# EOCENE RHAMPHOSIDAE (TELEOSTEI: SYNGNATHIFORMES) FROM THE BOLCA *LAGERSTÄTTE*, ITALY

PIETRO CALZONI[1]*, JACOPO AMALFITANO[1], LUCA GIUSBERTI[1], GIUSEPPE MARRAMÀ[2] & GIORGIO CARNEVALE[2]

[1]Dipartimento di Geoscienze, Università di Padova, Via Gradenigo, 6-35131 Padova, Italy; E-mail: pietro.calzoni@phd.unipd.it, jacopo.amalfitano@unipd.it, luca.giusberti@unipd.it
[2]Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, 35 I-10125 Torino, Italy; E-mail: giuseppe.marrama@unito.it, giorgio.carnevale@unito.it
*Corresponding Author.

*Abstract*. The Rhamphosidae is an extinct family of syngnathiform fishes from the lower Eocene deposits of Europe, primarily known from specimens derived from the Ypresian *Konservat-Lagerstätte* of Bolca (Verona province, Italy). A descriptive analysis of 28 specimens of *Rhamphosus* from Bolca revealed the existence of six species, showing a greater taxonomic diversity compared to the previous scenario of only two species (the type species *Rhamphosus rastrum* and *Rhamphosus biserratus*). Four new species are established herein: *Rhamphosus bloti* n. sp., characterized by a peculiar and unique rostrum with a discoid shape; *Rhamphosus brevirostris* n. sp., which exhibits a moderately large size associated with a relatively short rostrum; *Rhamphosus longispinatus* n. sp., characterized by having the longest dorsal-fin spine and rostrum of all the *Rhamphosus* species; *Rhamphosus tubulirostris* n. sp., which shows a peculiar slim rostrum, long-based dorsal and anal fins, and a unique squamation characterized by the presence of numerous bucklers. The species from Bolca are also compared to the only other known *Rhamphosus* species, *Rhamphosus rosenkrantzi*, from the Fur Formation, Denmark. A number of morphological features support the assignment of the Rhamphosidae to the syngnathiform clade Dactylopteroidei, together with the extant families Dactylopteridae and Pegasidae, representing the sister group to the Pegasidae.

## INTRODUCTION

The Eocene fish assemblage from the Bolca *Lagerstätte* (northeastern Italy) represents one of the richest and most diverse known fossil ichthyofaunas, which provides a unique window into the early Cenozoic shallow tropical marine biodiversity (e.g.,

Marramà et al. 2016a; Friedman & Carnevale 2018). The Bolca fish assemblage includes the earliest documented record for a number of teleost lineages currently inhabiting a variety of coastal marine biotopes, thereby providing substantial evidence of the stability of the structural features of the tropical shallow marine ichthyofaunas throughout the Cenozoic (Bellwood & Wainwright 2002; Carnevale 2006; Carnevale et al. 2014; Marramà et al. 2016b, c). Overall, the Bolca ichthyofauna represents a

peri-reefal assemblage (Marramà et al. 2016a) strongly dominated by percomorphs in terms of taxonomic diversity. Up to date about 250 fish taxa have been described, including sharks, batoids, pycnodontiforms, crossognathiforms and crown teleosts (Carnevale et al. 2014). The recognition of such an amazing taxonomic diversity is the result of considerable efforts in the past four decades, resulting in the publication of several dozens of papers. Therefore, thanks to these efforts, the diversity of certain groups is currently well defined, including anguilliforms (Blot 1978, 1984), aulopiforms (Marramà & Carnevale 2017), beryciforms (Sorbini 1975, 1984; Sorbini & Tirapelle 1975), clupeomorphs (Marramà & Carnevale 2015a, b, 2016, 2018; Marramà et al. 2019), lophiiforms (Carnevale & Pietsch 2009, 2010, 2011, 2012; Pietsch & Carnevale 2011; Carnevale et al. 2020), pharyngognaths (e.g., Bannikov & Carnevale 2010, 2012a) and tetraodontiforms (e.g., Tyler & Santini 2002). Other groups remain poorly or inadequately known and would certainly benefit from a detailed analysis of the available material. This is especially true for the numerous members of the Syngnathiformes (sensu Santaquiteria et al. 2021), whose diversity in the Bolca fish assemblage has been only marginally defined. Of the eight syngnathiform families (Aulostomidae, Centriscidae, Fistularioididae, Paraeoliscidae, Parasynarcualidae, Solenostomidae, Syngnathidae, Urosphenidae) listed by Blot (1980) only the ghost pipefishes of the family Solenostomidae have been described in detail (Bannikov & Carnevale 2017). In addition, Tyler (2004) provided an accurate overview of the extinct family Aulorhamphidae and, more recently, Carnevale & Bannikov (2019) described the earliest dragonet *Gilmourella minuta* based on a single specimen in part and counterpart.

One of the most elusive families of the Bolca fish assemblage is the Rhamphosidae, whose syngnathiform affinities were proposed by Agassiz (1839) and corroborated by Gill (1884), Eastman (1914) and Pietsch (1978), and reported elsewhere only from the Eocene Fur Formation of Denmark (Nielsen 1960). Although Blot (1980) recognized three species-level taxa pertaining to the Rhamphosidae in the Bolca ichthyofauna, he placed these species among the Scorpaeniformes. Despite the efforts by Pietsch (1978), our knowledge of the morphology of these fishes is very limited and

their phylogenetic affinities remain elusive. The goal of this paper is therefore to provide a detailed morphological analysis of the Rhamphosidae of the Bolca *Lagerstätte* in order to define their taxonomic diversity and discuss their affinities within the syngnathiform fishes.

## LOCALITY AND STRATIGRAPHY

All the *Rhamphosus* specimens known to date from the Bolca *Lagerstätte* were collected in the Pesciara site (Fig. 1A-B), in the eastern part of the Monti Lessini (Verona province, northeastern Italy). The intense tectonic activity that affected this area and the broad occurrence of volcanites made the study of the exposed Eocene sedimentary successions extremely difficult. The Pesciara succession was referred to the informal stratigraphic unit of the lower-middle Eocene "Calcari Nummulitici", widely exposed in northeastern Italy (Papazzoni et al. 2014; Friedman & Carnevale 2018).

The Pesciara (Vestenanova, Verona province), consists of a 20-meter-thick limestone block (an olistolith) packed into volcanic deposits (Fig. 1C-D). It is characterized by an alternation of finely laminated micritic limestones with fish, plants and invertebrates, and biocalcarenites/calcirudites with molluscs and larger foraminifera (Papazzoni & Trevisani 2006). Based on their larger benthic foraminifera and calcareous nannofossil content, the Pesciara limestones have been referred to the *Alveolina dainelli* Zone (Trevisani et al. 2005; Papazzoni & Trevisani 2006), or SBZ11 Biozone (Sierra-Kiel et al. 1998) and to the calcareous nannofossil zones NP14 zone or CNE6 zone (Martini 1971; Agnini et al. 2014), dating back to the late Ypresian (48.96–48.50 Ma; Papazzoni et al. 2017).

The fossils found in the Pesciara are usually complete and very well-preserved, suggesting a rapid burial and accumulation of the carcasses over a poorly oxygenated substrate. The presence of microbial biofilms probably favoured fossil preservation by preventing a fast decay and the scavenging activity (Marramà et al. 2016a, 2021). Moreover, a lot of fish specimens show typical signs of muscular tetany, a factor which hints at how toxic algae blooming events could have been one of the causes of death of the marine lifeforms of the Pesciara paleobiotope (Marramà et al. 2016a, 2021).
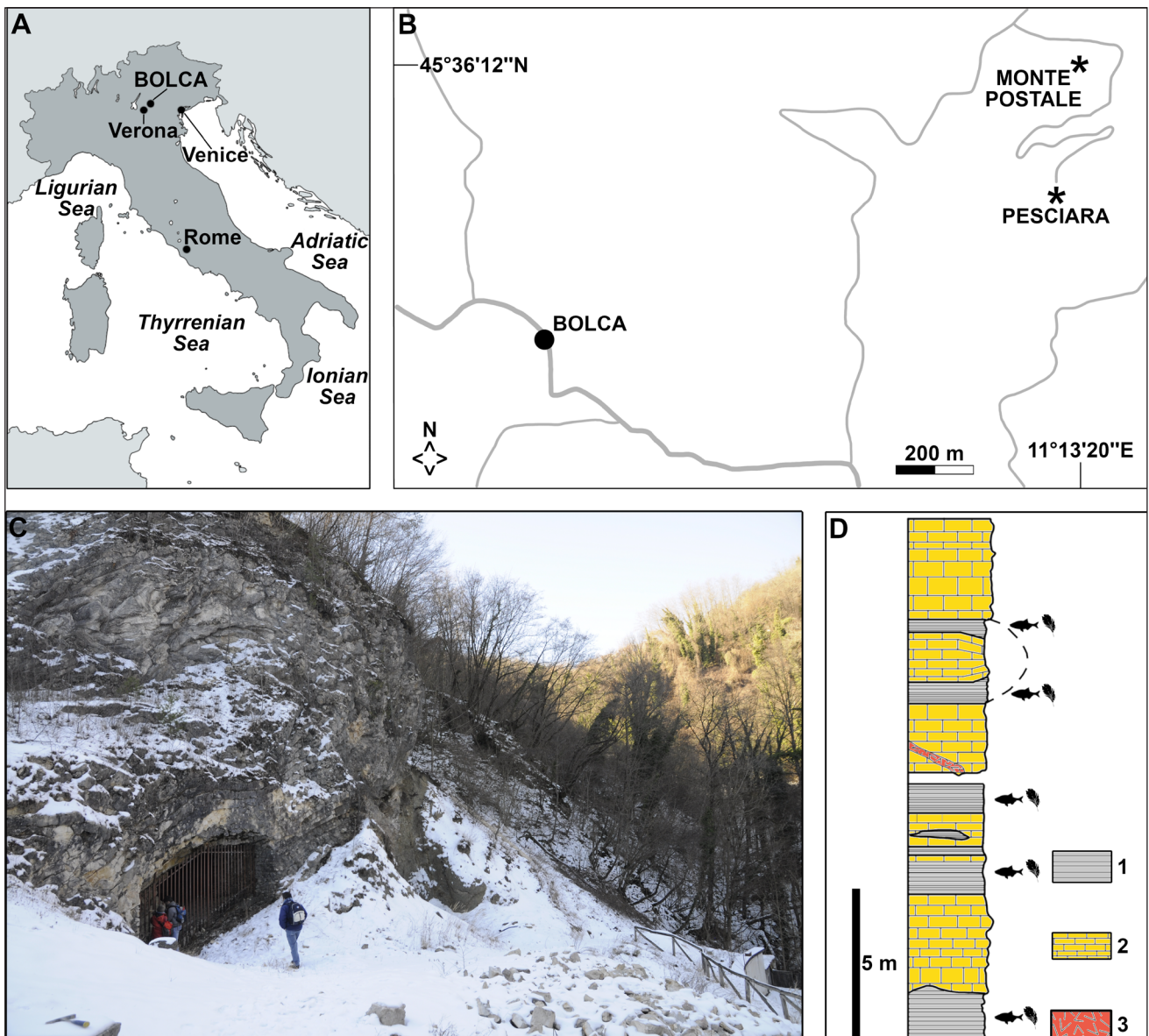
Fig. 1 - A) Sketch map of Italy showing the location of Bolca; B) sketch map of the Bolca area (modified from Pasini et al. 2022); C) photo of the outcrop of the Pesciara site (taken in Jan 2017); D) stratigraphic log of the Pesciara site. Legend: (1) fine-grained laminated micritic limestone with fish and plant remains; (2) coarse-grained biocalcarenite-biocalcirudite limestone with benthic fauna; (3) volcanic and basaltic rocks (modified from Marramà et al. 2023). Fish and plants silhouettes from www.phylopic.org.

The depositional context of the fossiliferous laminated micrites of the Pesciara site was an intraplatform basin with low energy and permanent anoxic or disoxic conditions on the seafloor (Marramà et al. 2016a).

## MATERIALS AND METHODS

The material examined in this study includes 28 articulated skeletons among which six species have been recognized. The skeletal anatomy of type species of the genus *Rhamphosus* – *R. rastrum* – has been described in detail herein in order to illustrate the osteological structure of the rhamphosid fishes, whereas the descrip-

tive analysis of the other species has been focused primarily on the diagnostic features.

Photos of the specimens were taken using a Sony α7R3 camera mounting a Sony FE 2.8/90 mm macro G OSS lens. Some specimens were photographed after being moistened with alcohol in order to emphasize the osteological details. Counts and measurements were taken directly on the specimens using a digital caliper or on digital photos using the software TpsDig (Rohlf, 2005). The specimens were studied with a stereomicroscope Wild Heerbrugg M5 equipped with a camera lucida drawing arm.

Anatomical terminology mostly follows Orr (1995).

**Institutional abbreviations**: CNHM: Carnegie Natural History Museum, Pittsburgh; CMC: Collezione Massimiliano Cerato; FUM: Fur Museum, Fur, Denmark; MCC: Museo Padre Aurelio Menin, Chiampo; MCSNV: Museo di Storia Naturale, Verona; MGPPD:

Sezione di Geologia e Paleontologia del Museo della Natura e dell'Uomo dell'Università di Padova (former Museo di Geologia e Paleontologia dell'Università di Padova), Padova; MNHN: Muséum national d'Historie Naturelle, Paris; NHMUK: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen.

**Anatomical abbreviations**: aa: angulo-articular; bas: basipterygium; br: branchiostegal rays; cor: coracoid; cl: cleithrum; den: dentary; ep: epural; epi: epioccipital; let: lateral ethmoid; fr: frontal; h: hypural; hspu2: haemal spine of the second preural vertebra; hspu3: haemal spine of the third preural vertebra; hyo: hyomandibula; io2: second infraorbital; io3: third infraorbital; iop: interopercle; la: lachrymal; mes: mesethmoid; mx: maxilla; na: nasal; nspu2: neural spine of the second preural vertebra; nspu3: neural spine of the third preural vertebra; op: opercle; pa: parietal; ph: parhypural; pmx: premaxilla; pop: preopercle; psp: parasphenoid; ptt: posttemporal; pro: prootic; pto: pterotic; q: quadrate; r: rays; rad: pectoral-fin radial; rpt: rayless pterygiophore; sca: scapula; sph: sphenotic; soc: supraoccipital; sop: subopercle; u: urohyal; un: uroneural; v: vertebra.

**Measurement abbreviations**: AFL: anal-fin base length; ARL: anal-fin ray length; BAS: basipterygium length; BD: maximum body depth; CP: caudal peduncle length; D1D2D: distance between first and second dorsal fins; DFL2: second dorsal-fin length; DRL2: second dorsal-fin ray length; HDS: first dorsal-fin spine length; HL: head length; O: orbit diameter; PA: preanal distance; PD1: predorsal distance; PD2: predorsal distance; PFL: pectoral-fin length; POO: postorbital distance; PRO: preorbital distance; PP: prepectoral distance; PV: prepelvic distance RL: rostral length (measured as horizontal distance between the anterior tip of the rostrum and the anterior tip of the premaxilla); RPT: rayless pterygiophore length; SL: standard length; TL: total length; VFL: pelvic-fin length.

## HISTORICAL NOTES

The monograph "*Ittiolitologia veronese del Museo Bozziano: ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti di fossili veronesi*" by the Abbott Giovanni Serafino Volta (1754-1842) was a first attempt to organically describe the extremely rich ichthyofauna coming from the Bolca *Lagerstätte* and constitutes the earliest paleoichthyological treatise (Carnevale et al. 2014). In this oeuvre, the author beautifully illustrated the Bolca fishes, including the description of more than 120 species (Carnevale et al. 2014). Volta erroneously referred the majority of the fossils to extant taxa, and only two genera and 15 species were described as new (Bannikov 2014; Carnevale et al. 2014), including the rhamphosid '*Uranoscopus*' *rastrum*, examined herein. Usually, the scholars referred to 1796 as the actual date for the creation of the taxa by Volta since that year was reported on the frontispiece of the "Ittiolitologia veronese". However, it is known that the publication of this monographic work started in 1796 and was officially completed in 1809, as testified by a colophon reported in its last page (see Riva 1966: 72). According to Gaudant (2011), the preparation of the

entire the "Ittiolitologia Veronese" required sixteen years (1793-1809). It was structured in sections of text ("quaderni") and their related plates were printed all over thirteen years, not in chronological order. Based on unpublished material, Gaudant (2011) provided a reconstruction of the troubled history of this monograph. The detailed work of Gaudant (2011), however, did not define a reconstruction of the precise date of printing of the various sections of text ("quaderni") and related plates. For the nomenclatural purpose of accurately determine the year in which the taxa created by Volta were actually published, we propose herein to apply the provisions of the Art. 21.6 of the ICZN Code (1999) affirming that "If the date of publication specified in a work is a range of dates, the work is to be dated from the final day of the range". As reported above, the "Ittiolitologia Veronese" was published between 1796 and 1809, and for this reason the work and the nomenclatural acts contained therein should be referred to 1809, not to 1796.

## SYSTEMATIC PALEONTOLOGY

Order **Syngnathiformes** sensu Nelson et al., 2016
Suborder **Dactylopteroidei** Betancur et al., 2017
Family Rhamphosidae Gill, 1884

**Diagnosis:** A family of the Syngnathiformes unique in having the following combination of features: anterior abdominal vertebrae elongate; 13 or 14 caudal vertebrae; head and nape encased in thick bony plates; mouth small and ventral; nasal bones fused along the midline forming a rostrum that extends anteriorly far beyond the mouth; rostrum tapering or spatulate distally; preopercle remarkably expanded medially; large rayless pterygiophore consolidated with the head shield; first dorsal fin inserted behind the head and consisting of a massive spine with serrated margins, followed by 2-4 thin, slender and flexible spines; first dorsal-fin spine articulated with the large rayless pterygiophore; second dorsal and anal fins placed posteriorly and approximately opposed to each other; caudal fin gently rounded with ten principal rays; pectoral fins inserting laterally on the body flanks and subhorizontally oriented; pectoral-fin rays unbranched; pelvic fins inserting just behind the pectoral fins and containing one spine plus five rays; caudal skeleton with hypurals, parhypural and uroneural consolidated into a single plate and two epurals; neural and haemal spines of the penultimate vertebra broadly expanded anteroposteriorly.

### Genus *Rhamphosus* Agassiz, 1835

**Type species (by monotypy):** *Rhamphosus aculeatus* Agassiz, 1835, objective junior synonym of *Centriscus aculeatus* de Blainville, 1818. Both species are junior synonyms of *Uranoscopus rastrum* Volta, 1809.
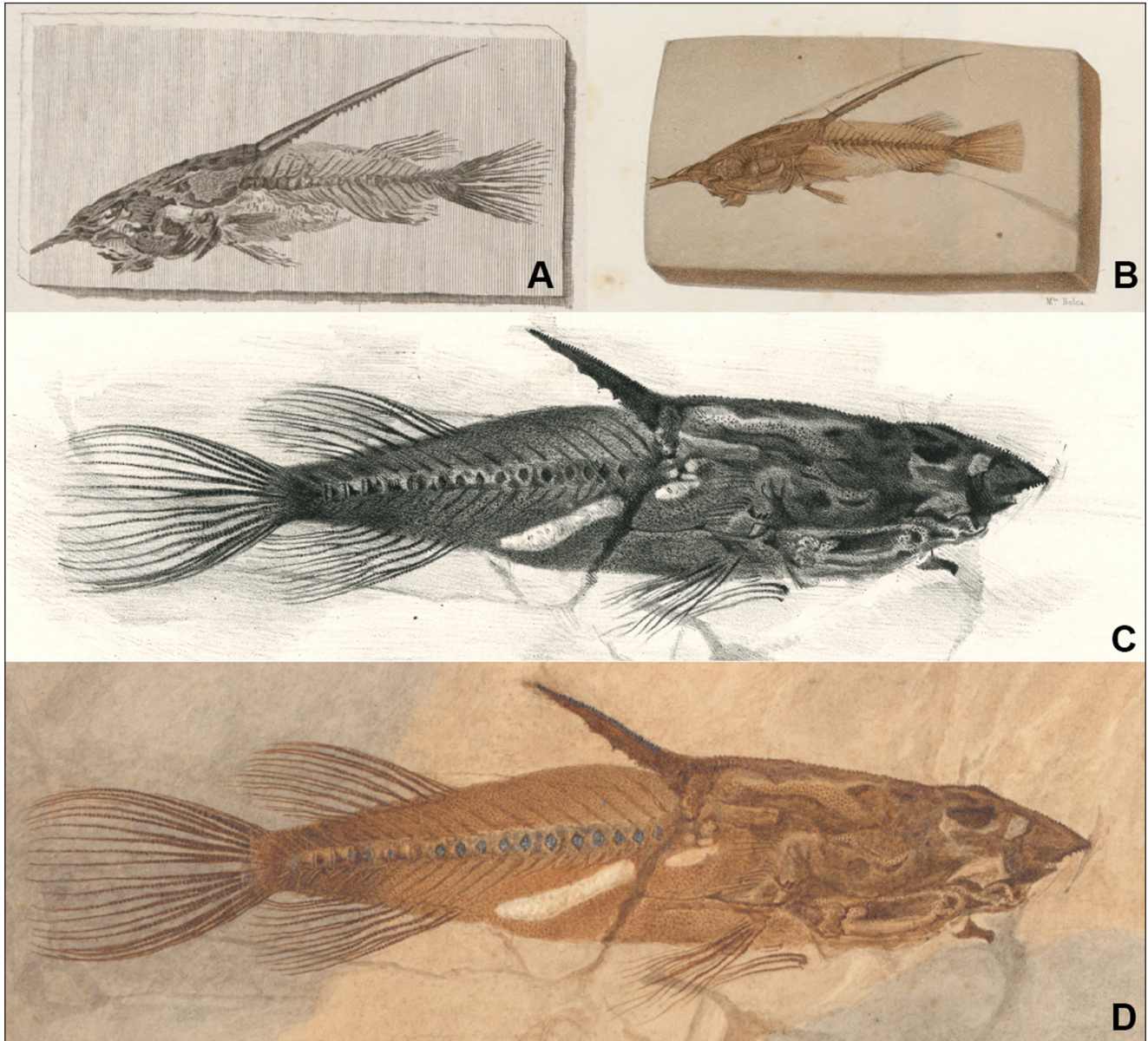
**Diagnosis:** As for the family.

