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THE YPRESIAN FISHES OF THE SOLTERI *LAGERSTÄTTE* (TRENTO, NORTHERN ITALY): A GLIMPSE INTO THE EARLY EOCENE TETHYAN MESOPELAGIC ASSEMBLAGES

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Keywords: bathyal; Teleostei; taxonomy; new taxa; early Paleogene; Tethys.

Abstract. A Ypresian fish-bearing site was discovered in the late 1970s at Solteri (Trento, northern Italy), but its ichthyofauna, dominated by pelagic bony fishes, remained almost completely neglected for decades despite its potential interest. In fact, it represents the nearly coeval pelagic equivalent of the *Lagerstätten* of Bolca (Verona province, northeastern Italy), worldwide known for their extremely abundant and diversified, reef-associated fish fauna. The Solteri ichthyofauna, represented by almost 300 specimens, comprises what appears to be a mesopelagic assemblage including stomiiforms (Gonostomatidae and Phosichthyidae), myctophiforms (Myctophidae) and certain percomorphs (Gempylidae and Centrolophidae), most of them represented by new, so far undescribed taxa, of which the following are established herein: *Ammutichthys loricatus* n. gen. et sp., *Eogorgon bizzarinii* n. gen. et sp., *Eomyctophum mainardii* n. sp., *Erebusia tenebrae* n. gen. et sp. *Krampusichthys tridentinus* n. gen. et sp., *Laurinichthys boschelei* n. gen. et sp., *Scopeloides bellator* n. sp., *Scopeloides violator* n. sp., *Solterichthys macrognathus* n. gen. et sp., and *Wudelenia diabolica* n. gen. et sp. Solteri is of extreme relevance not only because it represents one of the most ancient Cenozoic deep-water *Lagerstätten* known, but it also allows us to define the structure of the western Tethyan pelagic fish communities during the demise of the Early Eocene Climatic Optimum (EECO), the interval of the Cenozoic with the warmest long-term global average temperature and highest CO_2 levels (Filippi et al. 2024).

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Introduction

The European Paleogene fish record is one of the richest and most diversified in the world, with many sites of the Tethys and Paratethys documenting a variety of faunal assemblages (Bannikov & Erebakan 2023). Especially for the lower Paleogene, several localities show exquisite preservation of their fossil content, such as the lower Ypresian Fur Formation deposits of Denmark, which may comprise up to 60 species of bony fishes (Bonde 1966; Schrøder et al. 2023). Another relevant teleost assemblage that includes slightly less than 40 fish taxa is known from the Danata Formation (Turkmenistan), from strata that record the Paleocene–Eocene Thermal Maximum (PETM), a global warming event (Danil'chenko 1968; Bannikov 2010; Shcherbinina et al. 2016). Younger productive localities are those of the upper Ypresian London Clay Formation, England, with the peculiar three-dimensional preservation of its fossils (Casier 1966; Friedman et al. 2016), and the Pesciara and Monte Postale *Lagerstätten* of Bolca (northeastern Italy), which include about 250 bony fish species belonging to about 200 genera (Bannikov 2014; Carnevale et al. 2014). This area, located in the western portion of the Tethys Ocean, was part of an ancient biodiversity hotspot comparable to the current Indo-Pacific hotspot (Renema et al. 2008; Carnevale 2020). However, all these localities derive from neritic depositional settings, and, among the Tethyan fossil sites, those that reflect a deep-water ecosystem are extremely rare (Bannikov & Erebakan 2023). One of the few lower Eocene bathyal sites is that of Monte Solane (Verona province, Italy), which represents one of the oldest Cenozoic pelagic sites (late Ypresian, 50.4–49.1 Ma; Giusberti et al. 2014). At Monte Solane, more than 200 fossils have been retrieved, most of them pertaining to fish taxa typical of the mesopelagic zone. These fish assemblages are crucial in better defining the structure and composition of the pelagic fish communities in the aftermath of the K/Pg event, when a remarkable radiation of teleost fishes took place (Bannikov & Erebakan 2023). Not far from Solane, at the end of the 1970s, a pelagic fish-bearing *Lagerstätte* was discovered at Solteri, in the vicinity of the city of Trento (Trentino-Alto Adige region, northern Italy; see Venzo et al. 1986; Fig. 1). However, this site has never received proper attention except for preliminary stratigraphical studies that referred the fish-bearing beds to the Ypresian (Venzo et al. 1986), and for the recent description of its peculiar crustacean fauna (Garassino et al. 2024). The mesopelagic nature of this *Lagerstätte* is reflected by the fish assemblage, which comprises taxa that today typically live at depths below 200 m (i.e., Stomiiformes, Myctophiformes, Centrolophidae, and Gempylidae; Nakamura & Parin 1993; Harold 2002; Paxton & Hulley 2002). The upper bathyal setting is also corroborated by micropaleontological analyses that show how foraminiferal faunas are strikingly dominated by planktic foraminifera (planktic/benthic ratio is higher than 80–90%, indicating at least upper bathyal deposition, Garassino et al. 2024). The goal of this paper is to describe in detail the lower Eocene ichthyofauna of Solteri and to highlight its importance in expanding the knowledge of the pelagic faunas of the early Paleogene.

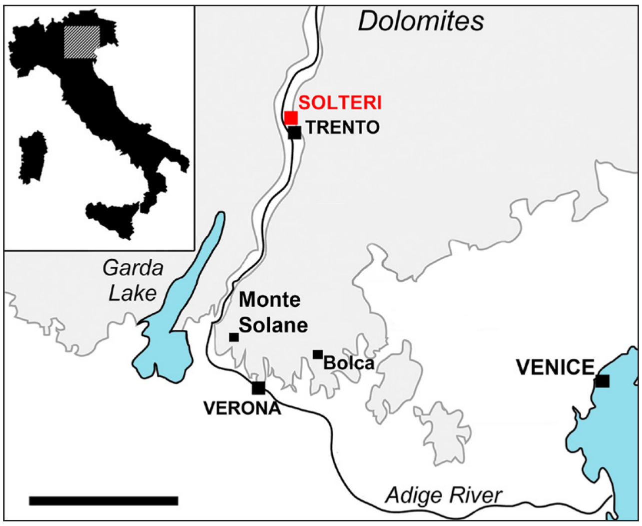


Fig. 1 - Sketch map showing the location of Solteri. Scale bar 50 km.

Geological setting

The fossils examined in this study come from an abandoned quarry (Angelini Quarry) located at Solteri on the northern outskirts of Trento (Trentino Alto-Adige, northern Italy; Fig. 1). In 1979, the succession cropping out around the Angelini Quarry was surveyed, and paleontological excavations were carried out in the fish-bearing bed. The section of Solteri (total thickness=65 m; Fig. 2) occurs at the core of a syncline with a NE-SW dip direction and was studied in detail stratigraphically and sedi-

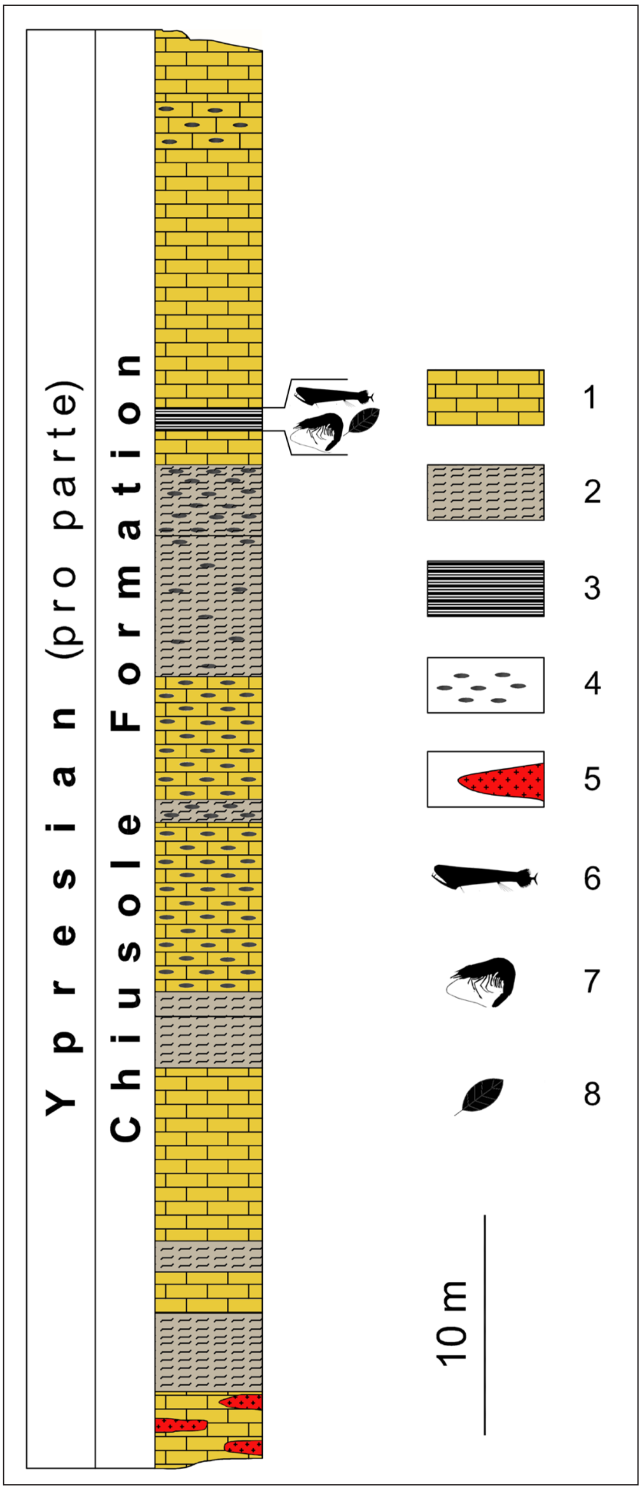


Fig. 2 - Stratigraphic log of the Chiusole Formation in the Solteri site (Trento) with indication of the fossiliferous interval (modified from Garassino et al. 2024). Legend: 1) limestones and marly limestones; 2) calcareous marls; 3) organic-rich black laminated calcareous marl; 4) chert; 5) hyaloclastites; 6) fish; 7) crustaceans; 8) vegetal remains. Fish and crustacean silhouettes from www.phylopic.org.

mentologically by Venzo et al. (1986). It belongs to the Chiusole Formation (e.g., Garassino et al. 2024) and mainly consists of greyish cherty limestones and marls, with black-greenish hyaloclastites occurring at its base and recently ascribed to the Lenzima Member of the Val Lagarina Basalt (Avanzini et al. 2010). According to Venzo et al. (1986), the fossiliferous interval is located in the upper half of the Solteri section and consists of a ca. 1.5 m thick package of black marls and calcareous marls characterized by thin lamination ("member XIV" of Venzo et al. 1986). Based on the planktic foraminiferal content, the section was referred by Venzo et al. (1986) to the Ypresian (early Eocene), and the fish assemblage was considered not much older than the famous fish *Konservat-Lagerstätte* of the Pesciara di Bolca (Fig. 1), deposited in a peri-reefal setting (e.g., Papazzoni & Trevisani 2006; Marramà et al. 2016, 2021). According to Venzo et al. (1986), the sedimentary rocks of Solteri document a persisting pelagic environment that records an upward oxygen content depletion in the water column, culminating in an anoxic environment that led to the deposition of the organic-rich, laminated lithology of the fossil-bearing bed. Avanzini et al. (2010) stated that the Chiusole Formation in the Trento area would indicate more periplatform deposit affinity rather than basinal affinity. Currently, most of the original Solteri section still crops out (including the fossiliferous horizon), even if protected by a metal rockfall drapery mesh. Around ten years ago, the fossiliferous interval was sampled by one of us (L.G.) in collaboration with staff from the Museo delle Scienze, Trento (MUSE) for stratigraphic investigations (Calzoni et al. in prep.). More detailed micropaleontological analyses on the calcareous nannofossils and planktic foraminifera are currently underway to achieve detailed stratigraphic correlation of Solteri with the nearly coeval and geographically close Monte Solane and Bolca fish localities (see Giusberti et al. 2014; Fig. 1).

Bony fishes constitute most of the fossils found at Solteri (almost 85%), while invertebrates are very uncommon and mainly represented by decapod crustaceans (e.g., Caridea, Penaeoidea, and Astacida), recently described by Garassino et al. (2024; Fig. 3A–B). Vegetal remains are mainly represented by red algae (cf. *Delesserites* Sternberg, 1883) and seagrasses (9%; Fig. 3D–G), along with other indeterminable remains. Sparse ichnofossils from the site have also been found in the collections of the Museo delle Scienze, Trento.

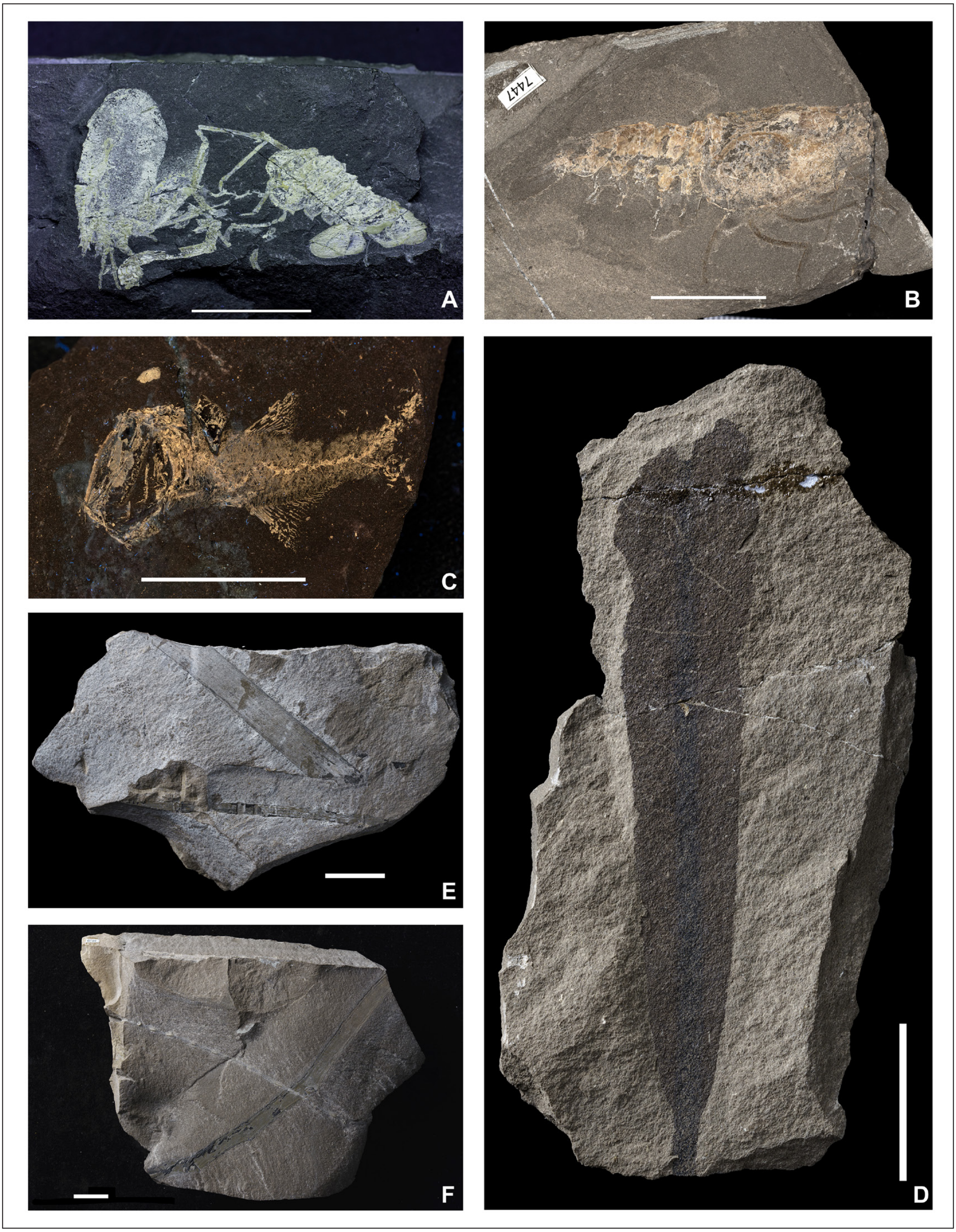


Fig. 3 - Selected fossils from the Solteri site. Under UV light: *Trentastacus levis* Garassino et al., 2024, MUSE-PAL 5542 (A). In natural light: undetermined Caridea, MUSE-PAL 7447 (B); under UV light: *Scopeloides bellator* n. sp., MUSE-PAL 1076 (C); Rhodophyta (cf. *Delesserites*), MUSE-PAL 3110 (D); undetermined marine seagrass, MUSE-PAL 6834, MUSE-PAL 6829 (E–F). Scale bars 20 mm (A–F).

MATERIALS AND METHODS

The material examined in this study includes 292 articulated skeletal remains of teleost fishes. The specimens are mainly housed in the collection of the Museo delle Scienze, Trento, and the Museo di Scienze e Archeologia, Rovereto. Photos of the specimens were taken using a Sony α7R3 camera mounting a Sony FE 2.8/90 mm macro G OSS lens. Various specimens were photographed under UV light to emphasize the osteological details by creating a distinct contrast in colour with the surrounding matrix. UV-A (peak emission at 368 nm), UV-B (peak emission at 318 nm), and UV-C (peak emission at 254 nm) wavelengths were produced with a 95 W discharge lamp from WayTooCool LLC. Most of the specimens were photographed with a combination of the three different wavelengths to have a greater contrast between the fossil and the matrix. The lamp was used with a custom design to better photograph the specimens; it was leaned on a wooden box perpendicular to the specimens and placed on a cardboard frame, obscured by different black fabrics to keep out the external light, to avoid the reflectiveness on the inside of the box and to protect the operator from any UV radiation. The specimens were studied with a stereomicroscope Wild Heerbrugg M5 equipped with a camera lucida drawing arm. Measurements were taken directly on the specimens using a digital caliper.

Institutional abbreviations: MCR: Museo di Scienze e Archeologia di Rovereto, Rovereto (Trento), MGP-PD: Museo della Natura e dell'Uomo dell'Università di Padova, Padova, MUSE-PAL, MUSE-PAL-SB: MUSE–Museo delle Scienze di Trento, Trento.

Anatomical abbreviations: aa: anguloarticular; AC: series of photophores posterior to the anal-fin origin; AO: anal organs; achy: anterior ceratohyal; afr: anal-fin ray; apt: anal-fin pterygiophore; art: articular; asmx: anterior supramaxilla; br: branchiostegal rays; bas: basipterygium; bsph: basisphenoid; cb: ceratobranchial; cor: coracoid; cl: cleithrum; dfpt: dorsal-fin pterygiophore; dfr: dorsal-fin ray; dfs: dorsal-fin spine; den: dentary; dpcl: dorsal postcleithrum; ect: ectopterygoid; end: endopterygoid; ep: epural; epi: epioccipital; epin: epineural; epipl: epipleural; fr: frontal; h: hypural; hh: ventral hypohyal; hsp: haemal spine; hspu2: haemal spine of the second preural vertebra; hspu3: haemal spine of the third preural vertebra; hyo: hyomandibula; iop: interopercle; IO: infraorbital; IP: isthmus photophore; la: lachrymal; let: lateral ethmoid; mes: mesethmoid; mtp: metapterygoid; mx: maxilla; na: nasal; nsp: neural spine; nspu2: neural spine of the second preural vertebra; nspu3: neural spine of the third preural vertebra; ORB1: preorbital photophore; ORB2: postorbital photophore; op: opercle; pa: parietal; pal: palatine; pchy: posterior ceratohyal; pcl: postcleithrum; pfr: pectoral-fin ray; ph: parhypural; pmx: premaxilla; pop: preopercle; pro: prootic; psmx: posterior supramaxilla; psp: parasphenoid; pto: pterotic; pts: pterosphenoid; ptt: posttemporal; PV: series of photophores between the bases of the pectoral and pelvic fins; q: quadrate; r: rays; rad: pectoral-fin radial; rart: retroarticular; rib: rib; sca: scapula; scl: supracleithrum; smx: supramaxilla; sn: supraneural; soc: supraoccipital; sop: subopercle; sph: sphenotic; steg: stegural; sym: symplectic; u: ural centrum; uhy: urohyal; un: uroneural; v: vertebra; vfr: pelvic-fin ray; VLO: supraventral organ; VO: ventral organs; vom: vomer; vpcl: ventral postcleithrum.

Measurement abbreviations: AFL: anal-fin base length; AFR; anal-fin ray length; ARL: anal-fin ray length; BD: maximum body depth; CPH: caudal peduncle height; CPL: caudal peduncle length; DFL: dorsal-fin base length; DRL: dorsal-fin ray length; HL: head length; O: orbit diameter; PA: preanal distance; PD: predorsal distance; PFL: pectoral-fin length; POO: postorbital distance; PRO: preorbital distance; PP: prepectoral distance; PV: prepelvic distance; PVD: distance between pectoral and pelvic fins; SL: standard length; TL: total length; VAD: distance between pelvic and anal fins; VFL: pelvic-fin length.

SYSTEMATIC PALEONTOLOGY

Infraclass **TELEOSTEI** Müller, 1845, *sensu* Arratia, 1999
Order **Stomiiformes** *sensu* Harold & Weitzman, 1996
Family Phosichthyidae Weitzman, 1974
Genus *Solterichthys* n. gen.

Type species (by monotypy): *Solterichthys macrognathus* n. gen. et sp.

Etymology: genus named after the type locality of Solteri (Trento Province, Italy), and the Greek word "ἰχθύς" meaning fish.

Diagnosis: A genus of the Phosichthyidae unique by having the following combination of features: mouth large with an elongate premaxilla that extends for more than half of the length of the maxilla, bearing about 30 minute needle-like teeth; maxilla bearing at least 12 needle-like teeth slightly longer than the premaxillary ones; mandibular joint behind the posterior edge of the orbit; lower jaw about the same size as the upper jaw and bearing about 20 needle-like teeth; 12 branchiostegal rays; pectoral fin with 13 rays, extending backwards up to the base of the pelvic girdle.

Remarks. This genus is referred to the family Phosichthyidae based on the presence of a greatly elongate premaxilla, which reaches more than half of the length of the maxilla, jaw teeth uniform in size, presence of photophores of the IP series, and presence of the post-orbital photophore (ORB2; Prokofiev 2005).

These features allow to exclude any possible attribution to the family Gonostomatidae, whose members are usually characterized by a premaxilla corresponding to one third or less of the length of the maxilla, teeth of different size forming an alternated pattern of long conical teeth separated by minute needle-like elements, and lack of ORB2 photophore as well as of photophores of the IP series (Harold 1998).

