, p. 48.

Referred material: MCSNV IG37528-37529.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The single available specimen, in part and counterpart, consists of a partially preserved upper jaw (Fig. 19). 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 nearly rounded in outline. The upper jaw bones are fully consistent with those of *Davichthys lacostei* (see Arambourg 1954; Forey 1973; Khalloufi 2010). Sorbini (1976) referred this specimen to *Holcolepis* sp. due to its similarity to *H.* (=*Davichthys*) *lacostei* from Jbel Tselfat (Arambourg 1954), which 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 11 Cretaceous genera, including *Apricenapiscis, Aquilopiscis*, *Elopopsis*, *Goulmimichthys*, *Greenwoodella*, *Lebrunichthys, Michin*, *Motlayoichthys*, *Nardopiscis*, *Pachyrhizodus*, *Rhacolepis*, *Stanhopeichthys*, and *Tingitanichthys* (see Arratia et al. 2018; Taverne & Capasso 2020a, b), plus the Eocene *Platinx* from Bolca. A revision of the limits and composition of the group formed by the genera *Rhacolepis*, *Pachyrhizodus*, and *Goulmimichthys* is necessary (see Cavin 2008).

Genus *Pachyrhizodus* Dixon, 1850

Pachyrhizodus subulidens (Owen, 1840)

Figs 20-21

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, figs 7-9.
1980 *Thrissopater magnus* - Sorbini, p. 119.
1980 *Pachyrhizodus subulidens* - Sorbini, p. 119 and unnumbered 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, figs 1-3.
1987 *Pachyrhizodus intermedius* n. sp. - Taverne, p. 136.
1990 *Pachyrhizodus* - Bizzarini & Coccioni, p. 79.
1990 *Thrissopater magnus* Woodward - Astolfi & Colombara, p. 147.
1990 *Pachyrhizodus subulidens* (Owen) - Astolfi & Colombara, p. 147.
1990 *Pachyrhizodus intermedius* Sorbini - Astolfi & Colombara, p. 148, figs 210-211.
1994 *Pachyrhizodus subulidens* - Colombara & Astolfi, p. 36.
1994 *Pachyrhizodus intermedius* - Colombara & Astolfi, p. 36.
1994 *Thrissopater magnus* (Woodward, 1899) - Sirna et al., 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.
2018 Elopide indeterminato – Bizzarini et al., p. 226, fig. 3.

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

Locality: Bomba Quarry (Cinto Euganeo), Carcoselle Quarry (Possagno), Valdagno-Schio tunnel.

Description and remarks. Several moderately to well-preserved specimens are referred herein to the species *Pachyrhizodus subulidens* (Fig. 20). All of these specimens exhibit a combination of features that support their assignment to this species (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 dentary 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).

Specimen MCSNV IG37495 (Fig. 21A) was designated by Sorbini (1976) as the holotype of *Pachyrhizodus intermedius*, although there are no substantial differences allowing a separation from *P. subulidens*. For this reason, *P. intermedius* is considered herein as junior synonym of *P. subulidens*.

The specimens MGCB IG37496 (Fig. 21B) and MCSNV 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).

Fig. 20 - *Pachyrhizodus subulidens* (Owen, 1840); Bomba Quarry (Cinto Euganeo), MGCB IG37491. Scale bar equals 100 mm.

Pachyrhizodus sp.

Figs 22-23

1976 Pachyrhizodontidae - Sorbini, p. 500, fig. 10, pls 17-18.
1987 *Pachyrhizodus* sp. - Taverne, figs 4-5.
1990 *Pachyrhizodus* - Bizzarini & Coccioni, p. 79.
1990 Pachyrhizodontidae - Astolfi & Colombara, fig. 212.
1994 Pachyrhizodontidae - Colombara & Astolfi, p. 36 and unnumbered fig. (p. 37).
2005 *Pachyrhizodus* sp. - Dalla Vecchia et al., p. 106-107.
2007 *Pachyrhizodus* sp. - Capasso, p. 189.

Referred material: MCSNV 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).

Description and remarks. The examined material includes several articulated caudal fins and their endoskeletal supports, associated in some cases with the caudal vertebrae (Fig. 22). The deeply

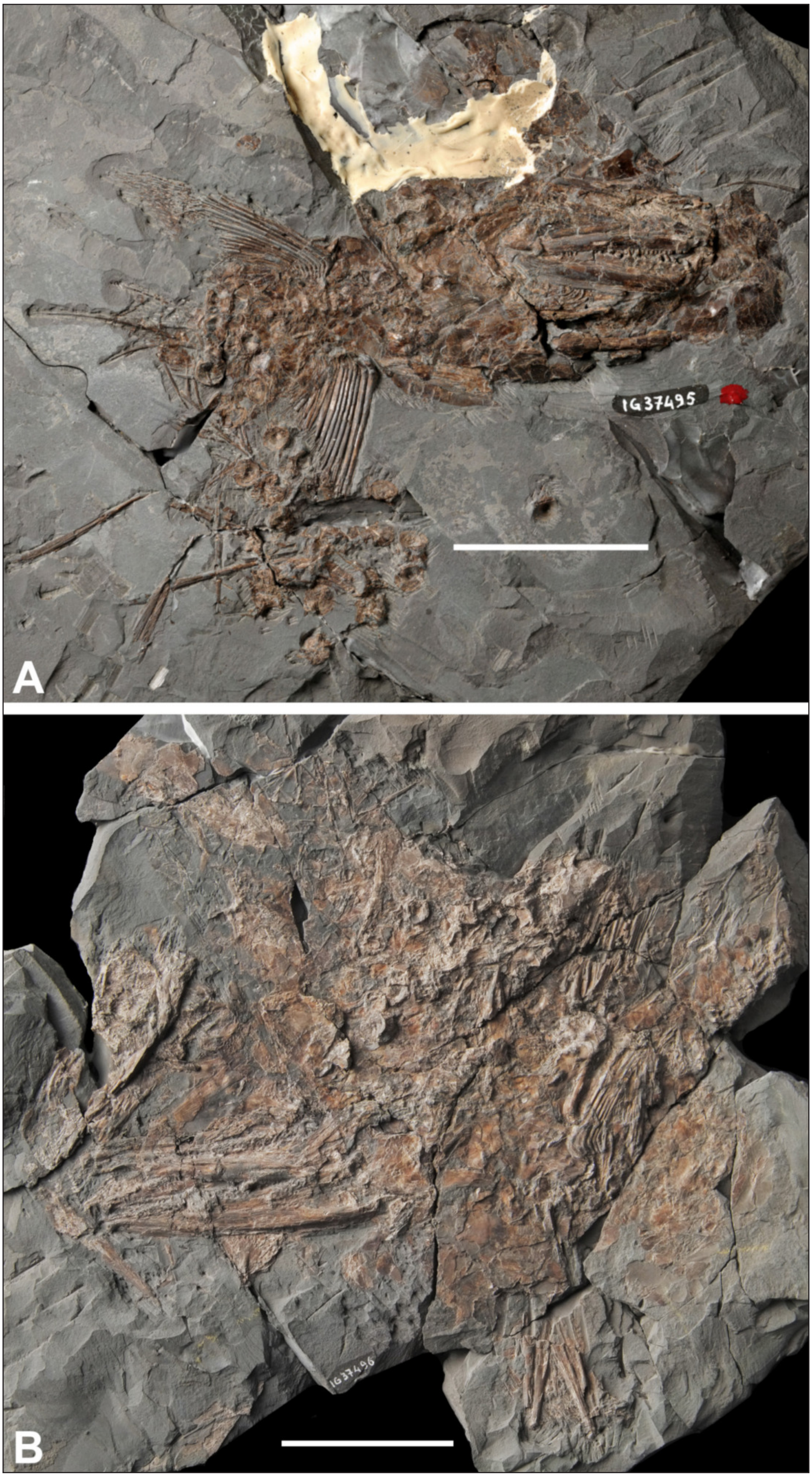

Fig. 21 - *Pachyrhizodus subulidens* (Owen, 1840); Bomba Quarry (Cinto Euganeo). A) MCSNV IG37495; B) MGCB IG37496. Scale bars equal 50 mm.

forked caudal fins exhibit a high degree of hypurostegy and the first uroneural extends forwards to the second preural vertebra (see Fig. 22A-B), revealing their affinity to the Pachyrhizodontoidei (sensu Cavin 2001). The presence of the hypurapophysis and the forked anterior extremity of the

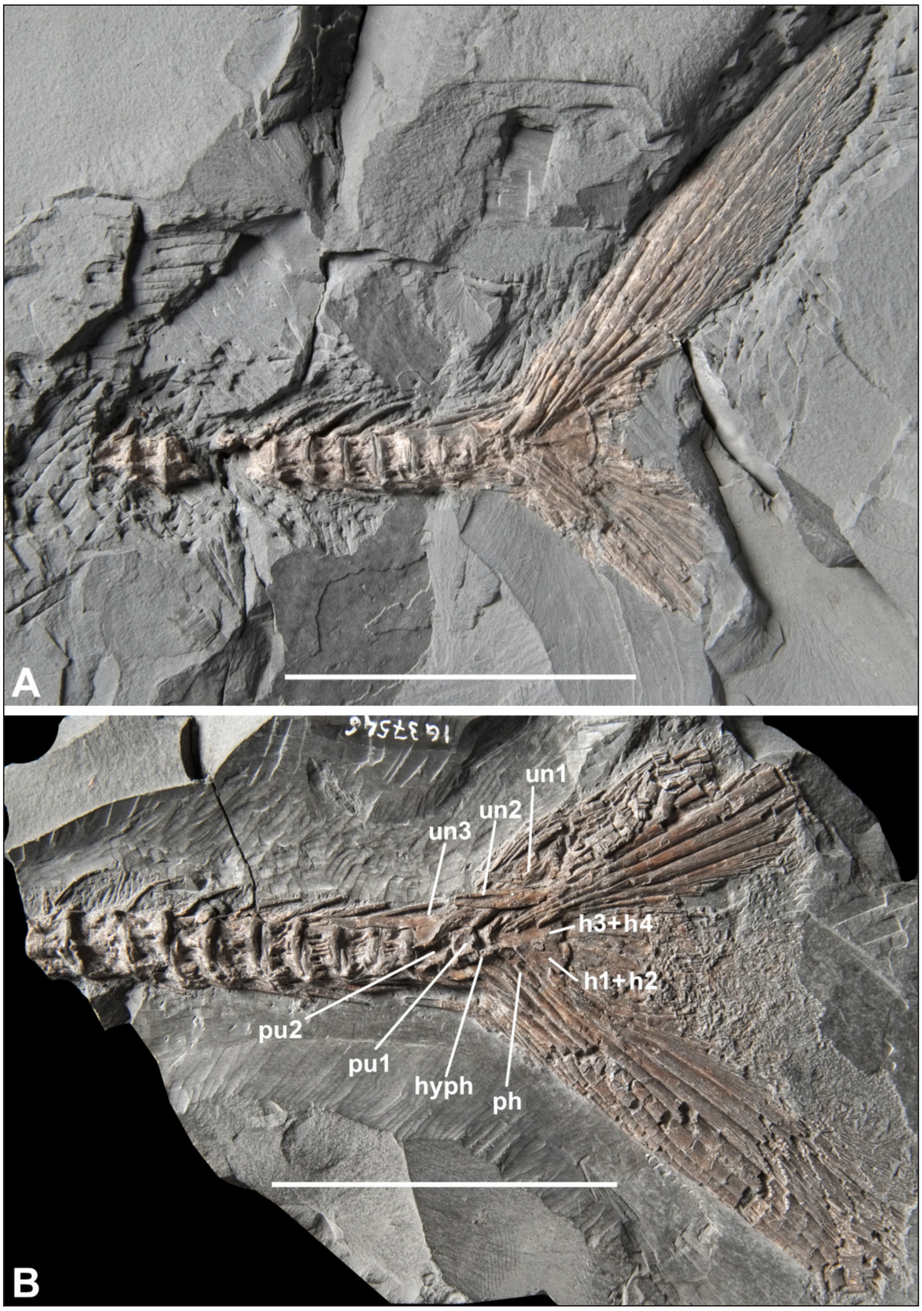

Fig. 22 - *Pachyrhizodus* sp.; Bomba Quarry (Cinto Euganeo). Posterior portion of the vertebral column, caudal skeleton and fin, A) MGCB IG37545, B) MGCB IG37546. Scale bars equal 50 mm.

anteriormost uroneural support their assignment to the family Pachyrhizodontidae (Cavin 2001). Within the Pachyrhizodontidae (sensu Cavin 2001) the closely related genera *Rhacolepis*, *Goulmimichthys* and *Pachyrhizodus* possess two hypural plates. In the specimens examined herein hypurals 1 and 2 are fused for more than half of their length and the dorsal hypurals are fused into a consolidated platted. 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 *Pachyrhizodus* (Cavin 2001), but *Pachyrhizodus* 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. 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. 23A). Finally, specimen MCV IG292958 (Fig. 23B) includes a large