Fig. 2 - *Rhamphosus rastrum* (Volta, 1809); A) drawing of the lost syntype (MHNH F.BOL33) figured in the "Ittiolitologia Veronese" (Volta 1809); B) drawing of the lost syntype (MHNH F.BOL33) figured in the fourth volume of the "Recherches sur les Poissons Fossiles" (Agassiz 1839). *Rhamphosus biserratus* Bassani, 1876; C) drawing of the holotype (MGPPD 8879-8880) figured by Bassani (1876); D) XIX century watercolor drawing of the holotype (MGPPD 8879-8880) housed in the Biblioteca di Geoscienze of the Università degli Studi di Padova.

**Remarks.** The skeletal anatomy of the recognized species is rather conservative, and the main interspecific differences are related to the general physiognomy and relative development of the rostrum, elongation of the dorsal-fin spine, and other morphometric and meristic features. Therefore, the osteology of the type species is described herein.

**Composition.** *Rhamphosus biserratus* Bassani, 1876; *Rhamphosus bloti* n. sp.; *Rhamphosus brevirostris* n. sp.; *Rhamphosus longispinatus* n. sp.; *Rhamphosus rastrum* (Volta, 1809); *Rhamphosus rosenkrantzi* Nielsen, 1960; *Rhamphosus tubulirostris* n. sp.

**Nomenclatural remarks.** The name *Rhamphosus* was created by Agassiz in a review of the fishes of Bolca illustrated and described by Volta in the "Ittiolitologia veronese" (Volta 1796-1809). Such Agassiz's paper was published twice in the same year in French and German. The French version appeared as offprint of the fourth "livraison" (instalment) of the monumental "Recherches sur les poissons fossiles" (Agassiz 1835a), while the German version was published in the journal "Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde" (Agassiz 1835b). We were un-

able to determine which of the two publications has priority, but fortunately it did not affect the establishment of the correct year of institution of *Rhamphosus* (Agassiz 1835a, b). *Rhamphosus* has been erected by indication (Art. 12.2.7 of the ICZN Code 1999) referring to the specimen originally figured by Volta as *Uranoscopus rastrum* (Volta 1796-1809: pl. 5, fig. 4) and renamed by Agassiz "*Rhamphosus aculeatus* Ag." (Agassiz 1835a, b). Agassiz attributed to himself the paternity of the specific epithet "*aculeatus*" already coined for the same Volta's specimen by de Blainville, who renamed it "*Centriscus aculeatus*" (de Blainville 1818: 339). *Centriscus aculeatus* has been erected by de Blainville (1818) explicitly and uniquely referring to the specimen figured by Volta (1796-1809: pl. 5, fig. 4; Fig. 2A). *Centriscus aculeatus* de Blainville, 1818 and *Rhamphosus aculeatus* Agassiz, 1835 share therefore the same name-bearing type and are to be considered objective synonyms (see the glossary of ICZN Code 1999).

Agassiz introduced some confusion using two different spellings of the genus ("*Rhamphosus*" and "*Ramphosus*") in the same works (e.g., Agassiz 1835a, b). He introduced the genus for the first time using "*Rhamphosus*" (Agassiz 1835a: p. 4 and Agassiz 1835b: p. 292), but in the subsequent pages of both papers both spellings were used. "*Ramphosus*" is reported at p. 21 in Agassiz (1835a), whereas at p. 39 "*Rhamphosus*" was used again. Similarly, in Agassiz (1835b) "*Rhamphosus*" occurs at p. 303, whereas "*Ramphosus*" was used at p. 314. In the volume IV of the text of the "Recherches", Agassiz uses both spellings. In the volume IV of the plates of the "Recherches", in which the fossil is illustrated, the spelling is *Rhamphosus* (Agassiz 1839: pl. 32, fig. 7; Fig. 2B). Based on what we observed in the cited papers, the original spelling of the name (sensu Art. 32 of ICZN Code 1999) is "*Rhamphosus*" and not "*Ramphosus*", which should be regarded as a lapsus calami or a printer's error propagated throughout the text. In any case, in the "Nomenclator Zoologicus" (Agassiz 1842-1846) *de facto* Agassiz acted as first reviser of spelling (sensu Art. 24.2.4 of ICZN Code 1999). Agassiz (1839) explained the etymology of this generic name from the Greek ῥάμφος (=rostrum) using the spelling "*Rhamphosus*". The initial misspelling of Agassiz has been perpetrated by some late authors and hence it is not uncommon in the literature to find the genus name spelled as "*Ramphosus*" (e.g., Berg 1947; Nielsen 1960; Pietsch 1978; Sorbini 1983; Carnevale 2020).

## *Rhamphosus rastrum* (Volta, 1809)

Figs. 3-8, 10A-11A

+1809 *Uranoscopus rastrum*; Volta, p. 22, pl. V, fig. 4.
1818 *Centriscus aculeatus*; de Blainville, p. 339.
1839 *Rhamphosus aculeatus* Ag.; Agassiz, pl. 32, fig. 7.
1842 *Ramphosus aculeatus* Ag.; Agassiz, p. 270.
1856 *Rhamphosus aculeatus* Ag.; Bronn, p. 698, pl. XLII⁵, fig. 2.
1848 *Rh. aculeatus* Ag.; Giebel, p. 99.
1888 *Rhamphosus aculeatus* Agass.; Vaillant, p. 339.
?1888 *Rhamphosus*; Woodward, p.39.
1901 *Rhamphosus aculeatus* (Blainville); Woodward, p. 377.
v1983 *Ramphosus aculeatus* (de Blainville); Sorbini, pl. 67 (non pl. 68 = *Rhamphosus brevirostris* n. sp.).

**Type series:** The original type series consists of the three specimens cited by Volta (1796-1809, p. 23), among which the author described and illustrated only one syntype (Volta 1796-1809: pl. V, fig. 4; Fig. 2A), originally pertaining to the "Gabinetto Bozziano" and later acquired by the Museum National d'Histoire Naturelle, Paris with several other fishes from Bolca. The two unfigured syntypes are untraceable and the syntype MNHN F.BOL33 (former 10919), figured also by Agassiz (1839), (Fig. 2B) is lost since the earliest part of 1990s and could not be traced (Alan Pradel pers. comm.). For this reason, we designate herein a neotype for *Rhamphosus rastrum* (Volta 1809).

**Neotype:** MCSNV T.286 (Figs. 3A-8, 10A, 11A), a complete specimen from the Pesciara site is designated herein as a neotype of *Rhamphosus rastrum* (Volta 1809). We designate this specimen as neotype due to its remarkable completeness and provenance from the locality of the original type series. Moreover, the selected neotype exhibits all the morphological characters of *R. rastrum*, it is consistent with the original illustration by Volta (1809) and allows to better define the diagnostic features of the species. In T.286 the head is intact as is the rest of the body, the fins are complete and even the ornamentation of the rostrum and cranial armor shows the complete pattern of minute tubercles and indentations.

**Referred material:** MCSNV IG.135681-135682, an incomplete articulated skeleton measuring 39.1 mm SL, in part and counterpart; MCSNV IG.135683, an incomplete articulated skeleton; MCSNV IG.186660, an incomplete articulated skeleton; MCSNV T.1002, a partially complete and modified articulated skeleton; MCSNV T.1003, a partially complete articulated skeleton measuring 52.6 mm SL; MCSNV VII C.11-12, a partially complete articulated skeleton measuring 50.5 mm SL, in part and counterpart; CMC 38 an incomplete articulated skeleton; MCC 19.1513 an incomplete and modified articulated skeleton; NHMUK P.5125, an incomplete articulated skeleton; NHMUK P.17494, a partially complete articulated skeleton measuring 59.3 mm SL; NHMUK P.17495, a partially complete articulated skeleton measuring 54.5 mm SL.

**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).

**Original diagnosis:** "*Uranoscopus* pinna dorsali priori uniradiata: radio osseo validissimo longitudine corporis, denticulato" (from Volta 1796-1809).

**Emended diagnosis:** A small-sized *Rhamphosus* species (less than 60 mm SL) characterized by the following combination of features: remarkably elongate dorsal-fin spine (between 50 and 60% SL), steeply inclined backward, extending posteriorly to the base of the caudal fin; rostrum well-developed (between 38.9 and 45.1% of SL) and distally pointed, ornamented with minute tubercles arranged in discrete rows; caudal fin with six-eight dorsal and six-seven ventral procurrent rays; first dorsal fin with three-four rays; pectoral fin up to 14 rays.
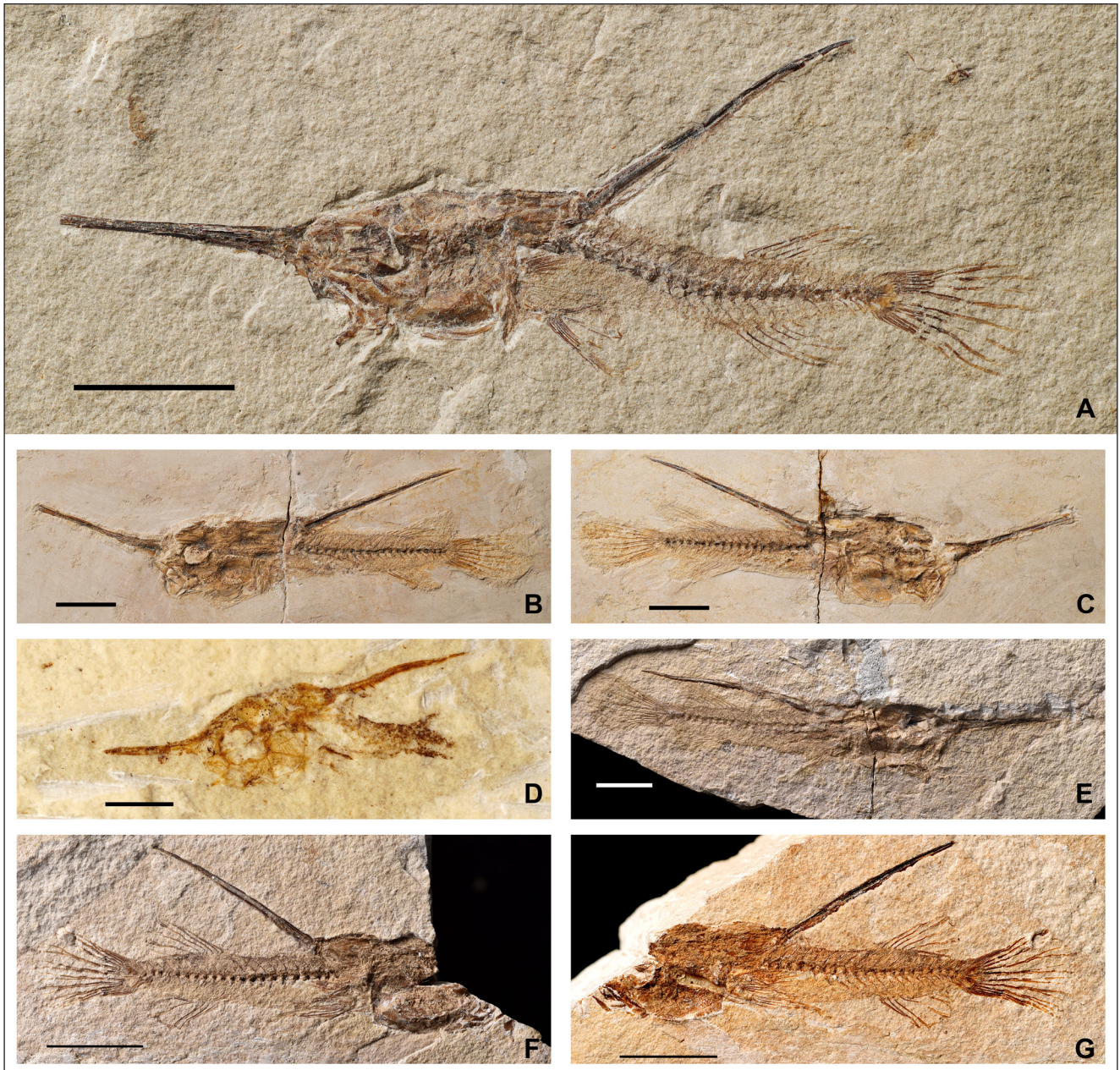
Fig. 3 - *Rhamphosus rastrum* (Volta, 1809), A) lateral view of the neotype MCSNV T.286. Lateral view of B) MCSNV VII C.11; C) MCSNV VII C.12; D) CMC 38; E) MCSNV T.1003; F) MCSNV IG.135681; G) MCSNV IG.135682. Scale bars = 10 mm (A, B, C, E, F, G). Scale bar = 2 mm (D).

**Description.** The peculiar body physiognomy of *Rhamphosus rastrum* is due to the combination of a large, armored head bearing a greatly elongate nasal rostrum and of a massive dorsal-fin spine with serrated posterior margin. The body is moderately depressed dorso-ventrally. The mouth is ventral, tubular, highly protrusible, with a moderately large gape, roofed by the pointed rostrum formed by the coalesced nasal bones. The caudal fin is gently rounded. The second dorsal fin originates in the posterior fourth of the body, the predorsal distance (PD2) ranges from 71.9 to 75.2% of SL,

except for the juvenile specimen (CMC 38; Fig. 3D) in which the second dorsal-fin origin is placed in close proximity to the caudal fin, thereby suggesting a delayed allometric development of the caudal peduncle (see Tab. 1). The opposite second dorsal and anal fins are compact, with the length of their bases not exceeding 12.3% SL (see Tab. 2).

The neurocranium (Figs. 5-6) occupies most of the cranial armor. All the dorsal and lateral neurocranial elements consist of thick bony plates showing a distinct ornamentation on their outer surface, with spines or tubercle-bearing ridges

| | *R. rastrum* | *R. biserratus* | *R. bloti* n. sp. | *R. brevirostris* n. sp. | *R. longispinatus* n. sp. | *R. tubulirostris* n. sp. | *R. rosenkrantzi* |
|---|---|---|---|---|---|---|---|
| SL (mm) | 36.9-59.3 | 143.3 | 71.4-88.3 | 82.1-84.5 | 22.7-42.9 | 51.4 | 25.5 |
| RL | 38.9-45.1 | 4.4 | 22-29.1 | 20.4-21.4 | 45.4-69 | 9.8 | 47.5 |
| PA | 72.6-74.8 | 73.6 | 62.6 | 68.3-73.8 | 71.6-79.1 | 65.1 | 72.9 |
| PD2 | 71.9-75.2 | 74 | 63.6 | 69.1-73.7 | 69.8-79.6 | 63.5 | 72.2 |
| HDS | 50-60.2 | 20.5 | 47.8-49.7 | 46.3-46.5 | 57.9-79.1 | 46.1 | 76.1 |
| DFL2 | 11.5-12.3 | 13.5 | 10.2 | 12.5- 12.8 | 10.3-13.2 | 31.3 | 13.3 |
| AFL | 11.3-12.3 | 13.2 | 10.9 | 12.1-13.5 | 10.2-13.3 | 28.1 | 12.9 |
| PRO | 44.4-49.9 | 10.8 | 29.6-35.4 | 27-27.8 | 51.8-77.1 | 14.4 | 56.5 |
| BD | 13.1-18.1 | 22.6 | 15-15.2 | 15.7-20.6 | 12.5-19.4 | 12.7 | 12.6 |
| CP | 6.5-9.2 | 9.5 | 5.6 | 13.1-15 | 6.8-12.1 | 8.6 | 10.2 |
| D1D2D | 17.1-22.2 | 22.6 | 18.5 | 22.6-23.8 | 18.3-23.5 | 16.8 | 25.1 |
| BAS | 5.2-10.5 | 15.1 | 4.2 | 11.2-13.2 | 5.8-10.6 | 5.2? | 5.9 |

Tab. 1 - Summary of the most relevant measurements of the various species of the genus *Rhamphosus*. Values are as percentage of SL.

forming a dense reticulate pattern that covers their entire surface. These ornamentations are more evident along the edges of the bones, where they appear as serrations. The two contralateral nasals are fused into an elongate rostrum, whose length ranges between 38.9 and 45.1% of SL. The base of the rostrum is robust, and it gradually tapers anteriorly becoming slightly spatulate distally and showing a rather deep horizontal concavity along its anterior border (Figs. 3A-B-C, 6, 10A). It is characterized by regularly spaced longitudinal ridges that are variously ornamented with tubercles and spines. The ridges that form lateral borders of the

rostrum bear a continuous and dense series of small retrorse spines. The upper margin of the rostrum is characterized by small, fine, and dense serrations towards the anterior extremity, which in turn become coarser and thicker, almost thorn-like, close to the base of the rostrum; spines are also present along the lower margin of the rostrum especially in the region just anterior to the mouth (Figs. 3A, 5, 10A). There is a broad concavity along the ventral surface of the proximal portion of the rostrum, which probably represents the outer border of a cavity in which the jaws were allocated when the mouth was closed. The nasals articulate poste-

| | MCSNV T.286 | MCSNV IG.135681-135682 | MCSNV T.1003 | MCSNV VII C.11-12 | NHMUK P.17494 | NHMUK P.17495 | Range |
|---|---|---|---|---|---|---|---|
| SL (mm) | 36.9 | 39.1 | 52.6 | 50.5 | 59.3 | 54.5 | 36.9-59.3 |
| TL (mm) | 61.5 | ? | 86.1 | 80.7 | 88.4 | 88.1 | 61.5-88.4 |
| HL | 34.3 | 34.3 | 30.5 | 30.5 | 32.2 | 31.9 | 30.5-34.3 |
| RL | 40.2 | ? | 41.7 | 40.2 | 45.1 | 38.9 | 38.9-45.1 |
| PP | 36.6 | 35.9 | 36.5 | 39.6 | 34.9 | 31.9 | 31.9-39.6 |
| PA | 74.8 | 72.6 | 72.6 | 74.1 | ? | 74.3 | 72.6-74.8 |
| PD1 | 46.9 | 48.9 | 47 | 50.3 | 48.1 | 46.6 | 46.6-50.3 |
| PD2 | 75.1 | 72.5 | 71.9 | 74.7 | ? | 75.2 | 71.9-75.2 |
| PV | 42.3 | 39.3 | 39.5 | 37 | 36.5 | 38.5 | 36.5-42.3 |
| HDS | 50.3 | 50 | 60.2 | 56.9 | 54.9 | 53.4 | 50-60.2 |
| DFL2 | 12.2 | 11.5 | 11.8 | 11.5 | ? | 12.3 | 11.5-12.3 |
| AFL | 11.4 | 12.2 | 12.3 | 11.3 | ? | 11.5 | 11.3-12.3 |
| VFL | 19.8 | 23.1 | 18.1 | 19.4 | 12.3? | 17.7 | 17.7-23.1 |
| PFL | 14.1 | 17.5 | 13.9 | 14.1 | 11 | 9.5 | 9.5-17.5 |
| PRO | 47.2 | ? | 47.5 | 49.9 | 48.4 | 44.4 | 44.4-49.9 |
| O | 10.3 | ? | 7.8 | 8.7 | 9.1 | 9.9 | 7.8-10.3 |
| POO | 18.2 | 19 | 15.2 | 15.4 | 18.6 | 17.1 | 15.2-19 |
| RPT | 18.7 | 21 | 20 | 20 | 17.1 | 18.5 | 17.1-21 |
| DRL2 | 18.3 | 17.6 | 17.1 | 21.2 | 16.9 | 19.6 | 17.1-21.2 |
| ARL | 17.4 | 14.8 | 12.4 | 14.5 | 10.5 | 13.4 | 10.5-17.4 |
| BD | 18.1 | 15.7 | 16 | 14.1 | ? | 13.1 | 13.1-18.1 |
| CP | 8.9 | 9.2 | 6.5 | 7.9 | 6.7 | 7.3 | 6.5-9.2 |
| D1D2D | 22.2 | 21.7 | 18.3 | 20.4 | 17.1 | 19 | 17.1-22.2 |
| BAS | 5.2 | 5.5 | 7.7 | 10.5 | 8.9 | ? | 5.2-10.5 |