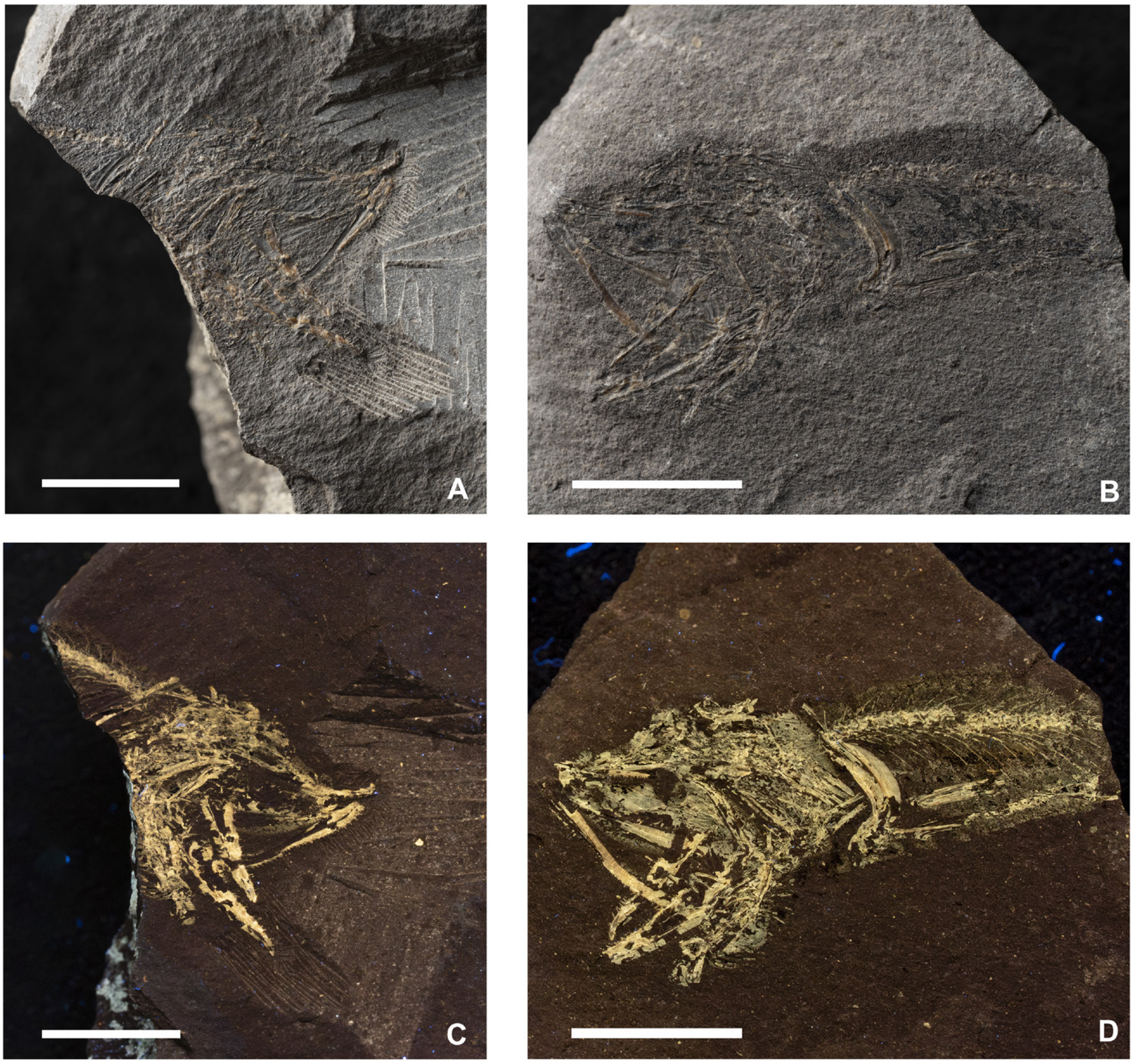


Fig. 4 - *Solterichthys macrognathus* n. gen. et sp. Lateral view of the holotype, MUSE-PAL 6792-6814, in natural light (A–B) and under UV light (C–D). Scale bars 10 mm.

Solterichthys macrognathus n. gen. et sp.

Figs. 4–6

Holotype (by monotypy): MUSE-PAL 6792-6814, an incomplete articulated skeleton lacking the posterior portion of the axial skeleton, including the median fins, in part and counterpart.

Etymology: Species named after the Latin *"macro"* meaning "big" and from the Greek *"γνάθος"* meaning "jaw".

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. The holotype, and only available specimen, is an incomplete articulated skeleton in part and counterpart, comprising only the head and the anterior portion of the body. The specimen has a preserved length of 33.8 mm, measured from the tip of the premaxilla to the last preserved vertebra. Overall, the body is rather slender and laterally compressed, showing its maximum depth in the head region. The mouth is terminal and large, with the mandibular joint located behind the posterior edge of the orbit (Figs. 4-5). The bones of the neurocranium are thin and delicate. The frontals are long, narrow, and triangular in outline, extending posteriorly behind the orbit. The parasphenoid is a thin, narrow, rod-like bone, passing through the

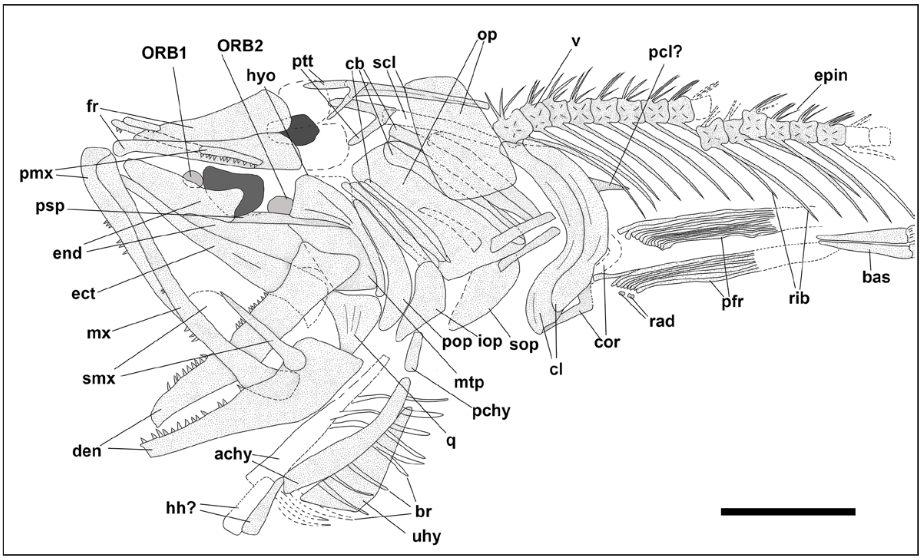


Fig. 5 - *Solterichthys macrognathus* n. gen. et sp. Holotype, MUSE-PAL 6792, interpretive reconstruction of the specimen. Scale bar 5 mm.

lower third of the orbit. The other bones of the neurocranium are poorly preserved and difficult to describe.

The upper jaw bears numerous teeth along the entire upper edge of the mouth. The premaxilla is straight and narrow, slightly more than half of the maxilla in length (54%) and bears a short triangular ascending process; the premaxilla bears about 30 small needle-like teeth, equally spaced and similar in size (Figs. 4–6). The maxilla is long, curved, and slightly expanded posteriorly, with equally developed needle-like teeth (of which at least 12 are preserved), slightly greater in size compared to those of the premaxilla. Of the anterior supramaxilla, only a feeble elliptic impression can be recognized (see MUSE-PAL 6792; Fig. 5), extending almost until the mid-length of the maxilla. The posterior supramaxilla is partially preserved, showing a slightly curved wedge-like shape, with a rounded base tapering into a pointed tip (see MUSE-PAL 6792; Fig. 5). The lower jaw is almost triangular in outline, with a short and vertical symphysis. The dentary is large and bears numerous small teeth similar in size and shape to those of the upper jaw. The anguloarticular is triangular in outline, and it is closely articulated to the dentary, occupying the posterior third of the lower jaw. The retroarticular is difficult to recognize.

The suspensorium is inclined forward. The quadrate is triangular in outline. The symplectic is not preserved. The ectopterygoid is straight, thin, posteriorly expanded, and slightly curved downwards. The endopterygoid has a triangular shape, while the metapterygoid is quadrangular. The hyomandibula is elongate and slightly curved anterodorsally; it has a narrow rod-like shaft and a broad dorsal triangular articular head; the opercular process is very short.

The preopercle is thin and ventrally curved, with an anterior margin closely associated with the hyomandibula. The opercle has a rectangular outline. The subopercle is poorly preserved and has rounded posterior and ventral margins. The interopercle is oblong and almost elliptical in outline.

At least 12 branchiostegal rays are preserved, mostly articulated to the long and rod-like anterior ceratohyal. The posterior ceratohyal is short and compact, while the hypohyals are subrectangular. The urohyal is broad and triangular (see MUSE-PAL 6792; Fig. 5), with a straight dorsal margin. Of the branchial arches, rod-like ceratobranchials bearing long gill rakers with small indentations are clearly exposed in MUSE-PAL 6814; Fig. 4D).

Of the vertebral column, only 20 abdominal vertebrae are preserved. The centra are almost squared, although some of them are rectangular, slightly longer than high. The contralateral neural arches and spines are not fused to each other. Long and curved ribs, not reaching the ventral margin of the body, articulate with the lateral sides of the vertebrae, except for the two anteriormost. Thin epineurals articulate with the base of the neural arches of all the vertebrae. The caudal portion of the vertebral column, including the caudal skeleton and the unpaired fins, is not preserved.

Some supraneurals are scarcely recognizable due to inadequate preservation.

The pectoral girdle is exposed in MUSE-PAL 6792 (Fig. 5). The posttemporal is relatively small and anteriorly bifurcated, bearing two anterior processes that articulate with the neurocranium. The crescent-shaped cleithrum is the largest bone of the pectoral girdle. The supracleithrum is thin and narrow. The coracoid is poorly preserved, and the scapula cannot be recognized at all. A single thin, curved and distally pointed postcleithrum is preserved (see MUSE-PAL 6792; Fig. 5). Only two ventral pectoral-fin radials are feebly recognizable. The pectoral fin is thin and elongate, inserting ventrally on the body. 13 pectoral-fin rays extend posteriorly up to the basipterygium.

The basipterygium is narrow and triangular, with very short iliac and ischial processes. The pelvic fins are not preserved.

Only a few photophores are recognizable. The photophores of the IP series are clearly recognizable in MUSE-PAL 6792. Other preserved photophores belong to the ORB series, including both the pre-orbital (ORB1) and the post-orbital photophore (ORB2). The pre-orbital photophore is placed above the anterior part of the ectopterygoid in front of the orbit, while the post-orbital photophore is placed posteroventrally to the orbit, over the pterygoids and anterior to the hyomandibula (Fig. 5). There is no evidence of the original squamation.

Discussion. Recent phylogenetic studies based on molecular and morphological data recognize the Phosichthyidae as non-monophyletic and include the genera traditionally referred to this family, plus *Triplophos* Bauer, 1902 (previously classified as a Gonostomatidae) within the Stomiidae (Smith et al. 2024). However, since there are still substantial morphological differences between the two families, for the sake of convenience, we still consider the Phosichthyidae as a separate family, following the classification of Nelson et al. (2016).

The Paleogene record of the family Phosichtyidae includes *Sytchevskia distincta* Danil'chenko, 1962 from the Eocene of Georgia (the Lutetian Dabakhana Formation; Prokofiev 2002a), the Oligocene *Eovinciguerria obscura* (Daniltchenko, 1946) (= *Vinciguerria obscura* according to Grădianu et al. 2020), and *Praewoodsia mesogeae* Arambourg, 1967 (e.g., Arambourg 1967; Popov et al. 2002; Prokofiev 2002a, 2005). Species of the genera *Ichthyococcus* Bonaparte, 1840, *Phosichthys* Hutton, 1872 and *Vinciguerria* Jordan & Evermann, 1896 (e.g., *V. orientalis* Nam et al. 2019) are known from Miocene deposits (e.g., Prokofiev 2005; Nam et al. 2019). Therefore, *Solterichthys macrognathus* n. gen. et sp. is the most ancient Phosichthyidae known to date, extending back the record of this family to the lower Eocene (Ypresian).

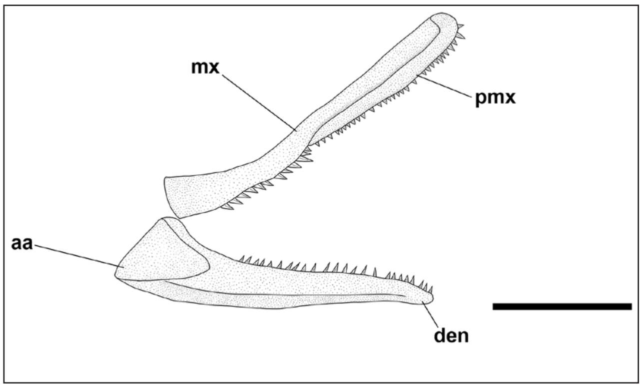


Fig. 6 - *Solterichthys macrognathus* n. gen. et sp.: interpretive reconstruction of the jaws. Scale bar 5 mm.

Due to the incompleteness of MUSE-PAL 6792-6814, the comparative analysis can be based exclusively on the characters of the head and anterior part of the axial skeleton. *Solterichthys macrognathus* n. gen. et sp. differs from the other genera of the Phosichthyidae by having a longer premaxilla, which is slightly more than half the length of the maxilla. The premaxilla of the other taxa known in the record is much shorter, ranging from extremely reduced (*Ichthyococcus*) to about one third of the length of the maxilla (*Vinciguerria*). The premaxillary teeth of *Solterichthys macrognathus* n. gen. et sp. are uniserial, unlike those of *Polymetme* McCulloch, 1926 and *Yarrella* Goode & Bean, 1896 which have biserial teeth on the premaxilla. As described above, the dentition of *Solterichthys macrognathus* n. gen. et sp. consists of minute needle-like teeth of similar shape and size that differ from those of *Phosichthys* and *Woodsia* Grey, 1859, which exhibit a jaw dentition characterized by teeth of two different sizes (Fig. 6B). *Solterichthys macrognathus* n. gen. et sp. exhibits both the orbital photophores (ORB1 and ORB2; Fig. 4B–5), while *Polymetme* and *Yarrella* lack the ORB2 photophore. *Solterichthys macrognathus* n. gen. et sp. differs from *Phosichthys* and *Woodsia* by having a lower number of branchiostegal rays (12 vs 17–21). *Solterichthys macrognathus* n. gen. et sp. differs from *Eovinciguerria* and *Vinciguerria* by lacking a spinous antero-ventral process of the hyomandibula that connects it to the endopterygoid (Grădianu et al. 2020). As far as the meristic is concerned, *Sol-*

terichthys macrognathus n. gen. et sp. shows more pectoral-fin rays than any other Phosichthyidae (13), with only *Vinciguerria* showing similar values, with a range of 8–12 pectoral-fin rays (Grădianu et al. 2020).

Family Gonostomatidae Gill, 1893
Genus *Scopeloides* Wettstein, 1886

Type species: *Osmerus glarisianus* Agassiz, 1844

Emended diagnosis: A genus of the Gonostomatidae characterized by the following combination of features: frontals sculptured with longitudinal striae; shortened premaxilla, representing between 1/4–1/5 of the length of the maxilla; maxillary teeth of two types (6–12 long pointed conical teeth, separated by numerous smaller needle-like teeth); two supramaxillae; small teeth on the ecto- and endopterygoid; hyomandibula inclined forward, with very short opercular process; vertebrae 35–43 (with 19–22 caudal); vertebral centra almost squared to rectangular, longer than high; epineurals in the caudal region inserting from the mid-point to the base of the neural spines; epipleurals of the caudal vertebrae inserting at about one third of the haemal-spine length; second ural vertebra present or reduced; six autogenous hypurals; two uroneurals; 14–15 dorsal-fin rays; anal-fin origin slightly behind the origin of the dorsal fin and comprising 24–30 rays; anterior rays of the anal fin more elongate compared to the following ones, forming a lobe; 9–15 pectoral-fin rays, extending posteriorly to the pelvic-fin insertion; 7–9 pelvic-fin rays, extending posteriorly to the anal-fin insertion.

Remarks and comparison. *Scopeloides* can be referred to the Gonostomatidae by having a short premaxilla, a developed posterior process of the palatine articulated with the pterygoids, IP and ORB2 photophores absent, maxillary teeth showing a distinct pattern with long, straight teeth separated by numerous small teeth (Harold 1998).

The frontals of *Scopeloides* exhibit a unique ornamentation characterized by numerous sculptured striae along their surface. The presence of two supramaxillae separates *Scopeloides* from the species of the genera *Gonostoma* Rafinesque, 1810 and *Cyclothone* Goode & Bean, 1883, as well as from *Ohuus kitamurai* Sato, 1962, *Primaevistomias weitzmani* Prokofiev, 2002 and *Kotlarczykia bathybia* Jerzmańska, 1974 (Sato 1962; Jerzmańska 1974; Harold 1998; Prokofiev 2002a, 2005). The anterior supramaxilla of *Scopeloides* extends anteriorly up to half of the length of the maxilla and is smaller if compared to the anterior supramaxilla of *Margrethia* Jespersen & Tåning, 1919, which has a size comparable to that of the maxilla. The premaxilla of *Scopeloides* (about 1/4–1/5 of the length of the maxilla) is longer than those of *Margrethia*, *Cyclothone,* and *Ohuus* (Sato 1962; Harold 1998) and comparatively shorter than that of *Primaevistomias* (being shorter than 1/3 of the length of the maxilla). *Scopeloides* can also be distinguished from *Cyclothone*, *Kotlarczykia,* and *Margrethia* for having a different vertebral count (from 35–43 vertebral centra vs 34 in both *Margrethia* and *Kotlarczykia*, and 30–35 for *Cyclothone*; e.g., Jerzmańska 1974; Přikryl & Carnevale 2017). *Scopeloides* differs from *Primaevistomias* by having the anal-fin origin slightly behind the origin of the dorsal fin, instead of an anal-fin insertion located at the end of the dorsal-fin base. The epipleurals associated with the caudal vertebrae of *Scopeloides* insert at about one third of the length of the corresponding haemal spine and differ from those of *Gonostoma* that articulate with the base of the haemal spine (Prokofiev 2005; Grădianu et al. 2017). *Scopeloides* exhibits a peculiar structure of the anal fin, with the anterior rays more elongate and forming a lobe; this feature has not been observed in *Gonostoma*, *Cyclothone* and *Primaevistomias*. Finally, *Scopeloides* differs from *Kotlarczykia* by having three (vs one) epurals and photophores of the OA series.

Scopeloides violator n. sp.

Figs. 7–10

Holotype: MUSE-PAL 2079, a nearly complete articulated skeleton, 83.4 mm SL.

Paratypes: MUSE-PAL 1014, a nearly complete articulated skeleton, 54.9 mm SL; MUSE-PAL 1015, a nearly complete articulated skeleton, 48.3 mm SL; MUSE-PAL 1016, a nearly complete articulated skeleton; MUSE-PAL 1017, a nearly complete articulated skeleton, 52.8 mm SL; MUSE-PAL 1023-1057, a nearly complete articulated skeleton, 59.8 mm SL, in part and counterpart; MUSE-PAL 1066, a nearly complete articulated skeleton, 36.9 mm SL; MUSE-PAL 5130, a nearly complete articulated skeleton, 45.8 mm SL; MUSE-PAL 6455, a nearly complete articulated skeleton.

Referred specimens: MUSE-PAL 1026, an incomplete articulated skeleton lacking the caudal skeleton; MUSE-PAL 1027, an incomplete articulated skeleton lacking the posterior portion of the axial skeleton; MUSE-PAL 1049, an incomplete articulated skeleton lacking the caudal skeleton MUSE-PAL 1068-1070, a nearly complete articulated skeleton, in part and counterpart; MUSE-PAL 1097, a nearly complete articulated skeleton; MUSE-PAL-SB 2453A-B, a partially complete skeleton, presenting the anterior portion of the axial skeleton detached from the rest of the body, in part and counterpart; MUSE-PAL-SB 2465A-B an incomplete articulated skeleton lacking the posterior portion of the axial skeleton, including the median fins, in part and counterpart.

Etymology: species named after the Latin word *"violator"*, meaning "defiler" (noun deriving from the Latin verb "*violare*", meaning "to violate"), for the large and menacing teeth.

Diagnosis: A medium-sized *Scopeloides* characterized by the following combination of features: body slender and elongate with a thin caudal peduncle (BD: 14.1–18.9% of SL; CPH: 6.5–9.1% of SL); premaxilla short, representing one fourth of the length of the maxilla, and bearing two long conical and pointed teeth, separated by 4–15 smaller needle-like teeth; maxilla with six-seven conical and

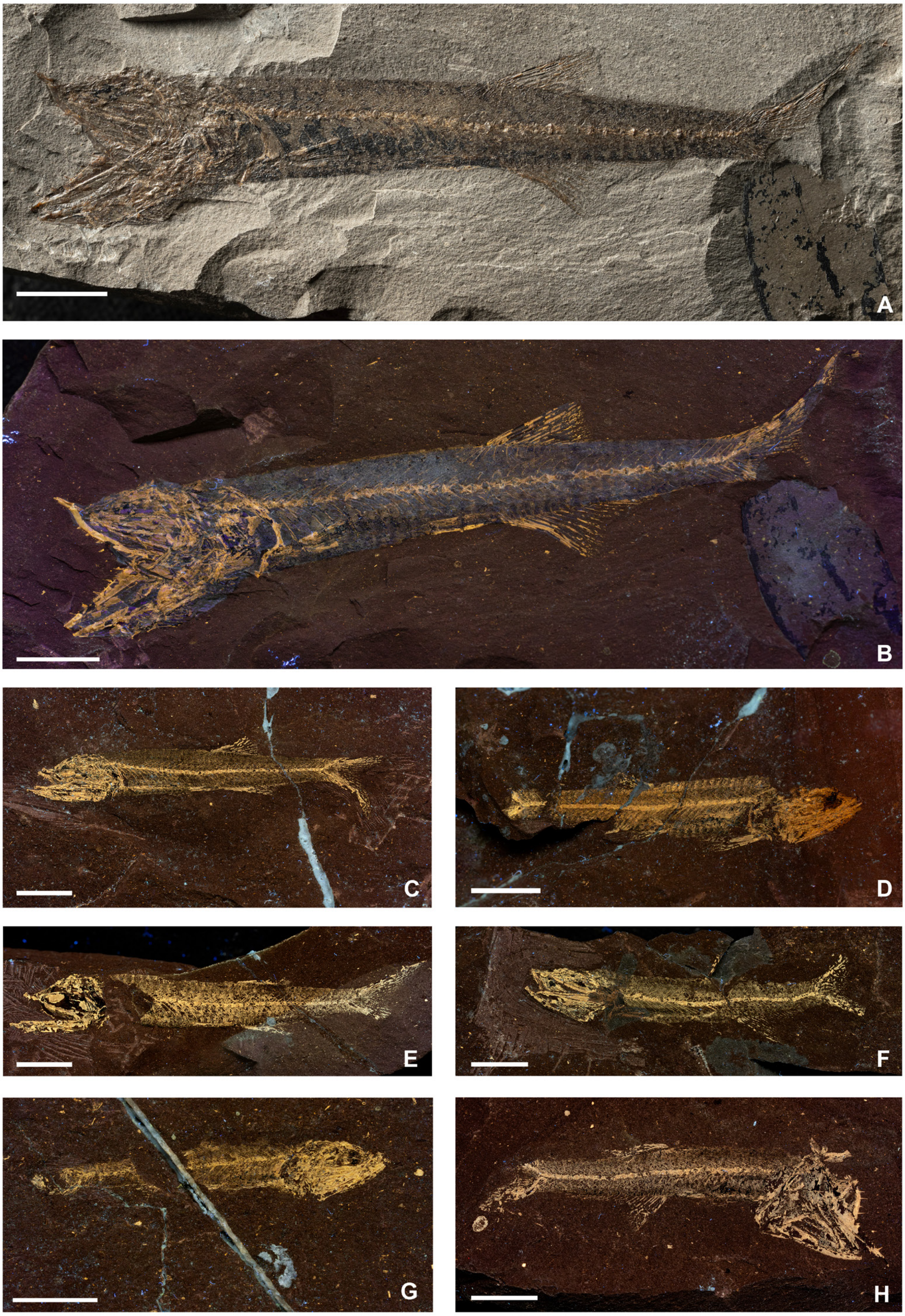


Fig. 7 - *Scopeloides violator* n. sp. Lateral view of the holotype, MUSE-PAL 2079, in natural (A) and under UV light (B). Lateral view of the paratypes under UV lights: C) MUSE-PAL 1014; D) MUSE-PAL 1015; E) MUSE-PAL 1016; F) MUSE-PAL 1017; G) MUSE-PAL 1066; H) MUSE-PAL 5130. Scale bars 10 mm.

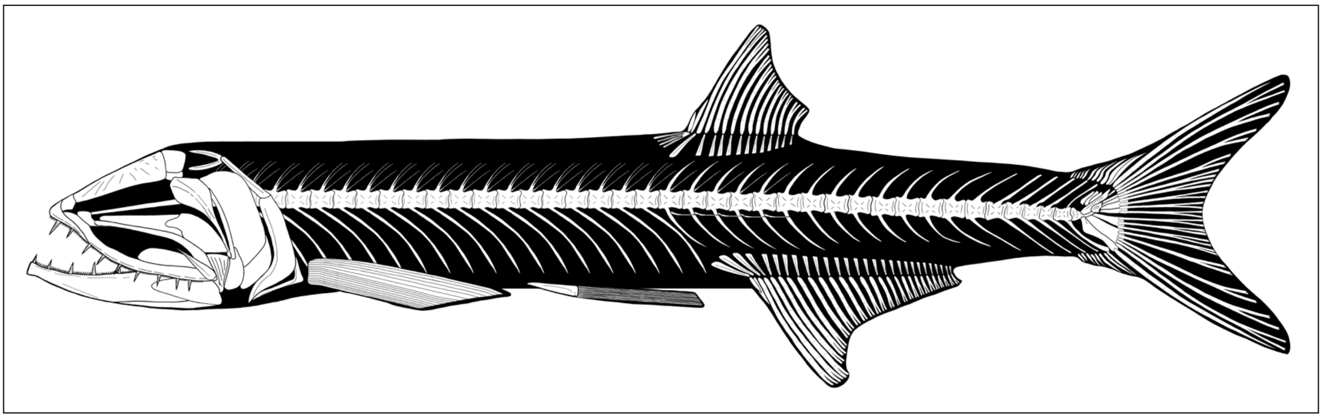


Fig. 8 - *Scopeloides violator* n. sp.: interpretive reconstruction of the skeleton.

pointed teeth, separated by 5–13 smaller needle-like teeth; large ovoid anterior supramaxilla extending anteriorly up to the mid-length of the maxilla; wedge-like posterior supramaxilla reaching one fourth of the length of the maxilla; dentary with five-six conical and pointed teeth separated by 6–10 smaller needle-like teeth; 12–14 branchiostegal rays; triangular urohyal with a slightly curved ventral and straight dorsal edge; 40–43 vertebrae (20–21 caudal); epineurals in the first five caudal vertebrae articulated close to the base of the neural arches rather than to half of the spine length; epipleurals up to the sixth caudal vertebra articulating at a third of the length of the haemal spine; second preural vertebra with a slightly expanded haemal spine; 8–11 dorsal and 7–9 ventral procurrent caudal-fin rays; pectoral fin comprising up to 15 rays.