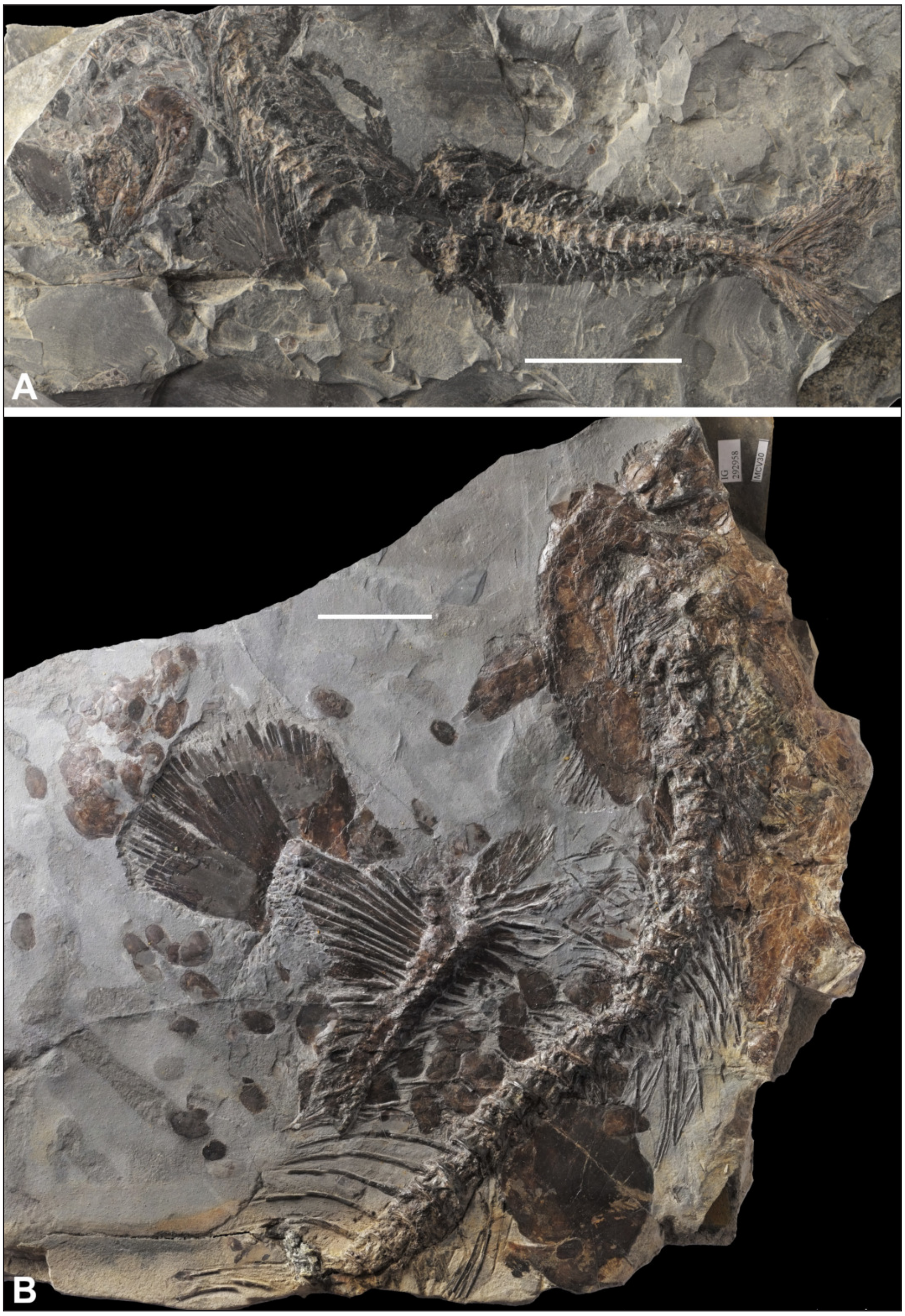

Fig. 23 - *Pachyrhizodus* sp. A) MCR 6136, Carcoselle Quarry (Possagno); B) MCV IG292958, Schio-Valdagno Tunnel. Scale bars equal 50 mm.

portion of the vertebral column, the dorsal fin containing 22 rays, two broad infraorbitals, and other poorly preserved cranial bones and some scales.

Order **Tselfatiiformes** Nelson, 1994
Family Plethodidae Loomis, 1900
Genus *Tselfatia* Arambourg, 1943

Tselfatia formosa Arambourg, 1943

Fig. 24

p.1976 *Tselfatia formosa* Arambourg 1943 - Sorbini, p. 518, figs 20, 22, pls 27, 29-30 (non pl. 28).
1980 *Tselfatia formosa* - Sorbini, p. 119.
1980 *Tselfatia formosa* Arambourg, 1943 - Bardack & Teller-Marshall, p. 1075, figs 1-3.
1983 *Tselfatia formosa* Arambourg, C., 1943 - Taverne, p. 165.
1990 *Tselfatia formosa* Arambourg - Astolfi & Colombara, p. 150, fig. 215.
1994 *Tselfatia formosa* Arambourg - Colombara & Astolfi, p. 38 and unnumbered fig.
1994 *Tselfatia formosa,* Arambourg, 1943 - Sirna et al., p. 271, 273.
2000a *Tselfatia formosa* - Taverne, p. 9, fig. 6-7.
2000b *Tselfatia formosa* - Taverne, p. 98, fig. 6D.
2000 *Tselfatia formosa,* Arambourg, 1943- Maisch & Lehmann, p. 500.
2001 *Tselfatia formosa* - Avanzini & Luciani, p. 195, figs 2-5.
2005 *Tselfatia formosa* - Dalla Vecchia et al., p. 106, fig. 80.
2005 *Tselfatia formosa* Arambourg, 1943 - Taverne & Gayet, p. 67, fig. 2.

Fig. 24 - *Tselfatia formosa* Arambourg, 1943; Bomba Quarry (Cinto Euganeo). A) MGCB IG37537; B) MCSNV IG37538, counterpart of specimen in A. Scale bars equal 50 mm.

2010 *Tselfatia formosa* - Khalloufi, p. 48.
2018 *Tselfatia formosa* - Bizzarini et al., p. 225, fig. 2.

Referred material: MGCB IG37537 and MCSNV IG37538; MCSNV IG37540-37544; MGCB IG295829; MGPPD 32090; MCSNVE 24522, 24545, 24547, 24548, 24549, 24564, 24565, 24567, 24570, 24571, 24574, 24592, 24702.

Locality: Bomba Quarry (Cinto Euganeo); Carcoselle Quarry (Possagno); Valdagno-Schio Tunnel; Schievenin Valley (Quero).

Description and remarks. Several specimens from four localities are referred herein to *Tselfatia formosa*. Among the available specimens, there is only one relatively large and moderately well-preserved specimen (MGCB IG37537 and MCSNV IG37538). 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 MCSNV 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; BD 95 mm; Fig. 24A-B). The skeleton is almost complete and, in large part articulated. The body is deep and laterally compressed, ovoid in outline. The head has a comvex antero-dorsal profile being particularly high at the occiput. The vertebral column contains about 71 vertebrae. The dorsal and anal fins are very long, both extending back to the caudal peduncle. The specimen also shows a series of characters that allow its assignment to the family Plethodidae (Taverne & 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 by a horizontal groove separating the plate into dorsal and ventral portions; 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 preopercle exhibits a ventral arm notably shorter than the dorsal one like in more advanced plethodids (Taverne & Gayet 2005). The specimen can be referred to the species *Tselfatia formosa* based on the following characters: head particularly high at the occiput; large dorsal- and anal-fin rays (the fifth and third ones, respectively) segmented and bearing a row of pseudo-fulcra all along their anterior border; neural and haemal arches partially or totally fused with the corresponding centra; tips of the dorsal- and anal-fin pterygiophores expanded in large semicircular plates; pectoral fin inserting just below the vertebral column; scales with pectinated posterior border (Bardack & Teller-Marshall 1980; Taverne & Gayet 2005). The first three of these characters are shared with *Dixonanogmius*, while the others are autapomorphic of *Tselfatia* (Taverne & Gayet 2005). *Dixonanogmius dalmatius* differs from *Tselfatia formosa* especially in the pectoral fin inserting just above the vertebral column (Bardack & Teller-Marshall 1980).

The other referred specimens mostly consist of 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.

Genus *Dixonanogmius* Taverne, 2000b

Dixonanogmius dalmatius (Bardack & Teller-Marshall, 1980)

Figs 25-27

p.1976 *Tselfatia formosa* Arambourg, 1943 - Sorbini, p. 518, fig. 21, pl. 28 (non figs 20, 22, pl. 27, 29-30).

Referred material: MCV IG292955; MCSNV IG37539.

Locality: Bomba Quarry (Cinto Euganeo); Valdagno-Schio Tunnel.

Description and remarks. MCSNV IG37539 (Figs 25-26) is probably one of the largest individuals ever reported (HL ca. 160 mm, BD ca. 320 mm); it consists of a moderately preserved partially complete articulated skeleton lacking the caudal region. It has a very deep body with the head particularly high at the occiput, reduced premaxillae, high and short lower jaw, large dorsal- and anal-fin rays, segmented and bearing a row of pseudo-fulcra all along their anterior border (Figs 25-26), neural and haemal arches almost fused with the corresponding centra, and pectoral-fin insertion located high on the body flanks, just above the level of the vertebral column (Taverne & Gayet 2005). This specimen was referred by Sorbini (1976) to *Tselfatia formosa*. Apparently, the fossil resembles *T. formosa* in the overall aspect and possession of a very large dorsal-fin ray. 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 & Teller-Marshall 1980; Taverne & Gayet 2005).

Specimen MCV IG292955 consists of an incomplete skeleton of a large individual lacking most of the head and the caudal fin (Fig. 27). Of the head, only part of the hyomandibula and the bones of the opercular series are preserved.

This is the first report of this taxon from the Bonarelli Level of Italy.

Fig. 25 - *Dixonanogmius dalmatius* (Bardack & Teller-Marshall, 1980); Bomba Quarry (Cinto Euganeo), MCSNV IG37539. The white arrow indicates the position of the pectoral-fin insertion located above the axis of the vertebral column. Scale bar equals 100 mm.

Order **Tselfatiiformes**? Nelson, 1994

"Protosphyraena" stebbingi Woodward, 1909

Fig. 28

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

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

Referred material: MGCB VT 001.
Locality: Sinigaglia Quarry (Teolo).

Description and remarks. The material is represented by a single isolated rostrum (Fig. 40) from the Sinigaglia Quarry near Villa di Teolo (Colli Euganei). The flattened aspect, blunt tip, lateral furrows and smooth surface are distinctive characters of rostra of '*Protosphyraena*' *stebbingi*. This taxon was reported before only from the English Chalk. A detailed analysis of this specimen has been recently presented by Amalfitano et al. (2019b) who also reported an additional more complete isolated rostrum found in the XIX century near Crespadoro (Lessini Mountains) and possibly coming from the Scaglia Variegata Alpina Formation (lower Aptian-Cenomanian; see Amalfitano et al. 2019b).

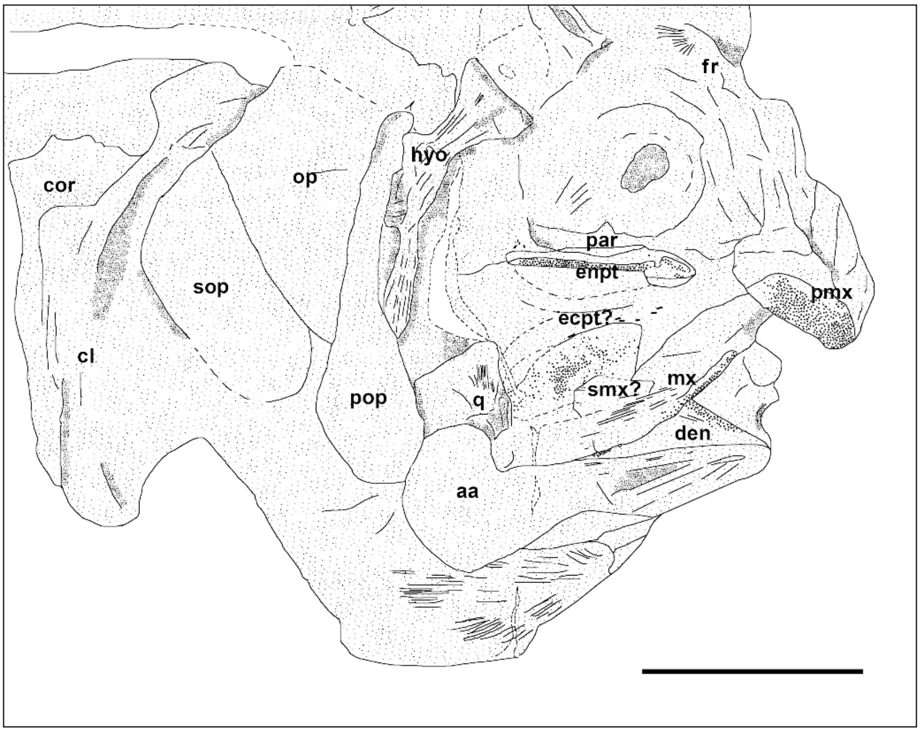

Fig. 26 - *Dixonanogmius dalmatius* (Bardack & Teller-Marshall, 1980). Interpretative reconstruction of the head of MCSNV IG37539. Scale bar equals 50 mm.

Fig. 27 - *Dixonanogmius dalmatius* (Bardack & Teller-Marshall, 1980); Schio-Valdagno Tunnel, MCV IG292955. Scale bar equals 100 mm

Fig. 28 - Isolated rostrum of *'Protosphyraena' stebbingi* Woodward, 1909; Sinigallia Quarry (Teolo), MGCB VT001. Scale bar equals 50 mm.