Tab. 2 - Measurements of *Rhamphosus rastrum* (Volta, 1809). Values are as percentage of SL.
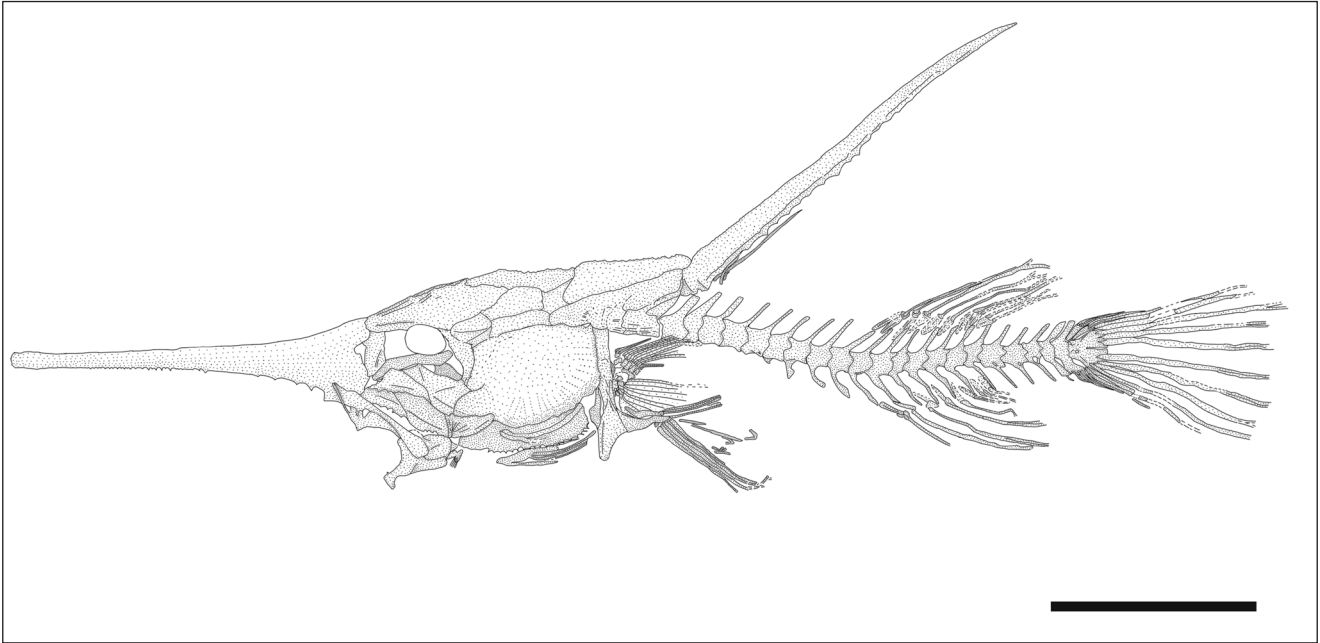
Fig. 4 - *Rhamphosus rastrum* (Volta, 1809), neotype MCSNV T.286: interpretative reconstruction. Scale bar = 10 mm.

riorly with the lateral ethmoids and posterodorsally with the mesethmoid and the frontals. The olfactory capsules are bordered by the nasals and lateral ethmoids. The frontals are the largest bones of the skull roof. The outer surface of the frontals exhibits some finely tuberculated longitudinal ridges. Spines can be recognized along the lateral margins of the frontals with some evident spines close to the edge of the orbit (Figs. 5-6). The frontals articulate anteriorly with the nasals, anteriorly and anterolaterally with the lateral ethmoids, postero-laterally with the sphenotic and posteriorly with the parietals and supraoccipital. The mesethmoid is a small median bone that articulates with the nasals anteriorly and the frontals posteriorly. The lateral ethmoid is a columnar bone with a constriction at its mid-height, forming the anterior border of the orbit. The lateral ethmoid articulates posterodorsally with the frontal, anteriorly with the nasal rostrum and ventrally with the lachrymal. The parietals are polygonal in outline and are separated from each other by the relatively large median supraoccipital. Each parietal articulates anteriorly with the frontal, laterally with the sphenotic and pterotic, medially with the supraoccipital and posteriorly with the epioccipital. The supraoccipital is a moderately large median bone that articulates anteriorly with the frontals, laterally with the parietals and epioccipitals and posteriorly with a large and ovoid rayless pterygiophore. The

sphenotic is triangular in shape, showing a gently curved anterior profile. The sphenotic articulates anterolaterally with the frontal, and posteriorly with the parietal and the pterotic. The pterotic is subrectangular in outline; it articulates anteriorly with the sphenotic, laterally with the parietal, posteriorly with the epioccipital and the posttemporal. The epioccipital articulates anteriorly with the parietal, medially with the supraoccipital, and laterally with the posttemporal. The posttemporals are notably expanded posteriorly and are consolidated with the neurocranium. The parasphenoid is stout and well-ossified, with an almost straight ventral margin. The anterior portion of the prootic is partially exposed in several specimens.

The lachrymal is a quadrangular bone with a thickened and serrated ventral border. It articulates dorsally with the lateral ethmoid, anteriorly with the nasal rostrum and posteriorly with the second infraorbital bone. The second and third infraorbital bones border the lower portion of the orbit; both these bones are closely associated to the expanded preopercle.

The premaxilla (Fig. 5) has a notably elongate ascending process, a slightly spatulate and vertically oriented articular process and a broad postmaxillary process. The alveolar process bears numerous small and delicate teeth (as shown in MSCNV T.286). The maxilla is rather elongate and distally expanded,
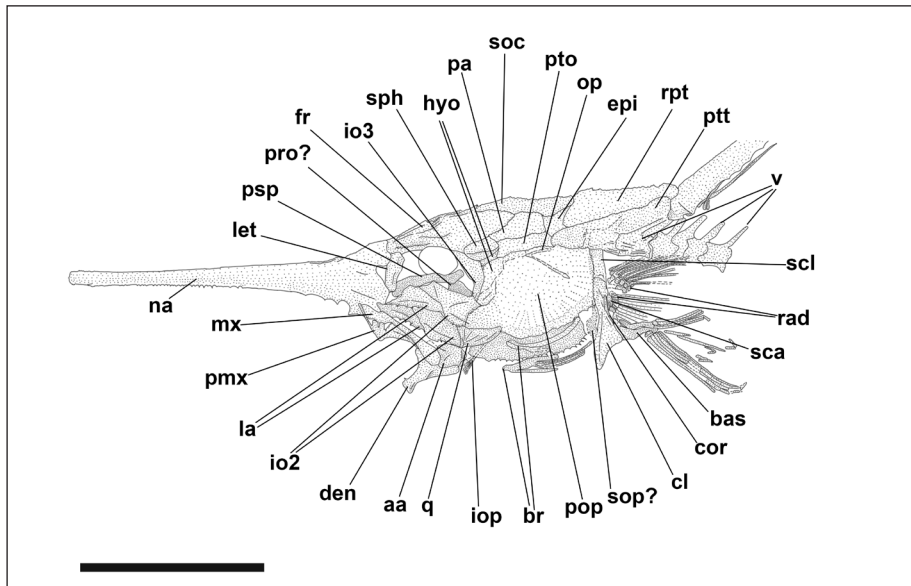
Fig. 5 - *Rhamphosus rastrum* (Volta, 1809), neotype MCSNV T.286: interpretative reconstruction of the neurocranium (lateral view). Scale bar = 10 mm.
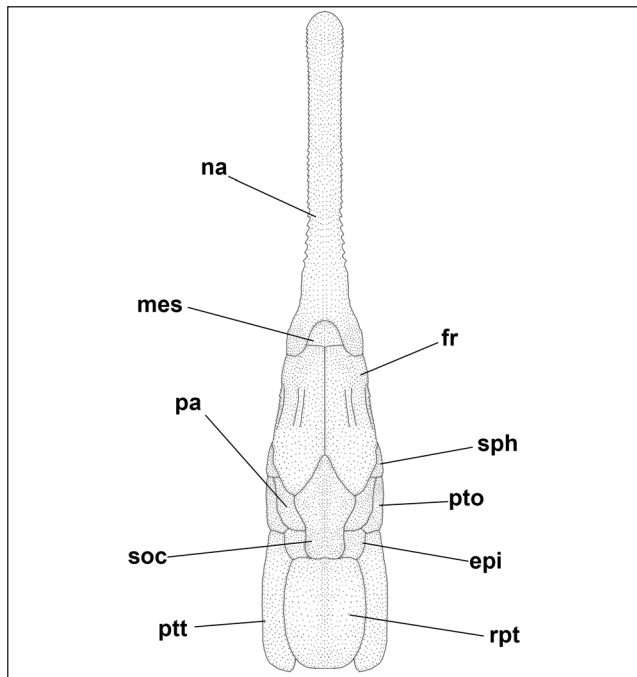


Fig. 6 - *Rhamphosus rastrum* (Volta, 1809), neotype MCSNV T.286: interpretative reconstruction of the neurocranium (dorsal view).

with a straight dorsal margin and a gently convex posterior half of the ventral margin. The dentary is well ossified, with an almost straight anterior margin, a moderately developed coronoid process, and a concave ventral margin. Small and delicate conical teeth similar to those of the premaxilla can be observed in certain specimens. The anguloarticular is anteroposteriorly compact.

The structure and composition of the suspensorium are difficult to define. The pterygoids and the palatine are difficult to recognize and were probably cartilaginous or almost completely absent in origin. The hyomandibula is broadly expanded dorsally and bears two articular heads for the neurocranium and a short opercular process. The quadrate is subtriangular in shape and bears a small articular condyle. The symplectic is scarcely recognizable.

The opercular series of *R. rastrum* is greatly expanded and covers a large part of the posteroventral portion of the head (Figs. 3A, 4, 5). All the opercular bones exhibit ornamentations similar to those of the bones of the neurocranium. The preopercle is remarkably enlarged, being also expanded medially almost approaching its antimere on the ventral midline of the head. The ventral margin of the preopercle is regularly serrated and its outer surface is extensively ornamented with ridges and pits forming a reticulate pattern similar to that of the neurocranial bones. The interopercle is rod-like and appears to be closely associated to the posterior border of the mandible. The opercle and subopercle are strongly reduced in size and widely separated from the interopercle. The opercle is very small, V-shaped, with a horizontal dorsal arm and an oblique ventral arm. The subopercle is narrow and almost vertical.

The hyoid bar appears to be short and stout and is partially exposed in MCSNV T.286. There are probably five thin and distally pointed branchiostegal rays. The elements of the branchial arches are not clearly recognizable.

The vertebral column (Figs. 4, 7) seems to comprise 26 vertebrae (?13 abdominals plus 13 cau-

Fig. 7 - *Rhamphosus rastrum* (Volta, 1809), neotype MCSNV T.286: interpretative reconstruction of the postcranial skeleton. Scale bar = 10 mm.
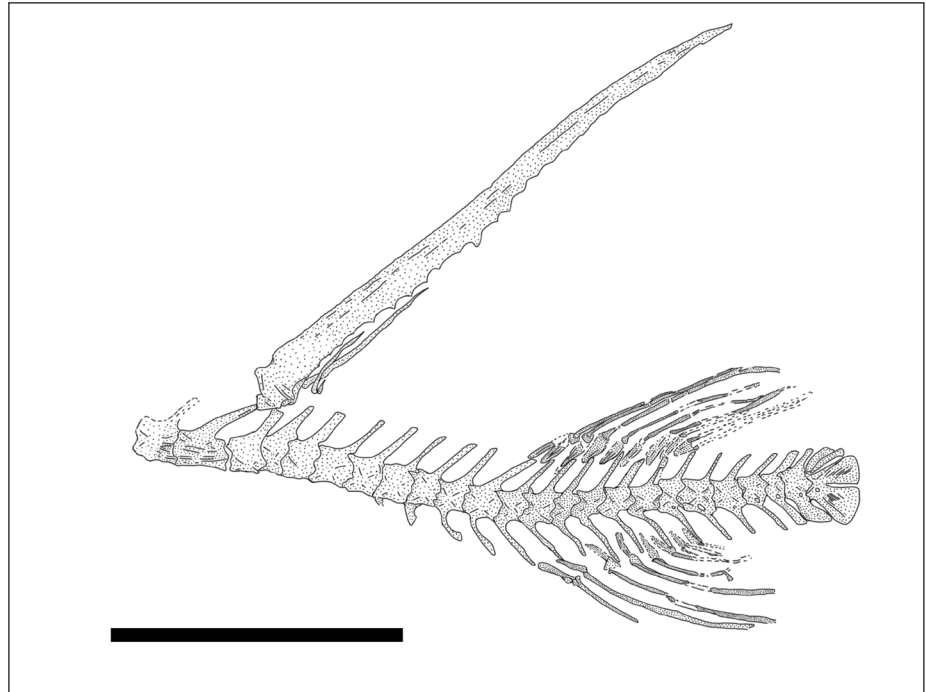


dal). Overall, the vertebral centra are rectangular, longer than high. The anterior centra are not clearly exposed, in large part covered by the posttemporal and other cranial bones, but they appear to be elongate compared to the subsequent elements. The neural arches and spines of the anterior abdominal vertebrae are anteroposteriorly expanded. The neural spines of the six posterior abdominal vertebrae as well as those of the caudal vertebrae are slender, straight, and distally pointed, obliquely emerging in the posterior third of each centrum. The haemal spines are slender. The haemal arches and spines originate ventrally from the anterior border of each caudal centrum. Dorsal prezygapophyses are well developed and partially overlap the neural arch of the preceding vertebra. The four posterior abdominal vertebrae bear thick parapophyses gradually increasing in size posteriorly. There is no evidence of ossified ribs. Epineurals are visible in the posterior abdominal and anterior caudal vertebrae where they articulate with the base of the parapophyses or of the haemal arch.

The neural and haemal spines of the second and third preural vertebrae are fused to their respective centra and are notably expanded anteroposteriorly, especially those of the second one (Fig. 8). The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two dorso-ventrally symmetric triangular plates separated by a deep and narrow median notch that
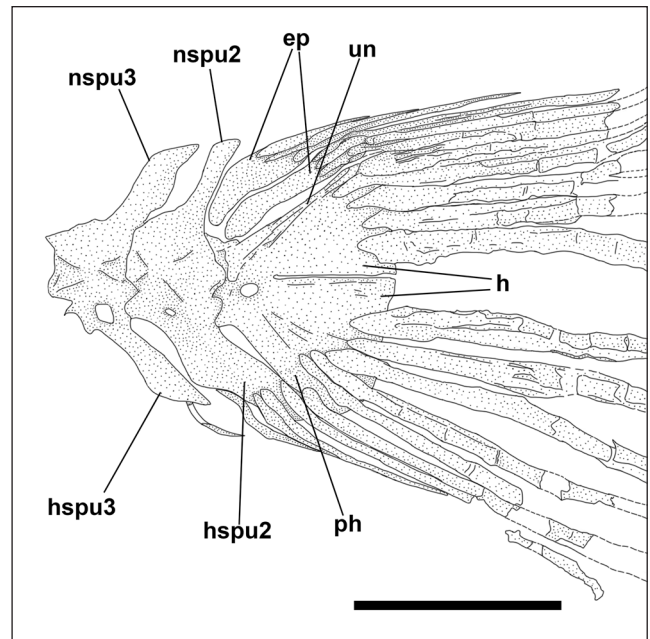


Fig. 8 - *Rhamphosus rastrum* (Volta, 1809), neotype MCSNV T.286: interpretative reconstruction of the caudal skeleton. Scale bar = 2 mm.

separates the epaxial and the hypaxial lobes from each other. The parhypural is consolidated with the hypural plate. There are two large epurals and a pair of uroneurals fused to the epaxial hypural plate (Fig. 8).

The caudal fin contains ten (I, 4-4, I) principal rays plus six to eight dorsal and six or seven ventral procurrent rays.

There are two dorsal fins separated by a large gap (Figs. 4, 7). The first dorsal fin consists of a hypertrophied and robust spine, followed by three or four slender and flexible spines. The spine is massive and greatly elongate, its length ranges between 50 and 60.2% of SL, extending posteriorly up to the base of the caudal-fin rays; overall, it is steeply inclined backwards and has a slightly curved apex. The anterior surface of the spine bears a series of regularly spaced longitudinal ridges ornamented by a dense series of minute tubercles, while its posterior margin is irregularly serrated, with thick and stout spines decreasing in size towards the apex. The massive dorsal-fin spine inserts over the nape, and its basal portion articulates with what we interpret as a rayless pterygiophore. This median bone is ovoid in outline and closely associated to the dermal neurocranial elements, showing a similarly ornamented outer surface. The posterior median portion of the rayless pterygiophore forms a sort of locking mechanism for the basal portion of the dorsal-fin spine. The pterygiophores associated with the massive dorsal-fin spine and the following flexible spines are partially recognizable in MCSNV IG.135682. The anterior dorsal-fin pterygiophore is large and robust, bearing a relatively short anterior process underlying the articulation between the spine and the rayless pterygiophore. The successive pterygiophores are notably smaller and weakly ossified.

The second dorsal fin inserts just above the third caudal vertebra and includes nine soft rays supported by nine feebly ossified pterygiophores. The first ray is the shorter of the series and is unbranched distally. The length of the rays increases gradually up to third or fourth element, decreasing posteriorly.

The anal fin is opposite to the second dorsal fin and seems to comprise nine rays supported by eight delicate and weakly ossified pterygiophores. Like in the second dorsal fin, the length of the rays increases posteriorly up to the third or fourth and then decreases posteriorly. The first anal-fin ray is unbranched and apparently unsegmented.

The pectoral fin inserts at the midheight of the body flanks and, based on the orientation of the rays, it probably was subhorizontal or slightly oblique in origin (Figs. 4-5). The fin contains up to 14 relatively short unbranched rays. The supracleithrum is oblong and laminar. The cleithrum is large, vertically oriented, and oblong in outline. The scapula is relatively small and quadrangular in outline. The scapular foramen appears to be anteriorly bordered by the cleithrum. The coracoid is delicate and slender. There is no postcleithrum. There are four short pectoral-fin radials that articulate with the pectoral-fin rays except for the two dorsalmost that articulate directly with the scapula.

The pelvic fins consist of a single slender spine plus five rays, longer than those of the pectoral fins. The pelvic fins originate just behind the pectoral-fin insertion. The basipterygium is relatively short with a poorly developed posterior process.

The trunk is entirely covered with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate. The lateral-line series is not evident in the available material.

### *Rhamphosus biserratus* Bassani, 1876
Figs. 9, 10B-11B

+v1876 *Rhamphosus biserratus* Bassani, 1876, p. 151, pl. II, fig. 3.
  1901 *Rhamphosus biserratus* Bassani; Woodward, p. 378.
 v1922 *Rhamphosus biserratus* Bassani; D'Erasmo, p. 89.

**Holotype (by monotypy):** MGPPD 8879-8880, a partially complete articulated skeleton measuring 143.3 mm SL, in part and counterpart.

**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).

**Emended diagnosis:** A large-sized *Rhamphosus* species showing the following combination of features: thick and robust first dorsal-fin spine steeply inclined backward, reaching about one fifth of SL (20.5% of SL), and extending posteriorly not beyond the insertion of the second dorsal fin, bearing a tuberculate anterior edge and serrated posterior edge; blunt and short rostrum (length 4.4% of SL), ornamented with minute tubercles and serrations; caudal fin with seven dorsal and seven ventral procurrent rays; first dorsal fin with a large spine followed by two thin and flexible spines; pectoral fin with 13 rays; second dorsal-fin origin in the posterior fourth of the body with a predorsal distance (PD2) reaching 74% of SL; second dorsal and anal fins opposite to each other, with their base lengths not exceeding 13.5% of SL (see Tab. 3).

**Description.** *Rhamphosus biserratus* is characterized by having a large size (143.3 mm SL) and rather deep body (body depth, BD: 22.6% of SL). The second dorsal fin originates in the posterior fourth of the body, with the predorsal distance (PD2) reaching 74% of SL. The opposite second dorsal and anal fins are compact, with the length of their bases not exceeding 13.5% SL (see Tab. 3).

The nasals are fused into a median short, compact, and blunt rostrum, whose length reaches
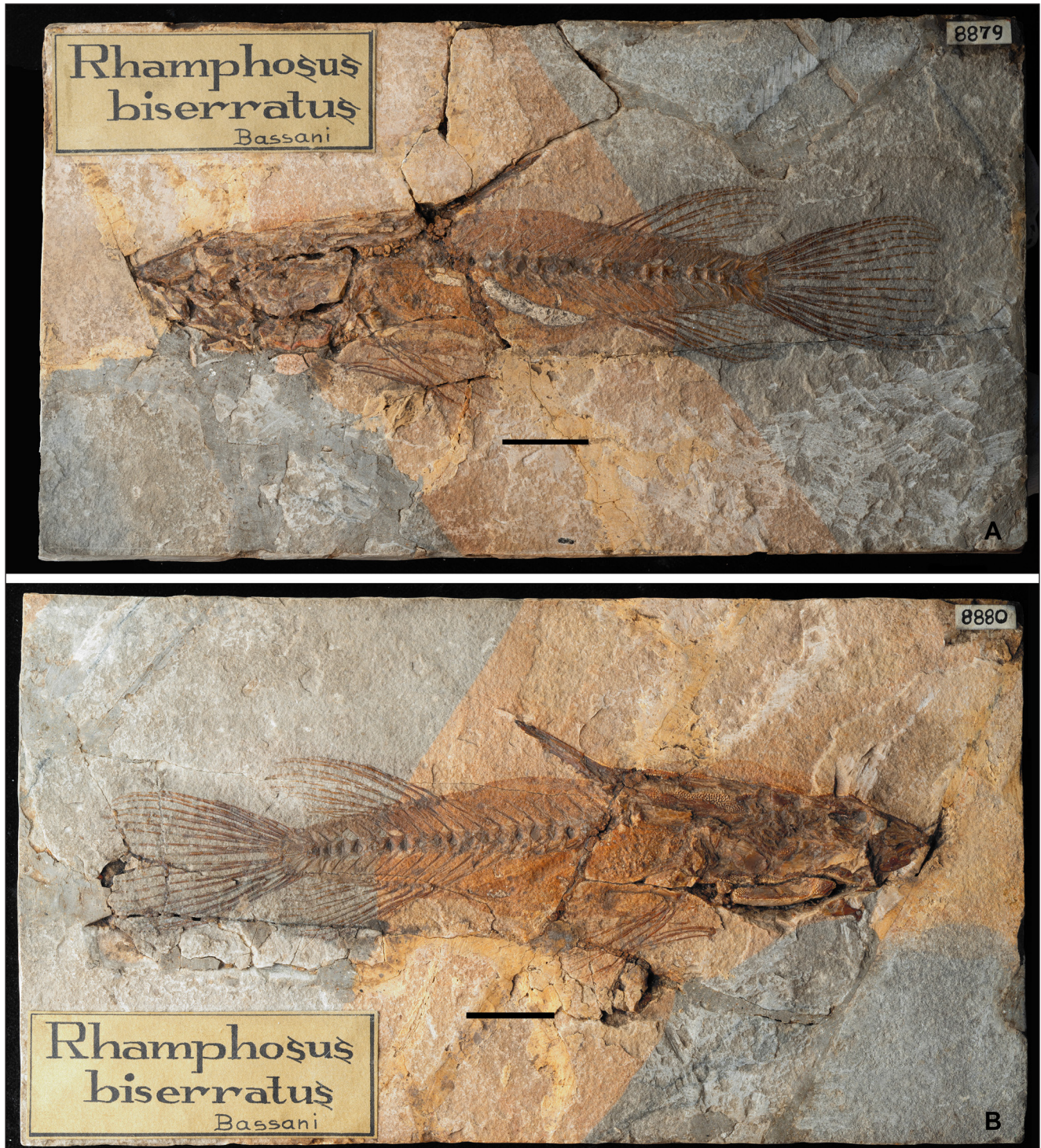
Fig. 9 - *Rhamphosus biserratus* Bassani, 1876, holotype MGPPD 8879-8880: lateral view of the holotype in part and counterpart. A) MGPPD 8879; B) MGPPD 8880. Scale bars = 20 mm.