Type horizon and locality: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Scopeloides violator* n. sp. exhibits a moderate size (between 45.8–83.4 mm SL) and a slender and elongate body. The maximum body depth is in the head region and immediately after, just behind the pectoral girdle. The head is large and deeper than the body. The orbit is rather small (between 4 and 7.9% of SL). The mandibular joint is placed well posterior to the orbit. The dorsal fin is anterior to the anal fin, and they are not opposite to each other (PD: 52.2–60% of SL; PA: 59–68.3% of SL; Tab.1).

The bones of the neurocranium are usually delicate and thin. The lateral ethmoid is difficult to see given its small size and poor preservation. The frontals are the largest bones of the skull roof; they are triangular, rather narrow anteriorly and wider posteriorly, ending right at the posterior end of the orbit and showing a peculiar ornamentation having the surface sculptured by longitudinal striae (Fig. 9). The parietals are polygonal in outline and commonly not easily recognizable. The pterotic is small and rectangular in outline. The supraoccipital, epioccipital and sphenotic are not preserved. The parasphenoid is a narrow and straight stick-like bone crossing the orbit on the mid-line.

The nasals are short and feebly thickened. The bones of the infraorbital series are not preserved. The premaxilla is small, with a mostly straight outline and a triangular ascending process; overall, the length of the premaxilla is approximately one fourth of the maxillary length and it bears two long conical teeth which are separated by several smaller needle-like teeth (ranging from 4–15). The maxilla is long and curved, almost sigmoid in shape, bearing six-seven long, conical teeth, separated by several minute needle-like teeth (ranging from 5–13). The anterior supramaxilla is usually preserved as an impression only; it is clearly exposed in some specimens (e.g., MUSE-PAL 2079; Fig. 8), showing an almost elliptic shape with a broad rounded base and slightly tapered; the anterior supramaxilla is around half the length of the maxilla. The posterior supramaxilla is wedge-like and it is shorter than the anterior supramaxilla; it has a rounded base and a pointed anterior end. The lower jaw is well-developed. The dentary is almost equal in size with the maxilla; it bears five to six large conical teeth separated by six to ten smaller needle-like teeth. The articular has an almost triangular shape.

The quadrate is triangular with gently rounded margins and a moderately developed anterior condyle for the articulation with the lower jaw. The quadrate-lower jaw joint is placed behind the posterior margin of the orbit (Figs. 8–9). The symplectic is thin (see MUSE-PAL 2079; Fig. 7A–B). The hyomandibula is inclined forward and shows a ventral rod-like shaft and a broad articular head. The opercular process of the hyomandibula slight-

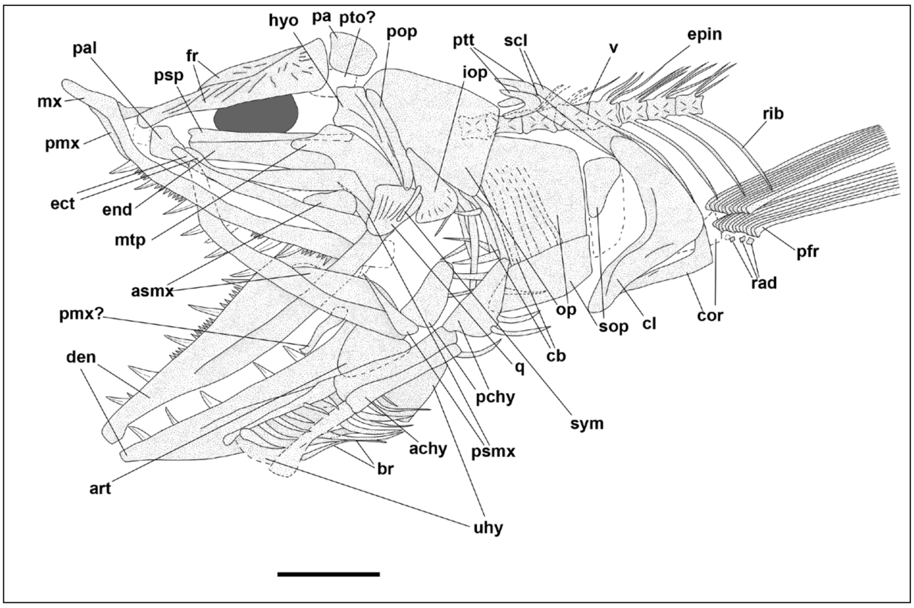


Fig. 9 - *Scopeloides violator* n. sp. Holotype, MUSE-PAL 2079, interpretive reconstruction of the head and anteriormost part of the body. Scale bar 5 mm.

ly extends posteriorly beyond the posterior margin of the bone. The ectopterygoid is long and narrow, slightly expanded posteriorly and tapered anteriorly (being also partially covered by the posterior supramaxilla, see MUSE-PAL 2079; Fig. 9). The endo- and metapterygoids are relatively large and flat. The metapterygoid exhibits a quadrangular shape, while the endopterygoid has a more triangular outline. The palatine has a short and stout body with an elongate posterior shaft ventral to the ectopterygoid. Some specimens show numerous pterygoid teeth on the medial surface of these bones, especially on the endopterygoid (better seen under UV light).

The preopercle has a narrow and curved shape. The opercle is the largest bone of the opercular series; it has a rectangular shape and is expanded posteroventrally, sometimes being completely displaced from the condyle of the hyomandibula and shifted posteriorly due to the inadequate preservation of some specimens (e.g., MUSE-PAL 2079; Fig. 9). The subopercle has a quadrangular shape. The interopercle is ovoid in outline.

The urohyal is usually preserved below the dentary (see MUSE-PAL 2079; Fig. 9); it has a large triangular shape with a gently rounded ventral margin. The anterior ceratohyal has a long and rod-like shape. The posterior ceratohyal has a thick and rectangular shape (see MUSE-PAL 2079; Fig. 9). There are 12–14 branchiostegal rays. The branchial arches are rarely preserved. In some specimens (see MUSE-PAL 2079; Fig. 9), there are some long and thin gill rakers (up to 11 or 12).

The vertebral column is inadequately preserved in certain specimens, thereby preventing a precise estimate of the vertebral number. Overall, the vertebral column contains more than 40 vertebrae (40–43 centra), with at least 20 caudal centra (21/22+20/21). The centra are rectangular, longer than high. The posterior caudal centra are extremely compact anteroposteriorly. The neural arches are attached to the anteriormost portion of the centrum: they are thin, slightly curved and extend posteriorly well beyond the end of their respective vertebral centrum. The haemal spines are thin and slender, almost identical to their opposite neural spines. There are long and thin ribs reaching the ventral margin of the body, articulating with the lateral sides of the abdominal vertebrae except for the first two centra. All the abdominal vertebrae bear thin epineural bones attached to the base of the neural arches; epineurals are also present in the first five caudal vertebrae, attached near the base of the neural spines (see MUSE-PAL 1016; Fig. 7A). There are up to six ossified epipleurals associated with the caudal vertebrae; these articulate with the haemal spines at around one third of their length (see, MUSE-PAL 2079, MUSE-PAL 5130; Figs 9A–B, H).

The elongate haemal spines of the second and third preural vertebrae are fused to the centrum, that of the second being slightly expanded (see MUSE-PAL 1016, MUSE-PAL 2079; Figs. 7A–B, E, 8, 10). The caudal skeleton consists of six autogenous hypurals, an expanded autogenous parhypural, two uroneurals, and three epurals (see

	MUSE-PAL 1014	MUSE-PAL 1015	MUSE-PAL 1017	MUSE-PAL 1023-1057	MUSE-PAL 1066	MUSE-PAL 2079	MUSE-PAL 5130	Range
SL (mm)	54.9	48.3	52.8	59.8	36.9	83.4	45.8	45.8-83.4
TL (mm)	64.7	48.3	60.7	68.8	43.2	94.9	55.9	48.3-94.9
HL	27	24.4	32.3?	23.3	32.4?	25.2	20.8	20.8-27
PD	59.3	55.6	60	?	52.2	59	58.8	52.2-60
PA	63.7	65.3?	68.3	64.4	?	60	59	59-68.3
PP	26.5	26.7	30.7	30.6	32.7	31.1	27.7	26.5-32.7
PV	52.5	53.1	57.1	49.3	51.7	51.1	46.1	46.1-57.1
DFL	14.2	12.2	?	?	?	12.2	14.7	12.2-14.7
AFL	26.2	?	21.5	27.9	?	25	28.7	21.5-28.7
PFL	18.1	17.4	12.1	19.8	14.5	15.6	16.7	12.1-21.3
VFL	10.5	10.1	8	10.8	?	9.8	9.4	8-12.7
PRO	5.8	4.4	5.3	4.2	7.7	5.2	5.8	4.2-7.7
O	6.2	5.7	5.6	6.1	3.5?	7.9	4	4-7.9
POO	13.7	11.3	16.3	14	20.3?	15.1	11.5	11.3-19.4
DRL	13.1	11	10.8	?	?	14.3	20.9	9.3-20.9
AFR	13.5	?	20.5	16.4	?	12.7	14.5	12.1-20.5
BD	15.5	14.1	14.9	15.1	17.3	14.5	16.4	14.1-18.9
CPL	5.7	?	6.6	9.1	?	8.5	8.5	5.7-9.4
CPH	7.3	9.1	7.5	7.2	7.5	6.5	7.9	6.5-9.1

Tab. 1 - Measurements of *Scopeloides violator* n. sp. Values are as percentage of SL.

MUSE-PAL 2079; Fig. 10). The caudal fin is forked and bears 19 (10+9) principal rays. In addition, there are eight to eleven dorsal and seven to nine ventral procurrent rays (8–11, I, 9+8, I, 7–9).

Some supraneurals are recognizable but poorly preserved. The dorsal-fin insertion is located anterior to that of the anal fin, the anal-fin origin being usually placed at the level of the fourth or fifth dorsal-fin pterygiophore. The dorsal fin consists of 14–15 rays, the first two being rather short, unsegmented, and unbranched. The third and fourth rays are the longest of the series. The dorsal fin is supported by 14–15 pterygiophores. The first two rays are supported by a large pterygiophore that is inclined forward, almost horizontally oriented. The successive pterygiophores are slender and thin. The length of the anal-fin base is about two times that of the dorsal fin (AFL: 21.5–28.7% of SL; DFL: 12.2–14.7% of SL; Tab. 1). The anal fin comprises up to 30 rays (range: 27–30) supported by 23 to 26 pterygiophores, which resemble those of the dorsal fin. The first two rays are reduced, unsegmented, and unbranched, and those from the third are longer, segmented, and distally branched. The third ray is the longest of the series and can be significantly longer than the successive rays (see MUSE-PAL 1017, Fig. 9F; AFR: 20.5% of SL; Tab. 1).

The pectoral girdle is crescent-shaped. The posttemporal is curved and has two well-developed anteriorly directed processes that articulate with the neurocranium. The supracleithrum is thin and rod-like, strongly inclined and projected anteriorly.

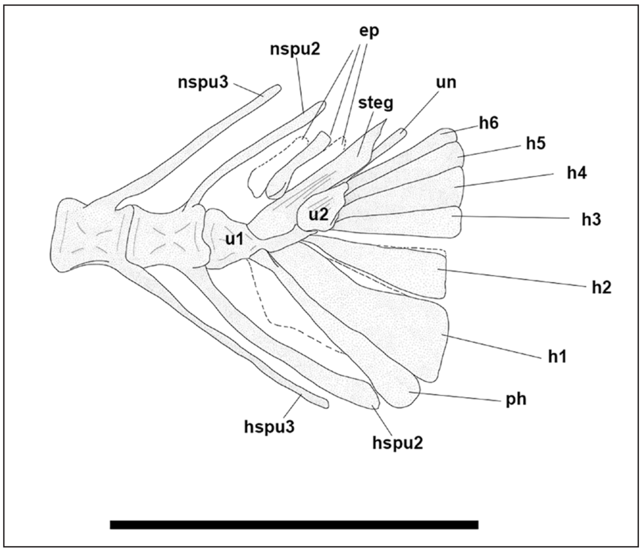


Fig. 10 - *Scopeloides violator* n. sp. Holotype, MUSE-PAL 2079, interpretive reconstruction of the caudal skeleton. Scale bar 5 mm.

The cleithrum is large and curved, posteroventrally expanded and anteriorly inclined; it also bears a distal pointed and curved tip bent downwards. The coracoid has a well-developed anterior process. The scapula is difficult to observe. There are four pectoral-fin radials. The pectoral fin inserts ventrally on the body and extends posteriorly to the pelvic girdle, containing up to 15 unbranched rays. The pelvic girdle is triangular and narrow. The pelvic fins contain seven to nine rays.

The photophores are usually poorly preserved and difficult to observe, in some cases preserved as impressions only. Up to 20 photophores on the AC series and from six to eight photophores of the PV series can be recognized.

The body is covered by thin and small cycloid scales with a rounded shape.

Scopeloides bellator n. sp.

Figs. 11–12

Holotype: MUSE-PAL 12a, a nearly complete articulated skeleton.

Paratypes: MUSE-PAL 12b, an incomplete articulated skeleton lacking the posterior portion of the axial skeleton including the pelvic fins; MUSE-PAL 1028-1053, a nearly complete articulated skeleton, 61.9 mm SL, in part and counterpart (only MUSE-PAL 1028 is present in Fig. 11 since is the most complete part); MUSE-PAL 5549, a nearly complete and articulated skeleton; MUSE-PAL 6125, a nearly complete articulated skeleton, 44.9 mm SL; MUSE-PAL 6449, a nearly complete articulated skeleton, 37.1 mm SL; MUSE-PAL 6984, a nearly complete articulated skeleton, 51.4 mm SL; MCR 3846 a nearly complete articulated skeleton, 62.8 mm SL; MGP-PD 33390, a nearly complete articulated skeleton, 54.3 mm SL; MGP-PD 33391, a nearly complete articulated skeleton.

Referred specimens: MUSE-PAL 4, a nearly complete articulated skeleton; MUSE-PAL 1029, an incomplete articulated skeleton, lacking the posterior portion of the axial skeleton, including the pelvic fins; MUSE-PAL 1045, a nearly complete articulated skeleton; MUSE-PAL 1076, a nearly complete articulated skeleton; MUSE-PAL 5550, a nearly complete articulated skeleton; MUSE-PAL-SB 2455A-B, a nearly complete articulated skeleton, in part and counterpart.

Etymology: species named after the Latin word *"bellator"*, meaning "warrior" or "fighter" for the fierce appearance of this fish, provided by its dagger-like teeth.

Diagnosis: A medium-sized *Scopeloides* characterized by the following combination of features: body moderately thick, with a deep caudal peduncle (BD: 20.4–31.4% of SL; CPH: 9.6–17.3% of SL); premaxilla short, being one fourth of the length of the maxilla, bearing two or three long conical teeth, separated by 4–12 smaller needle-like teeth; maxilla with six to eight long conical teeth separated by 6–13 needle-like teeth; large ovoid anterior supramaxilla reaching half the length of the maxilla; wedge-like posterior supramaxilla reaching one fourth of the length of the maxilla; dentary with seven or eight large, conical teeth separated by seven to ten needle-like teeth; 10-11 branchiostegal rays; triangular urohyal with a slightly curved margins; 35–39 vertebrae (18–20 caudals); epineurals in the first five caudal vertebrae articulate close to the base of the neural arches; epipleurals articulate with the first four or five caudal vertebrae at one third of the length of the haemal spine; haemal spine of the second preural centrum slightly expanded; seven to nine dorsal and six to seven ventral procurrent caudal-fin rays; pectoral fin with up to 14 rays.

Type horizon and locality: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Scopeloides bellator* n. sp. exhibits a moderate size (between 37.1–62.8 mm SL) and a rather thick and wide body. The maximum body depth is in the head region, just behind the pectoral girdle. The head is rather large and deeper than the body depth. The orbit is rather small. The mandibular joint is placed well posterior to the orbit. The dorsal fin is anterior to the anal fin, the two fins are not opposite to each other (PD: 55.7–57.5% of SL; PA: 53.6–67.1% of SL; Tab. 2).

The bones of the neurocranium are delicate and thin. The frontals are the largest bones of the skull roof; these are triangular, rather narrow anteriorly and wider posteriorly, ending at the posterior end of the orbit with a peculiar ornamentation of sculptured longitudinal striae. The parietals are quadrangular in shape. The pterotic is small and rectangular. The sphenotic, supraoccipital, and epioccipital are not preserved in the examined specimens. The parasphenoid is narrow and straight, crossing the orbit in its mid-depth.

The nasals are short and thickened (e.g., MUSE-PAL 12b, MUSE-PAL 1028-1053; Fig. 11A–B). The bones of the infraorbital series are not preserved.

The premaxilla is small with a triangular ascending process; the length of the premaxilla is around one fourth that of the maxilla; it bears two or three long conical teeth, separated by four to twelve smaller needle-like teeth. The maxilla is long and curved, almost sigmoid in shape, bearing up to eight long conical teeth (e.g., MUSE-PAL 1028-1053; Fig. 11B) separated by six to thirteen smaller needle-like teeth. The anterior supramaxilla is usually preserved as an impression only and is about half of the length of the maxilla; it is oblong with a broad rounded base slightly tapering dorsally (e.g., MUSE-PAL 1028-1053, MUSE-PAL 6449; Fig. 11B, I). The posterior supramaxilla is slender and wedge-like, half the length of the anterior supramaxilla; it has a rounded base and a pointed anterior end. The lower jaw is well-developed. The dentary

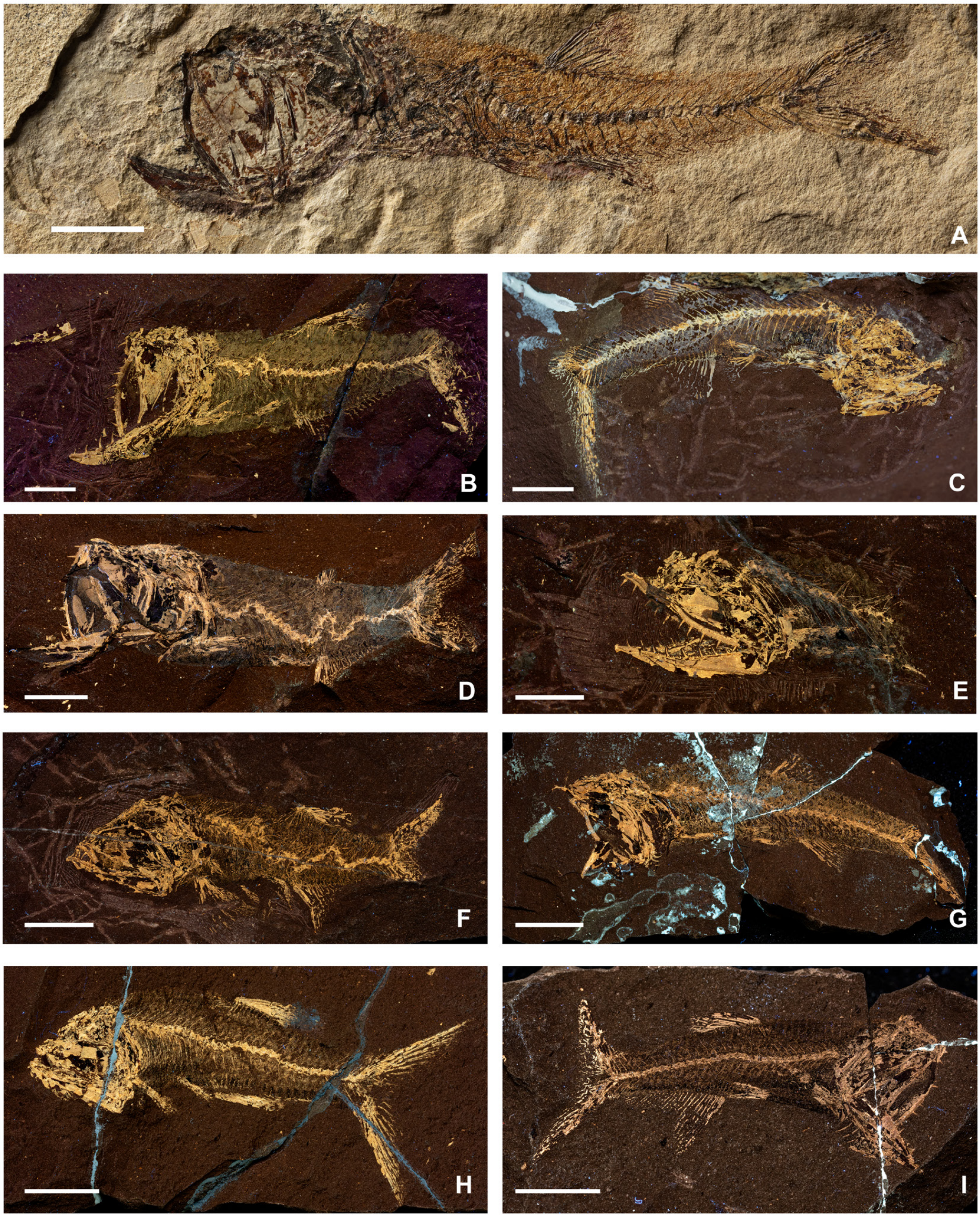


Fig. 11 - *Scopeloides bellator* n. sp. Lateral view of the holotype MUSE-PAL 12a, in natural light (A). Lateral view of the paratypes under UV lights: B) MUSE-PAL 1028; C) MCR 3846; D) MUSE-PAL 5549; E) MUSE-PAL 1029; F) MUSE-PAL 1045; G) MUSE-PAL 6984; H) MUSE-PAL 6125; I) MUSE-PAL 6449. Scale bar 10 mm.

is almost equal in size with the maxilla, bearing up to eight large conical teeth (e.g., MUSE-PAL 1029; Figs. 11E, 12), separated by seven to ten needle-like teeth. The articular has an almost triangular shape.

The quadrate is triangular with rounded margins and has a developed anterior condyle. The quadrate-lower jaw joint is placed well behind the posterior margin of the orbit. The symplectic is not preserved. The hyomandibula is inclined forward; it has a narrow ventral rod-like arm and a wide articular head. The opercular process of the hyomandibula slightly extends posteriorly beyond the posterior margin of the bone. The ectopterygoid is elongate, straight and narrow, slightly broadened posteriorly and tapering anteriorly. The posterior portion of the ectopterygoid is partially covered by the posterior supramaxilla. The endo- and metapterygoids are relatively large and flattened. The metapterygoid has a quadrangular shape, while the endopterygoid has a more triangular and elongate outline. Some specimens show many pterygoid teeth, especially on the endopterygoid (best seen under UV light, e.g., MUSE-PAL 1029, MCR 3846; Fig. 11C, E). The palatine has a short and rectangular body with an elongate posterior shaft that connects it to the ectopterygoid.

The preopercle has a narrow and slightly curved shape. The opercle is rectangular in outline, being expanded posteroventrally; occasionally it is completely displaced from the opercular process of the hyomandibula and shifted posteriorly (see MUSE-PAL 12a; Fig. 11A) or it is crushed and compressed (e.g., MUSE-PAL 1028-1053, MUSE-PAL 1029; Fig. 11B, E). The subopercle has a quadrangular shape. The interopercle is usually poorly preserved, with an ovoid shape.