Superorder **Euteleostei** Greenwood, Myers, Rosen & Weitzman, 1967

Euteleostei incertae sedis

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 & Weitzman 1982). Recently, Prokofiev (2005) excluded any relationship with the Stomiiformes (see also Carnevale 2002). 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

Figs 29-31

1976 *Paravinciguerria praecursor* Arambourg 1954 - Sorbini, p. 503, fig. 12, pls 20-21.
1976 *Protostomias maroccanus* Arambourg 1943 - Sorbini, p. 505, fig. 13, pl. 22.
1980 *Paravinciguerria praecursor* - Sorbini, p. 119.
1980 *Protostomias maroccanus* - Sorbini, p. 119.
1990 *Paravinciguerria praecursor* Arambourg - Astolfi & Colombara, p. 148.
1991 *Protostomias maroccanus* Arambourg 1943 - Taverne, p. 57.
1994 *Paravinciguerria praecursor* Arambourg- Colombara & Astolfi, p. 37.
1994 *Protostomias maroccanus* Arambourg - Colombara & Astolfi, p. 37.
1994 *Paravinciguerria praecursor* Arambourg, 1954 - Sirna et al., p. 271.
2005 *Protostomias maroccanus* - Dalla Vecchia et al., p. 106.
2010 *Protostomias maroccanus* - Khalloufi, p. 48.
2010 *Paravinciguerria praecursor* - Khalloufi, p. 48.

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

Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The available specimens are largely incomplete (Figs 41-44). Specimen MCSNV IG37510-37511 (Figs 29-30) is the only one with a nearly complete head skeleton (HL ca. 48 mm), showing several characters that unambiguously justify its 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; opercular series well-developed with a large opercle (see Arambourg 1943, 1954).

Specimens MGCB IG37548, 37551 and MCSNV IG37549 (Fig. 31) previously referred to *Paravinciguerria praecursor* by Sorbini (1976) are referred herein to *Protostomias maroccanus*. MGCB IG 37548 (Fig. 31A-B), the best preserved of these specimens, was already assigned, together with the specimen MCSNV IG 37507, to *Protostomias maroccanus* by Khalloufi (2010: 245) because its ectopterygoid extends beyond the dorsal edge of the quadrate and along the parasphenoid. Furthermore, the shape of the quadrate, characterized by an isosceles

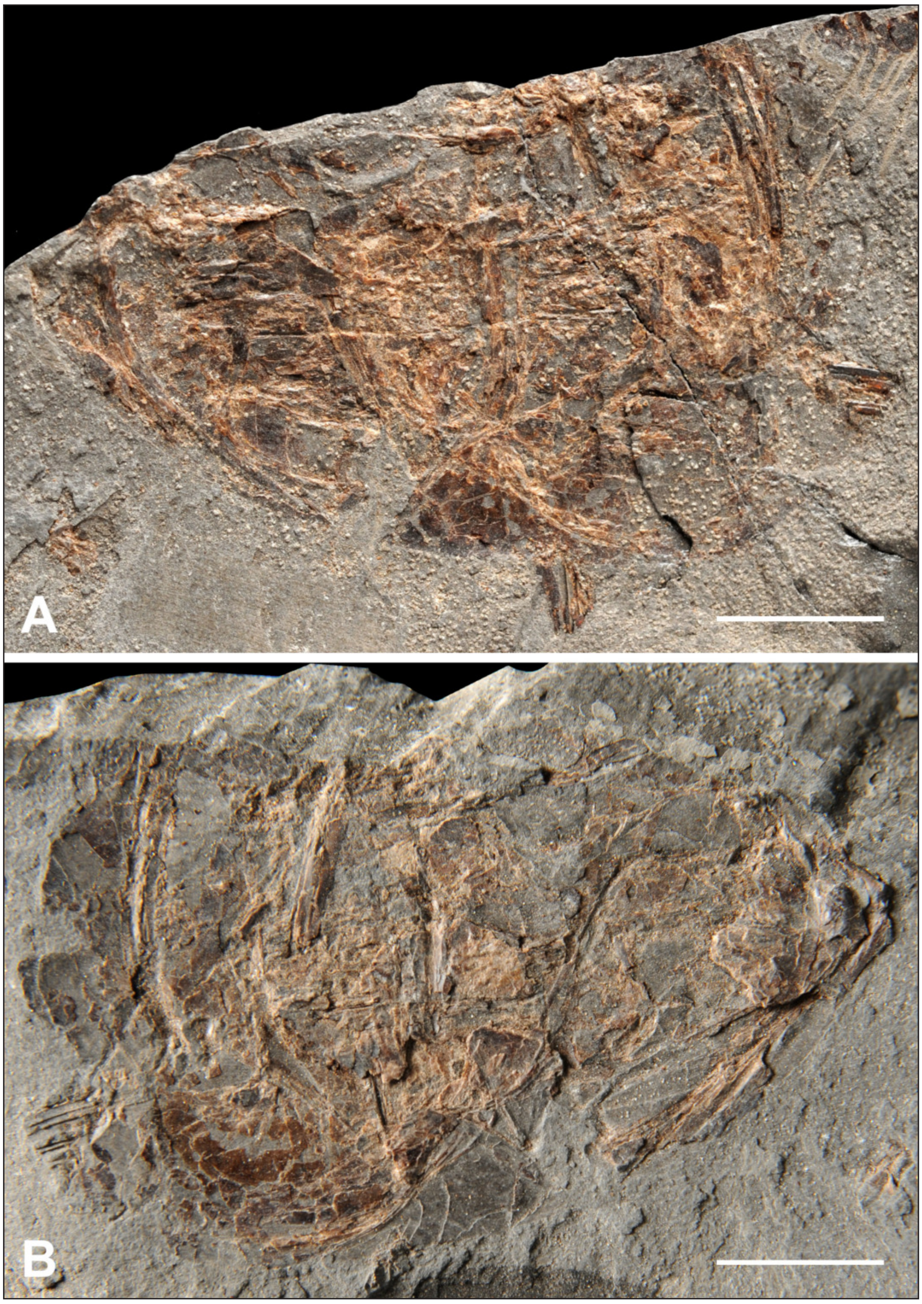

Fig. 29 - *Protostomias maroccanus* Arambourg, 1943; Bomba Quarry (Cinto Euganeo). A) MCSNV IG37510; B) MCSNV IG37511, counterpart of MCSNV IG37510. Scale bars equal 20 mm.

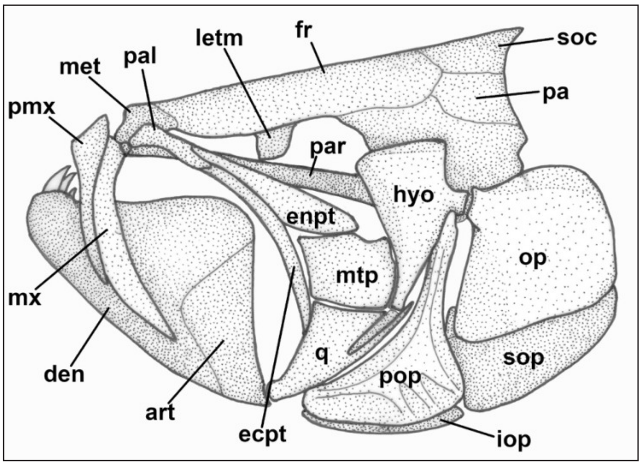

Fig. 30 - *Protostomias maroccanus* Arambourg, 1943. Interpretative reconstruction of the head based on material from the Bomba Quarry (Cinto Euganeo). Infraorbital bones omitted.

triangular outline with a short dorsal edge and an antero-ventral condyle, supports its attribution to *Protostomias*. The quadrate in *Paravinciguerria* has a more equilateral triangular outline, with a long dorsal edge, and a medio-ventral condyle.

Specimen MGCB IG37550 was previously referred to *Paravinciguerria praecursor* by Sorbini (1976) as the other specimens, probably due to its recurved maxilla (Fig. 31C). However, the dentary has a large coronoid process, which are not present in *Paravinciguerria praecursor*. The other specimens solely consist of fragmentary and scattered remains, which can be referred to *Protostomias* mostly because of their peculiar dentary (see e.g. Fig. 31D).

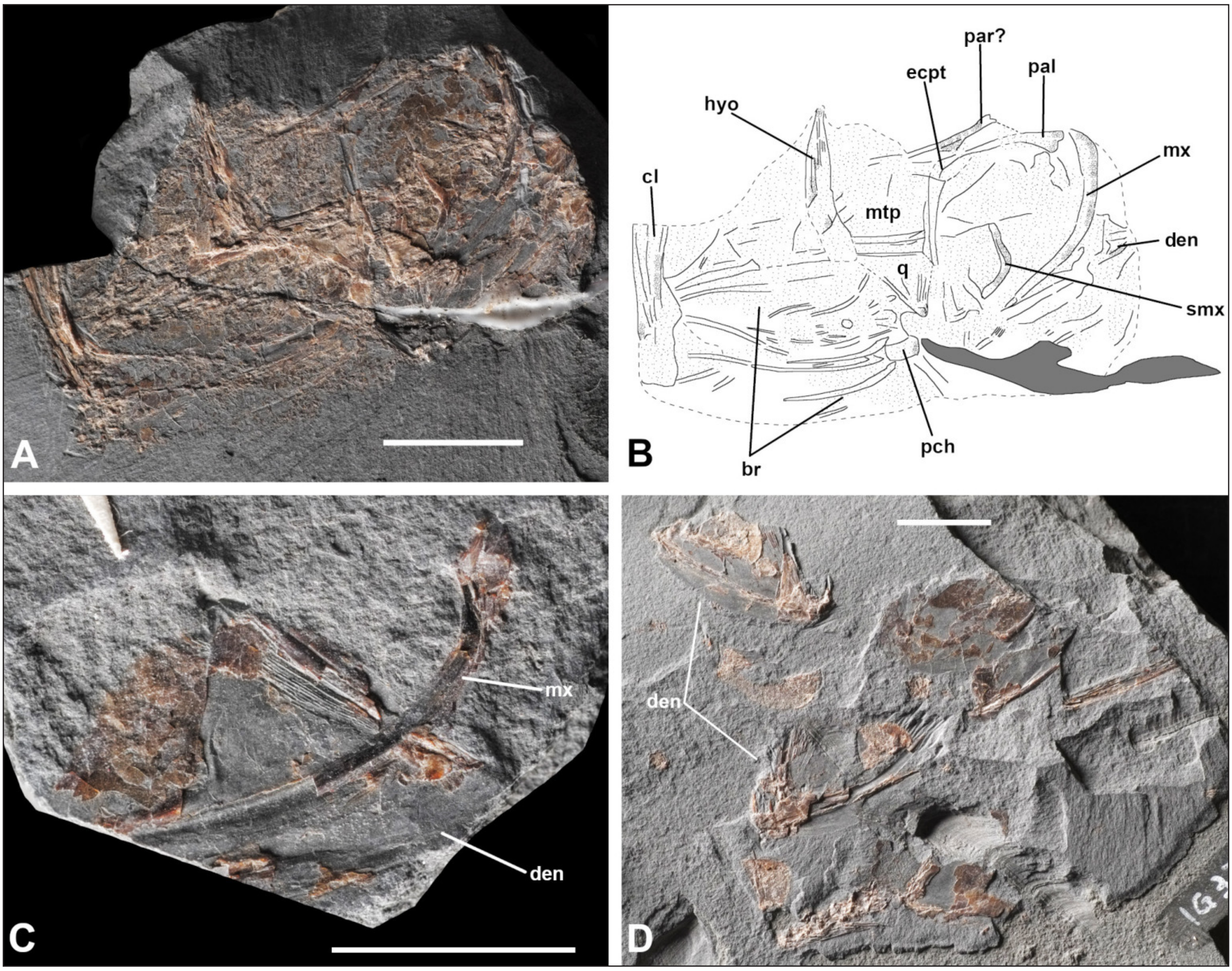

Fig. 31 - *Protostomias maroccanus* Arambourg, 1943; Bomba Quarry (Cinto Euganeo). A) MCSNV IG37548; B) interpretative drawing of MCSNV IG37548; C) MCSNV IG37550; D) MCSNV IG37509. Scale bars equal 10 mm.

Subdivision **Neoteleostei** Rosen, 1973
Section **Eurypterygii** Rosen, 1973
Order **Aulopiformes** Rosen, 1973 (sensu Nelson 1994)
Suborder **Ichthyotringoidei** Goody, 1969
Family Ichthyotringidae Jordan, 1905
Genus *Ichthyotringa* Cope, 1878

Ichthyotringa africana (Arambourg, 1954)

Figs 32-33

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 & Colombara, p. 149, fig. 213.
1990 *Rhinellus* sp. - Colombara & Astolfi, p. 37.
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, figs 1-7.
2010 *Ichthyotringa africana* - Khalloufi, p. 48.

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

Locality: Bomba Quarry (Cinto Euganeo); Carcoselle Quarry (Possagno).