4.4% of SL. The base of the rostrum is massive and robust. The ornamentation of the outer surface of the rostrum consists of tubercles and serrations dorsally, and spines ventrally, which are more developed in the basal region of the rostrum just above the mouth (Figs. 9-10B). The premaxilla bears an elongate ascending process, a vertically oriented, short, and enlarged articular process, and a slightly expanded postmaxillary process. Due to inadequate preservation, it is not possible to determine whether jaw teeth are present or not.

The vertebral column seems to comprise 26 vertebrae (?12+14), of which only 22 are clearly exposed. The four posterior abdominal vertebrae
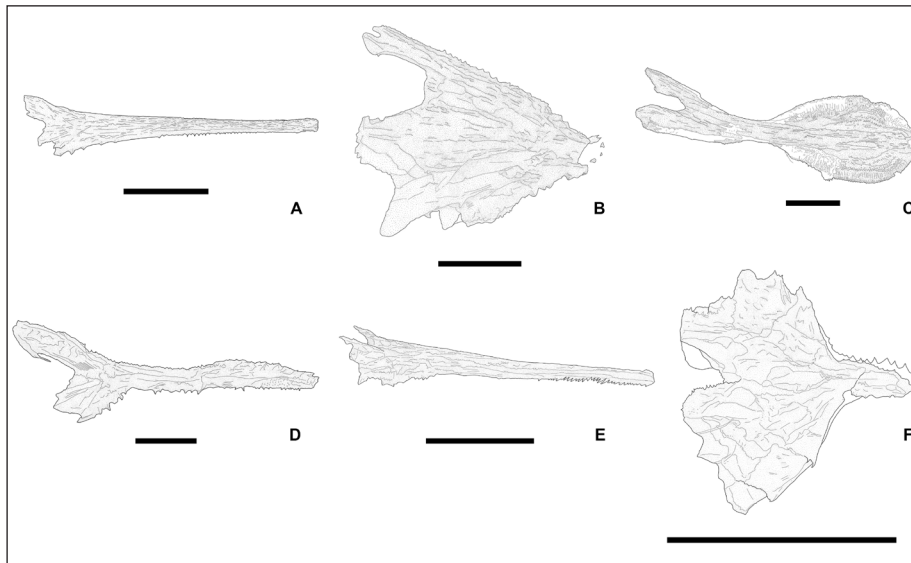
Fig. 10 - Interpretative reconstructions of the nasal rostrums of the *Rhamphosus* species. A) *Rhamphosus rastrum* (Volta, 1809); B) *Rhamphosus biserratus* Bassani, 1876; C) *Rhamphosus bloti* n. sp.; D) *Rhamphosus brevirostris* n. sp.; E) *Rhamphosus longispinatus* n. sp.; F) *Rhamphosus tubulirostris* n. sp. Scale bars = 5 mm.

|  | MGPPD 8879-8880 |
|---|---|
| SL (mm) | 143.3 |
| TL (mm) | 188.4 |
| HL | 31.9 |
| RL | 4.4 |
| PP | 35.5 |
| PA | 73.6 |
| PD1 | 46.4 |
| PD2 | 74 |
| PV | 33.1 |
| HDS | 20.5 |
| DFL2 | 13.5 |
| AFL | 13.2 |
| VFL | 23.6 |
| PFL | 11.5 |
| PRO | 10.8 |
| O | 6 |
| POO | 18.7 |
| RPT | 22 |
| DRL2 | 23.7 |
| ARL | 22.6 |
| BD | 22.6 |
| CP | 9.5 |
| D1D2D | 22.6 |
| BAS | 15.1 |

Tab. 3 - Measurements of *Rhamphosus biserratus* Bassani, 1876. Values are as percentage of SL.

bear thick parapophyses, gradually increasing in size posteriorly. Epineurals are associated with the posterior abdominal and anterior caudal vertebrae.

The caudal skeleton is structurally similar to those of other species of the genus *Rhamphosus*. The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two dorsoventrally symmetric triangular plates separated by a deep median notch. There are two large epurals, a single uroneural fused to the epaxial hypural plate and a parhypural fused to the hypaxial hypural lobe. The neural and haemal spines of the second and third preural vertebrae are greatly expanded antero-posteriorly. This is most evident for the second preural vertebra (see Fig. 9), which

has a broadly expanded and subtriangular haemal spine, contacting the preceding haemal spine anteriorly and the parhypural posteriorly. The caudal fin contains ten principal rays (I,4-4,I) plus seven dorsal and seven ventral procurrent rays. The two dorsal fins are separated by a large gap (22.6% of SL). The first dorsal fin consists of a thick and robust dorsal-fin spine, followed by two thin and flexible spines (Fig. 11B), which can reach half the length of the first spine. The first dorsal-fin spine is massive, its length does not exceed 20.5% of SL, extending posteriorly not beyond the insertion of the first ray of the second dorsal fin. The entire anterior surface of the spine bears numerous longitudinal ridges ornamented with tubercles; few heavy spines gradually decreasing in size distally emerge along the posterior edge of the spine. The dorsal-fin spine inserts over the nape, and its basal portion articulates with an elongate rayless pterygiophore (22% of SL). The pterygiophores associated with the massive dorsal-fin spine and the successive flexible rays are not clearly recognizable in the examined material. The second dorsal fin includes nine rays supported by nine pterygiophores. The anal fin is opposite to the second dorsal fin, and it includes nine rays supported by eight pterygiophores. The pectoral fin contains 13 relatively short, unbranched, and unsegmented rays. The pelvic fins consist of a single slender spine plus five rays, definitively longer than those of the pectoral fins. The basipterygium is notably developed (15.1% of SL), with a greatly elongate and posteriorly expanded posterior process that tapers posteriorly into a pointed end, clearly

Fig. 11 - First dorsal-fin spines of the *Rhamphosus* species. Interpretative reconstructions of: A) *Rhamphosus rastrum* (Volta, 1809); B) *Rhamphosus biserratus* Bassani, 1876; C) *Rhamphosus bloti* n. sp.; D) *Rhamphosus brevirostris* n. sp.; E) *Rhamphosus longispinatus* n. sp.; F) *Rhamphosus tubulirostris* n. sp. Scale bars = 5 mm.
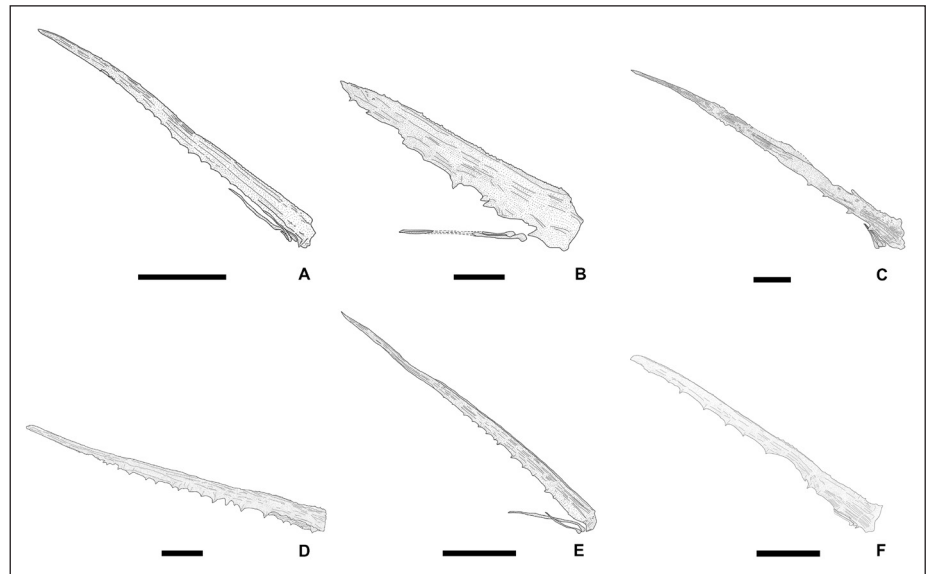
exposed at the level of the dorsal-fin spine insertion (see Fig. 9). As far as the squamation is concerned, the trunk is entirely covered with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate. The lateral-line series is not evident in the specimen.

**Discussion.** *Rhamphosus biserratus* is the largest species of the genus *Rhamphosus* (reaching 143.3 mm SL and 188.4 mm TL). The blunt rostrum emerging from a massive base, characteristic of *R. biserratus,* is the shortest among the *Rhamphosus* species (4.4% of SL). *R. tubulirostris* n. sp. is the only other species besides *R. biserratus* whose rostrum is poorly developed. The ornamentation of the rostrum consists of minute tubercles and spines, with the latter being more pronounced ventrally close to the rostrum base (Fig. 10B). These spines, however, are not as developed as those observed in the small-sized species (*R. rastrum*, *R. longispinatus* n. sp.). Another peculiar trait of *R. biserratus* is its first dorsal-fin spine; it is the shortest and thickest of all the species of the genus (20.5% of SL). As reported above, the relatively short first dorsal-fin spine of *R. tubulirostris* n. sp. reaches more than 46% of SL (see Tab. 1). *R. biserratus* has a considerable body depth (measured behind the dorsal-fin spine), its body being deeper than that of any other *Rhamphosus* species (22.6% of SL; see Tab. 1). The basipterygium in *R. biserratus* is especially developed, being the largest of any other *Rhamphosus* species (15.1% of SL). Its posterior process is greatly elongated and posteriorly expanded, tapering into a thin and pointed end, extending posteriorly up to the level of the first

dorsal-fin spine insertion. As far as the meristics is concerned, *R. biserratus* can be distinguished from its congenerics by having two rays just behind the dorsal-fin spine, 14 caudal vertebrae (feature shared only with *R. tubulirostris* n. sp.), seven dorsal and seven ventral procurrent rays in the caudal fin and 13 unbranched and unsegmented pectoral-fin rays. The subtriangular haemal spine of the second preural vertebra is greatly expanded antero-posteriorly, and the neural spine of the second preural vertebra is also expanded but to a lesser extent.

### *Rhamphosus bloti* n. sp.

Figs. 10C-11C-12

v1980 *Rhamphosus* sp.; Blot, p. 366.

**Holotype:** MCSNV VII C.13-14, a partially complete articulated skeleton measuring 88.3 mm SL, in part and counterpart.

**Paratype:** MCSNV VII C.15-16, a partially complete articulated skeleton measuring 71.4 mm SL, in part and counterpart.

**Etymology:** Species named after the French paleoichthyologist Jacques Blot (1924-1988), who kept separate this morphotype of Rhamphosidae from the hitherto known species of the genus *Rhamphosus* (Blot, 1980).

**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).

**Diagnosis:** A medium-sized *Rhamphosus* species showing the following combination of features: elongated first dorsal-fin spine steeply inclined backward, reaching between 47% and 50% SL and extending posteriorly up to the base of the caudal fin, and bearing an anterior edge with minute tubercles along its lower half and a serrated posterior edge; well-developed rostrum (length between 22% and 29.1% of SL), expanded anteriorly into a large horizontal ovoid structure with extensively ornamented dorsal surface and small and thick serrations along the lateral margins, showing a median deep concavity on its distal tip; caudal fin with at least four dorsal and se-

| | MCSNV VII C.13-14 | MCSNV VII C.15-16 | Range |
|---|---|---|---|
| SL (mm) | 88.3 | 71.4 | 71.4-88.3 |
| TL (mm) | 113.3 | 103.5 | 103.5-113.3 |
| HL | 31.1 | 28.6 | 28.6-31.1 |
| RL | 22 | 29.1 | 22-29.1 |
| PP | 32.3 | ? | 32.3 |
| PA | 62.6 | ? | 62.6 |
| PD1 | 40.5 | 41.3 | 40.5-41.3 |
| PD2 | 63.6 | ? | 63.6 |
| PV | 29.5 | 30.4 | 29.5-30.4 |
| HDS | 47.8 | 49.7 | 47.8-49.7 |
| DFL2 | 10.2 | ? | 10.2 |
| AFL | 10.9 | ? | 10.9 |
| VFL | 14 | 16.1 | 14-16.1 |
| PFL | 11.1 | ? | 11.1 |
| PRO | 29.6 | 35.4 | 29.6-35.4 |
| O | 6.3 | 5.3 | 5.3-6.3 |
| POO | 13.9 | 18.1 | 13.9-18.1 |
| RPT | 20.3 | 19.5 | 19.5-20.3 |
| DRL2 | 15.7 | ? | 15.7 |
| ARL | 17.5 | ? | 17.5 |
| BD | 15.2 | 15 | 15-15.2 |
| CP | 5.6 | ? | 5.6 |
| D1D2D | 18.5 | ? | 18.5 |
| BAS | 4.2 | ? | 4.2 |

Tab. 4 - Measurements of *Rhamphosus bloti* n. sp. Values are as percentage of SL.

ven ventral procurrent rays; first dorsal fin with a large spine followed by three thin and slender spines; pectoral fin with 10-11 rays; second dorsal-fin origin in the posterior fourth of the body with a predorsal distance (PD2) not exceeding 64% of SL; second dorsal and anal fins opposite to each other with their base lengths not exceeding 11% of SL (see Tab. 4).

**Description.** *Rhamphosus bloti* n. sp. exhibits a relatively large size (71.4-88.3 mm SL) coupled with an elongate nasal rostrum characterized by a peculiar discoid outline, and a large first dorsal-fin spine with a tuberculated anterior edge and a serrated posterior edge. The second dorsal fin originates in the posterior fourth of the body, with the predorsal distance (PD2) reaching 63.6% of SL. The opposite second dorsal and anal fins are compact, with the length of their bases not exceeding 11% (see Tab. 4). The nasals are fused into a median elongate rostrum, whose length ranges between 22% and 29.1% of SL. The base of the rostrum is rather thick, then it is horizontally expanded into an ovoid structure with a deep concavity along its anterior border (Figs. 10C, 12A-C-D) and extensively ornamented along its dorsal surface and bearing small

and thick serrations along the lateral margins. This horizontal expansion can also have a more rounded shape, with the length almost equal to its width. The ornamentation of the rostrum consists of spiny tubercles and irregular furrows dorsally, small and thick serrations laterally and possibly some spines ventrally (Figs. 10B, 12C-D). Furthermore, the ovoid/circular expanded portion of the rostrum shows an internal structure consisting of radiating grooves or ducts which extend from the centre to the lateral edges (Figs. 10B, 12). The vertebral column seems to comprise 26 vertebrae (?13+13), of which only 20 or 21 are clearly exposed, the anteriormost being hidden by the posttemporal and other cranial bones. The four posterior abdominal vertebrae bear parapophyses gradually increasing in size posteriorly. Epineurals are associated with the posterior abdominal and anterior caudal vertebrae (Fig. 12A-D). The caudal skeleton is structurally similar to that of other *Rhamphosus* species. The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two dorso-ventrally symmetric triangular plates separated by a deep median notch, which divides the epaxial lobe from the hypaxial lobe (Fig. 12A). The parhypural is fused to the hypaxial hypural lobe. The number of epurals and uroneurals cannot be determined due to the inadequate preservation of the caudal skeleton in the available material. The neural and haemal spines of the second and third preural vertebrae are anteroposteriorly expanded; this is especially evident in the second preural vertebra (Fig. 12A), which has a greatly expanded haemal spine, displaying a subtriangular shape, and contacting the haemal spine of the third preural centrum anteriorly and the parhypural posteriorly. The caudal fin is preserved only in MCSNV VII C.13 and contains ten principal rays (I, 4-4, I) plus seven ventral procurrent rays. Due to inadequate preservation of the available specimens, the original number of dorsal procurrent rays cannot be determined. The two dorsal fins are separated by a considerable gap (18.5% of SL). The first dorsal fin consists of an elongate and massive spine, followed by three thin and flexible spines, which can reach about one tenth of the length of the first spine (Figs. 11C-12A). The first dorsal-fin spine is inclined backward with a slightly curved apex and has a length ranging from 47.8% to 49.7% of SL, extending posteriorly to the base of the caudal fin. The anterior surface of this spine is characterized
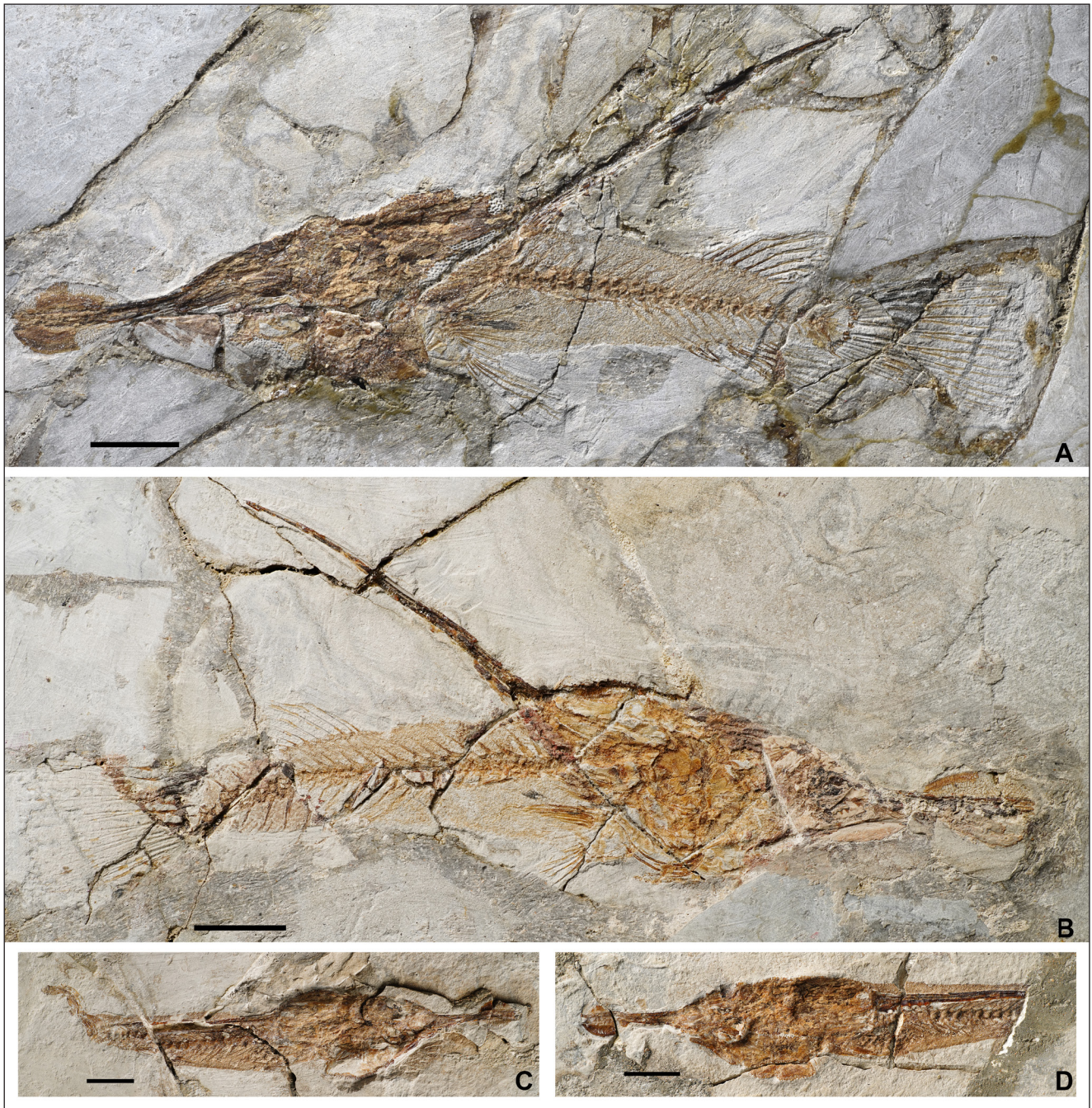
Fig. 12 - *Rhamphosus bloti* n. sp., lateral view of the holotype in part and counterpart: A) MCSNV VII C.13; B) MCSNV VII C.14, dorso-lateral view of the paratype in part and counterpart; C) MCSNV VII C.15; D) MCSNV VII C.16. Scale bars = 10 mm.

by several longitudinal ridges ornamented with minute tubercles, more evident in the lower half of the spine (Figs. 11C-12A); the posterior margin shows thick and irregularly spaced spines decreasing in size towards the apex. The first dorsal-fin spine inserts over the nape, and its basal portion articulates with a broad ovoid rayless pterygiophore (19.5-20.3% SL), which is closely associated to the dermal neurocranial elements, showing a similarly ornamented outer surface. The pterygiophores associated with the first dorsal fin are not recognizable in the examined material. The second dorsal fin includes nine rays supported by nine pterygiophores. The anal fin is opposite to the second dorsal fin and it includes nine rays supported by eight pterygiophores. The pectoral fin contains 10-11 relatively short, unbranched and unsegmented rays. The pelvic fins consist of a single slender spine plus five rays, definitively longer than those of the pectoral fins. Despite the pelvic girdle area is badly preserved in our

material, the basipterygium appears to be short with a scarcely developed posterior process (Fig. 12A).