The urohyal has a large triangular shape with a gently rounded ventral margin. The anterior ceratohyal is elongate and rod-like (see MUSE-PAL 1028-1053; Fig. 11B). The posterior ceratohyal is poorly preserved. There are 10-11 branchiostegal rays. Of the branchial skeleton, only rod-like ceratobranchials are noticeable, bearing up to eight long and thin gill rakers (e.g., MUSE 12a-b, MUSE-PAL 1028-1053; Fig. 11A–B).

The vertebral column is usually inadequately preserved, preventing a precise estimate of the vertebral number (e.g., MUSE-PAL 1045; Fig. 11F). However, it is reasonable to estimate that the vertebral column contains less than 40 vertebrae, most likely between 35 and 39, of which no more than 20 are caudal (18–20+18–20). The vertebrae are almost squared, being only slightly longer than high. The posterior caudal centra are much compact antero-posteriorly compared to the abdominal ones and the preceding caudal vertebrae (see MCR 3846, MUSE-PAL 12a; Fig. 11A, C). The neural arches are attached to the anteriormost portion of the centrum. The neural spines are long, thin, and slightly curved, extending posteriorly well beyond the end of their respective vertebral centrum. The haemal spines are thin, elongate, and curved backwards, very similar to their opposite neural spines. There are thin and curved ribs that almost reach the ventral margin of the body, articulating with the lateral sides of the abdominal vertebrae except for the first two. All the abdominal vertebrae bear thin epineurals attached to the base of the neural arches; epineurals are also present in the first five caudal vertebrae, inserting near the base of the neural arches. There are four or five ossified epipleurals associated with the caudal vertebrae. The epipleurals articulate with the haemal spines at about one third of their length (e.g., MUSE-PAL 12a, MUSE-PAL 6449; Fig. 11A, I).

The elongate haemal spines of the second and third preural vertebrae are fused to their respective vertebral centra, with the haemal spine of the second preural vertebra being slightly expanded (e.g., MCR 3846, MUSE-PAL 6984; Fig. 11C, G). The caudal skeleton consists of six autogenous hypurals, an autogenous wedge-like parhypural, two uroneurals, and three thin and subrectangular epurals (e.g., MUSE-PAL 12a, MUSE-PAL 1028-1053; Fig. 11A–B). The caudal fin is forked, bearing 19 (10+9) principal rays. In addition, there are six to nine dorsal and six to seven ventral procurrent rays (6–9, I, 9+8, I, 6–7).

Some supraneurals are recognizable but poorly preserved. The dorsal-fin insertion is slightly anterior to that of the anal fin, with the anal-fin origin usually located at the level of the third to fifth dorsal-fin pterygiophore. The dorsal fin consists of 14–15 rays, supported by 14–15 pterygiophores. The first two rays are short, unsegmented, and unbranched, while the third and fourth rays are the longest of the series. The first pterygiophore is large and almost horizontally oriented; the successive pterygiophores are slender and thin. The length of the anal-fin base is two times that of the dorsal

Tab. 2 - Measurements of *Scopeloides bellator* n. sp. Values are as percentage of SL.

	MUSE-PAL 1028-1053	MUSE-PAL 6125	MUSE-PAL 6449	MUSE-PAL 6984	MCR 3846	MGPPD 33390	Range
SL (mm)	61.9	44.9	37.1	51.4	62.8	54.3	37.1-62.8
TL (mm)	79.1	57.6	43.2	59.7	64.9	62.6	43.2-79.1
HL	25.9	29.4	30.7	30.9	27.1	29.8	27.1-30.9
PD	55.9	56.3	55.7	57.5	62?	57.1	55.7-57.5
PA	53.6	53.9	61.2	67.1	60.3	62.1	53.6-67.1
PP	22.1	28.2	29.3	34.3	28.4	31.9	22.1-34.3
PV	43.1	43.4	49.1	52.5	50.2	51.6	43.1-52.5
DFL	15.4	14.4	15.6	15.3	?	9.4	9.4-15.6
AFL	31.8	28.5	25.5	21.6	25.8	24.3	21.6-31.8
PFL	19.5	16.1	18.4	15.7	18.7	15.3	15.7-19.5
VFL	11.3	11.3	12.4	10	9.2	10.9	9.2-12.4
PRO	6	8.8	5.8	10.1	7.9	9.6	5.8-10.1
O	8	9.9	9.3	6.5	5.6	7.9	5.6-9.9
POO	18.8	13.4	15.3	15.6	11	8.8	8.8-18.8
DRL	20.1	18.7	18.2	11.4	?	12.7	11.4-20.1
AFR	?	21.5	22.8	15.5	11.7	9.9	9.9-22.8
BD	30.9	31.4	28.1	23.6	22.4	20.4	20.4-31.4
CPL	11.2	12.1	6.8	8.5	7.8	10.3	6.8-12.1
CPH	14.5	17.1	12	9.9	13	9.6	9.6-17.3

fin (AFL: 21.6–31.8% of SL; DFL: 9.4–15.6% of SL). The anal fin comprises up to 29 rays (range: 24–29), supported by 22 to 26 pterygiophores. The first two rays are very reduced, unsegmented, and unbranched; the third ray is the longest of the series and is significantly longer than the successive rays (e.g., MUSE-PAL 6125, MUSE-PAL 6449; Fig. 11H–I; AFR: 21.5% and 22.8% of SL, respectively; Tab. 2).

The pectoral girdle is crescent-shaped. The posttemporal has two well-developed anterior processes. The supracleithrum is thin and narrow, rodlike. The cleithrum is large, curved, and posteroventrally expanded. The coracoid has a well-developed anterior process; the posterodorsal portion is rather short and vertically oriented. The scapula is only rarely preserved (see MUSE-PAL 1029; Fig. 11E). There are four pectoral-fin radials. The pectoral fin inserts ventrally on the body and extends posteriorly to the pelvic girdle, containing up to 14 unbranched rays. The basipterygium is triangular and narrow. The pelvic fins contain seven to nine rays.

The photophores are usually poorly preserved and difficult to recognize, preserved as impressions only. Up to 18 photophores on the AC series and from six to eight photophores of the PV series can be recognized.

The body is covered by thin and small cycloid scales with a rounded shape.

Discussion. The cranial anatomy of the different *Scopeloides* species is rather conservative, and the main interspecific differences are related to the general physiognomy of the body, as well as to morphometric and meristic traits. *Scopeloides violator* n. sp. is characterized by a remarkably elongate and thin body with a maximum body depth lower than that of *Scopeloides bellator* n. sp., which is considerably higher (BD:14.1–18.9% and 20.4–31.4% of SL, respectively; see Tab. 1–2). The height of the caudal peduncle of *S. violator* n. sp. is also remarkably lower compared to that of *S. bellator* n. sp. (CPH: 6.5–9.1% and 9.6–17.3% of SL, respectively; see Tab. 1–2). The dentition of the different species is quite consistent, with some differences in the premaxillary teeth: *S. violator* n. sp. shows two large conical teeth, fewer than *S. bellator* n. sp. (up to three) and *Scopeloides glarisianus* (Agassiz, 1844) (up to four). As for the number of minute needle–like teeth the difference is minimal (4–15 vs 4–12, for *S. violator* n. sp. and *S. bellator* n. sp., respectively) and could easily be linked to a taphonomic artifact, while there are slightly less in *S. glarisianus* (3-10; Prokofiev 2005). The maxilla of *S. violator* n. sp. bears six or seven large conical teeth, slighlty less than *S. bellator* n. sp. (up to eight) and *S. glarisianus* (9–12; see Prokofiev 2005). The lower jaw of *S violator* n. sp. shows five or six large conical teeth, fewer than *S. bellator* n. sp. (up to eight) but similar to that of *S. glarisianus* (six; Tab. 3). The minute needle-like teeth in the dentary of *Scopeloides violator* n. sp. range from five to 13, similar to *S. bellator* n. sp., while in *S. glarisianus* they range from three to ten (Prokofiev 2005). The pos-

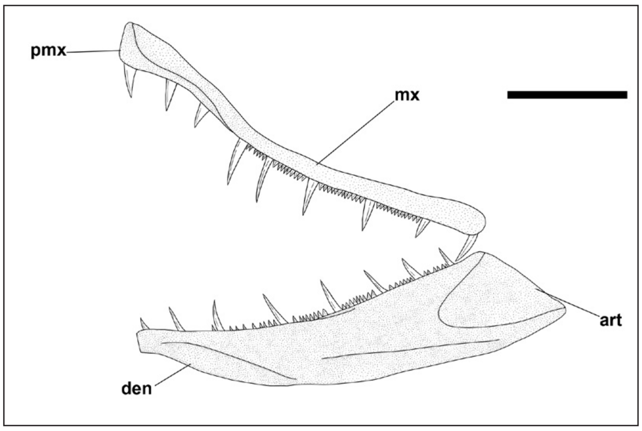


Fig. 12 - *Scopeloides bellator* n. sp.: interpretive reconstruction of the jaws. Scale bar 5 mm.

	Scopeloides violator n. sp.	*Scopeloides bellator* n. sp.	*Scopeloides glarisianus*
Dorsal-fin rays	14-15	14-15	14-15
Anal-fin rays	27-30	24-29	26-29
Pectoral-fin rays	10-15	9-14	11-12
Pelvic-fin rays	7-9	7-9	7-8
Caudal-fin rays (principal)	19 (10+9)	19 (10+9)	19 (10+9)
Caudal-fin rays (procurrent)	8-11 + 7-9	6-9 + 6-7	6-7 + 6-7
Vertebrae (caudals)	40-43(20-21)	35-39 (18-20)	39-40 (21-22)
Branchiostegal rays	10-14	10-11	9
Fangs (pmx)	2	2-3	2-4
Fangs (mx)	6-7	6-8	9-12
Fangs (den)	5-6	7-8	6
Ph PV	6-8	6-8	9-10
Ph AC	20	18	20
Epin.	5	5	7-8
Epipl.	6	4-5	6-7

Tab. 3 - Summary of the meristic traits of the different species of the genus *Scopeloides*. Includes new data and data from Gregorova (1997), Prokofiev (2005) and Gradiănu et al. (2017).

terior supramaxilla is rod-like in *S. glarisianus*, while it is wedge-like in *S. violator* n. sp. and *S. bellator* n. sp., with a rounded base and a tapering dorsal end. Furthermore, the posterior supramaxilla in *S. violator* n. sp. and *S. bellator* n. sp. is around half the length of the anterior supramaxilla, while in *S. glarisianus* the two supramaxillae are comparable in size (Prokofiev 2005). The anterior supramaxilla in *S. violator* n. sp. and *S. bellator* n. sp. is ovoid, representing half of the length of the maxilla, being substantially larger than that of *S. glarisianus,* which is narrow and reaches just one quarter of the length of the maxilla. *S. violator* n. sp. has the highest number of branchiostegal rays (12–14) when compared to the other species (10–11 in *S. bellator* n. sp. and nine in *S. glarisianus*; Tab. 3). The urohyal of *S. violator* n. sp. and *S. bellator* n. sp. shows a triangular shape with a mostly straight or slightly curved ventral edge, unlike the urohyal of *S. glarisianus,* which exhibits a concave ventral profile (Grădianu et al. 2017). The vertebral count of *S. violator* n. sp. is the highest of the genus with more than 40 vertebrae (40–43), more than *S. bellator* n. sp. (35–39) and *S. glarisianus* (39–40; Tab. 3). In *S. violator* n. sp. and *S. bellator* n. sp., the epineurals of the caudal centra are attached at one third of the length of the neural spine (e.g., MUSE-PAL 1016; Fig. 8), while they articulate at mid-length of the neural spines in *S. glarisianus*. Moreover, in *S. violator* n. sp. and *S. bellator* n. sp., the first five caudal vertebrae bear epineurals, while in *S. glarisianus* epineurals are present until the seventh or eighth caudal centrum (Grădianu et al. 2017). The epipleurals of *S. violator* n. sp. are attached near the base up to around the first third of the length of the haemal spines of the first five or six caudal vertebrae; a condition similar to *S. glarisianus*, where epipleurals are present up to the sixth or seventh caudal centrum, while in *S. bellator* n. sp. the epipleurals are present until the fourth or fifth vertebra. The caudal skeleton of *S. violator* n. sp. and *S. bellator* n. sp. differs from that of *S. glarisianus* in the presence of a slightly expanded haemal spine of the second preural centrum. Moreover, several meristic differences help in distinguishing these three species (e.g., number of the pectoral-fin rays and of the caudal–fin procurrent rays; see Tab. 3). The number of photophores of *S. violator* n. sp. (PV: 6–8; AC: 20) is comparable to that of *S. bellator* n. sp. (PV: 6–8; AC: 18) and *S. glarisianus* (PV: 9–10; AC: 20; Gregorová 1997; Tab. 3). In addition, some specimens show evidence of trophic interactions, exemplified by remains of the vertebral column of other teleosts in the abdominal area (see also Přikryl et al. 2012).

Order **Myctophiformes** sensu Johnson, 1982

Family Myctophidae Gill, 1893

Subfamily Eomyctophinae Prokofiev, 2006

Genus *Eomyctophum* Daniltschenko, 1947

Type species: *Eomyctophum koraense* Daniltshenko, 1947

Emended diagnosis: A genus of the Myctophidae characterized by the following combination of features: mouth large with mandibular joint placed at one orbit diameter or more from the posterior margin of the orbit; small and uniform teeth in both jaws; one small supramaxilla; maxilla with a slightly widened posterior end; 30–36 vertebrae (16–18 caudals); six autogenous hypurals; presence of a reduced second ural centrum; cleithrum with well–developed posterior lamina and weakly or moderately developed posteromedial shelf; basipterygium narrow; cycloid scales.

Remarks and comparison: *Eomyctophum* can be referred to the family Myctophidae by having a premaxilla with reduced ascending and articular processes; a reduced supramaxilla; presence of suborbital shelf; 28 to 45 vertebrae; elongate vertebral centra without developed lateral ridges; second ural centrum present but extremely reduced in size; anal-fin insertion located just behind the end of the dorsal-fin base; presence of photophores (see Prokofiev 2006).

These traits allow to exclude any attribution to the family Neoscopelidae, which is characterized by having one or two well-developed supramaxillae; a premaxilla with developed articular and ascending processes; lack of subocular shelf; presence of free second ural centrum; short vertebral centra with developed ridges, and anal-fin origin placed significantly behind the end of the dorsal-fin base (Prokofiev 2006).

Furthermore, *Eomyctophum* (and the subfamily Eomyctophinae) differs from the members of the other subfamilies of the Myctophidae by having the mandibular joint placed more posteriorly compared to the Myctophinae; a reduced supramaxilla (absent in Lampanyctinae and extremely reduced or absent in Myctophinae); a broader posterior end of the maxilla (more slender in Lampanyctinae; e.g., *Oligophus moravicus* (Paucă, 1931) (see Přikryl et al. 2017); 30–36 vertebrae (vs 31–40 in Myctophinae and 28–45 in Lampanyctinae); a cleithrum with a well-developed posterior plate (weakly developed in Lampanyctinae) and a moderately developed posteromedial shelf (absent in Myctophinae; Paxton 1972; Prokofiev 2006).

Eomyctophum mainardii n. sp.

Figs. 13–16

Holotype: MUSE-PAL 5472, a nearly complete articulated skeleton, 68.1 mm SL.

Paratypes: MUSE-PAL 1022, an incomplete articulated skeleton lacking the posterior portion of the axial skeleton; MUSE-PAL 1038-1100, a nearly complete articulated skeleton, in part and counterpart; MUSE-PAL 1074, a nearly complete articulated skeleton, 45.6 mm SL; MUSE-PAL 1102, an incomplete articulated skeleton lacking the posterior portion of the axial skeleton; MUSE-PAL 3912 a nearly complete articulated skeleton, 47.1 mm SL; MCR 3841, a nearly complete articulated skeleton; MUSE-PAL-SB 2454, a nearly complete articulated skeleton.

Referred specimens: MUSE-PAL 1084, an incomplete articulated skeleton, lacking the posterior portion of the axial skeleton, including the median fins; MUSE-PAL 3316, a partially complete articulated skeleton missing the dorsal portion of the cranium; MUSE-PAL 6806, an incomplete articulated skeleton represented by the head and the anterior part of the axial skeleton.

Etymology: Species named after the late Italian naturalist and science communicator Danilo Mainardi (1933-2017).

Diagnosis: A moderate-sized and relatively robust species of *Eomyctophum* characterized by the following combination of features: mouth large with mandibular joint at least one orbit diameter behind the posterior margin of the orbit; a single reduced supramaxilla; 32–34 vertebrae, (16–17 caudals); forked caudal fin with 19 principal plus five to eight dorsal and seven to nine ventral procurrent rays; dorsal fin containing 13–15 rays; anal fin containing 13–17 rays; pectoral fin comprising 12–14 rays; large pelvic fins with 9 rays; posterior lamina of the cleithrum well developed and posteromedial shelf moderately developed; pectoral fins short and narrow, smaller than the pelvic fins; basipterygium inserting at the level of the posterior margin of the pectoral girdle; prepelvic distance reduced (PV: 43.6% of SL; Tab. 4–5); length of basipterygium corresponds to the length of four to five vertebrae; pelvic fins elongate and almost two times the length of the pectoral fins (VFL: 20.6% of SL; PFL: 8.5% of SL; Tab. 4–5); distance between pectoral and pelvic–fin insertion shorter than distance between pelvic and anal fins (PVD: 10.7% of SL; VAD: 26.2% of SL; Tab. 4–5).

	***Eomyctophum mainardii* n. sp.**
SL (mm)	68.1
TL (mm)	70
HL	28.4
PD	48.6
PA	66.7
PP	32.2
PV	43.6
DFL	18.8
AFL	14.4
PFL	8.5
VFL	20.6
PVD	10.7
VAD	26.2
PRO	6.2
O	6.7
POO	15.5
DRL	21.2
AFR	13.1
BD	26.9
CPL	10.1
CPH	16.3

Tab. 4 - Measurements of *Eomyctophum mainardii* n. sp. Values are as percentage of SL.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Eomyctophum mainardii* n. sp. has a moderate size (45.6–68.1 mm SL). Some partially complete specimens could have reached a size surely above 80 mm SL (e.g., MCR 3841; Fig. 12H). The body is robust and compact, with a deep caudal peduncle, reaching the maximum depth at the level of the dorsal fin. The head is rather short, with a rounded and blunt snout. The anal–fin origin is placed posterior to the end of the dorsal-fin base.

The bones of the neurocranium are usually poorly preserved due to their small size and delicate texture. The mesethmoid and lateral ethmoid are difficult to observe. The frontals are the larg-

	***Eomyctophum mainardii* n. sp.**	***Eomyctophum koraense***	***Eomyctophum cozlae***
SL (mm)	68.1	26-57	36
TL (mm)	70	?	46
HL	28.4	27.8-38.9	36.1
PD	48.6	44-48.6	47.2
PA	66.7	66.7-72.9	66
PP	32.2	?	?
PV	43.6	49.1-54.3	51-52
DFL	18.8	13.9-16.7	?
AFL	14.4	18.6-22.8	?
PFL	8.5	16-21.9	?
VFL	20.6	10-16	?
PVD	10.7	13.3-18.5	12.5
VAD	26.2	16-20.4	18.9
PRO	6.2	?	8.9
O	6.7	?	6.1
POO	15.5	?	16.7
DRL	21.2	?	?
AFR	13.1	?	?
BD	26.9	16.7-31.7	19-20
CPL	10.1	11-14	?
CPH	16.3	10-15	13

Tab. 5 - Measurements of various species of the genus *Eomyctophum*. Values are as percentage of SL. Includes new data and data from Ciobanu (1977), Gregorovà (2004), and Prokofiev (2006).

est bones of the skull roof; they are triangular with rounded margins, being narrow anteriorly and wider posteriorly (Figs. 14–15). The parietals are small, compact, and quadrangular in shape. The pterotic and the sphenotic are poorly preserved and difficult to recognize. The supraoccipital and epioccipitals are not preserved. The parasphenoid is narrow, straight, and rod-like, passing throughout the orbit.

The nasals are short and stout (e.g., MUSE-PAL 3912; Fig. 13H). The bones of the infraorbital series are rarely preserved, partially exposed in certain specimens (see MUSE-PAL 1102; Fig. 13 F). The lachrymal is rather stout. The second infraorbital is short, whereas the third one is the largest of the series, being enlarged posteriorly, and characterized by a subocular shelf (e.g., MUSE-PAL 3912, MUSE-PAL 1102; Fig. 15).

The premaxilla is elongate and slightly curved anteriorly, with scarcely developed ascending and articular processes (Fig. 15), and bears numerous minute conical teeth. The maxilla is narrow and slightly curved, with a slightly expanded posterior end, and it is completely excluded from forming the mouth gape by the premaxilla. There is a single and small supramaxilla, with a roughly triangular outline and gently rounded margins (Fig. 15). The dentary is large and bears a dense band of small conical teeth like those of the upper jaw. The articular has a triangular outline and firmly fits in the posterior portion of the dentary (e.g., MUSE-PAL 1074, MUSE-PAL 5472; Fig. 15).

The quadrate is triangular in outline. The symplectic is difficult to recognize. The quadrate-lower jaw joint is placed more than one orbit diameter beyond the posterior edge of the orbit. The hyomandibula is oblique and anterodorsally inclined; it has a narrow and slightly curved ventral shaft, two dorsal articular heads, and a posteriorly developed opercular process (e.g., MUSE-PAL 5472; Fig. 15). The ectopterygoid is narrow and straight, slightly expanded posteriorly and tapering anteriorly into a pointed end. The endopterygoid has a triangular shape, narrow anteriorly and expanded posteriorly. The metapterygoid has a larger, trapezoid shape. The palatine is not preserved in the examined specimens.

The preopercle is thin and slightly curved, inclined anteriorly, following the profile of the hyomandibula, to which it is closely associated anteriorly. The opercle is the largest bone of the opercular series, with a rectangular outline and straight anterior and posterior margins. The interopercle has an ovoid shape, while the subopercle is quadrangular.

The hyoid apparatus is poorly preserved. The branchiostegal rays are usually scattered and difficult to count, given the dorsoventral preservation of some specimens and inadequate preservation. The branchial skeleton is not preserved in the available material, and only in a few specimens it is possible to recognize some ceratobranchials with long and slender spinous gill rakers (e.g., MUSE-PAL 1038-1100, MUSE-PAL 1074; Fig. 13D, G).