Description and remarks. The specimens are mainly represented by isolated jaw elements. There are also partially complete but isolated head skeletons (e.g. MCSNV IG37515; Fig. 32A) and few postcranial remains (e.g. MCSNV IG 37517; Fig. 32C). The specimens can be referred to the genus *Ichthyotringa* because of the following combination of characters (Fig. 33): head very shallow and elongated anteriorly into a prominent rostrum (premaxilla), dermal bones of the head smooth and not ornamented, teeth present on premaxilla, palatine, ectopterygoid and dentary, jaw suspension slightly inclined forward, vertebral centra longer than deep (Goody 1969). Sorbini (1976) referred these speci-

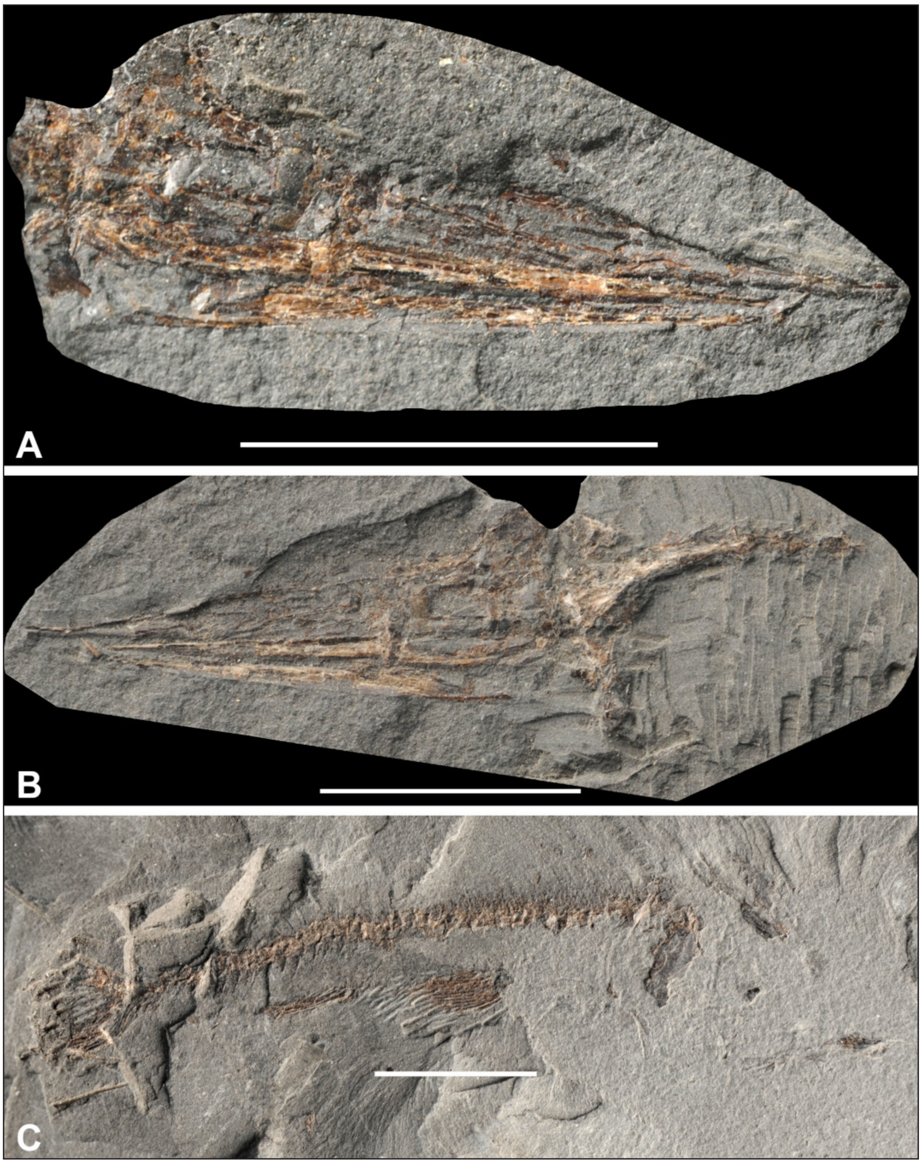

Fig. 32 - *Ichthyotringa africana* (Arambourg, 1954); Bomba Quarry (Cinto Euganeo). A) MCSNV IG37515, partially complete head skeleton; B) MCSNV IG37520, partially complete head skeleton and anterior portion of the vertebral column; C) MCSNV IG37517, partially complete axial skeleton. Scale bars equal 10 mm.

mens to “*Rhinellus*” (=*Ichthyotringa*) sp. whereas, more recently Taverne (2006) assigned them to *Ichthyotringa africana*.

Specimens MCSNV IG37504 and MGCB IG37526 (Sorbini 1976: pl. 21) consists of part and counterpart of the cranial remains of a single individual. These remains are represented by a neurocranium exposed in dorsal view. The outer surface of the bones of the skull roof is smooth and unornamented. The frontals are long and slender

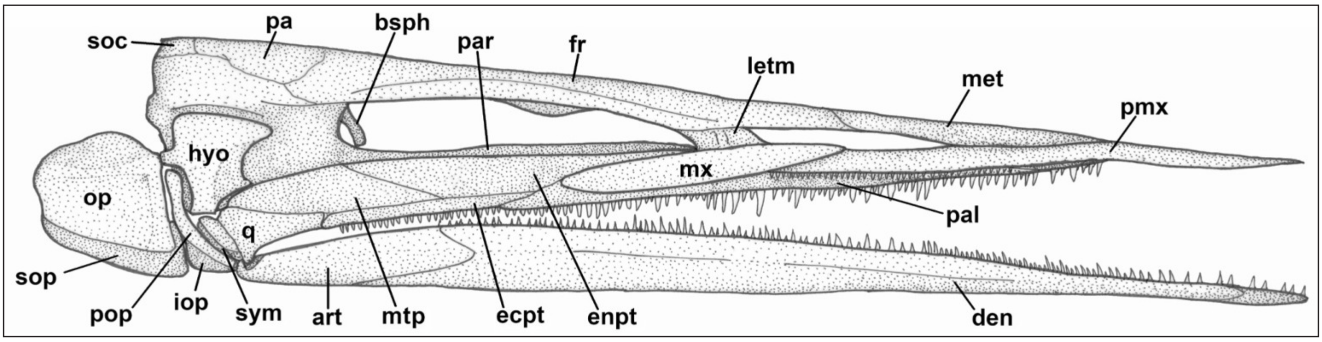

Fig. 33 - *Ichthyotringa africana* (Arambourg, 1954). Interpretative reconstrunction of the the head based on material from the Bomba Quarry (Cinto Euganeo).

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 (MCSNV IG 37504), which could be interpreted as a frontoparietal depression or fontanelle. These neurocranial remains were referred to *Clupavus* cf. *maroccanus* by Sorbini (1976), although the pattern of branching of the suborbital sensory canal at the level of the sphenotic diverges into three separate elements in *Clupavus* (Taverne 2006; Khalloufi 2010). Therefore, the morphology of the bones of the skull roof and the pattern of branching of the suborbital canal are consistent with those of *I. africana*.

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

***Rhynchodercetis* sp.**

Fig. 34

1976 *Rhynchodercetis* sp. - Sorbini, p. 507, fig. 14, pl. 23.
1980 *Rhynchodercetis* sp. - Sorbini, p. 119.
1990 *Rhynchodercetis* sp. - Astolfi & Colombara, p. 149.
1994 *Rhynchodercetis* sp. - Colombara & Astolfi, p. 38.
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 *Rynchodercetis* sp. - Silva & Gallo, tab. 2.

Referred material: MGCB IG37514.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks. The only available specimen consists of a poorly preserved anterior portion of the body of a single individual (Fig. 34). The head is elongated and shallow. The jaw bones bear small, conical and posteriorly recurved teeth. The anterior vertebral centra are slender and elongated, with well-developed transverse processes. 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, thereby implying that the dentary does not reach the tip of the snout. This condition supports the attribution to the genus *Rhynchodercetis* (see Chalifa 1989 and Blanco & 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).

Family Enchodontidae Lydekker, 1889
Genus *Enchodus* Agassiz, 1835

Enchodus venator Arambourg, 1954

Fig. 35

1976 *Enchodus* cfr. *venator* Arambourg 1954 - Sorbini, p. 513, figs 16-19, pl.26.
1980 *Paravinciguerria praecursor* - Sorbini, p. 119.
1990 *Enchodus* cfr. *venator* Arambourg - Astolfi & Colombara, p. 150.
1994 *Enchodus* cfr. *venator* Arambourg - Colombara & Astolfi, p. 38.
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: MCSNV IG37498 and MGCB IG37499; MGCB IG37500-37501, U3S1/1; MCSNVE 24577, 24578, MCSNV IG37512-37513, 37490.
Locality: Bomba Quarry (Cinto Euganeo).

Description and remarks: All the available specimens are poorly preserved. Specimens MCSNV IG37498 and MGCB IG37499 (Fig. 35) are the most informative ones and represent part and counterpart of a single individual. They consist of partially complete articulated cranial remains, especially the jaws and the opercular series. A combination of characters allows to refer this 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 herein to *Enchodus venator* because of 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, the attribution to one of 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 & Gallo 2011; Cavin et al. 2012), while *E. marchesetti* has a completely different

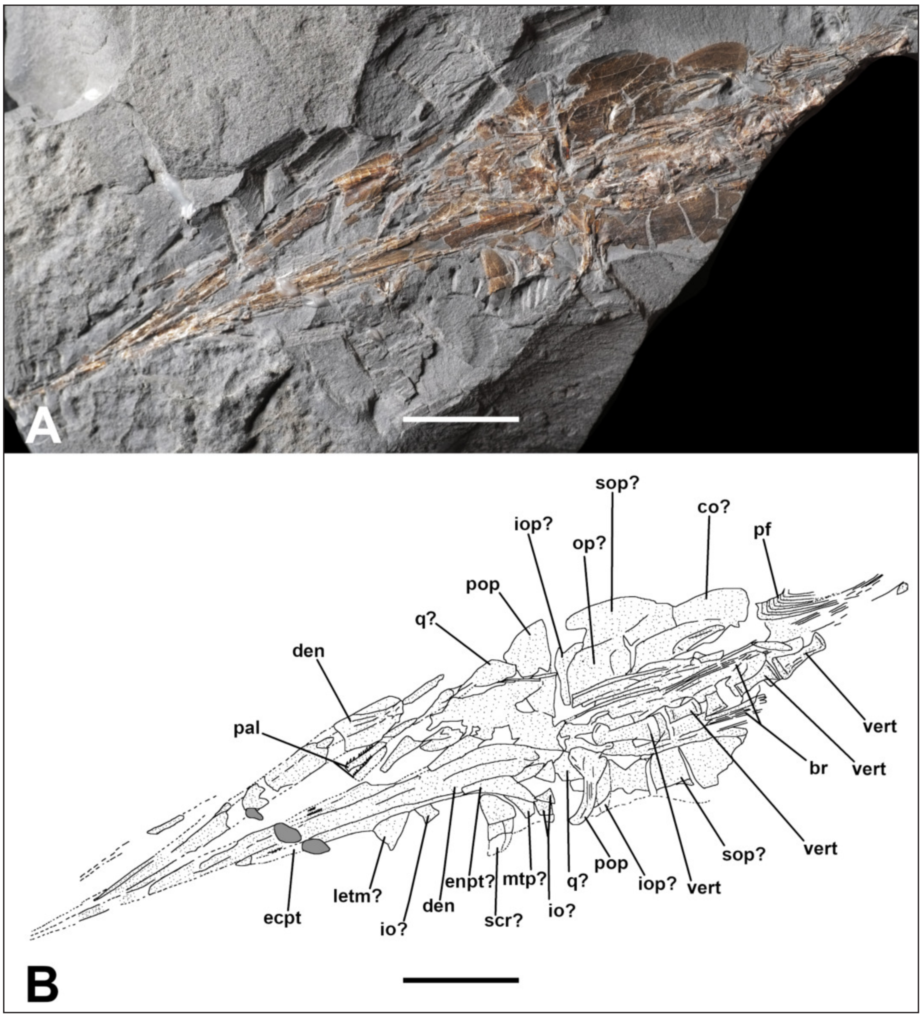

Fig. 34 - *Rhynchodercetis* sp.; Bomba Quarry (Cinto Euganeo). A) MGCB IG37514; B) interpretative drawing of MGCB IG37514. Scale bars equal 10 mm.

dermal pattern of the opercular bones (see Fielitz 2004: character 50). MCSNV IG37490, consists of a completely disarticulated and fragmentary skeleton, which 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. 36

1976 *Rharbichthys* cfr. *ferox* - Sorbini, p. 509, fig. 15, pl. 24.
1980 *Rharbichthys* cfr. *ferox* - Sorbini, p. 119.
1990 *Rharbichthys* cfr. *ferox* Arambourg - Astolfi & Colombara, p. 149, fig. 214.
1994 *Rharbichthys* cfr. *ferox* Arambourg - Colombara & Astolfi, p. 37.
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).

Description and remarks. The only specimen (Fig. 36) 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 palatine tooth with an elliptical cross section and an anterior cutting edge. This combination of these characters fits well the definition of *Rharbichthys ferox* provided by Fielitz (2004).

Sept **ACANTHOMORPHA** Rosen, 1973 (sensu Johnson & Patterson 1993)

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

Polymixiiformes indet.

Fig. 37

1976 *Omosoma simum* Arambourg 1954 - Sorbini, p. 524, fig. 23, pl. 31.
1980 *Paravinciguerria praecursor* - Sorbini, p. 119.
1990 *Omosoma simum* Arambourg - Astolfi & Colombara, p. 149, fig. 214.