The trunk is entirely covered with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate (Fig. 12). The lateral-line series is not evident in the available material.

**Discussion.** *Rhamphosus bloti* n. sp. exhibits a well-developed rostrum (rostrum length is between 22% and 29.1% SL), characterized by a peculiar and unique ovoid/discoid horizontal distal expansion that occupies more than half of the rostrum length. The ornamentation of the rostrum consists of minute and thick serrations and spines that cover all its surface including the lateral edges. The ventral portion close to the base of the rostrum is not exposed in any of the available specimens, even though in MCSNV VII C.15-16, it is possible to notice thick spines near the base of the rostrum, showing a condition more similar to that of the small-sized species (*R. rastrum* and *R. longispinatus* n. sp.). The rostrum of *R. bloti* n. sp. is shorter than that of the small-sized species (*R. rastrum*, *R. longispinatus* n. sp.; 38.9-45.1% and 45.4-69% of SL, respectively), more comparable to the length of the rostrum of *R. brevirostris* n. sp. (20.4-21.4% of SL; see Tab. 1) and definitively greater than that of *R. biserratus* and *R. tubulirostris* n. sp. (4.4% and 9.8% of SL, respectively). The dorsal-fin spine is elongate (from 47.8% to 49.7% of SL), extending posteriorly up to the base of the caudal fin. The length of the dorsal-fin spine of *R. bloti* n. sp. is consistent with those of *R. brevirostris* n. sp. and *R. tubulirostris* n. sp. (46.3-46.5% and 46.1% of SL, respectively), being shorter than those of the small-sized species (*R. longispinatus* n. sp. and *R. rastrum*) and, at the same time, by far longer than that of *R. biserratus* (20.5% of SL). Reaching a maximum size of 88.3 mm SL and 113.3 mm TL, *R. bloti* n. sp. is one of the largest species of the genus *Rhamphosus*, being comparable with *R. brevirostris* n. sp. (84.5 mm SL; 125.1 mm TL), but still smaller in size than *R. biserratus* (143.3 mm SL; 188.4 mm TL). *R. bloti* n. sp. exhibits a short predorsal (PD2) and preanal distance (PA); these parameters do not exceed 64% of SL in *R. bloti* n. sp., while in all the other taxa (except *R. tubulirostris* n. sp.) they exceed 70% of SL (see Tab. 1). The length of the caudal peduncle of *R. bloti* n. sp. is the shortest of any *Rhamphosus* species (5.6% of SL; see Tab. 1). The basipterygium is not especially large, representing the

less developed of any *Rhamphosus* species: 4.2% of SL), also lacking a particularly developed posterior process. As far as the meristic is concerned, *R. bloti* n. sp. can be distinguished from the other *Rhamphosus* species by having three short spines behind the dorsal-fin spine, 13 caudal vertebrae, with the last four abdominal vertebrae bearing parapophyses, a total of 10-11 unbranched and unsegmented pectoral-fin rays, and seven ventral procurrent rays. The haemal spine of the second preural centrum is broadly expanded anteroposteriorly (Fig. 12A), showing a subtriangular shape similar to that characteristic of *R. biserratus*.

### *Rhamphosus brevirostris* n. sp.
Figs. 10D-11D, 13

v1914 *Rhamphosus rastrum* (Volta); Eastman, p. 324, pl. XLIV, figs. 1-2 (non fig. 3 = *Rhamphosus longispinatus* n. sp.).
v1947 *Ramphosus rastrum* (Volta); Berg, fig. 185.
v1978 *Ramphosus rastrum* (Volta); Pietsch, p. 518, figs. 13, 14.
v1983 *Ramphosus aculeatus* (de Blainville); Sorbini, pl. 68 (non pl. 67 = *R. rastrum* (Volta, 1809).

**Holotype:** MCSNV T.1004-1005, a partially complete articulated skeleton measuring 82.1 mm SL, in part and counterpart.
**Paratype:** CNHM 5328, a partially complete articulated skeleton measuring 84.5 mm SL.
**Etymology:** From Latin *brevis* meaning "short" and *rostrum* for "snout or muzzle", in reference to the relatively short rostrum characteristic of this species.
**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).
**Diagnosis:** A medium-sized *Rhamphosus* species showing the following combination of features: elongate first dorsal-fin spine steeply inclined backward, reaching almost half of SL (around 46% SL) and extending posteriorly just beyond the end of the second dorsal fin, bearing a tuberculate anterior edge and a serrated posterior edge; rostrum moderately elongate (between 20.4% and 21.4% of SL) and slightly expanded distally, laterally ornamented with closely spaced serrations; caudal fin with eight dorsal and six ventral procurrent rays; pectoral fin with 10-12 rays; second dorsal-fin origin in the posterior fourth of the body, with a predorsal distance (PD2) reaching between 69.1% and 73.7% of SL; second dorsal and anal fin opposite to each other with the length of their bases not exceeding 13.5% of SL (see Tab. 5).

**Description.** *Rhamphosus brevirostris* n. sp. is characterized by a moderately large size (82.1-84.5 mm SL) associated with a relatively short nasal rostrum and a large first dorsal-fin spine ornamented with minute tubercles along the anterior edge and a serrated posterior edge. The second dorsal fin originates in the posterior fourth of the body, with the predorsal distance (PD2) ranging between 69.1% and 73.7% of SL. The opposite second dorsal and

anal fins are compact, with the length of their bases not exceeding 13.5% (see Tab. 5). The nasals are fused into a median rostrum, whose length reaches from 20.4% to 21.4% of SL. The rostrum has a broad base, then it gradually tapers anteriorly, being slightly expanded distally and showing a rather deep concavity along its anterior margin (Figs. 10D, 13). It is characterized dorsally by a series of longitudinal ridges bearing minute tubercles, laterally by minute and thick retrorse serrations that become more spaced towards the tip of the rostrum, and ventrally by some spines that slightly increase in size near the base of the rostrum (Figs. 10D, 13). The premaxilla bears a slender and thin ascending process, a vertically oriented and slightly expanded articular process and a posteriorly expanded postmaxillary process, which has an almost triangular shape. The presence of teeth on the premaxilla is difficult to determine. The vertebral column seems to comprise 26 vertebrae (?13+13), of which only 23 are clearly exposed, while the others are hidden by the overlying posttemporal and other posterior cranial elements. The four posterior abdominal vertebrae bear parapophyses gradually increasing in size posteriorly (Fig. 13A-B). A few epineurals are associated to the abdominal vertebrae. The structure and composition of the caudal skeleton are consistent to those of other *Rhamphosus* species (Fig. 8). The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two dorso-ventrally symmetric triangular plates separated by a deep median and narrow notch. There are two large epurals, a single uroneural fused to the epaxial hypural plate; the parhypural is fused to the hypaxial hypural lobe. The neural and haemal spines of the second and third preural vertebrae are greatly expanded antero-posteriorly; this is especially evident in the case of the second preural vertebra, in which the haemal spine is considerably expanded, displaying a subtriangular shape and being almost in contact with the haemal spine of the third preural vertebra anteriorly, and with the parhypural posteriorly. The neural spine of the second preural centrum is also expanded, but to a lesser extent. The caudal fin contains ten principal rays (I,4-4,I), plus eight dorsal and six ventral procurrent rays. The two dorsal fins are separated by a large gap (22.6-23.8% of SL). The first dorsal fin consists of an elongate first dorsal-fin spine, which is bent backwards along the dorsal margin of the body in MCSNV T.1004-

|  | MCSNV T.1004-1005 | CMNH 5328 | Range |
|---|---|---|---|
| SL (mm) | 82.1 | 84.5 | 82.1-84.5 |
| TL (mm) | 124 | 125.1 | 124-125.1 |
| HL | 33 | 31.9 | 31.9-33 |
| RL | 21.4 | 20.4 | 20.4-21.4 |
| PP | 32.8 | 33.1 | 32.8-33.1 |
| PA | 68.3 | 73.8 | 68.3-73.8 |
| PD1 | 45.9 | 47.2 | 45.9-47.2 |
| PD2 | 69.1 | 73.7 | 69.1-73.7 |
| PV | 34.6 | 36.8 | 34.6-36.8 |
| HDS | 46.5 | 46.3 | 46.3-46.5 |
| DFL2 | 12.8 | 12.5 | 12.5- 12.8 |
| AFL | 13.5 | 12.1 | 12.1-13.5 |
| VFL | ? | 23.5 | 23.5 |
| PFL | 16.2 | 10.6 | 10.6-16.2 |
| PRO | 27.8 | 27 | 27-27.8 |
| O | 7.9 | 8.4 | 7.9-8.4 |
| POO | 21.1 | 17 | 17-21.1 |
| RPT | 21.5 | 20.9 | 20.9-21.5 |
| DRL2 | 21.5 | 18.3 | 18.3-21.5 |
| ARL | 19.6 | ? | 19.6 |
| BD | 20.6 | 15.7 | 15.7-20.6 |
| CP | 13.1 | 15 | 13.1-15 |
| D1D2D | 23.8 | 22.6 | 22.6-23.8 |
| BAS | 11.2 | 13.2 | 11.2-13.2 |

Tab. 5 - Measurements of *Rhamphosus brevirostris* n. sp. Values are as percentage of SL.

1005, thus precluding the observation of the successive spines; in addition, there is no clear evidence of slender and flexible spines in the first dorsal fin of CNHM 5328 (Figs. 11D, 13). The first dorsal-fin spine is almost straight and exhibits a length ranging from 46.3% to 46.5% of SL, extending posteriorly slightly beyond the end of the second dorsal fin (Fig. 13). The anterior surface of the spine is characterized by longitudinal ridges ornamented with minute tubercles, more evident near the insertion of the spine; the posterior margin shows thick and irregularly spaced spines that decrease in size towards the apex. The dorsal-fin spine inserts over the nape, and its basal portion articulates with an elongate rayless pterygiophore (20.9-21.5% SL). The pterygiophore associated with the first dorsal-fin spine is not clearly recognizable in the examined material. The second dorsal fin includes nine rays supported by nine pterygiophores. The anal fin is opposite to the second dorsal fin and it includes nine rays supported by eight pterygiophores. The pectoral fin contains 10-12 relatively short, unbranched and unsegmented rays. The pelvic fin consists of a single slender spine plus five rays, definitively longer than those of the pectoral fins. The basipterygium is quite large
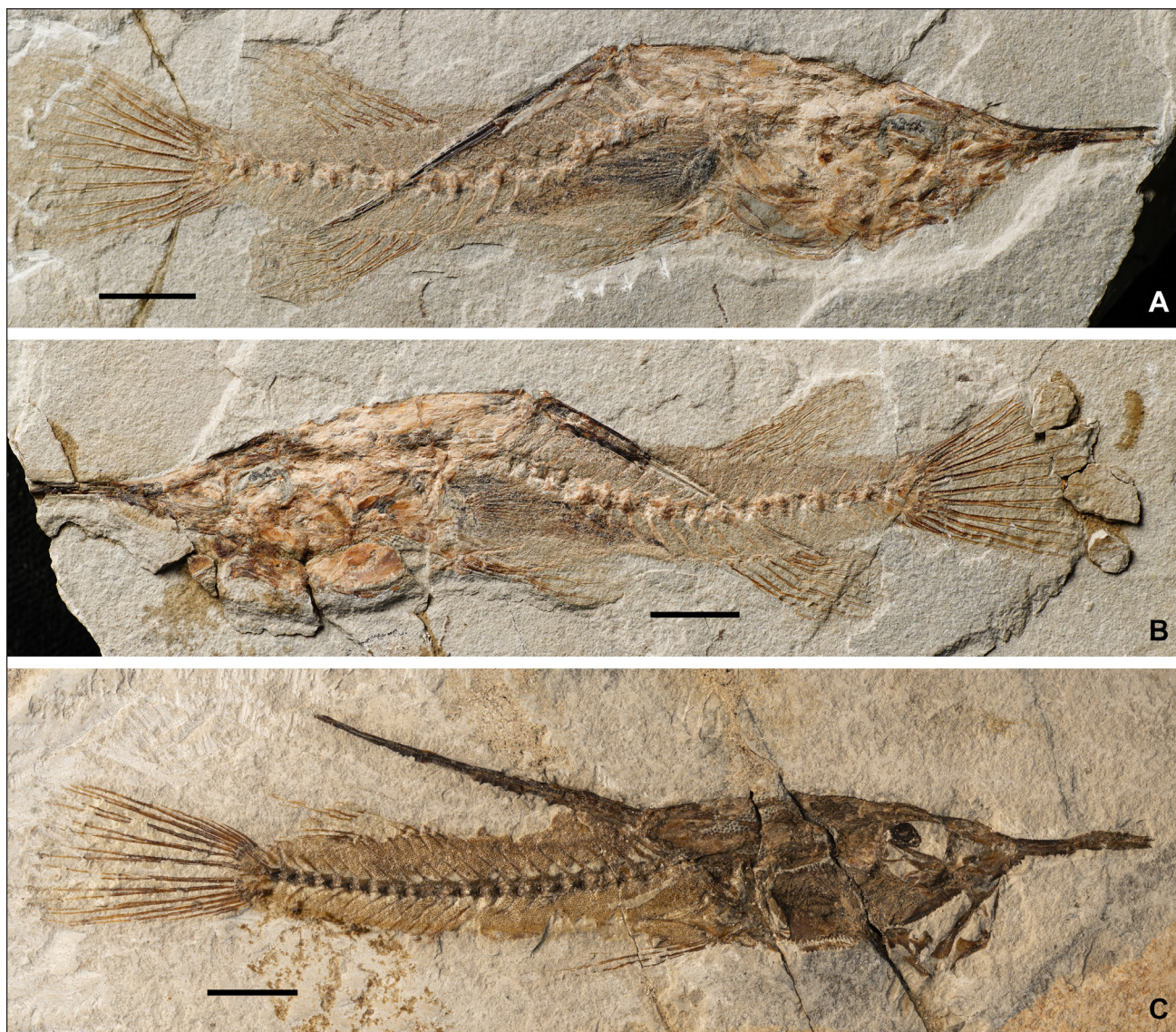
Fig. 13 - *Rhamphosus brevirostris* n. sp., lateral view of the holotype in part and counterpart. A) MCSNV T.1004; B) MCSNV T.1005, lateral view of the paratype; C) CMNH 5328. Scale bars = 10 mm.

(11.2-13.2% of SL), with an elongated posterior process that tapers posteriorly into a pointed end, extending backward to the level of the dorsal-fin spine insertion (Fig. 13C). As for the squamation, the trunk is entirely covered with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate (Fig. 13C). The lateral-line series is not evident in the available material.

**Discussion.** *Rhamphosus brevirostris* n. sp. has a relatively shorter rostrum (20.4-21.4% of SL) when compared to the small-sized species of the genus *Rhamphosus* (*R. rastrum* and *R. longispinatus* n. sp.). Moreover, the rostrum of *R. brevirostris* n. sp. is still slightly shorter compared to that of *R. bloti* n. sp., but definitely longer than those of *R. biserratus* and

*R. tubulirostris* n. sp. (see Tab. 1). The rostrum of *R. brevirostris* n. sp. has a straight outline being slightly expanded distally, where it shows a relatively deep concavity at its apex. Its ornamentation consists of minute tubercles dorsally, thick and continuous lateral serrations and scattered spines ventrally. The first dorsal-fin spine of *R. breviostris* n. sp. is elongate (46.3-46.5% of SL), extending posteriorly up to the end of the second dorsal fin. The length of the dorsal-fin spine of *R. brevirostris* n. sp. is comparable to those of *R. bloti* n. sp. and *R. tubulirostris* n. sp. (47.8-49.7% and 46.1% of SL, respectively), being shorter than those of the small-sized species (*R. rastrum* and *R. longispinatus* n. sp.) but, at the same time, considerably longer than that of *R. biserratus* (20.5% of SL;

| | CMNH 4213-4213a | CMNH 5310-5310a | MCSNV B.6 | MCSNV IG.186655-186656 | MCSNV T.429-IG.24560 | MCSNV T.1000-1001 | CMC 15 | MGPPD 8730-8731 | NHMUK P.9834-14400 | Range |
|---|---|---|---|---|---|---|---|---|---|---|
| SL (mm) | 31.1 | 27.3 | 42 | 22.7 | 31.7 | 23.2 | 42.9 | 38.1 | 40.7 | 22.7-42.9 |
| TL (mm) | 52.2 | 47.6 | 65 | 39.8 | 55.5 | 39.1 | 68.2 | 71.6 | 77.6 | 39.1-77.6 |
| HL | 35.1 | 34.4 | 35.8 | 38.2 | 35 | 33.3 | 40.9 | 31.3 | 32.8 | 31.3-40.9 |
| RL | 46.9 | 51.2 | ? | 51 | 47.1 | 53.3 | 45.4 | 69 | 64.2 | 45.4-69 |
| PP | 40.1 | 36.2 | 39.8 | 36.1 | 39.7 | 30.6 | 41.7 | 32.3 | 34.4 | 30.6-41.7 |
| PA | 76.3 | 73.3 | 69.7 | ? | 70.7 | 79.1 | 72 | 71.6 | 71.9 | 69.7-79.1 |
| PD1 | 51.8 | 50.9 | 49.5 | 49.8 | 50.8 | 47.8 | 48 | 46.7 | 49.2 | 46.7-51.8 |
| PD2 | 76.5 | 73.7 | 69.8 | ? | 70.4 | 79.6 | 71.6 | 71.3 | 74.7 | 69.8-79.6 |
| PV | 41.2 | 39.3 | 40 | 39.6 | 41 | 42.5 | 38.9 | 38.3 | 37.7 | 37.7-42.5 |
| HDS | 60.6 | 65.7 | 66.8 | 64.7 | 70.5 | 67.9 | 57.9 | 67.6 | 79.1 | 57.9-79.1 |
| DFL2 | 13.2 | 10.7 | 11.3 | ? | 11 | ? | 10.3 | 13.1 | 12.5 | 10.3-13.2 |
| AFL | 13.3 | 10.2 | 11 | ? | 11.4 | ? | ? | 12.2 | 12 | 10.2-13.3 |
| VFL | 18 | 20.5 | 22.4 | 19.8 | 24.6 | ? | 23.1 | ? | 19.3 | 18-24.6 |
| PFL | 7.5? | 20.4 | 15 | 14.1 | 12.7 | 14.2 | 11.2 | ? | 15.1 | 11.2-20.4 |
| PRO | 52.8 | 60.6 | 39.1 | 53.3 | 55.2 | 49.6 | 51.8 | 77.1 | 69.8 | 51.8-77.1 |
| O | 10.7 | 9.9 | 6.4 | 10.5 | 11 | ? | 8.2 | 8.6 | 6.5 | 6.4-11 |
| POO | 17.1 | 17.1 | 17.6 | 18.3 | 17.4 | 18.1 | 19.1 | 14.3 | 17.3 | 14.3-19.1 |
| RPT | 20.2 | 21.8 | ? | 23.4 | 20.9 | 18.1 | 19.4 | 24.9 | 20.3 | 18.1-24.9 |
| DRL2 | 9.6? | 19.1 | 16.9 | ? | 19.8 | 24.7 | 8.8? | 13.9 | 16.1 | 13.9-24.7 |
| ARL | 5.7? | 11 | 16.9 | 16.8 | 20.5 | 19 | 13.9 | 12.9 | 17 | 11-20.5 |
| BD | 12.6 | 12.5 | 15.9 | 19.2 | 12.7 | 19.4 | 16.4 | 18.8 | 15.5 | 12.5-19.4 |
| CP | 10.1 | 11.1 | 9.6 | 8.8 | 8.7 | 12.1 | ? | 6.8 | 10.6 | 6.8-12.1 |
| D1D2D | 18.3 | 20.7 | 21.1 | ? | 21.9 | 18.4 | 23 | 19.8 | 23.5 | 18.3-23.5 |
| BAS | 7.2 | 5.8 | ? | 7.7 | 10.6 | 6.2 | 8.7 | ? | 6 | 5.8-10.6 |

Tab. 6 - Measurements of *Rhamphosus longispinatus* n. sp. Values are as percentage of SL.

see Tab. 1). Reaching a maximum SL of 84.5 mm and a TL of 125.1 mm, *R. brevirostris* n. sp. is one of the largest species of the genus *Rhamphosus*, only *R. biserratus* shows a greater size (143 mm SL and 188.4 mm TL). The basipterygium of *R. brevirostris* n. sp. is one of the largest of any *Rhamphosus* species (between 11.2% and 13.2% of SL), second only to that of *R. biserratus*, with which it shares the presence of a rather elongated posterior process, with a posteriorly expanded shape tapering into a pointed end and extending posteriorly up to the level of the first dorsal-fin spine insertion. *R. brevirostris* n. sp. has the longest caudal peduncle of any *Rhamphosus* species (between 13.1% and 15% of SL; the other species do not exceed 11% of SL). Moreover, *R. brevirostris* n. sp. can be distinguished from the other species of the genus *Rhamphosus* by having a total of 13 caudal vertebrae and parapophyses in the last four abdominal vertebrae, plus eight dorsal and six ventral procurrent rays, and 10-12 unbranched and unsegmented pectoral-fin rays. The haemal spine of the second preural vertebra is anteriorly-posteriorly expanded (see MCSNV T 1004-1005), showing a subtriangular shape similar to that characteristic of *R. biserratus*. The neural spine of the second preural vertebra is also expanded, but to a lesser extent.