In several specimens (e.g., MUSE-PAL 1038-1100, MUSE-PAL 1102; Fig. 13F–G), the vertebral column is inadequately preserved, preventing a precise definition of the vertebral number. The vertebral column comprises 32–34 vertebrae (with 16–17 caudal centra). The centra are slightly elongate and rectangular, bearing weak longitudinal crests that cross the main body of the vertebral centra. The neural spines are attached to the anteriormost portion of the centrum; these neural spines are thin and straight, quite elongate, and extend posteriorly

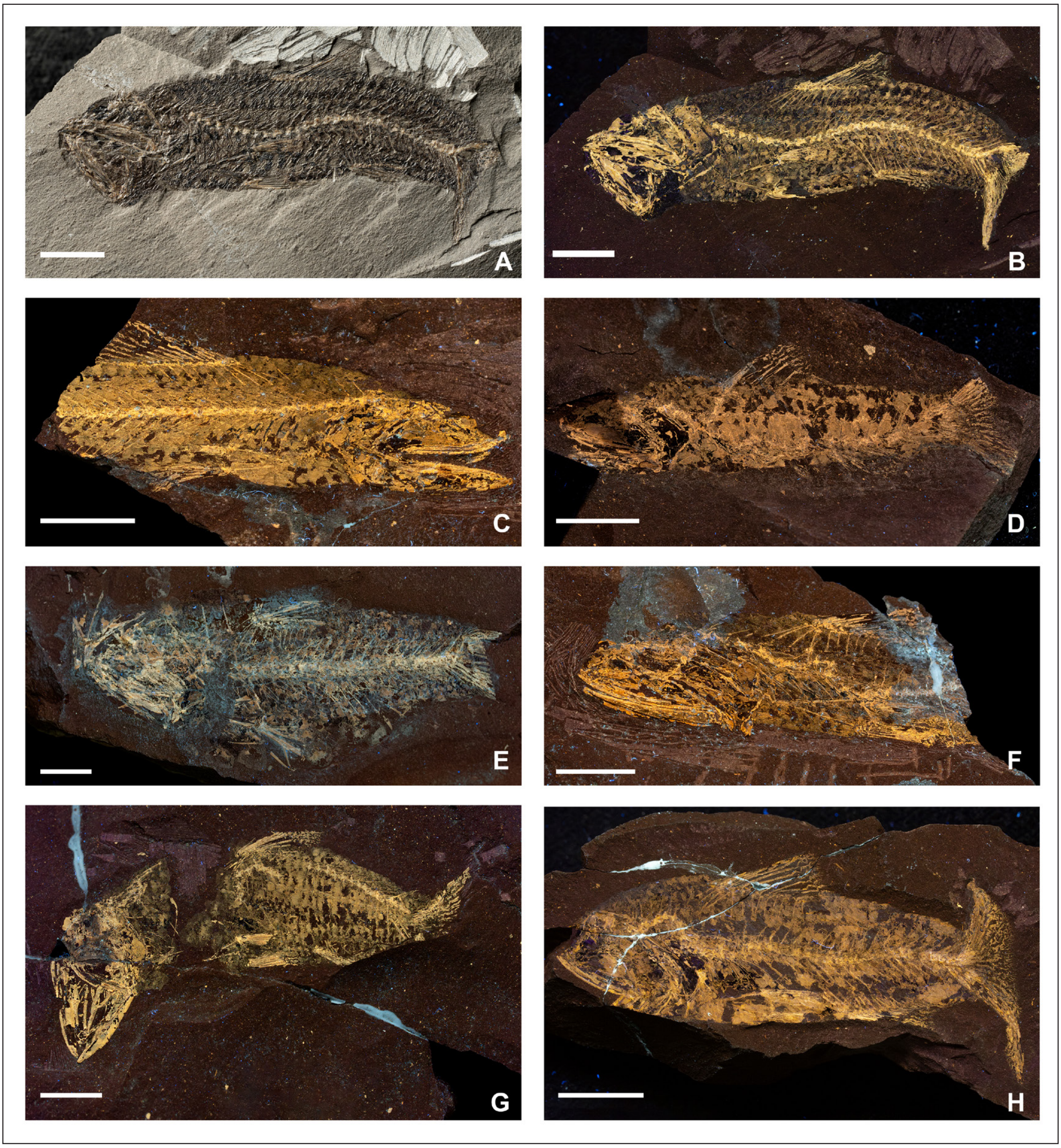


Fig. 13 - *Eomyctophum mainardii* n. sp. lateral view of the holotype, MUSE-PAL 5472, in natural (A) and under UV light (B). Lateral view of the paratypes under UV lights, C) MUSE-PAL 1022; D) MUSE-PAL 1074; E) MCR 3841; F) MUSE-PAL 1102; G) MUSE-PAL 1038; H) MUSE-PAL 3912. Scale bars 10 mm.

beyond the end of their respective vertebral centrum (Fig. 14). The haemal spines are straight and narrow, similar to their opposite neural spines. Long and curved ribs extend ventrally without reaching the ventral margin of the body and articulate with the lateral sides of the abdominal vertebrae, except for the first two. All the abdominal and most of the caudal vertebrae bear slender and straight epineurals, attached to the base of the neural spines. The haemal spines of the second and third preural vertebrae are autogenous, elongate, and slender. The neural spine of the second preural vertebra is significantly reduced and short. The caudal skeleton consists of six autogenous hypurals, a moderately

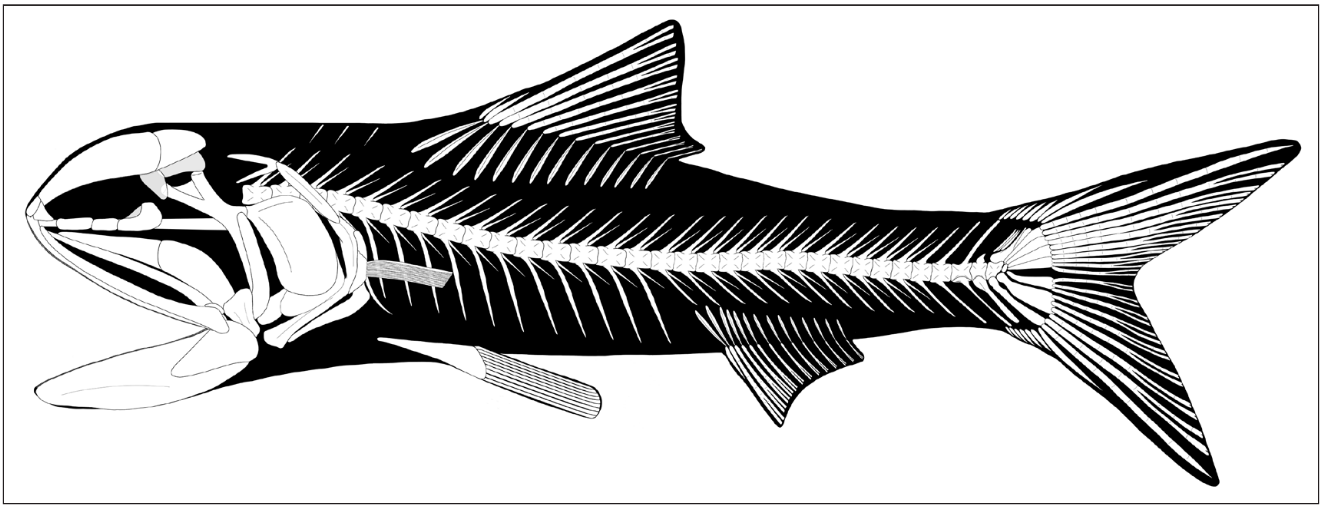


Fig. 14 - *Eomyctophum mainardii* n. sp., interpretive reconstruction of the skeleton.

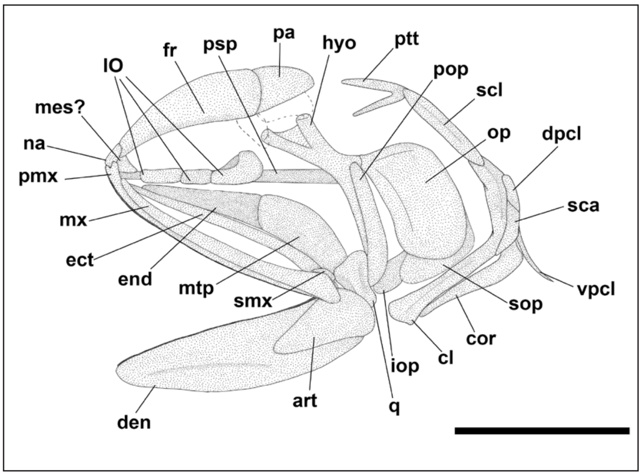


Fig. 15 - *Eomyctophum mainardii* n. sp., interpretive reconstruction of the cranium. Scale bar 10 mm.

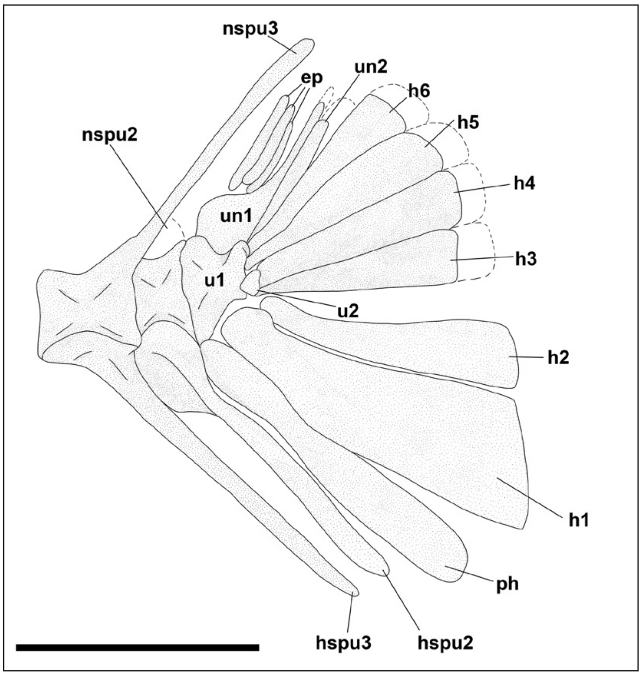


Fig. 16 - *Eomyctophum mainardii* n. sp. Paratype, MCR 3841, interpretive reconstruction of the caudal skeleton. Scale bar 5 mm.

expanded rod–like parhypural, two uroneurals, and three narrow and elongate epurals (see MUSE-PAL 3912, MUSE-PAL 5472; Fig. 16). It is possible to see a reduced second ural centrum, showing a small triangular shape (e.g., MUSE-PAL 5472, MCR 3841; Fig. 16). The caudal fin is forked and bears 19 (10+9) principal rays. In addition, there are five to eight dorsal and seven to nine ventral procurrent rays (5–8, I, 9+8, I,7–9).

There are three or four poorly preserved supraneurals (see MUSE-PAL 1022; Fig. 13C). The dorsal-fin insertion is located at the level of the eighth vertebra, and the dorsal-fin base ends at the level of the second caudal vertebra. The dorsal fin consists of 13–15 rays, with the first two being short, unbranched, and unsegmented. The third and fourth rays are the longest of the series. The dorsal fin is supported by 13–14 thin pterygiophores. The anal-fin origin is located just behind the posterior end of the dorsal fin. The anal fin contains up to 17 rays (range 13–17), with the first two very short, unbranched and unsegmented. The third and fourth rays are the longest of the series, with the successive rays being gradually shorter. The anal fin is supported by 14–15 pterygiophores that resemble those of the dorsal fin.

The pectoral girdle is notably curved. The extrascapulars are not preserved. The posttemporal is narrow and anteriorly bifurcated; its dorsal process is slightly longer than the ventral one. The supracleithrum is elongate and narrow. The cleithrum is arcuate, with a large ventral arm, well-developed posterior plate, and moderately large posteromedial shelf. The coracoid exhibits an elongate anterior process. The scapula is relatively small and quadrangular. The dorsal postcleithrum is ovoid and compact (see MUSE-PAL 3912, MUSE-PAL 5472; Fig. 15). The ventral postcleithrum is generally difficult to observe; it is arcuate, thin, and distally pointed (see MUSE-PAL 1022, MUSE-PAL 5472; Fig. 15). The pectoral-fin radials are usually poorly preserved; at least four hourglass-shaped radials are recognizable (see MUSE-PAL 1102; Fig. 13F). The pectoral fins are rather short, extending posteriorly up to the pelvic-fin insertion and contain 12–14 rays. The basipterygia insert at the level of the posterior margin of the pectoral girdle, being almost in contact with the posterior margin of the cleithrum (see MUSE-PAL 5472; Fig. 14); each basipterygium is triangular and rather large, its length corresponds to the length of four or five vertebral centra. The pelvic fins are considerably longer than the pectoral fins and contain nine rays.

The photophores are rounded, apparently not elevated with respect to the scales, and are generally poorly preserved in the available material. The photophore pattern cannot be properly deduced due to inadequate preservation. There is a single VLO photophore, just above the pelvic fin, at least three or four photophores of the VO series behind the pelvic fin, a single raised photophore above the AO series, and at least three photophores of the AO series (see MUSE-PAL 5472, MCR 3841; Fig. 13A–B, E)

The body is covered with large, almost rounded cycloid scales. The lateral line and a few lateral-line scales are rarely preserved (see MUSE-PAL 1074; Fig. 13D).

Discussion. Dating back to the Ypresian, the myctophids from Solteri are among the most ancient Cenozoic skeletal remains pertaining to this family (Prokofiev 2006; Schwarzhans & Carnevale 2021). Overall, the most ancient myctophids are known from the Maastrichtian of Japan, while the first myctophids of the Cenozoic, based on skeletal remains, belong to the genera *Eomyctophum* (with skeletal remains known from the Ypresian up to the Rupelian) and *Oligophus* (Rupelian; Schwarzhans & Carnevale 2021). The fossil myctophids described herein clearly differ from *Oligophus moravicus* (and other Lampanyctinae) by having a smaller number of vertebrae (32–34 vs 35–37 in *O. moravicus*), a higher number of pectoral-fin rays (12–14 vs 10 in *O. moravicus*), shorter pectoral fins, a maxilla with a broad posterior end (slender in *O. moravicus*), a reduced supramaxilla (absent in *O. moravicus*), a reduced second ural centrum (absent in *O. moravicus*), and a peculiar morphology of the cleithrum (Gregorová 2004; Prokofiev 2006). In *Eomyctophum mainardii* n. sp., the posterior lamina of the cleithrum is well developed and the posteromedial shelf is moderately pronounced, while in *O. moravicus,* the posterior lamina of the cleithrum is narrow and the posteromedial shelf is weakly developed (Gregorová 2004; Prokofiev 2006; Tab. 6).

Among the species of the genus *Eomyctophum*, *E. mainardii* n. sp. differs from *Eomyctophum polysarcus* (Kramberger, 1880) from the Oligocene of the Carpathians, by having more than 30 vertebrae ("around 30 vertebrae" in *E. polysarcus* vs 32–34 in *E. mainardii* n. sp.; see Tab. 6; Kramberger 1879-1880; Gregorová 2004; Prokofiev 2006).

E. mainardii n. sp. can be distinguished from *E. cozlae* (Ciobanu, 1977) (taxon that needs a modern revision, as most of the taxa described in Ciobanu 1977) from the Oligocene of Cozla, Romania, by having a lower number of vertebrae (32–34 vs 34–36 in *E. cozlae* Ciobanu 1977; see Tab. 6), a greater number of dorsal–fin rays (13–15 vs 12 in *E. cozlae* Ciobanu 1977; see Tab. 5), a shorter distance between the pectoral and pelvic fins and a larger distance between the pelvic and the anal fins (PVD: 10.7% of SL and VAD: 26.2% of SL vs PVD: 12.5% of SL and VAD: 18.9% of SL in *E. cozlae* Ciobanu 1977; Tab. 5), a thicker body and caudal peduncle (BD: 26.9% of SL and CPH: 16.3% of SL vs BD: 19–20% of SL and CPH: 13% of SL in *E. cozlae*; Ciobanu 1977; Tab. 5), and an overall larger body size (over 60 mm SL vs 36 mm SL in the holotype of *E. cozlae* Ciobanu 1977; see Tab. 5).

Eomyctophum mainardii n. sp. can be distinguished from *E. koraense* (the type species of the genus), based on a series of traits. The pectoral fins of *E. mainardii* n. sp. are less developed than those of *E. koraense* and shorter than the pelvic fins, almost half in length and barely reaching the insertion of the pelvic–fin rays (PFL: 8.5% of SL and VFL: 20.6% of SL in *E. mainardii* n. sp.; Tab. 5). On the other hand, in *E. koraense*, the pectoral fins

Tab. 6 - Summary of the meristic traits of the different species of the genus *Eomyctophum* and *Oligophus moravicus*. Includes new data and data from Ciobanu (1977), Gregorovà (2004), Prokofiev (2006).

	***Eomyctophum mainardii* n. sp.**	***Eomyctophum koraense***	***Eomyctophum cozlae***	***Eomyctophum polysarcus***	***Oligophus moravicus***
Dorsal-fin rays	13-15	12-14	12	10-14	12-14
Anal-fin rays	13-17	14-17	16	?	14-17
Pectoral-fin rays	12-14	12-15	?	?	10
Pelvic-fin rays	9	8	?	8-10	8
Caudal-fin rays (principal)	19 (10+9)	19 (10+9)	12?	?	19 (10+9)
Caudal-fin rays (procurrent)	5-8+7-9	8-9+7-8	10?	?	9+8
Vertebrae	32-34	32-34	34-36	30	35-37
Smx	yes	yes	yes	?	no
u2	yes	yes	yes	?	no
Size	>60 mm SL	<60 mm SL	<60mm SL	?	<60 mm SL

are longer than the pelvic fins, with the tips of the pectoral–fin rays extending beyond the insertion of the pelvic–fin rays (PFL: 16–21.9% of SL and VFL: 10–16% of SL in *E. koraense*; Prokofiev 2006; Tab. 5). The pelvic fin of *E. mainardii* n. sp. has nine rays, while that of *E. koraense* has eight rays. Furthermore, the basipterygium of *E. mainardii* n. sp. is placed rather anteriorly, much more than in *E. koraense*; in *E. mainardii* n. sp., the basipterygium inserts at the level of the posterior margin of the pectoral girdle, while in *E. koraense* the insertion of the basipterygium is located at the level of the dorsal–fin base origin. As a result, in *E. mainardii* n. sp. the distance between pectoral and pelvic fins is shorter than the distance between the pelvic and anal fins (PVD: 10.7% of SL and VAD: 26.2% of SL; Tab. 5), while in the type species these two measurements are fairly similar and comparable (PVD: 13.3–18.5% of SL and VAD: 16–20.4% of SL; Prokofiev 2006; Tab. 5). Therefore, *E. mainardii* n. sp. has the shortest prepelvic distance of all the species of the genus *Eomyctophum* (PV: 43.6% vs 49.1–54.3% of SL in *E. koraense* and PV: 51–52% of SL in *E. cozlae*; Ciobanu 1977; Prokofiev 2006; Tab. 5). Moreover, the basipterygium of *E. mainardii* n. sp. is larger than that of *E. koraense* (equal to the length of four to five vertebrae vs three, respectively; Prokofiev 2006).

Division **Percomorphacea** Wiley & Johnson, 2010
Order **Stromateiformes** *sensu* Pastana, Johnson & Datovo, 2022
Family Centrolophidae Bonaparte, 1846
Genus *Eogorgon* n. gen.

Type species (by monotypy): *Eogorgon bizzarinii* n. gen. et sp.

Etymology: Genus named from the ancient Greek word *"Ἠώς"*, meaning "dawn", also referring to the Eocene epoch, and the Greek *"Γοϱγών"*, referencing the Gorgons, Greek mythical creatures (Stheno, Euryale, and Medusa); especially Medusa, since this taxon is one of the most ancient genera of Centrolophidae (also known as medusafishes).

Diagnosis: A genus of the Centrolophidae characterized by the following combination of features: body moderately slender; upper jaw with uniserial, minute teeth; lower jaw with a few conical teeth; lachrymal expanded, ovoid in outline; preopercle large with smooth posterior and ventral margins; 32 (12+20) vertebrae; caudal skeleton with five autogenous hypurals and three epurals; caudal fin with 17 principal rays plus eight or nine dorsal and nine ventral procurrent rays; dorsal fin continuous and elongate, including four weakly developed spines and 30 soft rays; anal fin with three spines and 27–29 soft rays; pectoral fins containing 18 rays; pelvic fins developed, comprising one spine and five rays; scales cycloid.

Remarks and comparison. The new genus *Eogorgon* can be referred to the Stromateiformes (and the suborder Stromateoidei) by having uniserial premaxillary teeth, palatine teeth absent, anal fin containing more than 24 rays and pectoral fin with 18 or more rays (see Haedrich 1967; Pastana et al. 2022).

Eogorgon n. gen. cannot be assigned to the suborder Amarasipoidei (comprising the sole family Amarsipidae) as it exhibits a notably different vertebral count (32 vs 47), less than 13 ventral procurrent rays, a continuous dorsal fin with four spines (instead of two separate dorsal fins with 11 spines), and three anal-fin spines (vs none in Amarsipidae; Pastana et al. 2022).

Within stromateoid fishes, *Eogorgon* n. gen. can be tentatively referred to the family Centrolophidae by having an anterior ceratohyal without a beryciform foramen, a continuous dorsal fin; a reduced number of dorsal-fin spines (at least four), less than 35 dorsal-fin rays, and the anal fin containing three spines and 27–29 rays (see Pastana et al. 2022). Additional characters found in *Eogorgon* n. gen. and listed by Haedrich (1967) as diagnostic for centrolophids are: pelvic fins present in adults, toothless palatine and caudal skeleton with five autogenous hypurals plus an autogenous parhypural.

Eogorgon n. gen. differs from the extinct family Propercarinidae by having a different vertebral count (32 vertebrae vs 35–36 for *Propercarina* Paucă, 1929), and a continuous dorsal fin (instead of two fins separated by five to six rayless pterygiophores as in Propercarinidae; Přikryl et al. 2014).

Eogorgon n. gen. cannot be assigned to the Nomeidae due to having a single continuous dorsal fin instead of two separate dorsal fins, and for lacking the characteristic curved ventral limb of the coracoid typical of the Nomeidae (Pastana et al. 2022).

Eogorgon n. gen. also differs from the Tetragonuridae by having a different vertebral count (32 vs 53 vertebrae in tetragonurids), a single continuous dorsal fin (instead of two separate dorsal fins) and different compositions of the dorsal (IV+30 vs XIX+14 in Tetragonuridae) and anal fins (III+27–29 vs I+11 in Tetragonuridae; Pastana et al. 2022).

Any attribution to the Ariommatidae can be ruled out as well since *Eogorgon* n. gen. exhibits a different structure of the caudal skeleton (five autogenous hypurals vs a single autogenous dorsal hypural and a ventral hypural plate fused to the compound centrum in Ariommatidae), a single continuous dorsal fin (vs two separate dorsal fins), and fewer pectoral-fin rays (18 vs 20 in Ariommatidae; Pastana et al. 2022).

Lastly, *Eogorgon* n. gen. differs from the Stromateidae by having fewer anal-fin rays (27–29 vs 34–39 in Stromateidae) and by maintaining the pelvic fins in adults (absent in Stromateidae; Pastana et al. 2022).

Eogorgon bizzarinii n. gen. et sp.

Figs. 17–20

Holotype: MCR 3840-3842, a nearly complete articulated skeleton, 97.9 mm SL, in part and counterpart.

Paratype: MUSE-PAL-SB 2462A-B, a nearly complete articulated skeleton, in part and counterpart.

Etymology: Species named after the late Italian paleontologist Fabrizio Bizzarini (1947-2024) in recognition of his valuable contributions to the paleontology of northeastern Italy.

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. The body is moderately elongate and robust, with the maximum body depth (BD: 43.3% of SL) located in the pelvic area. The head is rather large with a blunt snout, a short preorbital area, and a large orbit. The mouth is moderately large and terminal. The pelvic fins are thoracic, at the level of the pectoral girdle. The height of the caudal peduncle is less than one third of the maximum body depth (CPH: 13.6% of SL; Tab. 7–9).

The neurocranium is rather deep with a low supraoccipital crest and a large orbit. The ethmoid region of the neurocranium is short and compact. The lateral ethmoid forms the anterior wall of the orbit and is stout and robust. The mesethmoid is large and squared. The frontals are the largest bones of the skull roof, being enlarged posteriorly and gradually tapered anteriorly. The parietal, sphenotic, and pterotic are difficult to recognize due to inadequate preservation. The epioccipital is not preserved. The pterosphenoid occupies the posterodorsal wall of the orbit. The basisphenoid is barely visible in our material. The parasphenoid is straight and rod-like, slightly expanded posteriorly.

The nasals are almost triangular, bearing a narrow anterior projection. Of the infraorbital bones, only the lachrymal is partially preserved. In MCR 3840-3842, the lachrymal exhibits an ovoid shape, rounded posteriorly and slightly tapering anteriorly with smooth margins (Figs. 17A–D, 18–19). Fragments of the other infraorbitals are difficult to recognize.

The premaxilla is large and bears a short ascending process. A deep notch separates the ascending process from the articular process (see MCR 3840-3842; Figs. 18–19). The globular articular process is slightly taller and larger than the ascending process. The premaxilla bears a single series of extremely minute and uniserial conical teeth, which primarily occur in its anterior portion. The maxilla is elongate and expanded distally; its anterior head has two processes for the articulation with the premaxilla and the palatine. There is a single supramaxilla that shows a splint-like shape, representing almost one fourth of the length of the maxilla. The lower jaw is shorter than the upper jaw. The dentary has a narrow, triangular shape. The teeth of the lower jaw are conical, larger than those of the upper jaw, recognizable in MUSE-PAL-SB 2462A-B (Fig. 17E–F). The anguloarticular is stout and triangular in outline. The retroarticular is poorly preserved and occupies the posteroventral corner of the mandible.

	MCR 3840-3842
SL (mm)	97.9
TL (mm)	128.3
HL	34.3
PD	34.8
PA	44.2
PP	39.7
PV	28.2
DFL	?
AFL	44.4
VFL	19.8?
PRO	10.9
O	11.6
POO	11.9
PRO (%HL)	31.8
O (%HL)	33.9
POO (%HL)	34.5
DRL	?
AFR	13.4
BD	43.3
CPL	13
CPH	13.6

Tab. 7 - Measurements of *Eogorgon bizzarinii* n. gen. et. sp. Values are as percentage of SL.

The quadrate is triangular, with a large anterior condyle for the articulation with the anguloarticular. The symplectic is thin and short. The hyomandibula has an elongate and narrow vertical shaft. The ectopterygoid is straight and elongate, tapering anteriorly. The endo- and metapterygoid are large and flat, quadrangular and almost triangular in outline, respectively. The palatine is ovoid in shape, slightly enlarged anteriorly, and toothless.