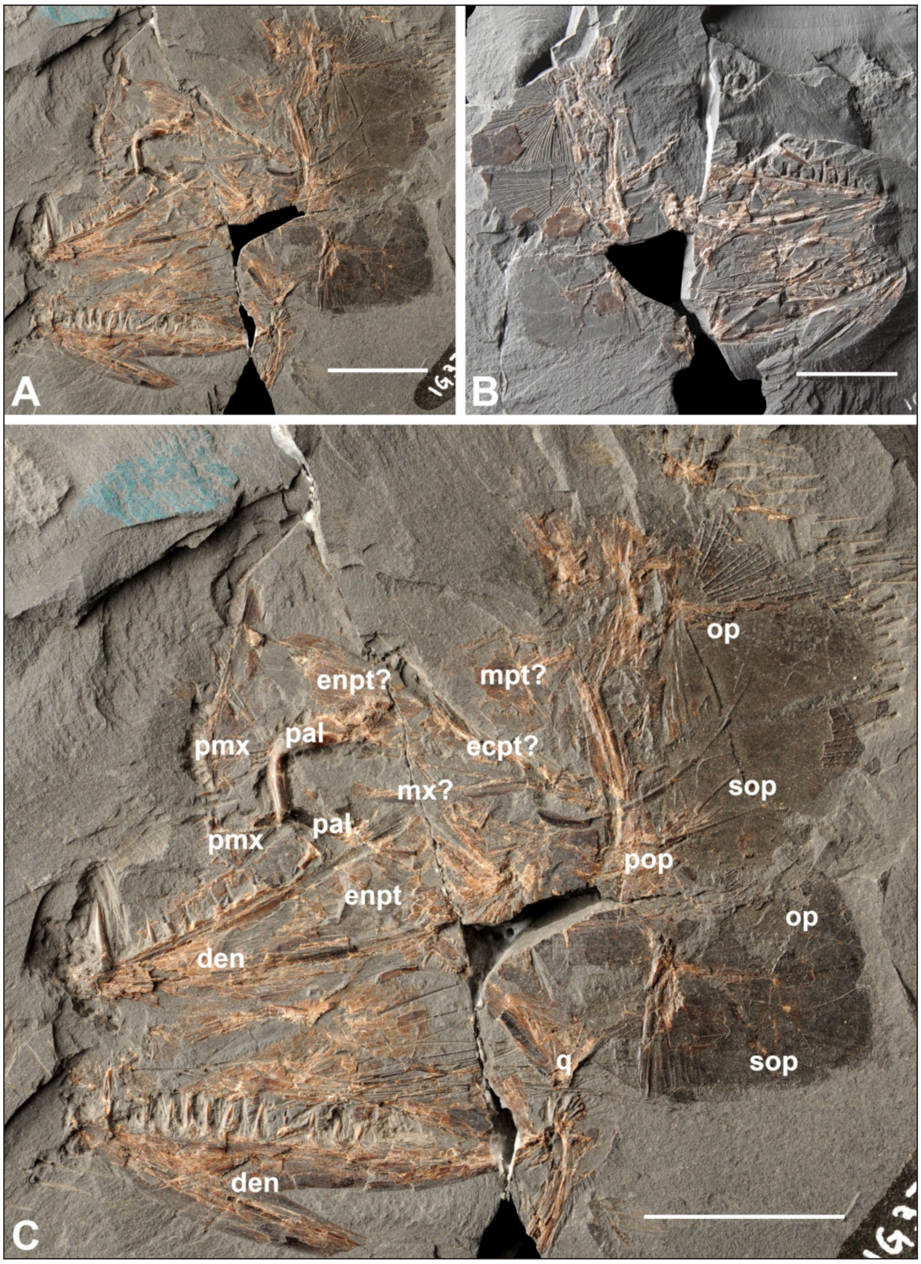

Fig. 35 - *Enchodus venator* Arambourg, 1954; Bomba Quarry (Cinto Euganeo). A) MCSNV IG37498; B) MGCB IG37499, counterpart of MCSNV IG37498; C) detail of MCSNV IG37498. Scale bars equal 20 mm.

1994 *Omosoma simum* Arambourg - Colombara & Astolfi, p. 39.
2005 *Omosoma simum* - Dalla Vecchia et al., p. 106.
2010 *Omosomopsis simum* - Khalloufi, p. 48.

Referred material: MCSNV IG37524 and MGCB IG37523.
Locality: Bomba Quarry (Cinto Euganeo, Padova).

Description and remarks. MCSNV IG37524 (Fig. 37) and MGCB IG37523 are part and counterpart of an incomplete specimen represented by a portion of the axial skeleton. It also includes 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 & Patterson 1993). Sorbini (1976) referred these remains to the polymixiid *Omosoma simum* known from the Cenomanian of Jbel 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.

Superorder **Acanthopterygii** (sensu Johnson & Patterson, 1993)
Series **Euacanthopterygii** (sensu Johnson & Patterson, 1993)
Order **Beryciformes** Regan, 1909

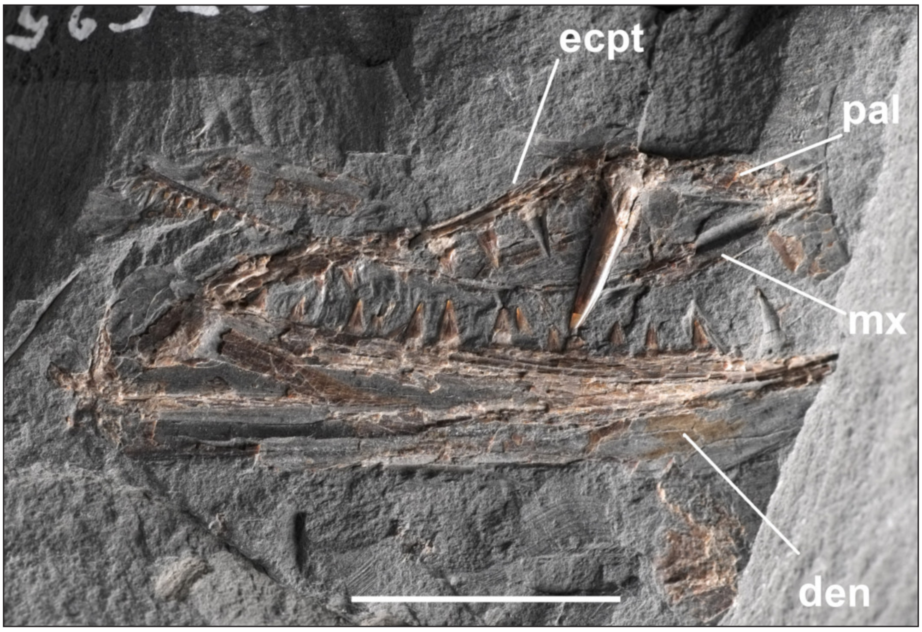

Fig. 36 - *Rharbichthys ferox* Arambourg, 1954; Bomba Quarry (Cinto Euganeo), MGCB IG37525. Scale bar equals 10 mm.

Fig. 37 - Polymixiiformes indet.; Bomba Quarry (Cinto Euganeo), MCSNV IG37524. Scale bar equals 10 mm.

?Beryciformes indet.

Fig. 38

Referred material: MGCB VT 002.

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

Description and remarks. Specimen MGCB VT 002 (Fig. 38) consists of the anterior portion a spinous dorsal fin. Dorsal-fin spines represent an apomorphic character of Acanthomopha (Johnson & 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 originally, supported by the sixth pterygiophore of the series and mostly preserved as impression only. It exhibits also a chain-link articulation of dorsal fin-spines, a char-

Fig. 38 - ?Beryciformes indet.; Sinigallia Quarry (Teolo), MGCB VT002. Scale bar equals 20 mm.

acteristic shared by beryciforms and percomorphs (Johnson & Patterson 1993). Due to the paucity of genuine Cenomanian percomorphs, 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. 39

Referred material: MGCB U3S1/2.

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

Description and remarks. The specimen consists of an isolated opercle. It is deeper than long, with two prominent spines along the posterior margin. The dorsal margin of the opercle is rounded, followed by two concavities and by an oblique and crenulated posteroventral margin converging into an acute angle with the anterior margin. The opercle exhibits a marked horizontal ridge ending with a small spine posteriorly plus some other shallow ridges also diverging from the articular condyle. The overall morphology of the opercle is reminiscent of that of the known species of trachichthyoid genus *Hoplopteryx* (see Patterson 1964), from which it differs by having two concavities and the two spines along the posterior margin.

This is the first report of the genus from the Bonarelli Level of northeastern Italy.

Discussion

The fish assemblage of the BL from northeastern Italy is characterized by a high diversity of taxa. The list of the taxa provides an insight into the results of our study (see Tab. 1). There are at least 27 taxa, versus 23 previously recognized by Sorbini (1976, 1980) and 16 reported by Khalloufi (2010). Khalloufi (2010) did not consider the chondrichthyans, but even considering the actinopterygians only our study evidences the presence of at least 21 taxa. The chondrichthyans are much more diverse than previously thought.

Fig. 39 - *Hoplopteryx* sp., Bomba Quarry (Cinto Euganeo), MGCB U3S1/2. Scale bar equals 5 mm.

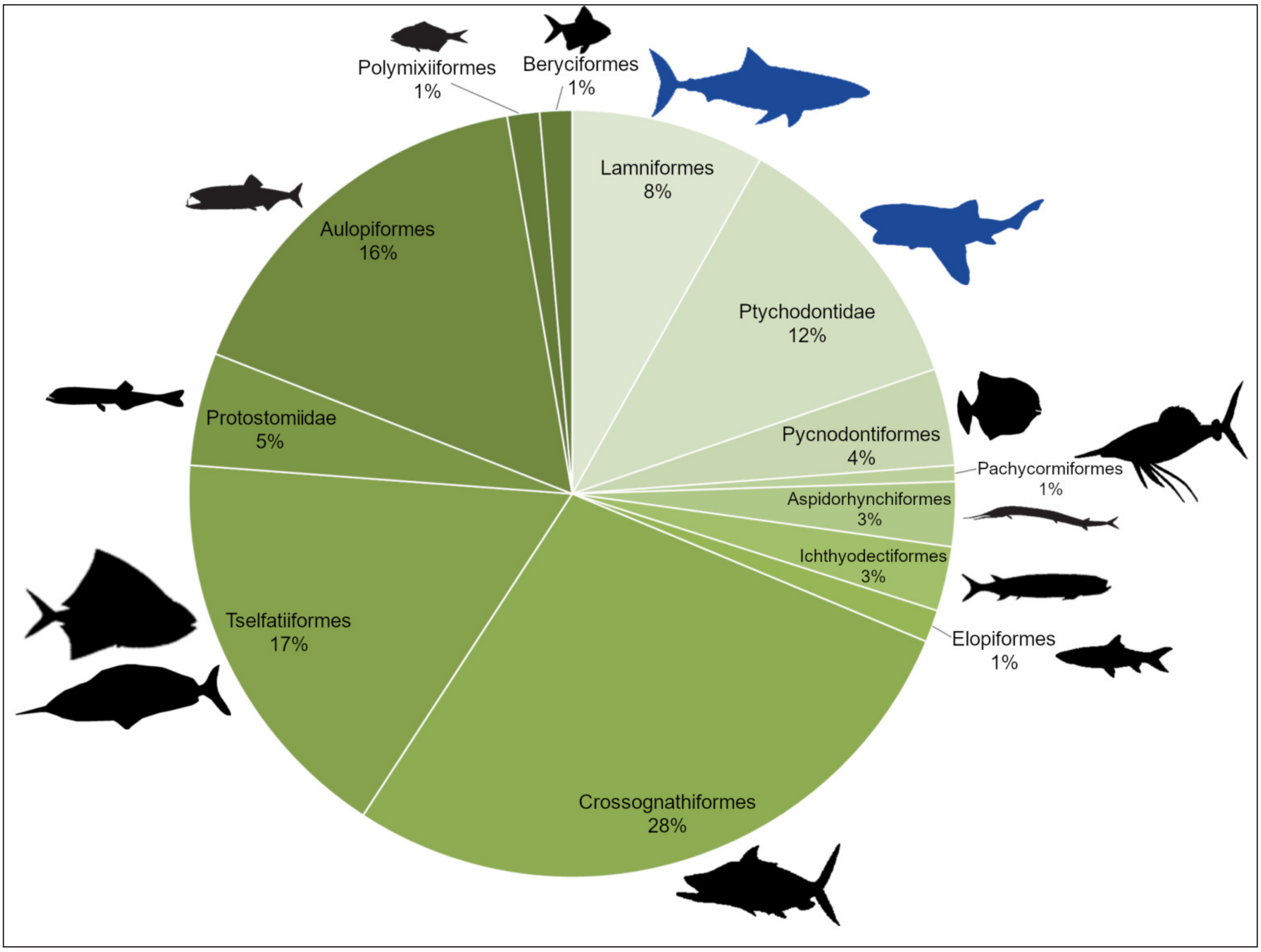

Fig. 40 - Taxonomic composition of the ichthyofauna of the Bonarelli Level from northeastern Italy. Blue color indicates the chondrichthyans, while the black color indicates the actinopterygians.

As far as the overall taxonomic composition of the recognized fish assemblage is considered (Fig. 40), despite it is possibily affected by sampling or preservation biases (Sorbini 1976; Patterson 1993), it appears to be dominated by crossognathiforms, tselfatiiforms and aulopiforms. Ptychodontids and lamniforms also represent a rather significant component 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 tselfatiiforms are usually interpreted as pelagic fishes by modern analogy (see Forey et al. 2003 and Taverne & Gayet 2005). Therefore, the ichthyofauna primarily consists of pelagic open water taxa. This is consistent with the general depositional environment of the BL in northeastern Italy (basinal and pelagic plateau setting).

Despite this study is based on material housed in museum collections in many cases with no associated field information and coming from only one official excavation (Bomba Quarry), it is possible to discuss some qualitative taphonomical aspects. The preservation of the specimens is generally poor, and the high degree 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 were buried more quickly than the carcasses of larger individuals, with the latter being likely exposed on the sea floor for a prolonged period. 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 degree 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 at the water-sediment interface (Lyman 1994; Chellouche et al. 2012). Other possible factors that can produce strongly disarticulated carcasses are currents or predation/scavenging activities. There is no direct evidence of biological disturbance of the fish remains from BL. There are also no clear tractive patterns on the fish remains produced by 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 presence of a high number of caudal remains has been elegantly discussed and explained by Chellouche et al. (2012: 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 body portions 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 degree 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 might represent a direct consequence of this mechanism occurring on the carcasses.