### *Rhamphosus longispinatus* n. sp.

Figs. 10E-11E, 14

?1888 *Rhamphosus*; Woodward, p.39.
v1898 *Rhamphosus aculeatus* Agassiz; Bassani, p. 82; pl. IX, fig. 4.
1911 *Rhamphosus aculeatus* (Blainville); Eastman, p. 362.
v1914 *Rhamphosus rastrum* (Volta); Eastman, p. 324, pl. XLIV, fig. 3 (non figs. 1-2 = *Rhamphosus brevirostris* n. sp.).
v1978 *Ramphosus rastrum* (Volta); Pietsch, p. 518 (non figs. 13-14= *Rhamphosus brevirostris* n. sp.).
v2011 *Rhamphosus aculeatus* (de Blainville, 1818); Cerato, fig. in text, p. 107.
v2014 *Rhamphosus rastrum* (Volta, 1796); Carnevale et al., p. 42, fig. 4b.
v2020 *Ramphosus rastrum*; Carnevale, fig. 3f.
v2022 *Rhamphosus*; Zorzin, fig. in text, p. 110.

**Holotype:** MCSNV IG.24560-T.429, a nearly complete articulated skeleton measuring 31.7 mm SL, in part and counterpart.

**Paratypes:** MCSNV B.6, a partially complete articulated skeleton measuring 42 mm SL; CMC 15, a partially complete articulated skeleton measuring 42.9 mm SL; MCSNV IG.24483, an incomplete articulated skeleton; MCSNV IG.186655-186656, a partially complete articulated skeleton measuring 22.7 mm SL, in part and counterpart; MCSNV T.1000-1001, a partially complete articulated skeleton measuring 23.2 mm SL, in part and counterpart; MGPPD 8730-8731 a partially complete articulated skeleton measuring 38.1 mm SL, in part and counterpart; CNHM 4213-4213a, a partially complete articulated skeleton measuring 31.1 mm SL, in part and counterpart; CNHM 5310-5310a, a partially complete articulated skeleton measuring 27.3 mm SL, in part and counterpart; NHMUK P.9834-14400, a partially complete articulated skeleton measuring 40.7 mm SL, in part and counterpart.

**Etymology:** Species named after Latin *longus* meaning "long" and *spinatus* for "spiny", in reference to its remarkably elongate dorsal-fin spine.

**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).

**Diagnosis:** A small-sized *Rhamphosus* species showing the following combination of features: remarkably elongate dorsal-fin spine steeply inclined backward, whose length ranges from 57.9% to 79.1% SL, extending posteriorly almost well beyond the insertion of the caudal-fin rays, and bearing minute tubercles on the anterior edge and serrations along the posterior edge; massive and distally pointed rostrum (between 45.4% and 69% of SL), ornamented with minute tubercles dorsally, with serrations laterally and with spines ventrally, near the base of the rostrum; caudal fin with five to eight dorsal and

four to six ventral procurrent rays; first dorsal fin containing up to three thin and flexible spines; pectoral fin with up to 15 rays; second dorsal-fin origin located in the posterior fourth of the body, with a predorsal distance (PD2) ranging between 69.8% and 79.6% of SL; second dorsal and anal fins opposite to each other with their base length not exceeding 13.3% of SL.

**Description.** *Rhamphosus longispinatus* n. sp. is characterized by a relatively small size (22.7–42.9 mm SL) and a slender body, associated with a greatly elongate nasal rostrum and a massive dorsal-fin spine with a serrated posterior margin. The second dorsal fin originates in the posterior fourth of the body, the predorsal distance (PD2) ranges from 69.8% to 79.6% of SL (see Tab. 6). The second dorsal fin and its opposite anal fin are compact, with the length of their bases not exceeding 13.3% of SL (see Tab. 6). The nasals are fused into a median elongate and massive rostrum, whose length ranges between 45.4% and 69% of SL (almost equal to the length of the body just behind the insertion of the dorsal-fin spine). The rostrum is massive basally, and then it gradually tapers anteriorly becoming slightly spatulate at its distal end and showing a horizontal concavity along its anterior border (Figs. 10E, 14D). The ornamentation of the rostrum consists of regular longitudinal ridges bearing minute tubercles dorsally and short retrorse spines ventrally and laterally. These ventral spines are much developed near the base of the rostrum, just anterior to the mouth (see Fig. 14A-B-C). The premaxilla bears a thin and elongate ascending process, a vertically oriented and slightly enlarged articular process, and a slightly expanded postmaxillary process. Small granular teeth can be observed along the alveolar process (Fig. 14A-B-D). The vertebral column comprises 26 (13+13) vertebrae. The anterior abdominal centra are rarely exposed, being hidden under cranial and pectoral girdle bones. These anterior vertebrae are more elongate compared to the subsequent elements. The three posterior abdominal vertebrae bear parapophyses gradually increasing in size posteriorly. Epineurals are associated with the abdominal and anterior caudal vertebrae (Fig. 14A-B-C-E-F-G-H) The overall structure of the caudal skeleton is consistent with that of *R. rastrum* described above. The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two dorso-ventrally symmetric triangular plates separated by a deep median and narrow notch, which divides the epaxial lobe from

the hypaxial lobe. There are two epurals, a single uroneural fused to the epaxial hypural plate, and the parhypural is fused to the hypaxial hypural lobe. The neural and haemal spines of the second and third preural vertebrae are slightly expanded antero-posteriorly (Fig. 14A-B). The caudal fin contains ten principal rays (I, 4-4, I) plus five to eight dorsal and four to six ventral procurrent rays. The two dorsal fins are separated by a large gap (18.3-23.5% of SL). The first dorsal fin consists of a greatly elongate massive dorsal-fin spine, followed by two or three slender and flexible spines that can reach up to one fourth of the length of the massive spine (Figs. 11E, 14A-B). The length of the first dorsal-fin spine ranges between 57.9% and 79.1% of SL, extending posteriorly well beyond the insertion of the caudal-fin rays and almost reaching the end of the fin itself in some of the available specimens (Fig. 14A-B-E-F). This spine is steeply inclined backward with a slightly curved apex. The anterior surface of the first dorsal-fin spine bears a series of longitudinal ridges, ornamented with minute tubercles that are more evident near the base; along the posterior margin, there are irregularly spaced thick and stout spines that decrease in size towards the apex (Fig. 14A-B). The first dorsal-fin spine inserts over the nape, and its basal portion articulates with the rayless pterygiophore, which has an ovoid outline, and it is closely associated to the dermal neurocranial elements, showing a similarly ornamented outer surface. The rayless pterygiophore is oblong (18.1-24.9% SL; see Tab. 6). The pterygiophore associated with the dorsal-fin spine is large and moderately ossified, while the subsequent flexible and thin spines are supported by feebly ossified pterygiophores, well recognizable in the holotype. The second dorsal fin includes nine rays supported by nine feebly ossified pterygiophores. The anal fin includes

Fig. 14 - *Rhamphosus longispinatus* n. sp., lateral view of the holotype in part and counterpart. A) MCSNV IG.24560; B) MCSNV T.429. Lateral view of paratypes C) CMNH 5310; D) CMC 15; E) NHMUK P.9834; F) NHMUK P.14400; G) MGPPD 8730; H) MGPPD 8731. Scale bars= 10 mm.

Figure 14

nine rays apparently supported by eight delicate pterygiophores. The pectoral fin contains up to 15 relatively short, unbranched and unsegmented rays. The pelvic fin consists of a single slender spine plus five rays, longer than those of the pectoral fins. The basipterygium is relatively short with a poorly developed posterior process (Fig. 14A-B). As far as the squamation is concerned, the trunk is covered with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate (Fig. 14C-D). The lateral-line series is not evident in the available material.

**Discussion.** *Rhamphosus longispinatus* n. sp. is the smallest species of the genus *Rhamphosus* (22.7–42.9 mm SL). On the other hand, the rostrum of *R. longispinatus* n. sp. is the longest among the *Rhamphosus* species (45.4-69% of SL), characterized by a remarkably large and stout base especially considering the reduced size of this species. *R. rastrum* is the only other species with a very large rostrum, which is shorter (38.9-45.1% of SL) and with a smaller base compared to *R. longispinatus* n. sp. These two small-sized species are the only ones who can be defined as "longirostrate", showing a rostral length (RL) that easily exceeds 35% of SL, while none of the other *Rhamphosus* species reaches 30% of SL (see Tab. 1). The ornamentation of the rostrum is consistent with that of the type species and shows dorsal minute tubercles, lateral small and thick serrations (see CNHM 5310, Fig. 14C) and ventral spines, all of which are more pronounced near the base of the rostrum. The spines are particularly evident in this species, more than in any other *Rhamphosus* (Figs. 10E, 14A-B-C). *R. longispinatus* n. sp. also has the longest dorsal-fin spine among the species of the genus *Rhamphosus* (57.9-79.1% of SL), extending backward well beyond the insertion of the caudal-fin rays and, in some specimens, almost reaching the distal end of the caudal fin (Fig. 14A-B-E-F). Even for this feature, *R. rastrum* is the only other species with a comparable spine length (50-60.2% of SL), despite being still substantially shorter than that of *R. longispinatus* n. sp. The length of the dorsal-fin spine of the other *Rhamphosus* species does not exceed 50% of SL (see Tab. 1). As a matter of fact, it is interesting to note that the smallest species of the genus *Rhamphosus* (*R. longispinatus* n. sp. and *R. rastrum*; 22.7-42.9 mm SL and 36.9-59.3 mm SL, respectively) are the ones who also exhibit the longest rostrum and dorsal-fin spine (see RL

and HDS; Tab. 1). Despite their overall similarity, *R. longispinatus* n. sp. and *R. rastrum* represent two separate species that can be recognized from each other based on a specific set of morphological features. *R. longispinatus* n. sp. differs from *R. rastrum* by having a larger relative size of the rostrum and dorsal-fin spine (see Tab. 1). An inverse ontogenetic relationship between the body size and the length of the rostrum and dorsal-fin spine can be ruled out given that even the smallest specimen of *R. rastrum* (MCSNV T.286, 36.9 mm SL) has a shorter rostrum and dorsal-fin spine compared to *R. longispinatus* n. sp. (see Tab. 1-2-6). *R. longispinatus* n. sp. can also be distinguished from the other species of the genus *Rhamphosus* by having one to three spines behind the dorsal-fin spine, with these reaching up to one fourth of the length of the spine (Fig. 11E). The first dorsal fin of *R. rastrum* contains up to four rays, which can reach one third of the length of the spine (Fig. 11A). *R. longispinatus* n. sp. has 13 caudal vertebrae, unlike some *Rhamphosus* species (*R. biserratus* and *R. tubulirostris* n. sp.), five to eight dorsal and four to six ventral procurrent rays and up to 15 unbranched and unsegmented pectoral-fin rays. The neural and haemal spines of the second preural vertebra are weakly expanded antero-posteriorly, showing a subtriangular shape. The expansion of the haemal spine of the second preural vertebra is substantially different from the remarkably expanded haemal spines of *R. biserratus*, *R. bloti* n. sp. and *R. brevirostris* n. sp., being also less pronounced than that of *R. rastrum*.

### *Rhamphosus tubulirostris* n. sp.
Figs. 10F-11F, 15

**Holotype (by monotypy):** CNHM 4227-5312, a partially complete articulated skeleton measuring 51.4 mm SL, in part and counterpart. The specimen is housed in the Carnegie Museum of Natural History, Pittsburgh.

**Etymology:** From Latin *tubulus* meaning "tubule" and *rostrum* for "snout or muzzle", in reference to the peculiar shape of the slim and tubular rostrum characteristic of this species.

**Type locality and horizon:** Pesciara site, Bolca *Lagerstätte*, northeastern Italy; lower Eocene, upper Ypresian, middle Cuisian, slightly less than 49 Ma (Papazzoni et al. 2017).

**Diagnosis:** A small-sized *Rhamphosus* species (less than 52 mm SL) characterized by the following combination of features: dorsal-fin spine elongate (46.1% SL), steeply inclined backwards, extending backward not beyond the end of the second dorsal fin; rostrum very short (9.8% of SL), slender and tubular, laterally ornamented with a few serrations; first dorsal fin with a large spine followed by two thin and smaller spines; second dorsal fin with 13 rays; second dorsal-fin insertion placed in the posterior third of the body, predor-

Fig. 15 - *Rhamphosus tubulirostris* n. sp., lateral view of the holotype in part and counterpart. A) CMNH 5312; B) CMNH 4227. Scale bars = 10 mm.
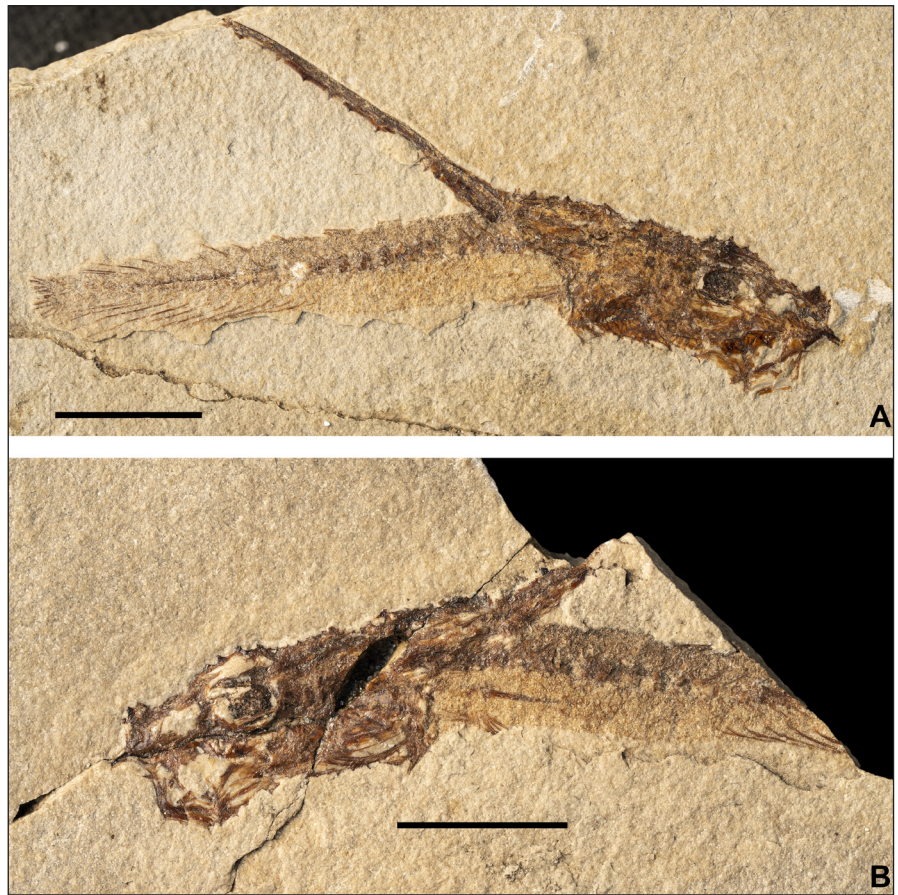


sal distance (PD2) reaching 63.5% of SL; second dorsal and anal fins approximately opposite to each other, with the length of their bases being about 31% and 28% SL, respectively (see Tab. 7); anal fin with 12-13 rays; posterior anal-fin rays considerably elongate; pectoral fin with ten rays; ventral portion of the trunk characterized by the presence of bucklers of different size.

**Description.** *Rhamphosus tubulirostris* n. sp. is characterized by a small body size (51.4 mm SL), associated with an elongate dorsal-fin spine and a short, slender and tubular rostrum. The body is elongate and slender. The second dorsal fin originates in the posterior third of the body and its predorsal distance reaches 63.5% of SL. The opposite second dorsal and anal fins are notably elongate, extending backwards up to the level of the caudal fin rays, with the length of their bases reaching 31.3% and 28.1%, respectively (see Tab. 7). The nasals are fused into a short and slender rostrum, whose length reaches 9.8% of SL. The base of the rostrum is broad and abruptly tapers into a tubular rod-like structure; the ornamentation consists of ridges bearing minute tubercles and spines dorsally and serrations laterally; the ventral side of the rostrum is not exposed (Figs. 10F, 15). The premax-

illa has an elongate ascending process, a vertically oriented and enlarged articular process (extending up to the level of the ascending process) and an expanded postmaxillary process (Fig. 15B), almost triangular in outline. The premaxilla of CNHM 5312 bears minute and delicate teeth. The ornamentation of the cranium consists of numerous pronounced spines, which cover the cranial armor, being most evident along the edges of various bones of the cranium and of the opercular region. The vertebral column comprises 26 vertebrae (?12+14), of which 24 are clearly exposed, while the two (elongate) anterior are hidden by the posttemporal and the other posterior cranial elements. The centra of the posterior nine caudal vertebrae exhibit a more stretched and elongate shape when compared to the more square-like preceding caudal and abdominal vertebrae. The three posterior abdominal vertebrae bear delicate parapophyses gradually increasing in length posteriorly. A few epineurals are associated to the posterior abdominal and the anterior caudal vertebrae. The caudal skeleton is only partially preserved. The compound centrum is fused with a consolidated hypural plate. The hypural plate consists of two

dorso-ventrally symmetric triangular plates separated by a deep median and narrow notch. There is a single uroneurals fused to the epaxial hypural plate and a parhypural fused to the hypaxial hypural lobe. There are two poorly preserved epurals. The neural and haemal spines of the second and third preural vertebrae appear to be not significantly expanded. The caudal fin is only partially preserved and contains ten principal rays (I,4-4,I); the number of dorsal and ventral procurrent rays cannot be properly determined. The two dorsal fins are separated by a large gap (16.5% of SL). The first dorsal fin consists of an elongate dorsal-fin spine, followed by two short, thin and flexible spines whose length reaches less than one tenth of the length of the massive first dorsal-fin spine (Fig. 11F). The first dorsal-fin spine is inclined backwards with a slightly curved apex and has a length of 46.1% of SL, extending posteriorly not beyond the end of the second dorsal fin. The anterior surface of the first dorsal-fin spine is characterized by various longitudinal ridges ornamented with many minute tubercles along the whole anterior edge; the posterior margin bears some thick and irregularly spaced spines, which slightly decrease in size towards the apex (Fig. 15A). The first dorsal-fin spine inserts over the nape, and its basal portion articulates with an ovoid rayless pterygiophore (16.9% of SL). The pterygiophores associated with the massive first dorsal-fin spine and the following short and flexible spines are not clearly recognizable in the examined material. The second dorsal fin inserts just above the last abdominal vertebra and includes 13 rays supported by 13 feebly ossified pterygiophores. The distal portion of the rays of the second dorsal fin is not preserved. The anal fin is almost opposite to the second dorsal and contains (12) 13 soft rays

supported by at least 11 feebly ossified pterygiophores. Like in the second dorsal fin, the distal portion of the majority of the anal-fin rays is not preserved. Only some of the very long posterior anal-fin rays are almost entirely preserved, extending posteriorly beyond the posterior margin of the hypural plate. The pectoral fin contains ten relatively short, unbranched, and unsegmented rays. The pelvic fin consists of a single slender spine plus five rays, longer than those of the pectoral fins. The basipterygium is relatively small and poorly developed, apparently devoid of the posterior processes (Fig. 15B). As far as the squamation is concerned, the trunk is covered dorsally with a dense cover of scale plates bearing a short upright spine emerging from a polygonal basal plate. There is no evidence of the lateral-line series. Aside from the scales, the hypaxial portion of the trunk is covered with bucklers of various sizes. These structures are scattered on the body, starting from the pectoral-fin insertion to the level of the sixth or seventh anal-fin ray.

**Discussion.** The rostrum of *Rhamphosus tubulirostris* n. sp. is very short (9.8% of SL; only *R. biserratus* has a shorter rostrum), slender and tubular and only weakly projected anteriorly, without any distal expansion; it bears small lateral serrations and lacks the thick spines on the ventral margin of the base of the rostrum that are characteristic of some of its congenerics. The first dorsal-fin spine is elongate (46.1% SL), extending posteriorly up to the posterior sector of the second dorsal fin. The length of the first dorsal-fin spine of *R. tubulirostris* n. sp. is consistent with those of *R. bloti* n. sp. and *R. brevirostris* n. sp. (47.8-49.7% and 46.3-46.5% of SL, respectively), shorter than those of *R. rastrum* and *R. longispinatus* n. sp. but, at the same time, being more than two times that of *R. biserratus* (which is 20.5% of SL). *R. tubulirostris* n. sp. is smaller in size compared to that of the largest taxa of this genus (*R. biserratus, R. brevirostris* n. sp., *R. bloti* n. sp.) and definitively larger compared to *R. longispinatus* n. sp. (see Tab. 1). With a SL of 51.4 mm, *R. tubulirostris* n. sp. falls in the size range of *R. rastrum* (36.9-59.3 mm SL). A unique feature of this new species is the presence of very pronounced spines and thorns on the cranial armor and of many bucklers along the body; the latter is a trait unique to this species, not observed in any other species of *Rhamphosus*. The bucklers are scattered randomly on the whole body, from the pectoral-fin insertion to the pos-

|  | CMNH 4227-5312 |
|---|---|
| SL (mm) | 51.4 |
| TL (mm) | 56.2 |
| HL | 32.7 |
| RL | 9.8 |
| PP | 34.1 |
| PA | 65.1 |
| PD1 | 47.5 |
| PD2 | 63.5 |
| PV | 34.7 |
| HDS | 46.1 |
| DFL2 | 31.3 |
| AFL | 28.1 |
| VFL | 11.7? |
| PFL | 11.7? |
| PRO | 14.4 |
| O | 9.2 |
| POO | 15.2 |
| RPT | 16.9 |
| DRL2 | 8.9 |
| ARL | 14.4 |
| BD | 12.7 |
| CP | 8.6 |
| D1D2D | 16.8 |
| BAS | 5.2? |

Tab. 7 - Measurements of *Rhamphosus tubulirostris* n. sp. Values are as percentage of SL.

terior end of the dorsal and anal fins (around the sixth-seventh anal fin ray). *Rhamphosus tubulirostris* n. sp. is unique in having very long second dorsal and anal fins, much more developed compared to all the other *Rhamphosus* species (LD2: 31.3% and LA: 28.1% of SL; in the other species these do not exceed 14% of SL), both ostensibly comprising 13 rays. *R. tubulirostris* n. sp. is the only species that has more than nine rays in the second dorsal and anal fins. The presence of a very long second dorsal and anal fins in *R. tubulirostris* n. sp. results in a rather short caudal peduncle (8.6% of SL), reduced predorsal and preanal distance (respectively 63.5% and 65.1% of SL), and the shortest gap between the two dorsal fins (16.8% of SL, with all the other taxa being above 17% and reaching 23.8% SL) compared to any other *Rhamphosus* species. Due to inadequate preservation, both these fins are incomplete; however, the posterior rays of both these fins are greatly elongate so that the penultimate anal-fin ray extends backward beyond the posterior margin of the hypural plate. The caudal fin is incomplete, and only the basal portions of ten principal rays are clearly recognizable and some of the procurrent rays are not preserved. The pectoral fins include ten rays, more evident in CNHM 4227. The vertebral column of *R. tubulirostris* n. sp. comprises 26 (12+14) vertebrae, of which the first two are possibly rather elongate. Parapophyses are present in the three posterior abdominal vertebrae. The posterior nine caudal centra are rectangular, longer than high, being more elongate than the preceding caudal and abdominal vertebrae. This is a unique feature of this species since in all the other *Rhamphosus* species the centra of the posterior caudal vertebrae are almost squared, similar to the preceding caudal and abdominal vertebrae.