The bones of the opercular series are poorly preserved in the available specimens. The preopercle is crescent-shaped and anteroventrally expanded, with a curved outline and smooth posterior and ventral margins. The opercle is almost trapezoid in outline. The subopercle is almost triangular with curved margins. The interopercle is not preserved in any of the available specimens.

The anterior ceratohyal is subrectangular, slightly constricted in the middle, not pierced by a beryciform foramen (see MCR 3840; Fig. 19). The posterior ceratohyal is almost triangular (see MUSE-PAL-SB 2462A–B; Fig. 17E–F). The hypohyals are not preserved. There are six curved and thick branchiostegal rays, three of which articulate with the anterior ceratohyal. Of the branchial skeleton, only fragments of the ceratobranchials bearing thin gill filaments are preserved. There is no evidence of the pharyngeal sac, a structure that is scarcely prone to fossilization.

The vertebral column contains 32 vertebrae, of which 19–20 are caudal. In the holotype, there are 12 abdominal plus 20 caudal vertebrae, whereas in the paratype only 25 centra are preserved. The centra are squared and bear a medial-lateral ridge. The neural spines emerge from the central portion of each centrum. The neural spines are thin and straight. The curved haemal spines emerge from the posterior portion of the anterior half of the centrum and are often in contact with the anal-fin pterygiophores, especially the anterior ones. Moderately large parapophyses are present in the posterior four abdominal vertebrae. There are elongate ribs that articulate laterally on the abdominal vertebrae (due to inadequate preservation, it is difficult to determine their articulation with the two anteriormost centra), extending ventrally without reaching the ventral margin of the body. There are some thin, straight, and short epineurals inserting on the base

	***Eogorgon bizzarinii* n. gen. et sp.**	***Butyrumichthys henricii***	***Zorzinia postalensis***	***Petrodavia nirvanae***	***Agarcia agarciaensis***	***Centrolophus***	***Tubbia***	***Icichthys***
SL (mm)	97.9	58.4-214.7	35-43	28	35-47	722-1198	60.7-110	69-435
HL	34.3	28.7-39	26-29	?	30-32	20.7-24.5	23.5-28.7	18.7-30.8
PD	34.8	29-38	58-61	43	38-40	28.8-36.8	22.3-28.8	42-43
PA	44.2	51.3-70.2	59-61	62	58-63	54.9-58.4	45.1-53	55-63
PP	39.7	31.9-39.9	?	?	?	?	23.3-27.1	?
PV	28.2	25.8-41	?	?	??	24.2-29.3	25.5-28.3	23.6-30.1
DFL	?	45.6-53	?	?	41-45	46.9-56.5	63.1-70.7	38.4-53.4
AFL	44.4	17.4-23.5	30-31	35	31-35	26.4-29.4	40-47.1	21.7-28.8
VFL	19.8?	?	?	?	?	?	4.8-6.8	?
O	11.6	8.1-14	8-9	?	10-12	?	5.2-7	?
POO	11.9	13.6-19.8	11-14	?	?	?	12.9-17.4	?
BD	43.3	37.3-55.3	25-26	38-39	31-35	24.7-29.6	30.1-39.3	25.6-34.1
CPL	13	8.5-12.2	?	?	?	?	5.6-8.7	?
CPH	13.6	12.3-16.7	10	?	8-11	?	8.8-10.5	?

Tab. 8 - Summary of the most relevant measurements of various Centrolophidae. Values are as percentage of SL. Includes new data and data from McDowall (1982), Last et al. (2013), Pastana et al. (2022) and Schrøder et al. (2023).

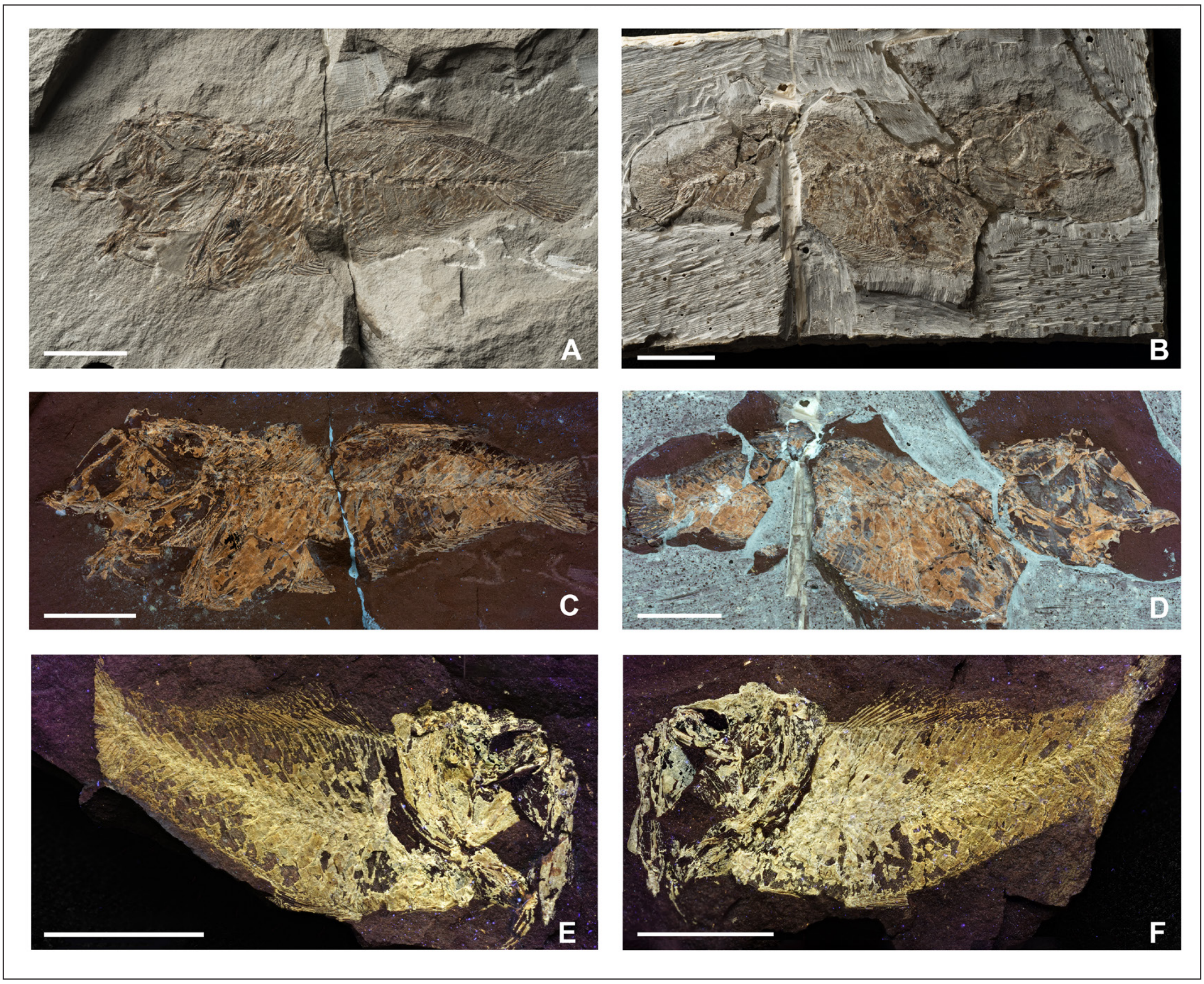
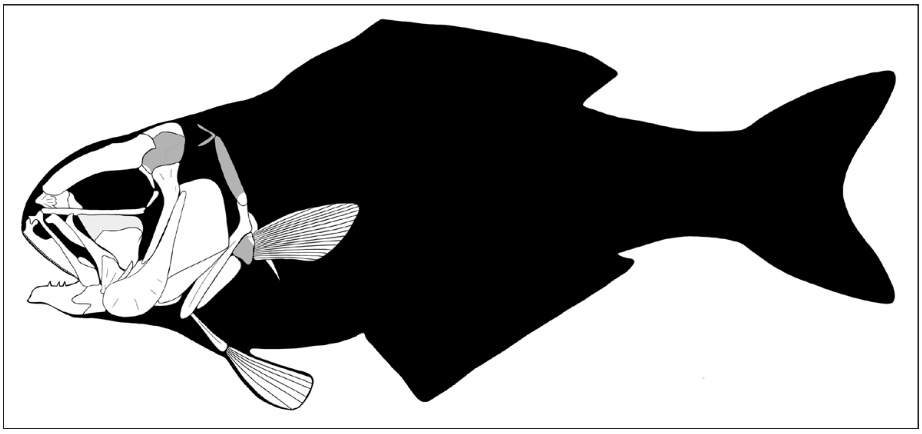


Fig. 17 - *Eogorgon bizzarinii* n. gen. et sp. Lateral view of the holotype, MCR 3840-3842, in natural (A–B) and under UV light (C–D). Lateral view of the paratype, MUSE-PAL-SB 2462A-B, under UV light (E–F). Scale bars 10 mm.

of the neural spines of the abdominal centra.

The haemal spines of the second and third preural vertebrae are autogenous and thin, with the haemal spine of the second preural vertebra being slightly wider. The neural spine of the second preural vertebra is notably shortened. The caudal skeleton consists of five autogenous hypurals, an autogenous parhypural (without parhypurapophy-

Fig. 18 - *Eogorgon bizzarinii* n. gen. et sp., interpretive reconstruction of the body outline with the isolated cranium and girdles (infraorbital bones are omitted).



	***Eogorgon bizzarinii* n. gen. et sp.**	***Butyrumichthys henricii* (average)**
SL (mm)	97.9	103.7
HL	34.3	34.7
PD	34.8	34.5
PA	44.2	65.1
PP	39.7	37.9
PV	28.2	39.2
DFL	?	49
AFL	44.4	20.2
VFL	19.8?	?
PRO	10.9	12.6
O	11.6	11.7
POO	11.9	16.8
DRL	?	22.6
AFR	13.4	20.9
BD	43.3	49.1
CPL	13	10.6
CPH	13.6	15.1

Tab. 9 - Summary of the most relevant measurements of *Eogorgon bizzarinii* n. gen. et. sp. and of *Butyrumichthys henricii*. Values are as percentage of SL. Includes new data and data from Schrøder et al. (2023).

sis), three epurals, and a single uroneural (Fig. 20). The epurals are slightly curved and expanded ventrally. The caudal fin is forked (see MUSE-PAL-SB 2462A-B; Fig. 17E–F) and bears 17 (9+8) principal rays. In addition, there are eight or nine dorsal and nine ventral procurrent rays (8–9, I, 8+7, I, 9).

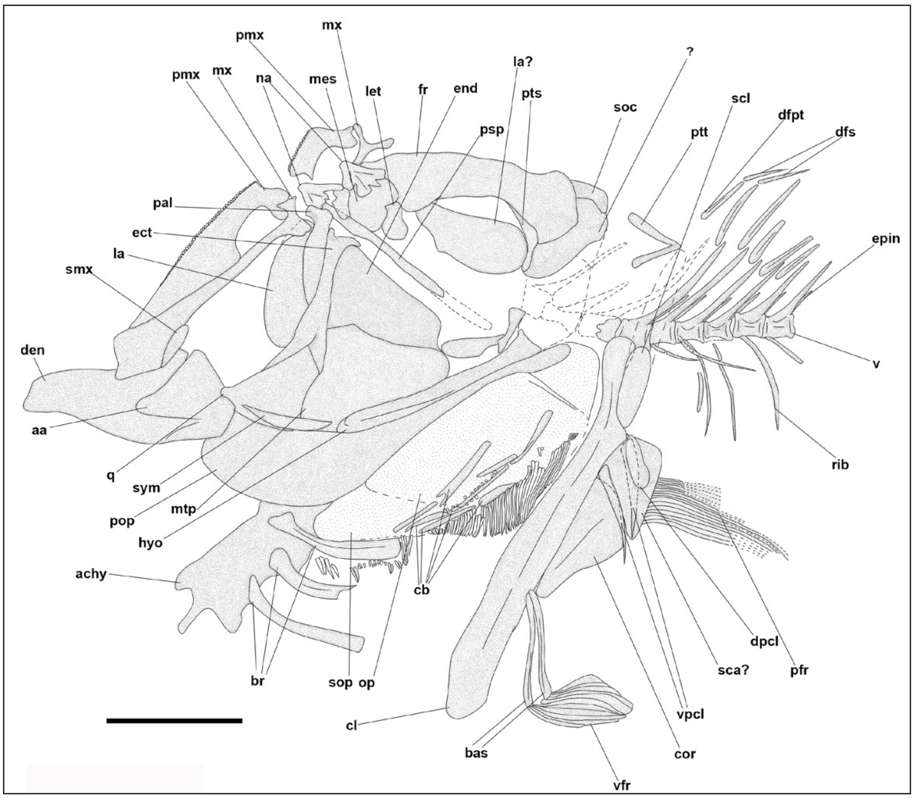
There are no traces of supraneurals, most likely as a result of inadequate preservation. The dorsal fin comprises at least four small and delicate spines followed by at least 30 elongate and distally branched rays (see MUSE-PAL-SB 2462A-B Fig. 17E–F). The anterior rays are the longest of the series, and their length gradually decreases posteriorly. The pterygiophores are thin, elongate, and straight. Due to inadequate preservation of the anterior portion of the vertebral column, it is difficult to determine the dorsal-fin pterygiophore formula. The anal fin inserts quite forward, before the midpoint of the body and comprises three short spines followed by 27–29 soft rays. Most of the anal-fin rays are not completely preserved. The anal-fin pterygiophores are slender and characterized by a straight profile; the first anal-fin pterygiophore is by far the largest of the series, and the following pterygiophores are progressively shorter posteriorly. Due to poor preservation of several anal-fin pterygiophores, it is difficult to determine the anal-fin formula.

The pectoral girdle is incomplete in the examined specimens. The posttemporal is bifurcate anteriorly. The supracleithrum appears to be narrow and oblong. The cleithrum is large, curved, and slightly expanded ventrally. The coracoid is almost triangular, tapering ventrally into a pointed tip. The morphology of the scapula is difficult to determine (see MCR 3840-3842; Fig. 19). The dorsal postcleithrum is ovoid, while the ventral one is thin and curved (see MCR 3840-3842; Fig. 19). The pectoral-fin radials are poorly preserved. The pectoral fin inserts low on the body flanks and appears to be characterized by 18 rays (see MCR 3840; Fig. 19). The basipterygium is delicate, weakly ossified, triangular in outline, with a scarcely developed median process. The pelvic fins are inserted slightly before the pectoral fins, and each of them contains a single spine plus five soft rays. The distal portion of the pelvic-fin rays is not well preserved, but these were likely shorter than the pectoral-fin rays in origin.

The body is covered by small and circular cycloid scales. The lateral line is poorly preserved, partially visible around the mid-length of the body, above the first caudal vertebrae, where a few lateral-line scales are preserved (see MCR 3842; Fig. 17B, D).

Discussion. As discussed above, *Eogorgon bizzarinii* n. gen. et sp. is tentatively referred to the Centrolophidae due to the presence of a supramaxilla (absent in the other Stromateoid families), toothless palatine, five autogenous hypurals and parhypural, continuous dorsal fin and pelvic fins present in adults (Haedrich 1967; Schrøder et al. 2023). However, some morphology-based phylogenetic studies (Horn 1984; Doiuchi et al. 2004; Pastana et al. 2022) do not consider the Centrolophidae as monophyletic, even though molecular phylogenies recurrently recognize it as monophyletic (e.g., Doiuchi & Nakabo 2006; Miya et al. 2013; Friedman et al. 2019). Pastana et al. (2022) separated the family into a basal clade containing three extant genera (*Icichthys* Jordan & Gilbert, 1880, *Tubbia* Whitley, 1843 and *Centrolophus* Lacepède, 1802) from the other four extant genera, which are regarded as successive sister groups of a clade containing the remaining families of the Stromatoidei. We consider *E. bizzarinii* n. gen. et sp., as related to the clade formed by *Icichthys*, *Tubbia,* and *Centrolophus,* with which it shares a continuous dorsal

Fig. 19 - *Eogorgon bizzarinii* n. gen. et sp. Holotype, MCR 3840, interpretive reconstruction of the cranium. Scale bar 10 mm.



fin with five or fewer spines, up to 35 dorsal-fin rays, and ceratohyal lacking a beryciform foramen (see Pastana et al. 2022). *E. bizzarinii* n. gen. et sp. mainly differs from the other extant Centrolophidae of this more basal clade on the vertebral count. It has a lower number than *Icichthys* and *Tubbia* (32 vs 49–51 and 40–45 vertebrae, respectively; McDowall 1982; Last et al. 2013; Pastana et al. 2022) and a higher number compared to *Centrolophus* (32 vs 25 total vertebrae; McDowall 1982). Furthermore, the counts and measurements of these three extant genera are different from those of *E. bizzarinii* n. gen. et sp. (See Tab. 8–10).

Eogorgon bizzarinii n. gen. et sp. is one of the most ancient stromateiforms known to date. The putative centrolophid *Butyrumichthys henricii* Schrøder et al., 2023, from the lower Eocene Fur Formation (Denmark), is older (dating back to 56–54 Ma; Schrøder et al. 2023). We distinguish *E. bizzarinii* n. gen. et sp. from *Butyrumichthys henricii* by having a generally more slender and less deep body (BD: 43.3% vs 37.3–55.3% of SL in *B. henricii*; Tab. 8–9), a lower number of vertebrae (32 vs 37–38 in *B. henricii*), anal fin with three spines and 27–29 rays (vs two spines and no more than 20 rays in *B. henricii*), preopercle with a smooth ventral margin instead of spine-bearing, longer anal-fin base (AFL: 44.4% vs 17.4–23.5% of SL in *B. henricii*; Tab. 8–9) and shorter preanal distance (PA: 44.2% vs 51.3–70.2% of SL in *B. henricii*; Tab. 8–9; Schrøder et al. 2023).

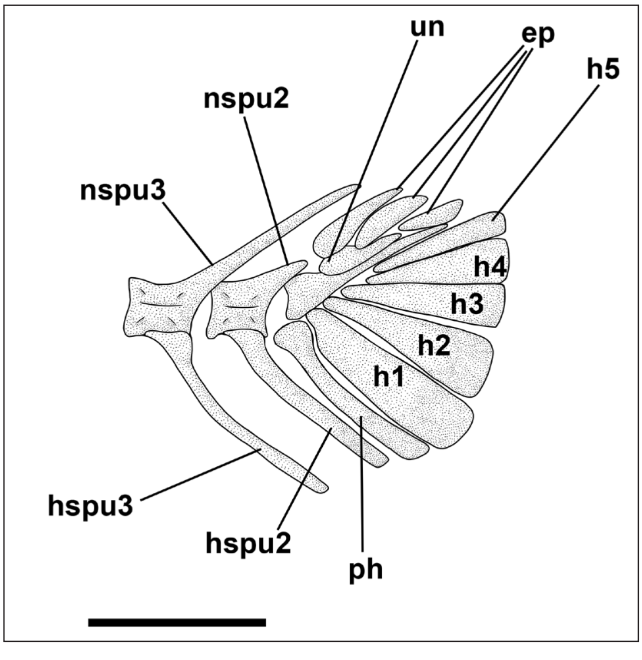


Fig. 20 - *Eogorgon bizzarinii* n. gen. et sp. Holotype, MCR 3840, interpretive reconstruction of the caudal skeleton. Scale bar

	***Eogorgon bizzarinii* n. gen. et sp.**	***Butyrumichthys henricii***	***Zorzinia postalensis***	***Petrodavia nirvanae***	***Agarcia agarciaensis***	***Centrolophus***	***Tubbia***	***Icichthys***
Dorsal-fin rays	IV, 27-30	V-VI, 27-28	VI, 17	X, 18	VIII-IX, 16-17	37-42	IV-VI, 42-49	38-40
Anal-fin rays	III, 27-29	II, 19-20	III, 18-19	III, 23	III, 20	24-27	II-III, 29-35	25-28
Pectoral-fin rays	18	25	?	15-16	12	20-23	18-21	16-18
Pelvic-fin rays	I+5	I+5	I+5	I+5	I+5	?	?	?
Caudal-fin rays (principal)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)
Caudal-fin rays (procurrent)	8-9+9	7-10+9	6+6	6-8+6-8	8+7	?	9-13+9-13	?
Vertebrae (caudals)	32 (12+20)	37-38 (17-18+20)	24 (10+14)	26 (11+15)	25 (10+15)	25	40-45	49-51
Branchiostegal rays	6	6	?	?	7	?	?	?
epurals	3	3	2	3	3	3	3	3
supraneurals	0?	3	3	3	3	?	?	9-11

Tab. 10 - Summary of the meristic traits of *Eogorgon bizzarinii* n. gen. et. sp. compared with different centrolophid genera. Includes new data and data from McDowall (1982), Bannikov (2000), Baciu & Bannikov (2004), Last et al. (2013), Pastana et al. (2022) and Schrøder et al. (2023).

Another Eocene putative member of the Centrolophidae is *Zorzinia postalensis* Bannikov, 2000 (see Bannikov 2000) from the Monte Postale site, near Bolca. This taxon is both stratigraphically and geographically close to Solteri, but it can be easily separated from *E. bizzarinii* n. gen. et sp. since it shows a longer vertebral column (32 vs 24 total vertebrae in *Zorzinia postalensis*), three (vs two) epurals, a deeper body with a rather large mouth (vs slender body and small mouth in *Z. postalensis*; BD: 43.3% vs 25–26% of SL in *Z. postalensis*; Tab. 8), as well as a different set of meristic and morphometric traits (see Tab. 8), especially regarding the dorsal fin, which in *Z. postalensis* originates remarkably posteriorly compared to *E. bizzarinii* n. gen. et sp. (PD: 34.8% vs 58–61% of SL in *Z. postalensis;* Tab. 8; Bannikov 2000).

The other two putative fossil Centrolophidae are known from the lower Oligocene of Romania, *Petrodavia nirvanae* Baciu & Bannikov, 2004 and *Agarcia agarciaensis* Baciu & Bannikov, 2004. *E. bizzarinii* n. gen. et sp. differs from *Petrodavia nirvanae* by having a different vertebral count (32 vs 26 in *Petrodavia nirvanae*), a preopercle with smooth ventral margin and lacking serrations, a slightly arcuate ventral postcleithrum (vs straight and vertical in *P. nirvanae*), plus some morphometric differences, especially the predorsal and preanal distance (PD: 34.8% vs 43% of SL in *P. nirvanae*; PA: 44.2% of SL vs 62% of SL in *P. nirvanae*; Tab. 8); in addition, the dorsal fin in *E. bizzarinii* n. gen. et sp. comprises a lower number of spines and more rays than that of *P. nirvanae* (IV+30 vs X+18 in *P. nirvanae*; Baciu & Bannikov 2004; Tab.10).

E. bizzarinii n. gen. et sp. also differs from *Agarcia agarciaensis* by having a lachrymal with a smooth lower margin instead of a serrated one, higher number of vertebrae (32 vs 25 vertebrae in *A. agarciaensis*; see Tab.10), a supramaxilla, preopercle with smooth ventral and posterior margins and without any serrations, an arcuate ventral postcleithrum (vs straight and vertical in *A. agarciaensis*), plus other meristic and morphometric traits such as the preanal distance, anal-fin length, maximum body depth and caudal peduncle height (PA: 44.2% vs 58–63% of SL in *A. agarciaensis*; AFL: 44.4% vs 31–35% of SL in *A. agarciaensis*; BD: 43.3% vs 31–35% of SL in *A. agarciaensis*; CPH: 13.6% vs 8–11% of SL in *A. agarciaensis*; Tab. 8). Moreover, the dorsal fin in *E. bizzarinii* n. gen. et sp. comprises fewer spines and more rays than that of *A. agarciaensis* (IV+30 vs VIII–IX+16 in *A. agarciaensis*; Baciu and Bannikov 2004; See Tab.10).

Order **Scombriformes** *sensu* Johnson, 1986

Suborder **Trichiuroidea** *sensu* Nakamura & Parin, 1993

Family Gempylidae Gill, 1862

Genus *Krampusichthys* n. gen.

Type species (by monotypy): *Krampusichthys tridentinus* n. gen. et sp.

Etymology: Genus named after the fictional creature *Krampus*, typical of the folklore of the Trentino-Alto Adige region (where the type locality and horizon are located), given the long “fang-like” teeth of this taxon reminding of the foul appearance of the *Krampus* and from the Greek word *"ἴχθύς"* meaning "fish".