PALEOBIOGEOGRAPHIC REMARKS

The comparative analysis of the composition of the BL ichthyofauna from NE Italy with those of other coeval assemblages may contribute to improve our knowledge of the mid-Cretaceous Tethyan paleoichthyogeography. Forey et al. (2003) compared the remarkably diverse Cenomanian fish assemblages from the Lebanese localities of Hakel, Hajoula and Namoura with those of other Cenomanian Tethyan (Israel, Morocco, Portugal, Slovenia) and boreal (English Chalk) localities, without considering the Italian assemblage described herein. Their study evidenced that, taking it as a whole, the Lebanon fauna appears to be similar to the fish faunas from Komen and Morocco (and perhaps also Portugal and Isreael) compared to the English Chalk. Forey et al. (2003) suggested that it was a genuine biogeographic pattern, not affected by sampling or taphonomic artifacts. Differences might have been related to the marked boundary of distributions running at 30°N and identified by Voigt (1996) for inoceramids and rudists. Forey et al. (2003) supposed that the boundary reflected cool, humid conditions to the north, which contrasted with the southern arid conditions, characterized by higher temperatures and development of carbonate platforms (for a general overview on Cretaceous climate see Hay & Floegel 2012). Forey et al. (2003) also presumed that the boundary could only be maintained through the Cenomanian by a distinct ocean circulation, which led to 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 & Gallo (2016) on the paleobiogeography of enchodontoid fishes seem to support this assumption, because they recognized a generalized NW-SE track during the Cenomanian probably related to a northern cold current reaching North Africa and the 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 lower taxonomic levels they may appear much more restricted in their range. According to Cavin (2008), the Cenomanian ichthyogeography is characterized by both vicariance and dispersal events (see also Silva & Gallo 2016). This is probably because the separation between Laurasia and Gondwana was already underway in the Late Jurassic and affected only weakly the Cretaceous faunas (Cavin 2008). There is also an east-west pattern concerning mainly taxa from Africa versus South America and Central versus Western Tethys in the mid-Cretaceous. The results are in accordance with the time of the opening of the Atlantic Ocean starting in the South and then extending northwards (Cavin 2008). Within this framework, we performed statistical (PCA and

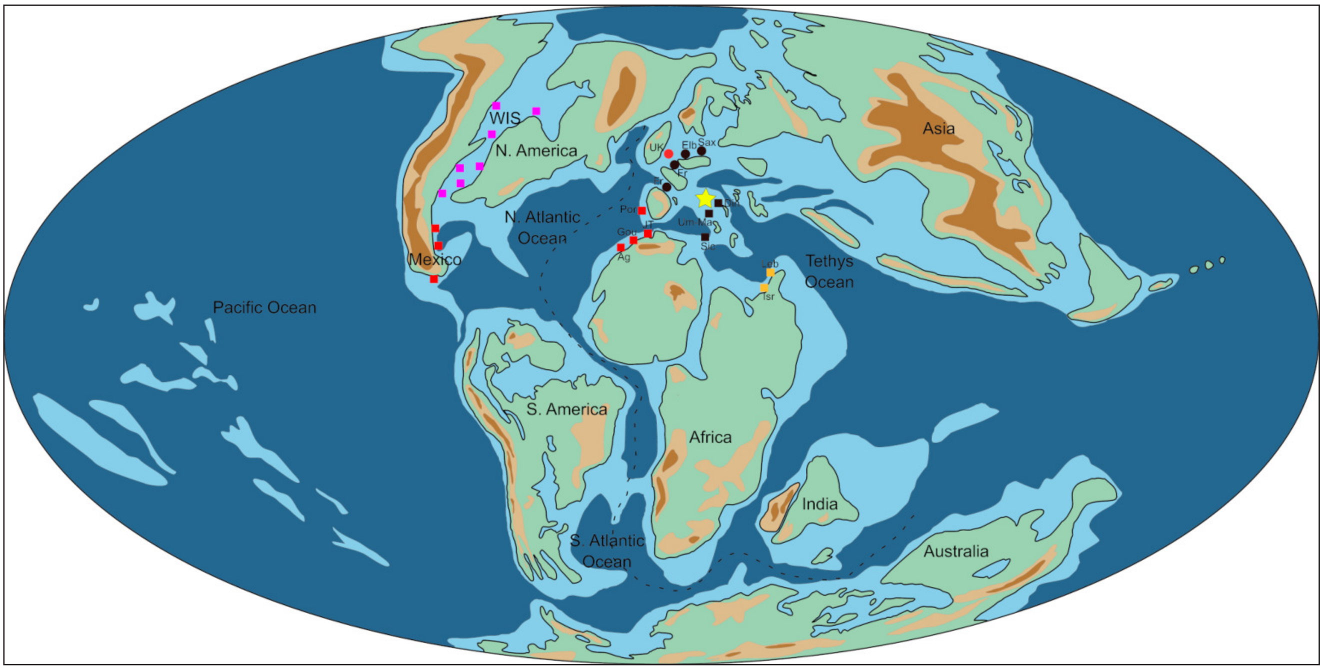

Fig. 41 - Reconstruction of the paleogeography during the Cenomanian (modified from Scotese 2014), with indication of the localities and assemblages listed in Tab. 1 and S.1. The yellow star indicates the position of the fossiliferous localities of northeastern Italy. Circles indicate the northern/boreal localities. Squares indicate Tethyan, N. Atlantic and WIS localities. Squares in Mexico (red squares) and in the WIS (purple squares) represent clusters of localities with assemblages from local formations included in the analysis. Abbreviations: Ag = Agoult; Din = Dinarids (Komen-Kras assemblages); Elb = Elbtal Group (Westphalia, Germany); Fr = French assemblages; Gou = Goulmima (Morocco); Isr = Israel; JT = Jbel Tselfat (Morocco); Leb = Lebanese assemblages; Por = Portugal; Sax = Saxony (Germany); Sic = Sicily (Italy); UK = English Chalk assemblage; Um-Ma = Umbria-Marche (Italy); WIS = Western Interior Seaway.

neighbor joining cluster analyses) analyses in order to interpret the mutual relationships between the mid-Cretaceous fish assemblages (see Figs 41-42 and Tab. 1). Considering cartilaginous and bony fishes together (Fig. 42A), the PCA evidences that the Lebanese and the English Chalk assemblages are completely different from the other assemblages. All other western Tethyan assemblages are grouped together. This would suggest the existence of a strong endemism of the English Chalk assemblage as also evidenced by Forey et al. (2003), Cavin (2008) and Friedman et al. (2016). The separation of the Lebanese localities in our analysis is certainly strongly affected by their enormous diversity, probably enhanced by Lagerstätte-effect and collection biases, as already evidenced in other studies (e.g. Guinot & Cavin 2016). The BL ichthyofauna is very close to the other localities from the western Tethys domain, especially the Jbel Tselfat (Morocco). Their similarities were already evidenced by Sorbini (1976), Khalloufi (2010) and Khalloufi et al. (2010). However, it exhibits also certain affinities 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 the patterns displayed in the PCA are confirmed by the neighbor joining cluster analysis (Fig. 55B-C). Considering the bony fishes alone (Fig. 42B), the PCA and cluster analyses almost perfectly match the results of the bony and cartilaginous fishes in the analysis. It is noteworthy to mention that the analysis of the cartilaginous fish dataset alone (Fig. 42C) shows a strong separation between chondrichthyan assemblages of the English Chalk and the North American Western Interior Seaway (WIS), which suggests the existence of a strong provincialism in these two assemblages. The analyses depict an overall provincialism during the Cenomanian/Turonian, already hypothesized also for 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 modern systematic revisions (see e.g. Cavin 2008), may become clear with increased interest in Cretaceous fishes resulting in 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

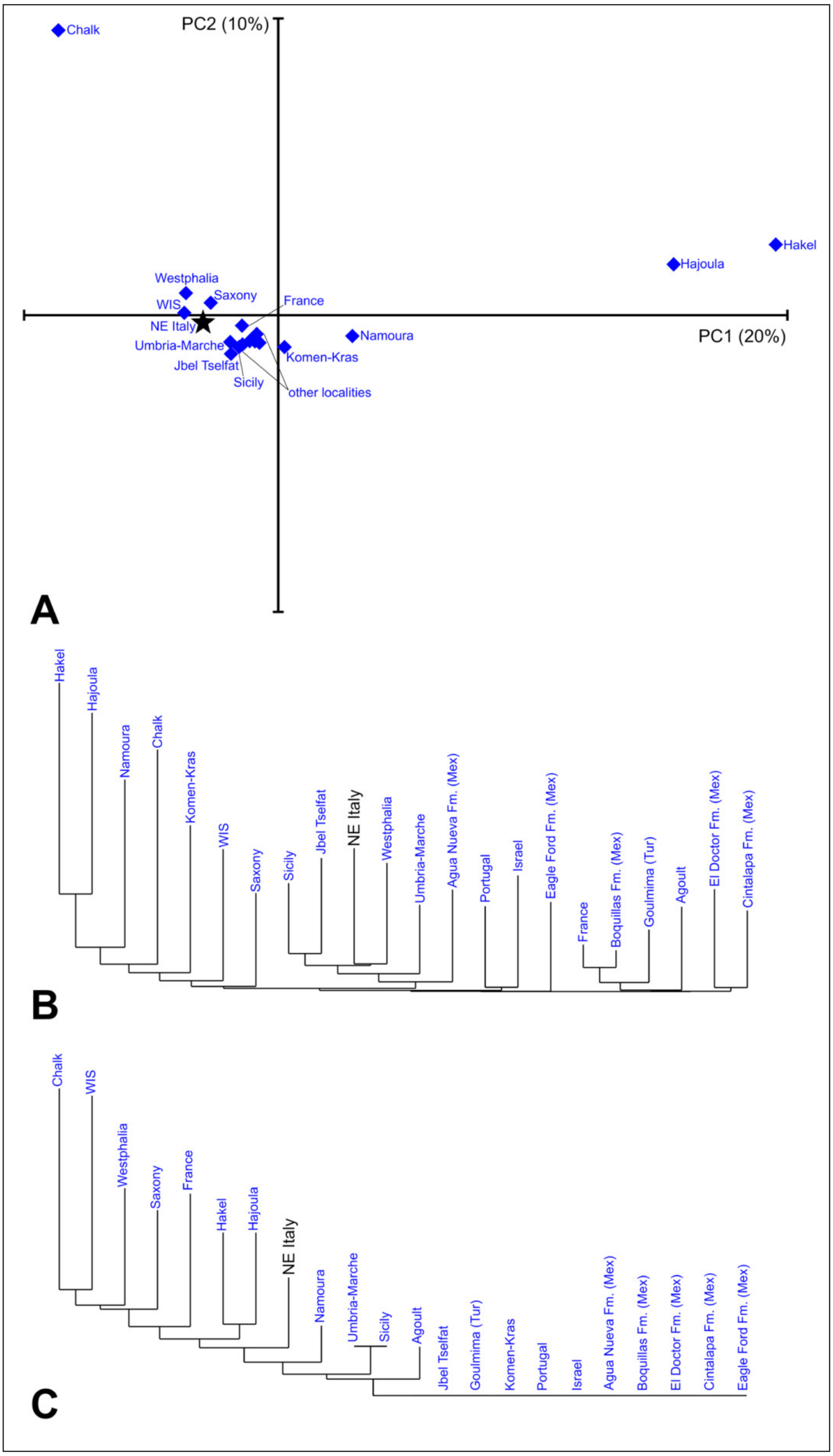

Fig. 42 - Diagram to illustrate the Cenomanian-Turonian ichthyofaunal relationships. A) PCA plot of cartilaginous and bony fishes data sets; B) neighbor joining cluster plot of bony fish data set; C) neighbor joining cluster plot of chondrichthyan data set. The names in the plots refer to the localities and assemblages listed in Tab. 1 and S.1. The black star indicates the ichthyofauna described in this paper. The label 'other localities' indicates the localities from Tab. 1 and S.1 that are not indicated in the plot. Abbreviations: Mex = Mexico; Tur = Turonian; WIS, Western Interior Seaway (North America).

studies utilizing additional specimens of all Tethyan localities will help to clarify the paleobiogeography of Cretaceous ichthyofaunas and the main drivers (climatic, tectonic, etc.) of their paleoecological and evolutionary dynamics (see e.g. Guinot & Cavin 2020).

Concluding remarks

The BL ichthyofauna from northeastern Italy was in need of an up-to-date revision also in order to include the material that was collected after the publication of the seminal paper on the Cinto

Euganeo ichthyofauna by Sorbini (1976). Our revision also considered the findings coming from three previously unrecognized localities: the Carcoselle Quarry, the Valdagno-Schio tunnel and Quero. We identified not less than 27 taxa, including nine new additions (*Scapanorhynchus raphiodon*, *Cretalamna appendiculata*, *Archaeolamna kopingensis*, '*Nursallia*' *tethysensis*, *Belonostomus* sp., *Dixonanogmius dalmatius*, '*Protosphyraena*' *stebbingi* and *Hoplopteryx* sp.). The overall assemblage primarily consists of crossognathiforms, tselfatiiforms and aulopiforms and possibly represents an open-water pelagic fauna. The degree of preservation seems to be consistent with the depositional setting. A brief comparison with coeval assemblages displays general similarities with nearby western Tethyan fish assemblages and especially with the Jbel Tselfat (Morocco) and the German assemblages. It is noteworthy to mention that during the late Cenomanian invasions of boreal/northern faunas from the high latitudes caused by the oceanic circulation disturbances induced by the cooling phases of the OAE2 has been observed in other taxonomic groups (see Jefferies 1962; Gale & Christensen 1996; Jarvis et al. 2011; Zheng et al. 2013; Jenkins et al. 2017). However, there is a consistent evidence of a certain degree of faunal separations during the Cretaceous (Cavin 2008). In any case, additional information would be necessary to more properly define the main global Cenomanian and Turonian ichthyogeographic distributional patterns.

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Tab. 1 - (p. 303- 308). List of known taxa from selected marine Cenomanian/Turonian localities. Grey-scale colors in columns indicate higher taxonomic levels. Abbreviations: Fm. = formation; NE = northeastern; Tur = Turonian; WIS = Western Interior Seaway.