## DISCUSSION

### Comments on *Rhamphosus rosenkrantzi*

*Rhamphosus rosenkrantzi* Nielsen, 1960 (Fig. 16), from the lower Eocene deposits of the Fur Formation (Denmark), is the only species of *Rhamphosus* found outside the Bolca *Lagerstätte*. The holotype of *R. rosenkrantzi* (a partially complete articulated skeleton, in part and counterpart, measuring 25.5 mm SL) shows most of the typical features of the Rhamphosidae, including head and nape encased in

thick bony plates, small ventral mouth, nasal bones fused into a median elongate rostrum extending anteriorly well beyond the mouth, massive and elongate dorsal-fin spine with a serrated posterior margin, peculiar ornamentation of the cranial armor, rostrum and dorsal-fin spine (consisting of numerous series of longitudinal tuberculated ridges), presence of a large rayless pterygiophore consolidated to the cranial armor, second dorsal and anal fins placed posteriorly and approximately opposed to each other, caudal skeleton with a consolidated hypural plate, caudal fin consisting of ten principal rays. Most of the meristic traits concerning the median and paired fins cannot be verified due to the inadequate preservation of the holotype (Nielsen 1960). *R. rosenkrantzi* has a body size (25.5 mm SL, 43.8 mm TL) closer to the small-sized species of *Rhamphosus* from Bolca (*R. rastrum*, *R. longispinatus* n. sp. and *R. tubulirostris* n. sp.), especially of *R. longispinatus* n. sp. (22.7–42.9 mm SL; see Tab. 1-6). Moreover, another trait shared by *R. rastrum* and *R. longispinatus* n. sp. is the anteriorly elongate and tapering rostrum (47.5% of SL), which shows a ventral margin characterized by some pronounced spines, especially near the base. The dorsal-fin spine of *R. rosenkrantzi* also shows a remarkable length (76.1% of SL; see Tab. 8), extending backward beyond the hypural plate, almost to the end of the caudal-fin rays. When compared to the Bolca species, the length of the dorsal-fin spine of *R. rosenkrantzi* is surpassed only by that of *R. longispinatus* n. sp. (HDS: 57.9-79.1% of SL; see Tab. 1-6). However, in the holotype of *R. rosenkrantzi*, the small slender spines following the enlarged first dorsal-fin spine appear to be absent. The second dorsal and anal fins of the holotype of *R. rosenkrantzi* are incom-

|  | **NHMD 164232a-b** |
|---|---|
| SL (mm) | 25.5 |
| TL (mm) | 43.8 |
| HL | 33.7 |
| RL | 47.5 |
| PP | ? |
| PA | 72.9 |
| PD1 | 47.8 |
| PD2 | 72.2 |
| PV | 37.3 |
| HDS | 76.1 |
| DFL2 | 13.3 |
| AFL | 12.9 |
| VFL | 20.4 |
| PFL | ? |
| PRO | 56.5 |
| O | 8.6 |
| POO | 16.1 |
| RPT | 18.8 |
| DRL2 | 9.8 |
| ARL | 12.2 |
| BD | 12.6 |
| CP | 10.2 |
| D1D2D | 25.1 |
| BAS | 5.2? |

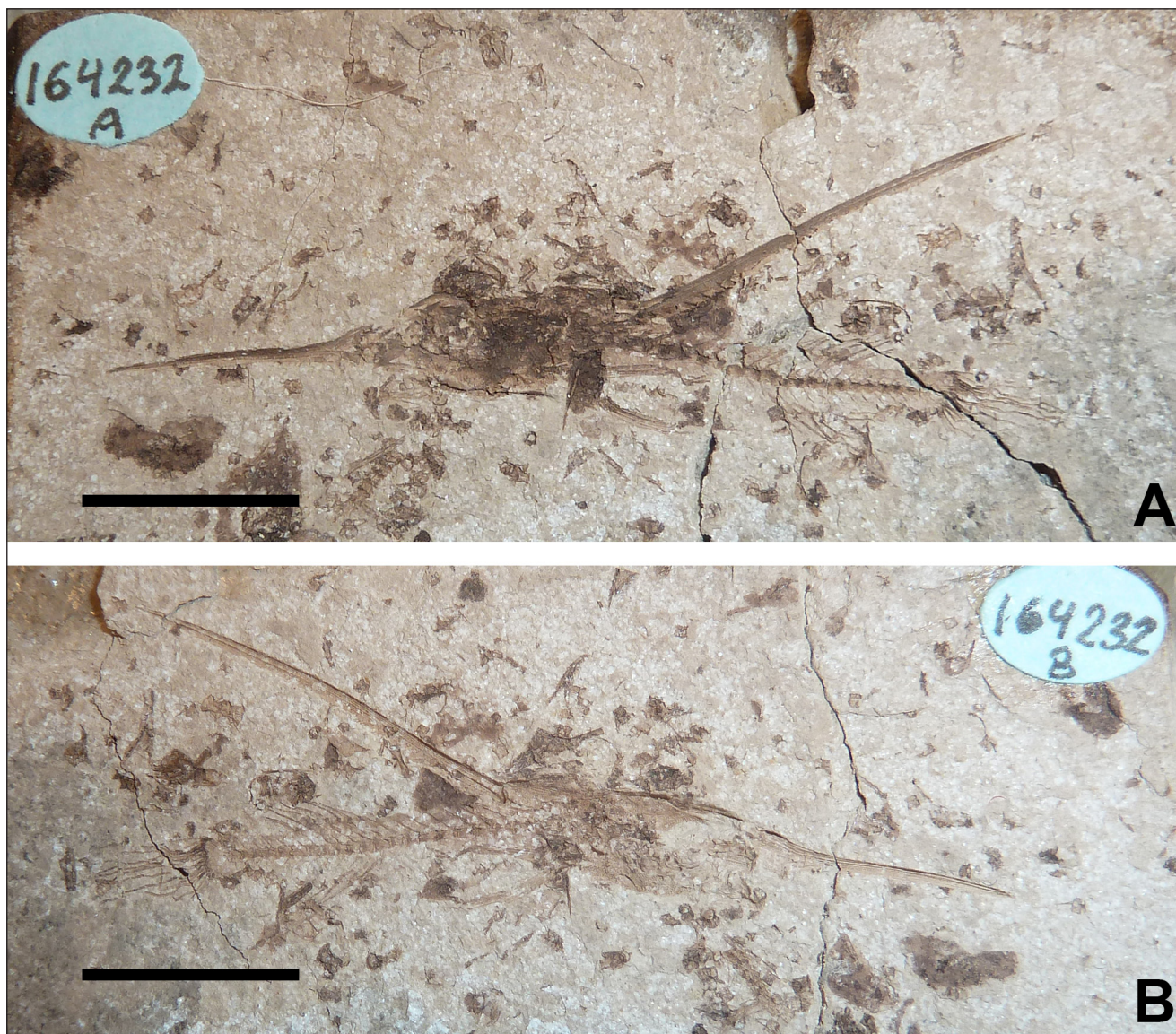Tab. 8 - Measurements of *Rhamphosus rosenkrantzi* Nielsen, 1960. Values are as percentage of SL.

Fig. 16 - *Rhamphosus rosenkrantzi* Nielsen, 1960, lateral view of the holotype in part and counterpart. A) NHMD 164232a; B) NHMD 164232b. Scale bars = 10 mm. Photos courtesy of Bent Erik Kramer Lindow.

plete and show eight and seven rays, respectively, far from the peculiar and unique longer dorsal and anal fins of *R. tubulirostris* n. sp. The basipterygium differs from that of the large-sized species (*R. biserratus*, *R. brevirostris* n. sp.) by being shorter and devoid of a posterior process. The posterior three abdominal vertebrae of *R. rosenkrantzi* bear thin parapophyses, as seen in NHMD 164232a (Fig. 16A). Due to the preservation of the holotype, it is difficult to determine if intermuscular bones were present or not in origin. The caudal skeleton is not especially well preserved and it is not possible to estimate the number of epurals and procurrent rays, as well as the degree of expansion of neural and haemal spines of the

second and third preural vertebrae. *R. rosenkrantzi* certainly differs from all the other *Rhamphosus* species from Bolca by having a long and uniquely ornamented dorsal-fin spine, characterized by heavy serrations along the whole posterior margin, and showing a slight bending towards the end of the spine itself (Nielsen 1960), and for the presence of slightly elongated anterior nine or ten abdominal vertebrae (Nielsen 1960).

The Fur formation dates back to 56-54 Ma being 7-5 Myr older than the carbonates of the Pesciara succession, thereby extending back the temporal range of the genus *Rhamphosus* and also expanding its geographic range up to the North Sea latitudes.

## The affinities of *Rhamphosus*

As evidenced by Pietsch (1978), most of the researchers that have examined *Rhamphosus* specimens have recognized its syngnathiform affinities (e.g., Agassiz 1835; Gill 1884; Vaillant 1988; Eastman 1914; Bonde 1966; Greenwood et al. 1966). Such a hypothesis was not supported by a few authors, who disagree with an alignment with the syngnathiform fishes and considered *Rhamphosus* as a perciform (Jurgensen 1908; Berg 1940; Nielsen 1960), or a scorpaeniform (Blot 1980).

Syngnathiform monophyly has been recently demonstrated by phylogenomic analyses that modified the composition of this clade, traditionally comprising several long-snouted lineages (see, e.g., Pietsch 1978; Orr 1995), with the inclusion of a heterogeneous set of primarily benthic groups like callionymoids, dactylopterids, mullids and pegasids that were previously associated with other percomorph orders (Longo et al. 2017; Santaquiteria et al. 2021). Due to this recent rearrangement of the limits and composition of the Syngnathiformes, morphological characters that can unite all the members of this clade remain elusive (e.g., Betancur-R et al. 2017). However, a series of morphological features, although not necessarily widespread within this group, might be regarded as diagnostic when found in combination (see Orr 1995). The putative diagnostic syngnathiform characters found in *Rhamphosus* include, among the others, a posttemporal consolidated with the cranium, anterior vertebrae elongate, ribs absent; anal-fin spine absent, postcleithrum absent, and pectoral-fin rays simple (see Orr 1995).

Within syngnathiforms, *Rhamphosus* was initially associated to the Fistulariidae (Giebel 1848; Woodward 1888), Centriscidae (Woodward 1901), Macrorhamphosidae (Greenwood et al. 1966) or assigned to a separate family, Rhamphosidae (Gill 1884; Eastman 1914). Pietsch (1978) hypothesized a sister group relationship between *Rhamphosus* and the Pegasidae, placing them within the new superfamily Pegasoidea, which was in turn considered as the sister group to the pair formed by the families Solenostomidae and Syngnathidae. The diagnosis of the Pegasoidea proposed by Pietsch (1978) was based on a large set of morphological features, the majority of which were confirmed in the phylogenetic survey conducted by Orr (1995). Pietsch (1978) also discussed a possible relationship between Pegasidae and the Dactylopteridae (=Cephalacanthidae) and evidenced a number of shared features, including mouth inferior, anterior abdominal vertebrae elongated, nasal fused along the midline and forming a cavity for the elements of the upper jaws, infraorbital bones connected with an enlarged preopercle, and head encased by thick ornamented bony plates. Johnson & Patterson (1993) excluded a possible affinity between syngnathiforms and dactylopterids based on a large set of morphological features. More recently, large-scale molecular datasets (e.g., Kawahara et al. 2008; Near et al. 2013; Song et al. 2014; Sanciangco et al. 2016) consistently suggested that the traditional long-snouted syngnathiform lineages form a monophyletic group with a peculiar group of benthic-associated fishes, among which pegasids and dactylopterids form a well-defined sister pair (Longo et al. 2017; Santaquiteria et al. 2021), which was named Dactylopteroidei by Betancur et al. (2017). Betancur et al. (2017) listed a single synapomorphy shared by these two families, fused nasal bones in the adult stage, a feature that is also characteristic of *Rhamphosus*. However, the placement of *Rhamphosus* within the Dactylopteroidei is supported by many other morphological traits (see also Gill 1890; Allis 1909; Rendahl 1930; Pietsch 1978; Gayet & Barbin 1985; Palsson & Pietsch 1989; Orr 1995; Eschmeyer 1997; Imamura 2000), including mouth ventral, infraorbital bones connected with the preopercle, head encased by thick bony plates, posttemporal consolidated with the neurocranium, suspensorium remarkably projected forward, anterior vertebral centra elongated, and short-based second dorsal and anal fin opposite and placed posteriorly on the body. Within the Dactylopteroidei, *Rhamphosus* shares some specialized features with the members of the family Pegasidae, including a variously developed nasal rostrum extensively ornamented with tubercles and spines (Rendahl 1930; Pietsch 1978; Palsson & Pietsch 1989), preopercle enormously expanded medially (Rendahl 1930; Pietsch 1978), hypurals (plus parhypural and uroneural) fused to form a solid bony plate (Pietsch 1978; Fujita 1990), and presence of a large rayless pterygiophore in the first dorsal fin (Pietsch 1978). These derived features may be considered as indicative of a genuine sister-group relationship between *Rhamphosus* and the Pegasidae, as formerly suggested by Pietsch (1978).

One of the most salient traits of *Rhamphosus* is the massive dorsal-fin spine, which is articulated anteriorly with a large median rayless pterygiophore. A very large dorsal-fin spine, in many ways similar to that characteristic of the species of the genus *Rhamphosus* is present in certain long-snouted syngnathiforms, including members of the family Centriscidae (e.g., *Macrorhamphosus*; Jurgensen 1908; Altermatt 1991), as well as in the Cretaceous *Gasterorhamphosus zuppichinii* from southern Italy (Sorbini 1981) and the Eocene *Protorhamphosus parvulus* from Turkmenistan (Danilchenko 1968). Although rayless pterygiophores have also been reported in *Macrorhamphosus*, these are not directly articulated with the expanded dorsal-fin spine (Jurgensen 1908; Altermatt 1991). Considering the presence of remarkable anatomical differences between these long-snouted syngnathiforms and *Rhamphosus*, it is very likely that the shared occurrence of an enormous dorsal-fin spine could be due to convergence, representing a further evidence of the rampant homoplasy characteristic of the syngnathiform lineage (see Orr 1995).

The presence of a massive dorsal-fin spine in *Rhamphosus* represents one of the most evident differences with the Pegasidae; a moderately enlarged first dorsal-fin spine is also distinctive of the members of the Dactylopteridae (Eschmeyer 1997). Pegasids lack a spinous dorsal fin, but like *Rhamphosus*, they exhibit a large rayless pterygiophore (Pietsch 1978; Orr 1995). Additional distinctive features of the pegasids, useful to separate them from *Rhamphosus*, include: body completely encased in fused dermal plates and tail encircled by bony rings, oral jaws toothless, premaxilla without ascending process, vertebral column comprising not more than 22 vertebrae, median-fin rays unbranched and unsegmented, second dorsal- and anal fins containing five rays; procurrent caudal-fin rays absent, three pectoral-fin radials, pelvic fin with a single short and modified spine used for "walking on the bottom" (Stivens 1964) plus two or three rays (Rendahl 1930; Pietsch 1978; Palsson & Pietsch 1989). In addition, pegasids (and dactylopterids) differ from *Rhamphosus* by having greatly enlarged and horizontally inserted pectoral fins.

Summarizing, substantial morphological evidence supports a placement of *Rhamphosus* within the Dactylopteroidei as sister-group to the family Pegasidae (Fig. 17). Given the phylogenetic rela-
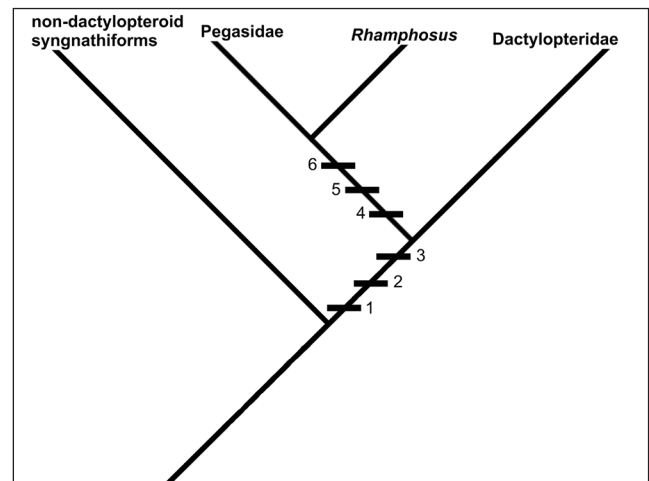


Fig. 17 - Cladogram showing hypothetical relationships of *Rhamphosus* within the Dactylopteroidei. Characters are: (1) nasal rostrum; (2) head encased by thick bony plates; (3) second dorsal and anal fins opposite and nearly equal in length; (4) preopercle enormously expanded medially; (5) rayless pterygiophore; (6) hypurals fused into a consolidated plate.

tionships hypothesized within the dactylopteroid fishes, the early Eocene age of *Rhamphosus* necessarily implies that both the Dactylopteridae and the Pegasidae were also in existence at that time. While the earliest confirmed representative of the Dactylopteridae, *Praevolitans faedoensis*, has been described based on a single specimen from late Eocene of Rio Faedo, in the vicinity of Priabona, northern Italy (Gayet & Barbin 1985), the fossil record of the Pegasidae remains elusive (see, e.g., Patterson 1993).

**Paleobiological remarks**

The overall physiognomy of the *Rhamphosus* species described herein, which includes the presence of a thick cranial bony armor and of a small and ventrally directed mouth, seems to indicate a benthic lifestyle, similar to that characteristic of the other dactylopteroids, the Dactylopteridae and the Pegasidae (e.g., Palsson & Pietsch 1989; Eschmeyer 1997). Goatley et al. (2010) considered the Rhamphosidae as daytime generalists, feeding on a broad array of easy-catch preys, such as small fishes or easily accessible benthic invertebrates. Such a hypothesis is partially confirmed by a cololite preserved in the holotype of *Rhamphosus biserratus* (MGPPD 8879) (Fig. 18), which shows different phosphatic fragments, including partially articulated vertebrae pertaining to small-sized fishes.

The overall configuration of the feeding apparatus of *Rhamphosus* is very similar to that

Fig. 18 - Cololite preserved in the ho-
lotype of *Rhamphosus biserra-
tus* Bassani, 1876, (MGPPD
8879) showing different
phosphatic fragments: in the
top left corner of the colo-
lite some partially articula-
ted vertebrae pertaining to
small-sized fished are visible.
Scale bar = 10 mm.

of pegasids described by Pietsch (1978, 1984), in which the elements of the upper and lower jaws are scarcely recognizable when the mouth is closed since they are covered by the lachrymal and folded and allocated within a cavity formed at the base of the rostrum (see, e.g., MCSNV T.429; Fig. 14A-B). Moreover, like in pegasids, there is no evidence of the palatine and pterygoids in the examined *Rhamphosus* specimens, although it is not possible to rule out that these skeletal elements were cartilaginous in origin. The peculiar jaw mechanism of the pegasids involves enlarged premaxillo-maxillary and maxillo-vomerine cartilages supported by premaxillomaxillary ligaments and strong ligaments extending from the dorsal portion of the maxilla to the ventral surface of the nasal rostrum; these cartilages and ligaments are closely associated with premaxillae, maxillae and dentaries to form a highly protrusible mouth (Pietsch 1978). When the upper jaw elements are unfolded and the mandible is completely depressed, pegasids are characterized by a very small buccal cavity, which becomes enormously expanded to form a long tubular mouth that allows the effective suction used to capture preys. Pietsch (1978) demonstrated that protrusion of the mouth in pegasids involves a single coupling by way of the hyoid apparatus. Given the substantial similarity of the bones of the feeding apparatus of *Rhamphosus* with those of pegasids, it is reasonable to hypothesize that these Eocene benthic fishes were characterized by a similar feeding mechanism.