Diagnosis: A genus of the Gempylidae characterized by the following combination of features: moderately elongate, deep and compressed body (BD: 30.5% of SL); low supraoccipital crest; palatine with small conical teeth; upper jaw with one or two long fangs and up to 29 smaller conical teeth; lower jaw with three long fangs and up to seven smaller teeth; ventral margin of the preopercle with minute serrations; deep opercular notch; seven or eight branchiostegal rays; 32 (14+18) vertebrae; parapophyses on the last three posterior abdominal vertebrae; epineurals present in the abdominal vertebrae; caudal fin forked with 17 principal rays (I,8+7,I) plus six or seven dorsal and six or seven ventral procurrent rays; five autogenous hypurals with small notch between the second and third hypurals; first dorsal fin with nine to 13 spines; second dorsal fin with one or two spines followed by 20 to 26 rays; anal fin with two spines and 14 to 19 rays; pectoral fin with 15 to 19 rays; pelvic fins with one spine plus five rays; dense squamation covering the whole body with large ctenoid scales showing up to 14 radii.

Remarks and comparison. *Krampusichthys* n. gen. is referred to the family Gempylidae by having: body semifusiform, elongate and laterally compressed; elongate mesethmoid and lateral ethmoid; lateral ethmoid with a short lateral process and a posterolateral process; reduced supraoccipital crest; mouth large with fangs in both upper and lower jaws; premaxilla with short ascending process and a postmaxillary process not expanded and not extending beyond the maxilla; a small supramaxilla; three branchiostegal rays articulated with the posterior ceratohyal; beryciform foramen absent; a deep opercular notch; a rounded dorsoanterior process of the subopercle; 32 vertebrae; caudal fin forked with the caudal-fin rays attached to the distal edge of the hypurals; two clearly separate dorsal fins; supracleithrum elongate; cleithrum without posterior protuberance; pectoral-fin length shorter than head length; pelvic fins short (e.g., Russo 1983; Nakamura & Parin 1993).

Krampusichthys n. gen. differs from the Euzaphlegidae by having: fangs in both upper and lower jaws; a supramaxilla; caudal skeleton with unfused hypural bones (vs two hypural plates); absence of rayless pterygiophores between the two dorsal fins, which are not separated by a large gap (present in Euzaphlegidae); different ray-counts of unpaired and paired fins (Monsch 2000; Monsch & Bannikov 2011; Tab. 11–12).

Krampusichthys n. gen. cannot be assigned to the Trichiuridae due to the presence of conical fangs with smooth edges (vs compressed in Trichiuridae), a different number of vertebrae (32 vertebrae vs more than 50 in Trichiuridae), a large caudal fin (small or absent in Trichiuridae), and first dorsal-fin base longer than the second dorsal-fin base (while the opposite occurs in Trichiuridae; Gago 1998).

With 32 vertebrae, *Krampusichthys* n. gen. differs from *Abadzekhia* spp. Bannikov, 1985 (34; Bannikov 2017), *Argestichthys vysotzkyi* Prokofiev, 2002 (35; Prokofiev 2002b; Bannikov 2017) and many extant gempylids (e.g., *Diplospinus* Maul, 1948, 57–62; *Paradiplospinus* Andriashev, 1960, 60–67; *Gempylus* Cuvier, 1829, 48; Nakamura & Parin 1993). Moreover, the dentition of *Krampusichthys* n. gen. (one or two fangs on the premaxilla and three fangs on the dentary) differs from that of several extinct (*Abadzekhia*; *Progempylus edwardsi* Casier, 1966; *Argestichthys vysotzkyi*; Prokofiev 2002b; Bannikov 2017; Beckett et al. 2018) and extant taxa (see Russo 1983; Nakamura & Parin 1993). By lacking finlets *Krampusichthys* n. gen. differs from the fossil genus *Abadzekhia* (Bannikov 2017) and many extant genera (*Gempylus*, *Hemithyrsites* Sauvage, 1873, *Lepidocybium* Gill, 1862, *Nealotus* Johnson, 1865, *Nesiarchus* Johnson, 1862, *Rexea* Waite, 1911, *Rexicthtys* Parin & Astakhov, 1987, *Ruvettus* Cocco, 1833, *Thyrsites* Lesson, 1831, *Thyrsitoides* Fowler, 1829, *Thyrsitops* Gill, 1862; see Russo 1983; Nakamura & Parin 1993). Due to its low supraoccipital crest, it is possible to separate *Krampusichthys* n. gen. from the fossil *Progempylus edwardsi* (Beckett et al. 2018) and the extant *Lepicydobium*, *Neoepinnula* Matsubara & Iwai, 1952 and *Ruvettus* (Nakamura & Parin 1993). Moreover, the developed pelvic fins of *Krampusichthys* n. gen. allow to separate it from the fossil *Chelifichthys goujeti* Carnevale, 2006 and the extant *Hemithyrsites*, *Nealotus*, *Rexea*, *Rexicthtys,* and *Nesiarchus* (Nakamura & Parin 1993). *Krampusichthys* n. gen. further differs from *Tongaichthys* Nakamura & Fujii, 1983 by not being characterized by hypurostegy (Nakamura & Fujii 1983). Various meristic differences of the median and paired fins between *Krampusichthys* n. gen. and several other extinct gempylids are summarized in Tab. 12.

Krampusichthys tridentinus **n. gen. et sp.**

Figs. 21–22

Holotype: MUSE-PAL 5473, a nearly complete articulated skeleton, 78.2 mm SL

Paratypes: MUSE-PAL 1033-1047, a nearly complete articulated skeleton, in part and counterpart; MUSE-PAL 1034, an incomplete articulated skeleton lacking the caudal skeleton and fin; MUSE-PAL 3567, an incomplete articulated skeleton lacking the caudal skeleton and fin; MUSE-PAL 6791 an incomplete articulated skeleton lacking the caudal skeleton and fin, in part and counterpart.

	***Krampusichthys tridentinus* n. gen. et sp.**	***Laurinichthys boschelei* n. gen. et sp.**	***Wudelenia diabolica* n. gen. et sp.**
1st Dorsal-fin rays	IX-XIII	XVIII	XII
2nd Dorsal-fin rays	I-II, 18-26	I, 15+	II, 31
Anal-fin rays	II, 14-19	I, 7+?	?
Pectoral-fin rays	15-19	14	18
Pelvic-fin rays	I+5	I+5	I+5
Caudal-fin rays (principal)	17 (9+8)	?	17 (9+8)
Caudal-fin rays (procurrent)	6-7+6-7	?	6+6
Vertebrae	32 (14+18)	25+ (16+9?)	40 (16+24)
Branchiostegal rays	8	5+?	7
Pmx teeth (fangs)	16-29 (1-2)	20 (1)	14-16 (2)
Den teeth (fangs)	7 (3)	9+ (1)	5 (3)

Tab. 11 - Summary of the meristic traits of the different gempylid taxa found in Solteri.

Referred specimens: MUSE-PAL 4317, an incomplete specimen lacking the posterior portion of the body and the caudal fin; MUSE-PAL 5131-6107, a nearly complete articulated skeleton, in part and counterpart.

Etymology: Species named after the Latin word *"tridentinus"*, meaning "coming from *Tridentum*" (Latin translation of Trento, the province of the type locality of this species).

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Krampusichthys tridentinus* n. gen. et sp. is a small-sized gempylid with a maximum length of less than 80 mm SL; however, some of the incomplete specimens were probably slightly longer in origin (e.g., MUSE-PAL 1033–1047; Fig. 21E–F). The body is deep, moderately elongate, and laterally compressed, showing its maximum depth around its mid-length at the level of the pelvic fins. The head is elongate and characterized by a pointed snout. The orbit is large, central, and slightly ovoid. The anal-fin origin is located at the level of the insertion of the second dorsal fin.

The neurocranium is elongate and anteriorly pointed. The ethmoid region is elongate and massive (Fig. 22A–B). The mesethmoid is trapezoid in shape, while the lateral ethmoid is almost triangular and forms the anterior margin of the orbit, bearing a lateral process. The vomer is anteroventrally expanded and bears minute teeth (e.g., MUSE-PAL 5473; Fig. 22A). The frontals are the largest bones of the skull roof; they are elongate and tapered anteriorly. The small parietals are only partially visible and poorly preserved. The pterotic is trapezoid. The sphenotic is almost triangular in outline. The supraoccipital exhibits a weakly developed crest. The morphology of the epioccipital is difficult to determine due to inadequate preservation. The pterosphenoid forms the posterodorsal margin of the orbit. The basisphenoid is short and slightly curved (see MUSE-PAL 3567; Fig. 22B) and bears a ventral process that contacts the parasphenoid. The prootic is poorly preserved in the examined specimens. The parasphenoid is narrow and rod-like.

The nasals are small and tubular. The lachrymal is the largest element of the infraorbital series; it is elongate and only slightly expanded at its extremities. The second infraorbital is always poorly preserved. The third infraorbital is curved and thin. The other infraorbitals are usually poorly preserved.

The premaxilla has a moderately developed ascending process and a shallow postmaxillary process. The premaxillary teeth are arranged in two rows, the outer one with several minute conical and slightly retrorse teeth (up to 29, see MUSE-PAL 6791a; Fig. 21G), and the inner one with one or two large fangs placed just below the ascending process (e.g., MUSE-PAL 1034, MUSE-PAL 5473; Figs. 21A–C, 22A). The maxilla has a robust articular head and a notably expanded distal end, characterized by a rounded profile. There is a thin and splint-like supramaxilla (see MUSE-PAL 3567; Fig. 22B). The lower jaw is large and protrudes anteriorly beyond the upper jaw. The dentary is prominent (e.g., MUSE-PAL 1033-1047; MUSE-PAL 1034; Fig. 21C, E–F). The mandibular teeth are arranged into a single row and characterized by two different sizes; there are seven conical teeth with slightly retrorse tips, larger than those of the premaxilla, plus three long and curved fangs, the first placed in the anteriormost tip of the dentary and the other two placed further back (e.g., MUSE-PAL 1034, MUSE-PAL 6791a; Fig. 21C, 22A). The anguloarticular is

	Krampusichthys	***Laurinichthys***	***Wudelenia***	***Abadzekhia***	***Eothyrsites***	***Progempylus***	***Argestichthys***	***Chelificthtys***	***Hemithyrsites***	***Epinnula***
1st Dorsal-fin rays	IX-XIII	XVIII	XII	XVI	?	?	XIV+	XIII	XVII-XVIII	XV-XVI
2nd Dorsal-fin rays	I-II, 19-26	I, 15	II, 31	I, 12	10+?	?	17	?	I, 17-20	I, 15-18
Anal-fin rays	II; 14-19	I, 7+	?	II, 13	?	?	II, 12	?	II, 16	III, 13-17
Pectoral-fin rays	15-19	14	18	12+	10+	?	14-16	16	13-14	15-16
Pelvic-fin rays	I+5	I+5	I+5	I+4-5	?	?	I+5	-	I, 0	I+5
Caudal-fin rays (principal)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	17 (9+8)	?	?	?	17 (9+8)	17 (9+8)
Caudal-fin rays (procurrent)	6-7+6-8	?	6+6	?	?	?	?	?	4+4	?
Vertebrae	32 (14+18)	25+ (16+9)	40 (16+24)	34 (16+18)	30+	?	35 (15+20)	17+	33-35 (16-20+14-16)	32-35
Branchiostegal rays	8	5+	7	?	?	2+	7	?	?	7
Pmx teeth (fangs)	14-21 (1-2)	20 (1)	14-16 (2)	25 (1)	9+ (1+)	?	16 (5)	?	? (0-3)	15-25 (2+3)
Den teeth (fangs)	7 (3)	9+ (1)	5 (3)	12-13 (0)	4+ (?)	4+(?)	9 (4-5)	?	? (1)	7-11 (2)

Tab. 12 - Summary of the meristic traits of different gempylid genera. Includes new data and data from Nakamura & Parin (1993), Prokofiev (2002b), Carnevale (2006), Monsch & Bannikov (2011), Bannikov (2017), Ho et al. (2017), Beckett et al. (2018), Monsch & Micklich (2018), Rust & Robinson (2023).

large and triangular in outline. The retroarticular is small, approximately triangular, and forms the posteroventral corner of the mandible (see MUSE-PAL 5473; Fig. 22A). The outer surface of the jaw bones exhibits a cancellous texture.

The quadrate is triangular and bears a stout articular condyle. The symplectic is small and narrow. The hyomandibula has a large articular head, a curved ventral shaft, and a short opercular process. The ectopterygoid is narrow and almost straight. The metapterygoid bears a narrow process that emerges from its posterodorsal corner and that articulates with the anterior margin of the hyomandibula (see MUSE-PAL 5473; Fig. 22A). The endopterygoid is toothless, broad, and plate-like. The palatine is narrow, slightly expanded anteriorly, and characterized by small teeth along its ventral margin (see MUSE-PAL 5473; Fig. 22A).

The preopercle is crescent-shaped and expanded anteroventrally, with a smooth posterior margin; delicate serrations, preserved as an impression only, are recognizable along the posterior margin of MUSE-PAL 5473 (Fig. 22A). The opercle has a polygonal shape and exhibits a deep and large notch along its posterior margin. The subopercle is arcuate and quite expanded anteriorly, with a smooth ventral margin. The interopercle is triangular and, like the subopercle, has a smooth ventral margin.

The hyoid apparatus is exposed and visible in certain specimens (e.g., MUSE-PAL 1034, MUSE-PAL 3567; Fig. 22B). The hypohyals are poorly preserved. The anterior ceratohyal is flat and quadrangular, devoid of a beryciform foramen. The posterior ceratohyal is compact and slightly tapering posteriorly. There are seven (or eight) sabre-like branchiostegal rays, three of which articulate with the posterior ceratohyal. The urohyal is long and thin. Of the branchial skeleton, it is possible to recognize the two hypobranchials and incomplete ceratobranchials (see MUSE-PAL 1034; Fig. 21C).

The vertebral column comprises 32 (14+18) vertebrae. The centra are rectangular in shape, slightly longer than high, characterized by a robust longitudinal ridge. The posterior caudal centra are slightly shorter and more compact. The neural and haemal pre- and postzygapophyses are well-developed. The neural spines are slender and thin. The haemal spines are long and slender, very similar to their opposite neural spines, and originate from the central portion of the ventral margin of the vertebra. The last three posterior abdominal vertebrae bear moderately large parapophyses. There are thin and posteriorly curved ribs that articulate with the lateral side of the abdominal vertebrae (except for the first two). Delicate and short epineurals are associated with the abdominal vertebrae.

The caudal skeleton consists of five closely associated autogenous hypurals, an autogenous parhypural, one thin epural, and one uroneural. The haemal spines of the second and third preural centra are autogenous. The neural spine of the second preural vertebra is reduced to a short crest. The caudal fin is forked and shows 17 (9+8) principal rays, plus six or seven dorsal and ventral procurrent rays (6–7, I, 8+7, I, 6–7).

There are two thin and poorly preserved supraneurals inserting in the preneural space (see MUSE-PAL 3567; Fig. 21D). There are two dorsal fins, separated by a short gap. The first dorsal fin

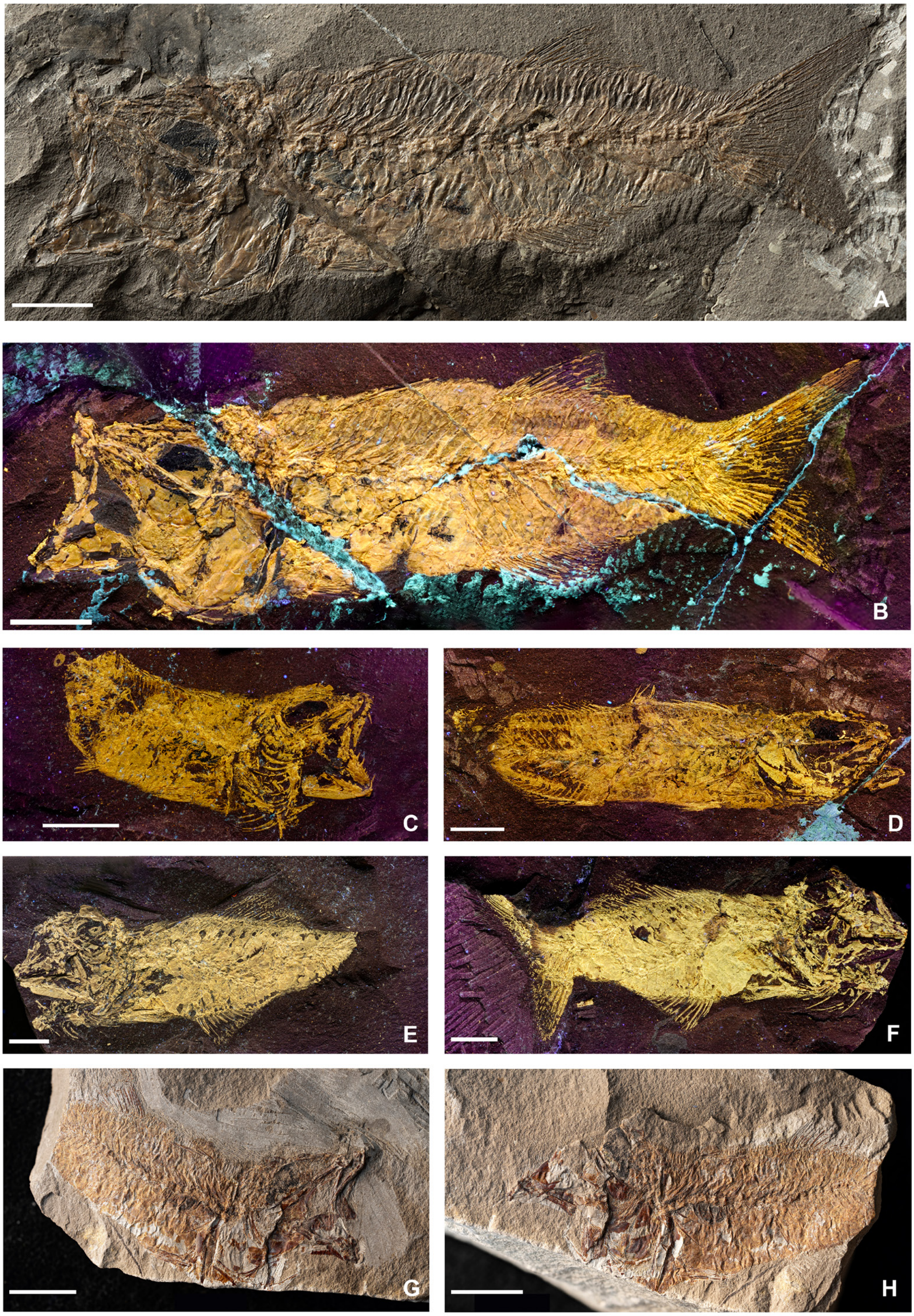


Fig. 21 - *Krampusichthys tridentinus* n. gen. et sp. Lateral view of the holotype MUSE-PAL 5473 in natural (A) and under UV light (B). Lateral view of the paratypes under UV light: C) MUSE-PAL 1034; D) MUSE-PAL 3567; E) MUSE-PAL 1033; F) MUSE-PAL 1047. Lateral view of the paratype MUSE-PAL 6791a-b in natural light (G-H). Scale bars 10 mm.

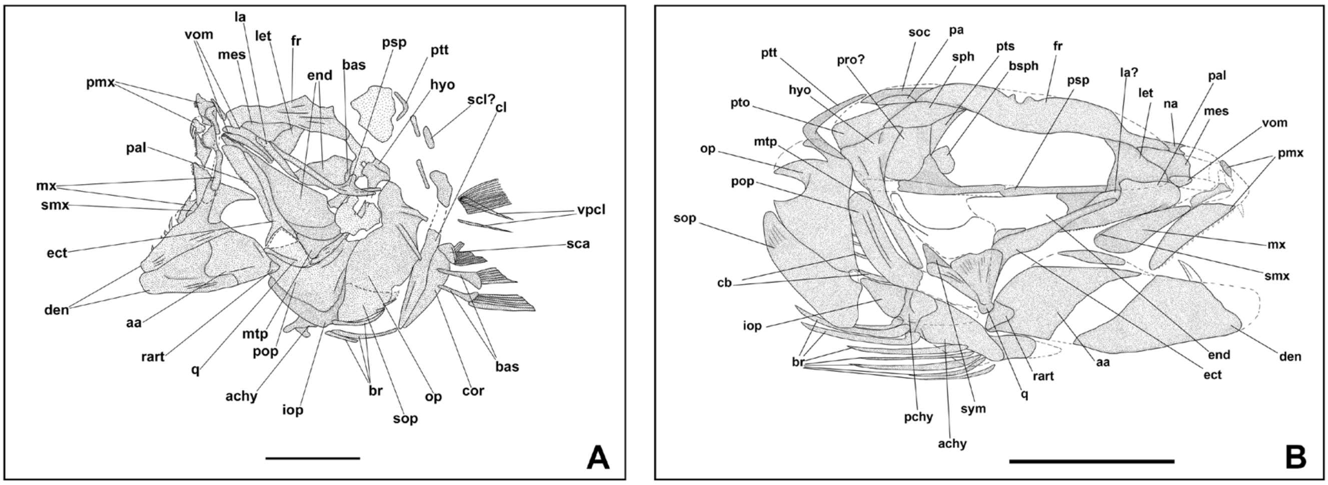


Fig. 22 - *Krampusichthys tridentinus* n. gen. et sp. Holotype, MUSE-PAL 5473 (A) and paratype MUSE-PAL 3567 (B), interpretive reconstructions of the cranium. Scale bars 10 mm.

seems to contain 9 to 13 thin and slender spines of similar length, supported by 9 to 13 pterygiophores. There is an anterior supernumerary spine on the first dorsal-fin pterygiophore, which inserts in the second interneural space (see MUSE-PAL 5473; Fig. 21A–B). The second dorsal fin contains one or two small spines, followed by up to 26 distally branched rays (see MUSE-PAL 1033-1047; Fig. 21E–F), of which the third, fourth, and fifth are the longest of the series. In general, the pterygiophores are thin and slender. The anal fin is similar in shape and size to the opposite second dorsal fin and its origin is just behind the insertion of the second dorsal fin; it contains two small spines followed by up to 19 distally branched rays. Like in the second dorsal fin, the third, fourth, and fifth rays are the longest of the series. The anal-fin pterygiophores are similar to their dorsal counterparts. There is no trace of dorsal and anal finlets.

The posttemporal is V-shaped, with two robust anterior processes diverging from a reduced posterior shelf. The supracleithrum has an elongate and rather broad ovoid shape, slightly tapering dorsally and quite expanded posteriorly. The cleithrum is large and curved (e.g., MUSE-PAL 1034, MUSE-PAL 3567; Fig. 21C–D). The coracoid is gently curved, ending anteroventrally into a blunt tip (see MUSE-PAL 1034; Fig. 21C). The scapula is quadrangular and is pierced by a relatively small scapular foramen. The dorsal postcleithrum is ovoid, with a rounded profile (see MUSE-PAL 1034; Fig. 21C). The ventral postcleithrum is rather elongate but does not reach the ventral margin of the body. The short pectoral fins insert in the lower third of the body flanks and contain 15–19 unbranched rays articulated with four pectoral-fin radials. The pelvic fin is thoracic and placed just behind the pectoral fin. The basipterygium contacts the pectoral girdle and bears an elongate and thin posterior process. The pelvic fin consists of one spine plus five rays, whose length is comparable to that of the pectoral rays.

Certain specimens show a dense squamation consisting of moderately large and rounded ctenoid scales (e.g., MUSE-PAL 6791a-b; Fig. 21G–H), characterized by small spiniform ctenii and up to 14 radii. The lateral line is generally poorly preserved. In the holotype, two canals of the lateral line are noticeable: the lower canal is visible in the mid-posterior portion of the body (where some tubular lateral-line scales are preserved); it runs above the caudal vertebrae and gradually moves downwards towards the caudal peduncle (see MUSE-PAL 5473; Fig. 21A–B). Portions of the upper canal of the lateral line and of a few tubular lateral-line scales are partially visible just below the second dorsal-fin base (see MUSE-PAL 5473; Fig. 21A–B).

Genus *Laurinichthys* n. gen.

Type species (by monotypy): *Laurinichthys boschelei* n. gen. et sp.

Etymology: Genus named after king *Laurin*, a mythological figure from the folklore of the Trentino-Alto Adige region (where the type locality and horizon are located) and from the Greek word *"ἰχθύς"* meaning "fish".