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
Higher systematic classification			***Taxa***	**NE Italy (this study)**	Umbria-Marche	Sicily	Jbel Tselfat	Agoult	Goulmima (Tur)	Komen-Kras	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoula (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
Chondrichthyes			Chondrichthyes indet.																	✓					
Elasmobranchii			Elasmobranchii indet.																	✓					
Euselachii	*incertae sedis*		*Cretomanta canadensis*																	✓					
Selacimorpha	Hybodontiformes		*Polyacrodus polyptychus*											✓											
			Hybodus sp.																	✓					
Squalomorphii	Hexanchiformes	Hexanchidae	*Hexanchus microdon*									✓													
			Gladioserratus aptiensis									✓													
	Squaliformes	Squalidae	*Protosqualus barringtonensis*									✓													
	Squatiniformes	Squatinidae	*Squatina (Cretascyllium) cranei*									✓			✓										
Galeomorphii	Heterodontiformes	Heterodontidae	*Heterodontus polydictyos*											✓											
			Heterodontus canaliculatus									✓			✓										
			Heterodontus sp. 1									✓													
	Orectolobiformes	Hemiscylliidae	*Mesiteia emiliae*														✓								
			Chiloscyllium greenei												✓					✓					
			Chiloscyllium sp. 2									✓													
			Chiloscyllium sp.										✓							✓					
			Pseudospinax pusillus												✓										
		Parascyllidae	*Pararhinchodon lehmani*														✓								
			Pararhynchodon? sp.																	✓					
		Ginglymostomatidae	*Cantioscyllium decipiens*									✓		✓											
			Cantioscyllium sp.																						
	Lamniformes	Alopiidae	*Paranomotodon angustidens*									✓		✓	✓										
		Anacoracidae	*Squalicorax falcatus*	✓								✓		✓					✓	✓					
			Squalicorax primolus												✓										
			Squalicorax curvatus																	✓					
			Squalicorax baharijensis										✓												
			Squalicorax sp.										✓							✓					
			Nanocorax sp.									✓													
			Palaeoanacorax aff. *pawpawnensis*									✓								✓					
			Microcorax crassus																	✓					
		Cardabiodontidae	*Cardabiodon venator*																	✓					
		Archaeolamnidae	*Archaeolamna kopingensis*	✓								✓								✓					
			Archaeolamna sp.										✓												
		Cretoxyrhinidae	*Cretoxyrhina mantelli*	✓								✓		✓						✓					
			Cretoxyrhina denticulata									✓			✓										
			Cretoxyrhina agassizensis																	✓					
			Dallasiella owstoni									✓													
		incertae familiae	*Dwardius woodwardi*									✓								✓					
		Otodontidae	*Cretalamna appendiculata*	✓								✓	✓	✓	✓					✓					
		Pseudoscapanorhynchidae	*Psedoscapanorhynchus compressidens*									✓	✓												
			Cretodus semiplicatus									✓	✓	✓			✓	✓		✓					
			Cretodus "longiplicatus"									✓						✓							
			Cretodus crassidens									✓													
			Leptostyrax sp.																	✓					
			Protolamna acuta											✓	✓										
			Protolamna sokolovi												✓										
			Protolamna compressidens										✓												
			Protolamna sp.									✓	✓												
		Haimirichiidae	*Haimirichia amonensis*					✓																	
		Mitsukurinidae	*Scapanorhynchus raphiodon*	✓								✓		✓											
			Scapanorhynchus minimus									✓	✓												
			Anomotodon sp.									✓													
			Anomotodon cf. *principalis*									✓													
		Odontaspididae	*Carcharias* sp.											✓											
			Carcharias saskatchewanensis																	✓					
			Carcharias amonensis										✓												
			Cenocarcharias tenuiplicatus																	✓					
			Cenocarcharias rochebrunei										✓												
			cf. *Johnlongia*																	✓					
			Johnlongia cf. *J. parvidens*																	✓					
			Posadaia nolfi									✓			✓										
			Pseudomegachasma comanchensis																	✓					
			Eostriatolamia (?) *subulata*									✓			✓										
			Roulletia bureaui										✓												
	Carcharhiniformes		Carcharhiniformes *incertae sedis*																	✓					
		Scyliorhinidae	*Scyliorhinus bloti*														✓								
			Scyliorhinus arambourgi															✓							
			Scyliorhinus antiquus									✓													
			Scyliorhinus dubius									✓													
			Cretascyliorhinus aff. *destombesi*												✓										
			Scyliorhinidae indet.															✓							
		Pseudoscyliorhinidae	*Pseudoscyliorhinus schwarzhansi*									✓		✓	✓										
			Diprosopovenator hilperti											✓	✓										
	Synechodontiformes	Palaeospinacidae	*Synechodus dubrisiensis*									✓													
			Synechodus nitidus									✓													
			Synechodus tenuis									✓													
Neoselachii *incertae sedis*		Ptychodontidae	*Ptychodus decurrens*	✓	✓	✓						✓		✓	✓					✓					
			Ptychodus mammillaris											✓						✓					
			Ptychodus anonymus																	✓					
			Ptychodus occidentalis																	✓					
			Ptychodus whipplei																	✓					
Batomorphii	Rajiformes	Rhinobatoidei incertae fam.	*Turoniabatis ornata*									✓			✓										
			Turoniabatis cappetai										✓												
			Squatirhina westfaica												✓										
	Rajiformes	*incertae sedis*	*Hamrabatis bernardezi*										✓												
	Rajiformes	Rhinobatidae	*Rhinobatos grandis*														✓								
			Rhinobatos hakelensis														✓								
			Rhinobatos maronita														✓								
			Rhinobatos whitfieldi															✓							
			Rhinobatos incertus																	✓					
			Rhinobatos sp.																	✓					
			Rhombopterygia rajoides															✓							
			Pseudohypolophus mcnultyi										✓							✓					

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
Higher systematic classification			***Taxa***	**NE Italy (this study)**	Umbria-Marche	Sicily	Jbel Tselfat	Agoult	Goulmima (Tur)	Komen-Kras	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoula (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
		Sclerorhynchidae	*Libanopristis hiram*														✓	✓							
			Micropristis solomonis															✓							
			Ischyrhiza avonicola																	✓					
			Ischyrhiza schneideri																	✓					
			Onchopristis dunklei																	✓					
			Ptychotrygon sp.																	✓					
			Sclerorhinchidae(?) *incertae sedis*																	✓					
			aff. Sclerorhynchidae gen. et sp. indet.										✓												
		Rajidae	*Rajorhina expansa*															✓							
		Cyclobatidae	*Cyclobatis major*														✓	✓							
			Cyclobatis olygodactylus														✓	✓	✓						
			Cyclobatis tuberculatus														✓								
Holocephali	Chimaeriformes		*Edaphodon mantelli*									✓													
			Edaphodon agassizi									✓													
			Edaphodon reedi									✓													
			Ischyodus thurmoni									✓													
			Elasmodectes willetti									✓													
Sarcopterygii	Coelacanthiformes		Latimeroidei indet.																						✓
		Latimeriidae	*Macropomoides orientalis*														✓	✓							
			Macropoma lewesiensis									✓													
			Macropoma praecursor									✓													
		Coelacanthidae	Coelacanthidae indet.																				✓		
Actinopterygii			Osteichthyes indet.																	✓					
	Macrosemiiformes		*Macrosemiocotzus americanus*																					✓	
		Agoultichthyidae	*Agoultichthys chattertoni*					✓																	
	Lepisosteiformes		*Herreraichthys coahuilaensis*																						✓
	Amiiformes		*Tomognathus mordax*									✓													
			Pachyamia latimaxillaris													✓									
			Paleamia cenomaniensis								✓														
			Caturidae indet.																	✓					
	Ionoscopiformes		*Spathiurus dorsalis*									✓					✓								
			Neorhombolepis excelsus									✓													
			Neorhombolepis ? punctatus									✓													
		Aphanepigydae	*Aphanepygus dorsalis*														✓								
			Petalopteryx syriacus														✓								
	Pycnodontiformes		Pycnodontiformes indet.																✓	✓			✓	✓	
		Coccodontidae	*Coccodus armatus*														✓								
			Coccodus insignis															✓							
			Ichthyoceros spinosus														✓								
			Hensodon spinosus														✓								
			Rhinopycnodus gabriellae														✓								
			Corusichthys megacephalus														✓								
			Paracoccodus woodwardi														✓								
		?Coccodontidae	*Cosmodus carentonensis*										✓												
		Trewavasiidae	*Trewavasia carinatus*														✓								
		Pycnodontiformes fam. indet.	*Akromystax tilmachiton*														✓		✓						
		Pycnodontidae	*Ocleodus costai*							✓															
			Coelodus saturnus							✓															
			Anomoedus angustus											✓											
			Anomoedus willetti									✓													
			Anomoedus muensteri											✓											
			"Nursallia" goedeli														✓	✓	✓						
			Paranursallia gutturosa	✓	✓	✓	✓								✓						✓				
			"Nursallia" thethysensis	✓																	✓				
			"Coelodus" fimbriatus																	✓					
			"Pycnodus" scrobiculatus											✓											
			Palaeobalistum sp.							✓										✓					
			Proscinetes sp.																✓						
			Scalacurvichthys naishi													✓									
			Haquelpycnodus picteti														✓								
			Flagellipinna rhomboides														✓								
			Sygmapycnodus giganteus														✓								
			Corusichthys magacephalus														✓								
			Micropycnodon kansasensis																	✓					
		Gladiopycnodontidae	*Gladiopycnodus karami*														✓								
			Gladiopycnodus byrnei															✓							
			Monocerichthys scheuchzeri															✓	✓						
			Rostropycnodus gayeti														✓								
			Joinvillichthys lindstroemi														✓								
			Joinvillichthys kriweti														✓	✓							
			Pankowskichthys libanicus														✓		✓						
			Hayolperichthys pectospinus														✓								
			Ducrotayichthys cornutus														✓								
			Tricertichthys wenzi														✓								
			Ichthyoceros spinosus														✓								
			Stenoprotome hamata														✓								
		Gebrayelichthyidae	*Gebrayelichthys uyenoi*														✓								
			Gebrayelichthys vexillarius														✓								
			Maraldichthys verticalis														✓								
		Pycnodontiformes fam. indet.	*Acrorhinichthys poyatoi*														✓		✓						
Teleostei	incertae sedis		?*Carsothrissops delorenzi*							✓															
			Idrissia jubae			✓	✓																		
			Teleostei indet. (sp. A)																	✓					
			Teleostei indet. (sp. B)																	✓					
			Teleostei indet. (sp. C)																	✓					
			Teleostei indet. (sp. D)																	✓					
		Araripichthyidae	*Araripichthys* sp.																		✓				
			Araripicthtys corythophorus						✓																
	Pachycormiformes		?*Protosphyraena* sp.									✓													
			Protosphyraena sp.											✓	✓					✓					
			Protosphyraena ferox	✓								✓													
			Protosphyraena minor									✓													
			Rhinchonichthys taylori									✓													

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
Higher systematic classification			***Taxa***	**NE Italy (this study)**	Umbria-Marche	Sicily	Jbel Tselfat	Agoult	Goulmima (Tur)	Komen-Kras	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoula (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
	Aspidorhynchiformes		*Belonostomus* sp. 1																✓						
			Belonostomus sp. 2																✓						
			Belonostomus cinctus									✓			✓										
			Belonostomus sp.	✓	✓			✓				✓								✓	✓				
			Belonostomus lesinaensis							✓															
			Belonostomus aff. *crassirostris*				✓																		
			Vinctifer sp.																				✓		
	Ichthyodectiformes		Ichthyodectiformes indet.																	✓			✓		
			Vallecillichthys multivertebratum																		✓				
			Ichthyodectoidei indet.	✓																				✓	
		Ichthyodectidae	Ichthyodectidae indet.											✓											
			Ichthyodectes "minor"									✓													
			Ichthyodectes sp.											✓											
			Grisichthys bardacki						✓																
			Xiphactinus audax																	✓					
			Xiphactinus mantelli									✓													
			Xiphactinus gaultinus									✓													
			Xiphactinus sp.												✓										
		Cladocyclidae	*Chirocentrites coronini*							✓															
			Chirocentrites sp.																✓						
			Heckelichthys vexillifer	✓			✓			✓															
			Heckelichthys microdon							✓															
			Heckelichthys preopercularis																				✓		
			aff. *Eubiodectes*																				✓		
			Eubiodectes libanicus														✓	✓	✓						
		Saurodontitidae	*Saurodon* sp.									✓													✓
			Prosaurodon sp.									✓													
			"Saurocephalidae" indet.									✓													
			"Saurodon" intermedius									✓													
			Gillicus arcuatus																						✓
Elopomorpha	Elopiformes		Elopiformes indet.	✓																					
			Laminospondylus sp.																						✓
	Elopiformes	Elopidae	*Davichthys gardnieri*														✓								
			Davichthys lacostei	✓	✓	✓	✓																		
			Ctenodentelops striatus																✓						
			Protelops anglicus									✓													
		Megalopidae	*Sedenhorstia libanica*														✓								
			Sedenhorstia dayi															✓							
			Sedenhorstia orientalis															✓							
		Osmeroididae	*Dinelops ornatus*									✓													
			Osmeroides lewesiensis									✓		✓											
			Osmeroides levis									✓													
			Osmeroides latifrons									✓													
			Osmeroides rheris						✓																
		Pterothrissidae	*Hajulia multidens*														✓	✓							
			?Istieus sp.			✓																			
	Albuliformes	Albulidae	*Lebonichthys lewisi*														✓								
			Lebonichthys namouriensis																✓						
			Albulidae indet.																	✓					
	Anguilliformes	Anguilloidei	*Anguillavus bathshebae*														✓	✓							
			Anguillavus mazeni																						
			Anguillavus quadripinnis															✓							
			Abisaadia hakelensis														✓								
			Urenchelys hakelensis														✓								
			Urenchelys germanus															✓							
			Luenchelys minimus																✓						
			Hayenchelus germanus															✓							
			Libanechelys bultyncki															✓							
		Saccopharyngoidei	*Enchelium montium*														✓	✓							
	Notacanthiformes		*Enchelurus anglicus*									✓													
Osteoglossomorpha	Osteoglossiformes		*Prognathoglossum kalassyi*																✓						
Clupeocephala	Crossognathiformes	Pachyrhizodontidae	*Pachyrhizodus megalops*									✓													
			Pachyrhizodus magnus									✓													
			Pachyrhizodus subulidens	✓								✓			✓										
			Pachyrhizodus basalis									✓													
			Pachyrhizodus dibleyi									✓													
			Pachyrhizodus caninus																		✓				
			Pachyrhizodus minimus																	✓					
			Pachyrhizodus leptopsis																	✓					
			Pachyrhizodus sp.	✓	✓									✓						✓					
			Elopopsis fenzli							✓															
			Elopopsis microdon				✓			✓					✓										
			Elopopsis crassus									✓													
			Elopopsis sp.																	✓					
			Apsopelix anglicus									✓													
			Goulmimichthys sp.																						✓
			Goulmimichthys arambourgi						✓																
			Goulmimichthys roberti																		✓				
			Kermichthys daguini			✓	✓																		
			Tingitanichthys sp.																		✓				
			Tingitanichthys heterodon				✓																		
			Motlayoichthys sergioi																				✓		
			Lebrunichthys nammourensis																✓						
			Stanhopeichthys libanicus															✓							
	Tselfatiiformes	Protobramidae	*Protobrama avus*															✓	✓						
			Protobrama woodwardi															✓							
			Absaadichthys libanicus															✓							
			Eusebichthys byblosi														✓								
			Eusebichthys sp. 1														✓								
			Eusebichthys sp. 2															✓							
			nov. gen, nov. sp.																✓						
		Plethodidae	*Bananogmius ornatus*			✓									✓										
			Plethodus expansus									✓													