As clearly demonstrated in the descriptive analysis of *Rhamphosus* above, the morphology of the rostrum is species-specific, showing a variety of forms from short and stout, to tubular, to enormously elongate and massive, to ovoid and spatulate. The possible function of the nasal rostrum in *Rhamphosus* is difficult to determine. However, considering the broad array of sizes and morphologies observed in the species of *Rhamphosus*, a pure defensive function appears to be unlikely, also because a horizontal bony extension located above and anterior to the jaws does not seem to offer the consistent defensive advantage that was certainly accorded by the massive first dorsal-fin spine, which is present in all the known species. The peculiar nasal rostrum of *Rhamphosus* likely was a multi-adaptative structure and we speculate that it also functioned as a sensory device. Although the thick and densely ornamented cranial bones prevented any observation of the cephalic sensory canals, it is likely that the cranial laterosensory system extended anteriorly into the nasals (like in pegasids; Pietsch 1978), which were probably occupied by the anterior terminations of the supraorbital and/or infraorbital canals. As described above, the nasal rostra of the majority of the *Rhamphosus* species exhibit a concavity along the anterior margin, which was probably connected with canals running through the entire length of the rostrum. As a matter of fact, an anterior extension of the sensory apparatus would have been beneficial for prey detection (see Johnson & Schnell 2015), especially for a benthic fish like *Rhamphosus*.

Overall, the rigid armored head, the variously developed rostrum and the enlarged first dorsal-fin spine characteristic of the *Rhamphosus* species result in a peculiar gestalt that is in some ways reminiscent of those of fossil and extant centriscoid fishes (e.g., Jurgensen 1908; Sorbini 1981; Bannikov & Carnevale 2012b) and of certain Cretaceous gladiopynodontids (e.g., Marramà et al. 2016). Centriscoid fishes (and likely also certain gladipycnodontids; Marramà et al. 2016d) can swim orienting the body vertically with the snout downwards primarily by sculling the pectoral fins (e.g., Stewart & Roberts 2004; Fish & Holzman 2019). This vertical posture is maintained by using the beating fins as the position of their center of buoyancy almost corresponds to the center of mass (Fish & Holzman 2019). The overall similarity with the body design of centriscoid fishes might suggest that *Rhamphosus* has a similar swimming capability, with the long anterior rostrum and first dorsal-fin spine counterbalancing each other to maintain a vertical posture over the substrate (when searching for food) possibly sculling the pectoral fins.

## References

Agassiz L. (1833-1844) - Recherches sur les poissons fossiles. Petitpierre, Neuchatel (four volumes, text and plates), 1420 pp.

Agassiz L. (1835a) - Revue critique des poissons fossiles figurés dans l'Ittiolitologia Veronese. Extraits de la 4me livre des Recherches sur les poissons fossiles, Neuchatel: Imprimerie de Petitpierre et Prince, 44 pp.

Agassiz L. (1835b) - Kritische revision der Ittiolitologia Veronese abgebildenten fossilen Fische. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1835: 290-316.

Agassiz L. (1839) - Recherches sur les poissons fossiles. 13 livraison. H. Nicolet (plates), Neuchâtel, vol. 4, pl. 26-36.

Agassiz L. (1942) - Recherches sur les poissons fossiles. 13 livraison. Petitpierre (text), Neuchâtel, vol 4, 205-291 pp.

Agassiz L. (1842-1846) - Nomenclator Zoologicus: continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum disposita, adjectis auctoribus, libris, in quibus reperiuntur, anno editionis, etymologia et familiis, ad quas pertinent, in singulis classibus. Soloduri, Sumtibus et typis Jent et Gassmann.

Agnini C., Fornaciari E., Raffi I., Catanzariti R., Palike H., Backman J. & Rio D. (2014) - Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes. *Newsletters on Stratigraphy*, 47: 131-181.

Allis E.P. (1909) - The cranial anatomy of the mail-cheeked fishes. *Zoologica*, 20: 1-219.

Altermatt R.U. (1991) - Zur Kopfanatomie des Schnepfenfisches *Macrorhamphosus scolopax* (Linnaeus, 1758) (Teleostei, Syngnathiformes). Eine beschreibend-morphologische Studie unter Berucksichtigung funktioneller Aspekte. Unpublished dissertation, Universität Basel, 117 pp.

Bannikov A.F. (2014) - The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Studi e Ricerche sui Giacimenti Terziari di Bolca,* 12: 23-34.

Bannikov A.F. & Carnevale G. (2010) - *Bellwoodilabrus landinii* n. gen., n. sp., a new genus and species of labrid fish (Teleostei, Perciformes) from the Eocene of Monte Bolca. *Geodiversitas*, 32: 201-220.

Bannikov A.F. & Carnevale G. (2012a) - *Frippia labroiformis* n. gen. n. sp., a new perciform fish from the Eocene of Pesciara di Bolca, Italy. *Bollettino della Societa Paleontologica Italiana*, 51: 155-165.

Bannikov A.F. & Carnevale G. (2012b) - A long-bodied centriscoid fish from the basal Eocene of Kabardino-Balkaria, northern Caucasus, Russia. *Naturwissenshaften*, 99: 379-389.

Bannikov A.F. & Carnevale G. (2017) - Eocene ghost pipefishes (Teleostei, Solenostomidae) from Monte Bolca, Italy. *Bollettino della Societa Paleontologica Italiana*, 56: 319-331.

Bassani F. (1876) - Pesci fossili nuovi del calcare eoceno di Monte Bolca. *Atti della società Veneto-Trentina di scienze naturali*, 5: 143-154.

Bassani F. (1898) - Aggiunte all'ittiofauna eocenica dei Monti Bolca e Postale con due tavole. *Paleontographia Italica*, 3: 77-88.

Bellwood R.D. & Wainwright P.C. (2002) - The history and biogeography of fishes on coral reefs. In: Sale P.F. (Ed.) - Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press.

Berg L.S. (1940) - Classification of fishes, both recent and fossil. *Trudy Zoologicheskogo Instituta*, 5: 85-517.

Berg L.S. (1947) - Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS*, 5: 88-517.

Betancur R., Wiley E.O., Arratia G., Acero A., Bailly N., Miya M., Lecointre G. & Ortí G. (2017) - Phylogenetic classification of bony fishes. *BMC Evolutionary Biology*, 17: 162.

Blot J. (1978) - Les Apodes fossiles du Monte Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 3: 1-260.

Blot J. (1980) - La faune ichthyologique des gisements du Monte Bolca (Province de Verone, Italie). Catalogue systematique prèsentant l'ètat actuel des 160 reserches

concernant cette faune. *Bulletin du Musèum national d'historie naturelle Paris*, 2: 339-396.

Blot J. (1984) - Les Apodes fossiles du Monte Bolca. II. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 4: 61-264.

Bonde N. (1966) - The fishes of the Mo-Clay Formation (Lower Eocene): A short review. *Meddelelser fra Dansk Geologisk Forening*, 16: 198-202.

Bronn H.G. & Roemer F. (1856) - Atlas zu H. G. Bronn's Lethea geognostica oder Abbildung und Beschreibung der fur dies Gebirgs-Formationen Bezeichnendsten Versteinerungen/bearbeitet von H.G. Bronn und F. Roemer. 3 Stark vermehrte Aufl; Stuttgart: E. Schweizerbart, 544 pp.

Carnevale G. (2006) - Morphology and biology of the Miocene butterflyfish *Chaetodon ficheuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society*, 146: 251-267.

Carnevale G. (2020) - I fossili di Bolca, icone della paleontologia italiana. *Geologicamente,* 2: 38-47.

Carnevale G. & Bannikov A.F. (2019) - A dragonet (Teleostei, Callionymoidei) from the Eocene of Monte Bolca, Italy. *Bollettino della Societa Paleontologica Italiana*, 58: 295-307.

Carnevale G., Bannikov A.F., Marramà G., Tyler T.C. & Zorzin R. (2014) - The Pesciara-Monte Postale Fossil-*Lagerstätte*. Fishes and other vertebrates. *Rendiconti della Società Paleontologica Italiana*, 4: 37-63.

Carnevale G. & Pietsch T.W. (2009) - An Eocene frogfish from Monte Bolca, Italy, the earliest known skeletal record for the family. *Palaeontology*, 52: 745-752.

Carnevale G. & Pietsch T. W. (2010) - Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae. *Zoological Journal of the Linnean Society*, 160: 621-647.

Carnevale G. & Pietsch T.W. (2011) - Batfishes from the Eocene of Monte Bolca. *Geological Magazine*, 148: 461-472.

Carnevale G. & Pietsch T.W. (2012) - †*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. *Journal of Systematic Palaeontology*, 10: 47-72.

Carnevale G., Pietsch T.W., Bonde N., Leal M.E.C. & Marramà G. (2020) - †*Neilpeartia ceratoi*, gen. et sp. nov., a new frogfish from the Eocene of Bolca, Italy. *Journal of Vertebrate Paleontology*, 40: e1778711.

Cerato M. (2011) - Cerato. I pescatori del tempo. Grafica Alpone, San Giovanni Ilarione, 180 pp.

Danilchenko P.G. (1968) - Ryby verkhnego paleotsena Turkmenii. In: Obruchev D.V. (Ed.) - Ocherki po filogenii i sistematike iskopayemykh ryb i bebeschelyustnykh. Nauka, Moscow, pp.113-156 [in Russian].

De Blainville H.D. (1818) - Des ichtyolites du Monte Bolca, ou Vestena Nuova dans le Veronais. *Nuoveau dictionnaire d'histoire naturelle*, 27: 334-361.

D'Erasmo G. (1922) - Catalogo dei pesci fossili delle tre Venezie. *Memorie dell'Istituto di Geologia della R. Università di Padova*, 6: 1-181.

Eastman C.R. (1911) - Catalog of fishes in the Carnegie Museum. Part I. Fishes from the Upper Eocene of Monte Bolca. *Memoirs of the Carnegie Museum*, 4: 349-391.

Eastman C.R. (1914) - Catalogue of the fossil fishes in the Carnegie Museum. Part II. *Memoirs of the Carnegie Museum*, 6: 315-348.

Eschmeyer W.N. (1997) - A new species of Dactylopteridae (Pisces) from the Philippines and Australia, with a brief synopsis of the family. *Bulletin of Marine Science*, 60: 727-738.

Fish F.E. & Holzman R. (2019) - Swimming turned on its head: stability and manoeuvrability of the shrimpfish (*Aeoliscus punctulatus*). *Integrative Organismal Biology*, 1: 1-14.

Friedman M. & Carnevale G. (2018) - The Bolca Lagerstatten: shallow marine life in the Eocene. *Journal of the Geological Society*, 175: 569-579.

Fujita K. (1990) - The Caudal Skeleton of Teleostean Fishes. Tokai University Press, Tokyo, 897 pp.

Gaudant J. (2011) - La publication de l'*Ittiolitologia Veronese* (1796-1809): Le triomphe de l'obstination au service d'une entreprise scientifique hors norme. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 13: 67-133.

Gayet M. & Barbin V. (1985) - Cephalacanthidae fossile du Priabonien des environs de Priabona (Italie). *Bulletin du Museum National d'Hisorie Naturelle*, Paris, 4e sér., 7, section C, n° 4: 263-283.

Giebel C. G. (1848) - Fauna der Vorwelt. 1, 3: Fische, pp. 97-100.

Gill T. (1884) - On the mutual relationships of the Hemibranchiate Fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 36: 154-166.

Gill T. (1890) - The characteristics of the Dactylopteroidea. *Proceedings of the United States National Museum*, 13: 243-248.

Goatley C.H.R., Bellwood D.R. & Bellwood O. (2010) - Fishes on coral reefs: changing roles over the past 240 million years. *Paleobiology*, 36: 415-427.

Greenwood P.H., Rosen D.E., Weitzman S.H. & Myers G.S. (1966) - Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, 131: 339-456.

ICZN (1999) - International Code of Zoological Nomenclature. Fourth Edition. http://iczn.org.code.

Imamura H. (2000) - An alternative hypothesis on the phylogenetic position of the family Dactylopteridae (Pisces: Teleostei), with a proposed new classification. *Ichthyological Research*, 47: 203-222.

Johnson G.D. & Patterson C. (1993) - Percomorph phylogeny: A survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, 52: 554-626.

Johnson G.D. & Schnell N.K. (2015) - Development of the rostrum and upper jaws in squirrelfishes and soldierfishes (Beryciformes: Holocentridae): A unique ontogenetic trajectory. *Copeia*, 103: 902-919.

Jurgensen H.F.E. (1908) - Ichthyotomical Contributions I. The structure of the genera *Amphisile* and *Centriscus*. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Raekke, Naturvidenskabeligog Matematisk Afdeling*, 6: 41-109.

Kawahara R., Miya M., Mabuchi K., Lavoué S., Inouem J.G., Satoh T.P., Kawaguchi A. & Nishida M. (2008) - Interrelationships of the 11 gasterosteiform families (sticklebacks, pipefishes, and their relatives): a new perspective based on whole mitogenome sequences from 75 higher teleosts. *Molecular Phylogenetics and Evolution*, 46: 224-236.

Longo S.J., Faircloth B.C., Meyer A., Westneat M.W., Alfaro M.E. & Wainwright P.C. (2017) - Phylogenomic analysis of a rapid radiation of misfit fishes (Syngnathiformes) using ultraconserved elements. *Molecular Phylogenetics and Evolution*, 113: 33-48.

Marramà G., Bannikov A.F., Kriwet J. & Carnevale G.

(2019) - An Eocene paraclupeid fish (Teleostei, Ellimmichthyiformes) from Bolca, Italy: the youngest marine record of double-armored herrings. *Papers in Palaeontology*, 5: 83-98.

Marramà G., Bannikov A.F., Tyler J.C., Zorzin R. & Carnevale G. (2016a) - Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the paleoecology and taphonomy of the fishes of assemblage of the Eocene Bolca Konservat Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.

Marramà G. & Carnevale G. (2015a) - Eocene round herring from Monte Bolca, Italy. *Acta Palaeontologica Polonica*, 60: 701-710.

Marramà G. & Carnevale G. (2015b) - The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy, and paleobiology. *Journal of Vertebrate Paleontology*, 35: e1014490.

Marramà G. & Carnevale G. (2016) - An Eocene anchovy from Monte Bolca, Italy: the earliest known record for the family Engraulidae. *Geological Magazine*, 153: 84-94.

Marramà G. & Carnevale G. (2018) - *Eoalosa janvieri* gen. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca, Italy. *Paläontologische Zeitschrift*, 92: 107-120.

Marramà G., Carnevale G. & Kriwet J. (2021) - Diversity, palaeoecology and palaeoenvironmental significance of the Eocene chondrichthyan assemblages of the Bolca Lagerstätte, Italy. *Lethaia*, 54: 736-751.

Marramà G., Garbelli C. & Carnevale G. (2016b) - A morphospace for the Eocene fish assemblage of Bolca, Italy: A window into the diversification and ecological rise to dominance of modern tropical marine fishes. *Bollettino della Societa Paleontologica Italiana*, 55: 11-21.

Marramà G., Garbelli C. & Carnevale G. (2016c) - A clade-level morphospace for the Eocene fishes of Bolca: Patterns and relationships with modern tropical shallow marine assemblages. *Bollettino della Societa Paleontologica Italiana*, 55: 139-156.

Marramà G., Villalobos-Segura E., Zorzin R., Kriwet J. & Carnevale G. (2023) - The evolutionary origin of the durophagous pelagic stingray ecomorph. *Palaeontology*, 66. e12669.

Marramà G., Villier B., Dalla Vecchia F.M. & Carnevale G. (2016d) - A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. *Cretaceous Research*, 61: 34-43.

Martini E. (1971) - Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci A. (Ed.) - Proceedings of the 2nd Planktonic Conference, vol. 2. Edizioni Tecnoscienza, Roma: 739-785.

Near T.J., Dornburg A., Eytan R.I., Keck B.P., Smith W.L., Kuhn K.L., Moore J.A., Price S.A., Burbrink F.T., Friedman M. & Wainwright P.C. (2013) - Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Sciences of the United States of America*, 110: 12738-12743.

Nelson J.S., Grande T.C. & Wilson M.H.V. (2016) - Fishes of the World. 5th ed. Wiley, Hoboken, 707 pp.

Nielsen E. (1960) - A new Eocene teleost from Denmark. *Meddelelser fra Dansk Geologisk Forening*, 14: 247-252.

Orr J.W. (1995) - Phylogenetic Relationships of Gasterosteiform Fishes (Teleostei: Acanthomorpha). Unpublished PhD Thesis, University of Washington, Seattle, 813 pp.

Palsson W.A. & Pietsch T.W. (1989) - Revision of the acanthopterygian fish family Pegasidae (Order Gasterosteiformes). *Indo-Pacific Fishes*, 18: 1-38.

Papazzoni C.A. & Trevisani E. (2006) - Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the 'Pesciara di Bolca' (Verona, northern Italy): an early Eocene Fossil-Lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 21-35.

Papazzoni C.A., Bassi D., Fornaciari E., Giusberti L., Luciani V., Mietto P., Roghi G. & Trevisani E. (2014) - Geological and stratigraphical setting of the Bolca area. *Rendiconti della Società Paleontologica Italiana*, 4: 19-28.

Papazzoni C.A., Fornaciari E., Giusberti L., Vescogni A. & Fornaciari B. (2017) - Integrating shallow benthic and calcareous nannofossil zones: the Lower Eocene of the Monte Postale section (northern Italy). *Palaios*, 32: 6-17.

Pasini G., Garassino A., Roberto Z. & Giusberti L. (2022) - An unexpected Cenozoic record of palinurid lobsters (Achelata) from the lower Eocene of "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza), northeastern Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 19: 5-34.

Patterson C. (1993) - Osteichthyes: Teleostei: 621-656. In: M. J. Benton (Ed.) - The Fossil Record 2. Chapman & Hall, London.

Pietsch T.W. (1978) - Evolutionary relationships of sea moths (Teleostei: Pegasidae) with a classification of gasterosteiform families. *Copeia*, 1978: 517-529.

Pietsch T.W. (1984) - Enlarged cartilages in the protrusible upper jaws of teleost fishes: phylogenetic and functional implications. *Copeia*, 1984: 1011-1015.

Pietsch T.W. & Carnevale G. (2011) - A new genus and species of anglerfish (Teleostei: Lophiiformes: Lophiidae) from the Eocene of Monte Bolca, Italy. *Copeia*, 2011: 64-71.

Rendahl H. (1930) - Pegasiden-Studien. *Arkiv för Zoologi*, 21: 1-56.

Riva F. (1966) - Le avventurose vicende dell'Ittiolitologia veronese del can. Giovanni Serafino Volta mantovano. *Civiltà Mantovana*, 1: 71-77.

Rohlf F.J. (2005) - tpsDig, version 2.04. Department of Ecology and Evolution, State University of New York, Stony Brook.

Sanciangco M.D., Carpenter K.E. & Betancur R.-R. (2016) - Phylogenetic placement of enigmatic percomorph families (Teleostei: Percomorphaceae). *Molecular Phylogenetics and Evolution*, 94: 565-576.

Santaquiteria A., Siqueira A.C., Duarte-Ribeiro E., Carnevale G., White W.T., Pogonoski J.J., Baldwin C.J., Ortì G., Arcila D. & Betancur R. (2021) - Phylogenomics and historical biogeography of seahorses, dragonets, goatfishes, and allies (Teleostei: Syngnatharia): assessing factors driving uncertainty in biogeographic inferences. *Systematic Biology*, 70: 1145-1162.

Sierra-Kiel J., Hottinger L., Caus E., Drobne K., Ferràndez C., Jauhri A.K., Less G., Pavlovec R., Pignatti J., Samsò J. M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998) - Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France*, 169: 281-299.

Song H.Y., Mabuchi K., Satoh T.P., Moore J.A., Yamanoue Y., Miya M. & Nishida M. (2014) - Mitogenomic circumscription of a novel percomorph fish clade

mainly comprising "Syngnathoidei" (Teleostei). *Gene*, 542: 146-155.

Sorbini L. (1975) - Gli Holocentridae di M. Bolca, II: *Tenuicentrum pattersoni* (nov. gen., nov. sp.). Nuovi dati a favore dell'origine monofiletica dei Beryciformi (Pisces). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 455-472.

Sorbini L. (1981) - Cretaceous fishes of Nardò. I. Order Gasterosteiformes (Pisces). *Bollettino del Museo Civico di Storia Naturale di Verona*, 8: 1-27.

Sorbini L. (1983) - La collezione Baja di pesci e piante fossili di Bolca. Museo Civico di Storia Naturale, Verona, 117 pp.

Sorbini L. (1984) - Les Holocentridae du Monte Bolca, III: *Berybolcensis leptacanthus* (Agassiz). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 4: 19-35.

Sorbini L. & Tirapelle R. (1975) - Gli Holocentridae di M. Bolca, I: *Eoholocentrum* (nov. gen.), *Eoholocentrum macrocephalum* (de Blainville) (Pisces, Actinopterygii). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 206-228.

Stewart A.L. & Roberts C.D. (2004) - New Zealand bellowfishes. *Seafood New Zealand*, 12: 61-63.

Stivens D. (1964) - Queer fish - they like to walk. *Frontiers*, 1964: 136-138.

Trevisani E., Papazzoni C.A., Ragazzi E. & Roghi G. (2005) - Early Eocene amber from the "Pesciara di Bolca" (Lessini Mountains, Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 223: 260-274.

Tyler J.C. (2004) - Review of the species of the Eocene of Monte Bolca, Italy, fish family Aulorhamphidae, new, related to Gasterosteiformes. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 37-54.

Tyler J.C. & Santini F. (2002) - Review and reconstruction of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 9: 47-119.

Vaillant L. (1888) - Expeditions Scientifiques du Travailleur et du Talisman 1880-1883. V.1 Poissons, G. Masson, Paris, 406 pp.

Volta G.S. (1796-1809) - Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti fossili veronesi. Stamperia Giuliari, Verona, I-LII+I-CCCXXIII, pl. I-LXXVI.

Woodward A.S. (1888) - Guide to the collection of fossil fishes in the department of Geology and Palaeontology, British Museum. 81 Woodcuts 8vo. 4d., VIII+51 pp.

Woodward A.S. (1901) - Catalogue of the fossil fishes in the British Museum (Natural History). Part IV. London: British Museum (Natural History), 636 pp.

Zorzin R. (2022) - Fossili e Rocce del Veronese. Cierre Edizioni, Verona, 224 pp.