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
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			Pentanogmius pentagon									✓													
			Tselfatia formosa	✓	✓	✓	✓								✓						✓				
			Tselfatia sp.																						✓
			Dixonanogmius dalmatius	✓						✓															
			Dixonanogmius oblungus									✓													
			Plethodontidae indet.																	✓					
	Tselfatiiformes?		*"Protosphyraena" stebbingi*	✓								✓													
			"Cylindracanthus" cf. *minor*												✓										
			nov. gen, nov. sp.															✓							
	incertae sedis		*Pseudoberyx syriacus*							✓							✓	✓							
			Pseudoberyx bottae							✓							✓	✓							
			Pseudoberyx grandis														✓								
Clupeomorpha		incertae sedis	*Ornategulum sardinoides*														✓		✓						
			Scombroclupea macrophthalma	✓						✓							✓	✓							
			Scombroclupea diminuta																✓						
			Scombroclupea javieri																					✓	
			Scombroclupea occidentalis																						✓
	Ellimmichthyformes	Ellimmichthyidae	*Armigatus* sp.				✓																		
			Armigatus brevissimus			✓				✓	✓				✓		✓	✓							
			Armigatus namouriensis																✓						
			Armigatus alticorpus																✓						
			Diplomystus birdi														✓	✓							
			Diplomystus 'paredentulous'									✓													
			Diplomystus sp.									✓													
		Paraclupeidae	*Triplomystus noorae*																✓						
			Triplomystus oligoscutatus																✓						
			Thorectichthys marocensis					✓																	
			Thorectichthys rhadinus					✓																	
			aff. *Paraclupea*																					✓	
			nov. gen. 1																✓						
			nov. gen. 2															✓							
			Scutatoclupea bacchiai																✓						
			Scutatoclupea applegati																					✓	
		Sorbinichthyidae	*Sorbinichthys elusivo*																✓						
			Sorbinichthys africanus					✓																	
	Clupeiformes		*Syllaemus anglicus*												✓										
			Clupeidae indet.																		✓				
Ostariophysii	Gonorhynchiformes		Gonorhynchiformes indet.																				✓		
		Charitosomidae	*Charitopsis spinosus*														✓	✓							
			Hakeliosomus hakelensis														✓	✓							
			Hakeliosomus sp. nov.																✓						
			Judeichthys haasi													✓									
			Ramallichthys orientalis													✓									
		Gonorhynchidae	*Parachanos* sp.		✓	✓				✓															
			Sapperichthys chapanensis																					✓	
Ostariophysii		incertae sedis	*Clupavus maroccanus*				✓								✓										
			Clupavus sp.		✓																				
		Clupavidae	*Lusitanichthys characiformis*								✓														
			Lusitanichthys africanus					✓																	
Euteleostei	Stomiiformes		*Paravinciguerria praecursor*			✓	✓																		
	incertae sedis		*Gaudryella gaudryi*														✓	✓	✓						
			Gharbouria libanica																✓						
			Ginsburgia operta														✓	✓							
			Salminops ibericus								✓														
			Barcarenichthys joneti								✓														
		Protostomiidae	*Protostomias maroccanus*	✓	✓		✓								✓										
Eurypterygii	Aulopiformes	*incertae sedis*	*Rharbichthys ferox*	✓		✓	✓								✓										
			Apateodus striatus									✓			✓										
			Yabrudichthys striatus													✓									
		Chirothricidae	*Exocoetoides minor*														✓	✓							
			Telepholis tenuis														✓	✓							
			Chirothrix libanicus																						
		Ichthyotringidae	*Ichthyotringa delicata*														✓	✓							
			Ichthyotringa africana	✓	✓		✓								✓										
			Ichthyotringa mexicana																				✓		
		Apatepopholidae	*Apatepopholis laniatus*														✓	✓	✓						
			Apatepopholis lanceolatus									✓													
			Apateopholis nov. sp.																✓						
			nov. gen, nov. sp.														✓								
		Cimolichthyidae	*Cimolichthys lewesiensis*									✓			✓										
			Cymolichthys nepaholica																	✓					
			Cimolichthys sp.											✓											
		Dercetidae	*Dercetis elongatus*									✓													
			Dercetoides venator													✓									
			Hastichthys gracilis													✓	✓		✓						
			Hastichthys sp.																		✓				
			Rhynchodecertis sp.	✓	✓									✓											
			Rhynchodercetis hakelensis														✓	✓							
			Rhynchodercetis serpentinus															✓							
			Rhynchodercetis yovanovitchi			✓	✓																		
			Rhynchodercetis gortani							✓															
			Rhynchodecertis regio																		✓				
			Leptotrachelus sp.												✓										
			nov. gen., nov. sp.															✓							
		Prionolepidae	*Prionolepis cataphractus*														✓	✓							
			Prionolepis angustus									✓													
		Aspidopleuridae	*Aspidopleurus kickapoo*																						✓
		Enchodontidae	*Enchodus lewesiensis*								✓			✓											
			Enchodus marchesetti														✓	✓							
			Enchodus mecoanalis																✓						
			Enchodus cf. *major*							✓															
			Enchodus dentex							✓															
			Enchodus lycodon							✓															

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
Higher systematic classification			***Taxa***	**NE Italy (this study)**	Umbria-Marche	Sicily	Jbel Tselfat	Agoult	Goulmima (Tur)	Komen-Kras	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoula (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
			Enchodus venator	✓		✓	✓								✓										
			Enchodus shumardi																	✓					
			Enchodus brevis													✓									
			Enchodus zimapanensis																				✓		
			Enchodus sp.																		✓				✓
			Enchodus gladiolus																	✓					
			Enchodus sp. 1														✓								
			Enchodus sp. 2																✓						
			Parenchodus longipterygius													✓									
		Eurypholidae	*Eurypholis boissieri*														✓	✓	✓						
			Eurypholis pulchellus									✓													
			Saurorhamphus freyeri							✓															
			Saurorhamphus judeaensis													✓									
			Saurorhamphus giorgiae																✓						
			nov. gen., nov. sp.																✓						
		Halecidae	*Phylactocephalus microlepis*														✓	✓							
			Hemisaurida hakelensis														✓								
			Hemisaurida neocomiensis							✓															
			Serrilepis longidens													✓									
			Serrilepis prymnostrigos																✓						
			Serrilepis minor																✓						
			Halec eurypterygius									✓													
			Halec haueri							✓															
		Aulopodidae	*Nematonotus bottae*							✓							✓		✓						
			Nematonotus longispinus															✓							
Ctenosquamata	?Myctophiformes	Aulolepidae	*Aulolepis typus*									✓			✓										
		incertae sedis	*Hakelia laticauda*														✓	✓							
		Sardinioididae	*Sardinioides minimus*														✓	✓							
			Sardinioides attenuatus														✓	✓							
			Sardinioides pontivagus														✓	✓							
			Sardinioides guestphaicus							✓															
			"Sardinioides" illustrans									✓													
			Acrognathus boops									✓													
			Acrognathus dodgei														✓	✓							
			Volcichthys sp.														✓								
	Ctenothrissiformes	Ctenothrissidae	*Ctenothrissa vexillifer*														✓								
			Ctenothrissa protodorsalis														✓								
			Ctenothrissa signifer															✓							
			Ctenothrissa radians									✓													
			Ctenothrissa microcephala									✓													
			Heterothrissa signeuxae															✓							
		Pattersonichthyidae	*Pateroperca libanica*															✓							
			Pteroperca robusta															✓							
			Pattersonichthys delicatus															✓							
			Phoenicolepis arcuatus															✓							
			Humilichthys orientalis															✓							
Acanthomorpha		*incertae sedis*	*Gigapteryx thethyestris*																✓						
			Protriacanthus gortanii							✓															
			Dalgoichthys tropicalis																				✓		
			Muhichthys cordobai																				✓		
			Paleocyttus princeps								✓														
			Xenyllion zonensis																	✓					
			?*Cylindracanthus libanicus*														✓	✓							
	Lampridomorpha		*"Aipichthys" nuchalis*									✓													
		Pharmacichthyidae	*Pharmacichthys venenifer*														✓								
			Pharmacichthys numismalis														✓								
			Pharmacichthys judensis													✓									
			Errachidia pentaspinosa					✓																	
			Homalopagus multispinosus					✓																	
			Freigichthys elleipsis															✓							
		Aipichthyidae	*Aipichthys minor*														✓	✓							
			Aipichthys velifer														✓								
			Aipichthys oblungus														✓								
			Aipichthys pretiosus							✓															
		Pycnosteroididae	*Aipichthyoides galeatus*													✓									
			Aipichthyoides formosus													✓									
			Aipichthyoides sp. nov.																✓						
			Maghrebichthys nelsoni					✓																	
	Polymixiiformes		*Paraipichthys lusitanicus*								✓														
	Polymixiiformes		*Pycnosteroides levispinus*															✓							
			Omosoma / gen. nov, sp. nov.																✓						
			Omosomopsis simum			✓	✓																		
			Berycopsis elegans									✓													
			Berycopsis pulcher															✓							
			Homonotichthys dorsalis									✓													
			Homonotichthys rotundus									✓													
			Homonotichthys pulchellus									✓													
Acanthopterygii			?Beryciformes indet.	✓																					
Acanthopterygii	Beryciformes	*incertae sedis*	*Plesioberyx maximus*														✓								
			Plesioberyx discoides														✓								
			Cryptoberyx minimus															✓							
			Cryptoberyx brevis								✓					✓									
			Pattersonoberyx pharsus														✓								
		Holocentroidei	*Stichocentrus liratus*															✓							
			Stichocentrus elegans															✓							
			Stichocentrus spinulosus															✓							
			Stychocentrus sp. nov.															✓							
			Paracentrus lebanonensis																✓						
			Paracentrus sp. nov.																✓						
			Trachichthyoides ornatus									✓													
		Trachichthyoidei	*Stychoberyx lewisi*														✓	✓							
			Stychoberyx polydesmus				✓																		
			Lissoberyx dayi															✓							

Taxonomy				Italy			Morocco			Dinarids	Portugal	England	France	Germany		Middle East				North America	Mexico				
Higher systematic classification			***Taxa***	**NE Italy (this study)**	Umbria-Marche	Sicily	Jbel Tselfat	Agoult	Goulmima (Tur)	Komen-Kras	Portugal	Chalk	Chalk and other localities	Saxony	Westphalia	Israel (Ein Yabrud, etc.)	Hakel (Lebanon)	Hajoula (Lebanon)	Namoura (Lebanon)	WIS (Greenhorn, etc.)	Agua Nueva Fm.	Boquillas Fm.	El Doctor Fm.	Cintalapa Fm.	Eagle Ford Fm.
			Lissoberyx arambourgi															✓							
			Lissoberyx denticulatus															✓							
			Lissoberyx anceps				✓																		
			Beryx dalmaticus							✓															
			Microcapros libanicus															✓							
			Libanoberyx spinosus															✓							
			Hoplopteryx sp.	✓																					
			Hoplopteryx lewesiensis									✓		✓											
			Hoplopteryx simus									✓													
			Hoplopteryx stachei							✓															
			Lobopterus pectinatus							✓															
			Judeoberyx princeps													✓									
			Hgulichthys spinus															✓							
			Zoqueichthys carolinae																					✓	
			Pepemkay maya																					✓	
		Pseudomonocentridae	*Handuichthys interopercularis*																				✓		
			Pseudomonocentris microspinosus																				✓		
	Tetraodontiformes	Plectocretacidae	*Plectocretacicus clarae*														✓								

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