Diagnosis: A genus of the Gempylidae showing a unique combination of features: body moderately deep and laterally compressed; upper jaw with one long fang and 20 smaller conical teeth; lower jaw with one long fang and at least nine smaller conical teeth; eight branchiostegal rays; 16 abdominal vertebrae; first dorsal fin with 18 spines; second dorsal fin with two spines followed by at least 15 rays; pectoral fin with 14 rays; scales highly deciduous and minute.

Remarks and comparison. *Laurinichthys* n. gen. is referred to the family Gempylidae by having: mouth large with fangs in both upper and lower jaws; elongate mesethmoid and lateral ethmoid; premaxilla with short ascending process and a postmaxillary process not expanded and not extending beyond the maxilla; a small supramaxilla; beryciform foramen absent; two clearly separated dorsal fins; first dorsal-fin base longer than that of the second dorsal fin; supracleithrum elongate; cleithrum without a posterior protuberance; pectoral fin with low insertion along the body flanks and pectoral-fin length shorter than head length (e.g., Russo 1983; Nakamura & Parin 1993).

Laurinichthys n. gen. differs from the Euzaphlegidae by having: fangs in both upper and lower jaws; a supramaxilla; rayless pterygiophores absent between the two dorsal fins, which are not separated by a large gap (present in Euzaphlegidae); different counts in both unpaired and paired fins (Monsch 2000; Monsch & Bannikov 2011; Tab. 11–12).

Laurinichthys n. gen. cannot be assigned to the Trichiuridae due to the presence of conical fangs with smooth edges (vs compressed in Trichiuridae) and a first dorsal-fin base longer than the second dorsal-fin base (while the opposite occurs in Trichiuridae; Gago 1998).

The dentition of *Laurinichthys* n. gen. (one fang in both the premaxilla and dentary) differs from that of several extinct (*Abadzekhia* spp.; *Progempylus edwardsi*; *Argestichthys vysotzkyi*; Prokofiev 2002b; Bannikov 2017; Beckett et al. 2018) and extant taxa (see Russo 1983; Nakamura & Parin 1993). By lacking finlets, *Laurinichthys* n. gen. differs from the extinct genus *Abadzekhia* (Bannikov 2017) and several extant genera (*Gempylus*, *Hemithyrsites, Lepidocybium, Nealotus, Nesiarchus, Rexea*, *Rexicthtys*, *Ruvettus*, *Thyrsites*, *Thyrsitoides, Thyrsitops*; see Russo 1983; Nakamura & Parin 1993). Due to its high supraoccipital crest, it is possible to separate *Laurinichthys* n. gen. from the fossil taxa *Argestichthys vysotzkyi* and *Abadzekhia* spp. (Prokofiev 2002b; Bannikov 2017) and from the majority of low-crested extant gempylids (see Russo 1983; Nakamura & Parin 1993). The developed pelvic fins of *Laurinichthys* n. gen. allow to separate it from the fossil *Chelifichthys goujeti* (Carnevale 2006) and the extant *Hemithyrsites*, *Nealotus*, *Rexea*, *Rexicthtys,* and *Nesiarchus* (Nakamura & Parin 1993).

Laurinichthys boschelei n. gen. et sp.

Fig. 23–25

Holotype (by monotypy): MUSE-PAL-SB 2464, an incomplete articulated skeleton lacking the caudal fin.

Etymology: Species named after Sergio Boschele, who found and secured the holotype and only known specimen of this species.

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Laurinichthys boschelei* n. gen. et sp. is solely represented by the holotype. The specimen has a length of 54 mm, measured from the tip of the premaxilla to the last preserved vertebra. Overall, the body is slender and elongate, with its maximum depth in the head region and near the pelvic fins. The head is rather elongate, tapering towards the snout with a large, central, and elliptical orbit.

The neurocranium is almost triangular. The lateral ethmoid is columnar and bears a developed posterolateral process (Figs. 24–25). The mesethmoid is stout and massive. The vomer appears to be rather thick. The frontals are the largest bones of the skull roof; they are elongate and tapered anteriorly, forming the dorsal margin of the orbit. The parietals are small and polygonal. The morphology of the sphenotic, pterotic, and epioccipital is difficult to determine due to inadequate preservation. The supraoccipital crest is particularly high and extends anteriorly over the entire length of the frontals, up to the ethmoid region. The pterosphenoid is rather large, well-exposed along the posterodorsal corner of the orbit. The basisphenoid is nearly vertical. The parasphenoid is robust and straight, apparently bearing a low flange emerging along its dorsal surface.

The nasals are not preserved. The lachrymal is elongate and slightly expanded posteriorly. The other elements of the infraorbital series are fragmentary and scarcely recognizable.

The premaxilla is mostly preserved as impression; the ascending process is short and thick, obliquely oriented; the premaxillary teeth are ar-

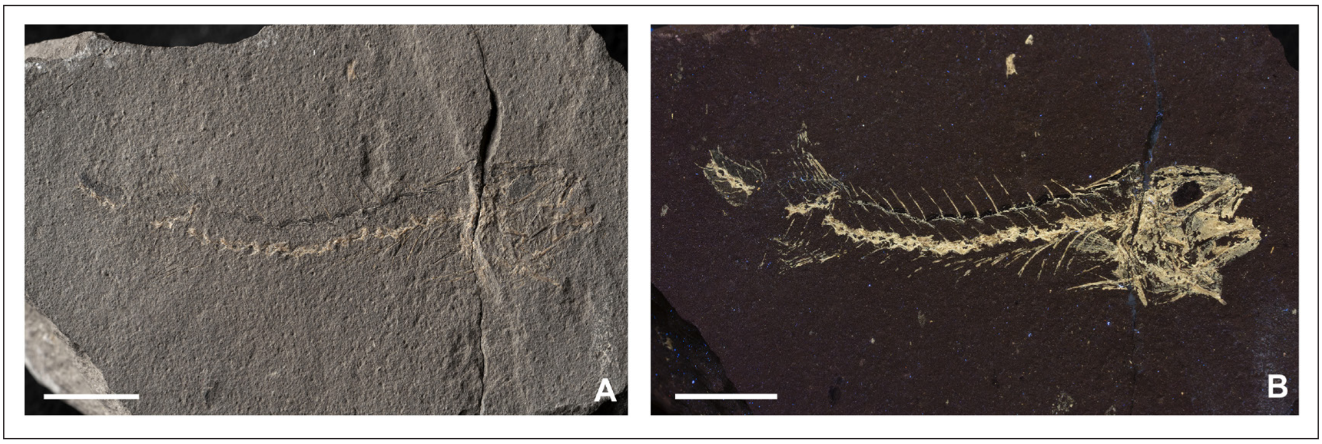


Fig. 23 - *Laurinichthys boschelei* n. gen. et sp. Lateral view of the holotype, MUSE-PAL-SB 2464, in natural (A) and under UV light (B). Scale bars 10 mm.

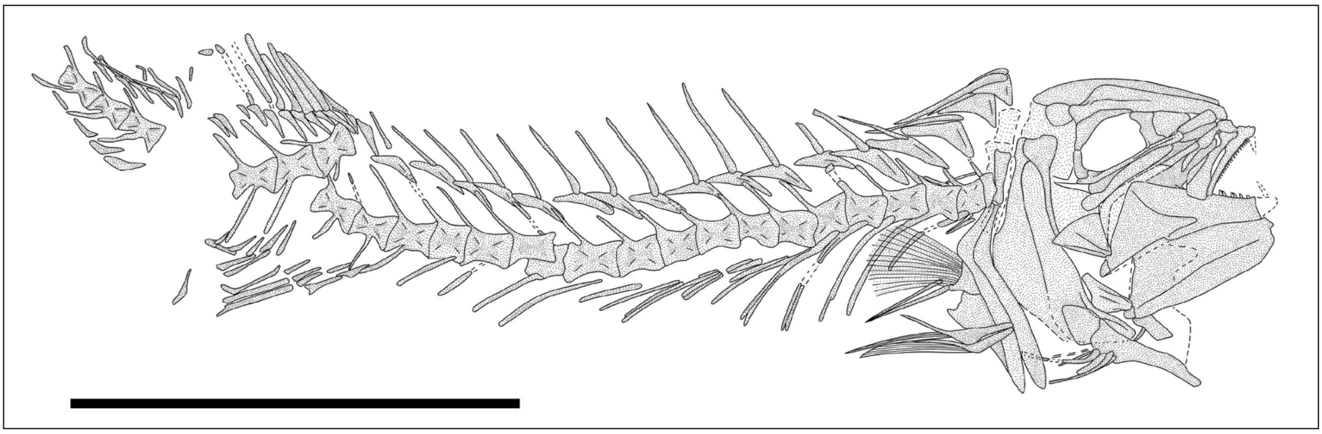


Fig. 24 - *Laurinichthys boschelei* n. gen. et sp. Holotype, MUSE-PAL-SB 2464, interpretive reconstruction. Scale bar 10 mm.

ranged into two series, an outer series of 20 small, conical and slightly retrorse teeth and an inner series with a single large fang placed just under the ascending process (Figs. 24–25). The maxilla is distally expanded and exhibits a well-developed articular head. There is a thin and splint-like supramaxilla. The lower jaw is rather large. The dentary is broad and triangular in outline. The lower jaw dentition consists of a single large fang plus at least nine smaller conical teeth with slightly retrorse tips, slightly larger than the premaxillary ones (Fig. 25). The anguloarticular is large and triangular. The small retroarticular is recognizable at the posteroventral corner of the mandible.

The quadrate is triangular in outline and displaced from its original position. The symplectic is small and narrow. The hyomandibula has a large head and a thin vertical shaft. The ectopterygoid is narrow and slightly expanded posteroventrally. The morphology of the metapterygoid is difficult to determine due to inadequate preservation. The endopterygoid is narrow, plate-like, and triangular in outline. The palatine is almost straight, slightly expanded anteriorly.

The preopercle is crescent-shaped, showing a smooth posterior margin and bearing a delicate serration along the ventral margin. The opercle is notably compressed and poorly preserved. The subopercle and interopercle are scarcely preserved.

The hyoid apparatus is exposed but poorly preserved. The anterior ceratohyal is quadrangular and tapers anteriorly. The posterior ceratohyal is triangular and very compact anteroposteriorly. At least five sabre-like branchiostegal rays articulated to the anterior ceratohyal are recognizable. The urohyal is poorly preserved. There are no preserved remains of the branchial skeleton.

The vertebral column is incomplete, lacking the posterior caudal vertebrae, thereby preventing an estimate of the number of vertebrae. There are

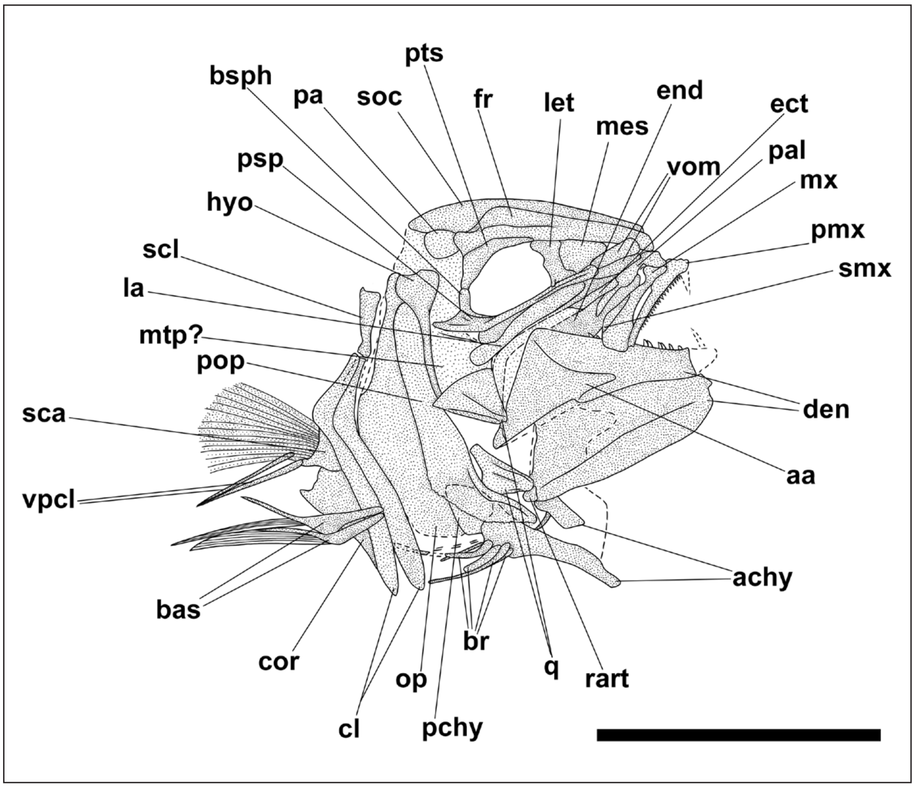


Fig. 25 - *Laurinichthys boschelei* n. gen. et sp. Holotype, MUSE-PAL-SB 2464, interpretive reconstruction of the cranium and girdles. Scale bar 10 mm.

25 preserved vertebrae, 16 of which are abdominal, characterized by elongate centra, subrectangular in outline, longer than high. The neural and haemal pre- and postzygapophyses are moderately developed. The neural spines are slender and thin. Only a few haemal spines are preserved; these are long, slender, and curved, extending posteriorly like their neural counterparts. The abdominal vertebrae, from the third one, bear long and curved ribs not reaching the ventral margin of the body. Fragments of thin epineurals inserting at the base of the neural spines are also recognizable.

There are no traces of supraneurals. The first dorsal fin contains 18 thin and slender spines, almost equal in size. There is an anterior supernumerary spine on the first dorsal-fin pterygiophore. Aside from the anterior portion of the fin, where the preservation of the pterygiophores is unclear, there is a one-to-one relationship between pterygiophores and interneural spaces. The second dorsal fin is incomplete and contains only a single spine followed by 15 distally branched rays, of which the second to fifth are the longest of the series. The pterygiophores are thin and delicate, anteroventrally oriented, and wedge-shaped with a narrow and pointed ventral portion. The anal fin is also incomplete and contains at least one short spine and seven rays.

The posttemporal and the supratemporal are not preserved. The supracleithrum is narrow, straight, and elongate. The cleithrum is large and crescent-shaped. The coracoid is narrow, tapered anteroventrally, and broader posterodorsally. The scapula is poorly preserved. The dorsal postcleithrum is scarcely recognizable. The ventral postcleithrum is elongate and does not reach the ventral margin of the body. The pectoral fins insert rather low in the body flanks; the fin is rather short and contains 14 unbranched rays. The basipterygium contacts the pectoral girdle anteriorly and bears a thin and elongate posterior process. The pelvic fins comprise one spine and five rays, whose length is similar to that of the pectoral fins.

The squamation is scarcely preserved, and only a few spots of the original squamation are preserved in the posterior portion of the body, represented by minute and delicate cycloid scales.

Genus *Wudelenia* n. gen.

Type species (by monotypy): *Wudelenia diabolica* n. gen. et sp.

Etymology: Genus named after the *Wudelen*, fictional creatures typical of the folklore of the Trentino-Alto Adige region (where the type locality and horizon are located), given the long fang-like teeth and elongate body of this taxon, reminding of the bizarre and scary appearance of the *Wudelen*.

Diagnosis: A genus of the Gempylidae characterized by the following combination of features: highly elongate and compressed body (BD: 14.1% of SL); low supraoccipital crest; upper jaw with two long fangs and 14–16 smaller conical teeth; lower jaw with three long fangs and five smaller conical teeth; preopercle with smooth ventral and posterior margins; deep opercular notch; seven branchiostegal rays; 40 vertebrae (16+24); caudal skeleton with five autogenous hypurals, three epurals and two uroneurals; forked caudal fin with 17 principal rays (9+8) plus six dorsal and six ventral procurrent rays; pectoral fin with 18 rays; first dorsal fin with 12 spines; second dorsal fin with two spines followed by at least 31 rays; (Tab. 11) dense squamation characterized by large ctenoid scales with up to 10 radii.

Remarks and comparison. *Wudelenia* n. gen. is referred to the family Gempylidae by having: elongate mesethmoid and lateral ethmoid; an elongate lachrymal; incomplete infraorbital ring; first and second infraorbital bones not tightly bound together; fang-like teeth in both upper and lower jaws; premaxilla with short ascending process and postmaxillary process not expanded and not extending beyond the maxilla; a small supramaxilla; three branchiostegal rays on the posterior ceratohyal; beryciform foramen absent; a deep opercular notch; two clearly separated dorsal fins; first dorsal-fin base longer than the second one; supracleithrum elongate; cleithrum without a posterior protuberance; short pectoral fins inserting low on the body flanks; pectoral-fin length shorter than head length; pelvic fins small (Russo 1983; Nakamura & Parin 1993).

The attribution of *Wudelenia* n. gen. to the extinct family Euzaphlegidae can be ruled out since it exhibits: fangs in both upper and lower jaws; a supramaxilla; caudal skeleton with five autogenous hypurals (vs two hypural plates in Euzaphlegidae); absence of rayless pterygiophores between the two dorsal fins, which are not separated by a large gap (present in Euzaphlegidae); different composition of unpaired and paired fins (e.g., Monsch 2000; Monsch & Bannikov 2011; see Tab. 11–12).

Wudelenia n. gen. cannot be referred to the Trichiuridae by having: conical fangs with smooth edges (vs laterally compressed and serrated in Trichiuridae); different vertebral number (40 vertebrae vs more than 50 in Trichiuridae); large caudal fin (smaller or absent in Trichiuridae); three epurals (vs one in Trichiuridae); first dorsal-fin base longer than the second dorsal-fin base (while the opposite occurs in Trichiuridae; Gago 1998).

With a total of 40 vertebrae, *Wudelenia* n. gen. differs from the extinct *Abadzekhia* spp. (34) and *Argestichthys vysotzkyi* (35; Prokofiev 2002b; Bannikov 2017) and some extant gempylids (*Diplospinus*, 57–62; *Paradiplospinus*, 60–67; *Gempylus*, 48; *Epinnula*, 32; Nakamura & Parin 1993). Moreover, the dentition of *Wudelenia* n. gen. (two fangs on the premaxilla and three fangs on the dentary) differs from that of several extinct (*Abadzekhia* spp.; *Progempylus edwardsi*; *Argestichthys vysotzkyi*; Prokofiev 2002b; Bannikov 2017; Beckett et al. 2018) and extant taxa (see Russo 1983; Nakamura & Parin 1993). By lacking finlets, *Wudelenia* n. gen. differs from the fossil genus *Abadzekhia* (Bannikov 2017) and from several extant genera (*Gempylus*, *Hemithyrsites, Lepidocybium, Nealotus, Nesiarchus, Rexea*, *Rexicthtys*, *Ruvettus*, *Thyrsites*, *Thyrsitoides, Thyrsitops*; see Russo 1983; Nakamura & Parin 1993). Due to its low supraoccipital crest, it is possible to separate *Wudelenia* n. gen. from the fossil *Progempylus edwardsi* (Beckett et al. 2018) and the extant genera *Lepicydobium*, *Neoepinnula,* and *Ruvettus* (Nakamura & Parin 1993). The developed pelvic fins of *Wudelenia* n. gen. allow to separate it from several taxa, including the fossil *Chelifichthys goujeti* (Carnevale 2006) and the extant *Hemithyrsites*, *Nealotus*, *Rexea, Rexichthtys,* and *Nesiarchus* (Nakamura & Parin 1993). *Wudelenia* n. gen. further differs from *Tongaichthys* by not being characterized by hypurostegy (Nakamura & Fujii 1983).

Wudelenia diabolica n. gen. et sp.

Figs. 26–28

Holotype: MUSE-PAL 1035-1036, a nearly complete articulated skeleton measuring 116.74 mm SL, in part and counterpart.

Paratype: MUSE-PAL 7027, a nearly complete articulated skeleton.

Referred specimens: MUSE-PAL 6764, an incomplete articulated skeleton, lacking the posterior portion of the axial skeleton, including the median fins.

Etymology: Species named after the Greek word "*διαβολικός*" meaning "devilish" or "diabolic", given the long, fang-like teeth and menacing appearance of this taxon.

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. The body is slender and elongate, reaching its maximum depth behind the head at the level of the pelvic fins. The head is elongate, with a pointed snout (Figs. 26–27). The orbit is large, its diameter being almost equal to the preorbital portion of the head. The anal fin is poorly preserved and its origin is placed slightly posterior to the second dorsal-fin insertion (see MUSE-PAL 7027; Fig. 26E–F).

The elongate neurocranium is partially preserved and exposed in lateral view in both the type specimens, showing a large and pointed ethmoid region. The mesethmoid and lateral ethmoid are elongate and trapezoid in shape. The vomer appears to be ovoid in outline and appears to be toothless. The frontals are the largest bones of the skull roof; they are highly elongate, tapering anteriorly and expanded posteriorly. The parietals appear to be small and polygonal in outline. The supraoccipital is not entirely preserved and appears to be scarcely developed. The sphenotic and pterotic are almost triangular in outline. The epioccipital is poorly preserved and only partially exposed in MUSE-PAL 7027 (see Fig. 26E–F). The prootic and pterosphenoid are difficult to recognize. The basisphenoid is small and articulates ventrally with the parasphenoid. The parasphenoid is stout and narrow.

The nasals are slender, short, and tubular. The lachrymal is the largest element of the infraorbital series; it is elongate (see MUSE-PAL 1036; Fig. 27) and has an expanded anterior portion bearing a spinous articular process (see MUSE-PAL 1035-1036; Fig. 27). The second infraorbital is small and slender, rod-like (see MUSE-PAL 1035-1036; Fig. 27). The third infraorbital is curved and thin and follows the posteroventral margin of the orbit (see MUSE-PAL 1035-1036; Fig. 27). The other infraorbitals are poorly preserved, small and compact (see MUSE-PAL 1035-1036; Fig. 27).

The premaxilla has a thick and short ascending process and a reduced postmaxillary process. The premaxillary teeth are arranged in two series, an outer series with least 14–16 minute conical and slightly retrorse teeth and an inner series of two large fangs placed close to the anterior end of the bone (e.g., MUSE-PAL 1035; Fig. 27). The maxilla has a large articular head and largely expanded posterior end. There is a small and thin splint-like supramaxilla that articulates with the posterodorsal portion of the maxilla. The lower jaw is long and slender, protruding forward beyond the upper jaw. The dentary is prominent and elongate, with a nearly vertical and low symphysis; the outer surface of the dentary exhibits a moderately cancellous texture. The dentary teeth are arranged into a single row characterized by up to five conical teeth with slightly retrorse tips, larger than the premaxillary ones, plus three long and slightly curved fangs, one of which is placed in the anterior portion of the dentary (see MUSE-PAL 1035-1036; Fig. 27). The anguloarticular is thick and triangular in outline. The retroarticular is pointed posteriorly and occupies the posterior tip of the mandible.

The quadrate is triangular and bears a developed anterior condyle. The symplectic is small and narrow. The hyomandibula has a large articular head, a short opercular process, and a slender and curved vertical shaft. The ectopterygoid is narrow and strongly curved, showing an expanded ventral arm and a slender and almost horizontal arm. The endopterygoid and metapterygoid are poorly preserved and extremely fragmentary. The palatine is almost straight and slightly expanded anteriorly; it is unclear whether it bears teeth along the ventral margin or not.

The preopercle is crescent-shaped, anteroventrally expanded, and characterized by smooth and gently convex posterior and ventral margins. The opercle is large and has a deep notch along its posterior margin. The subopercle is gently arcuate, thin posteriorly, and quite expanded anteriorly. The interopercle is poorly preserved, almost triangular (see MUSE-PAL 1035-1036; Fig. 27).

The hyoid apparatus is exposed and clearly visible in the holotype (Figs. 26A–D, 27). The basihyal is not preserved. The ventral hypohyal has a straight ventral profile. The dorsal hypohyal has a prominent knob-like dorsal process. The anterior ceratohyal is flattened, nearly rectangular, and tapering anteriorly; there is no evidence of the beryciform foramen. The posterior ceratohyal is compact and almost triangular in outline. There are seven saber-like branchiostegal rays, four of which articulate with the anterior ceratohyal, and three with the posterior ceratohyal. Interhyal and urohyal are not preserved. The branchial skeleton is mostly hidden by the opercular series bones; however, fragments of slightly curved ceratobranchials are partially exposed in the holotype.

The vertebral column is hidden by the dense scale cover in the holotype, making it difficult to determine the precise number of vertebrae. The paratype shows a complete vertebral column, although poorly preserved. Overall, the vertebral column of MUSE-PAL 7027 consists of 40 (16+24) vertebrae. The vertebral centra are rectangular, longer than high. The posterior caudal centra are slightly shorter compared to those of the preceding vertebrae. The neural and haemal pre- and postzygapophyses

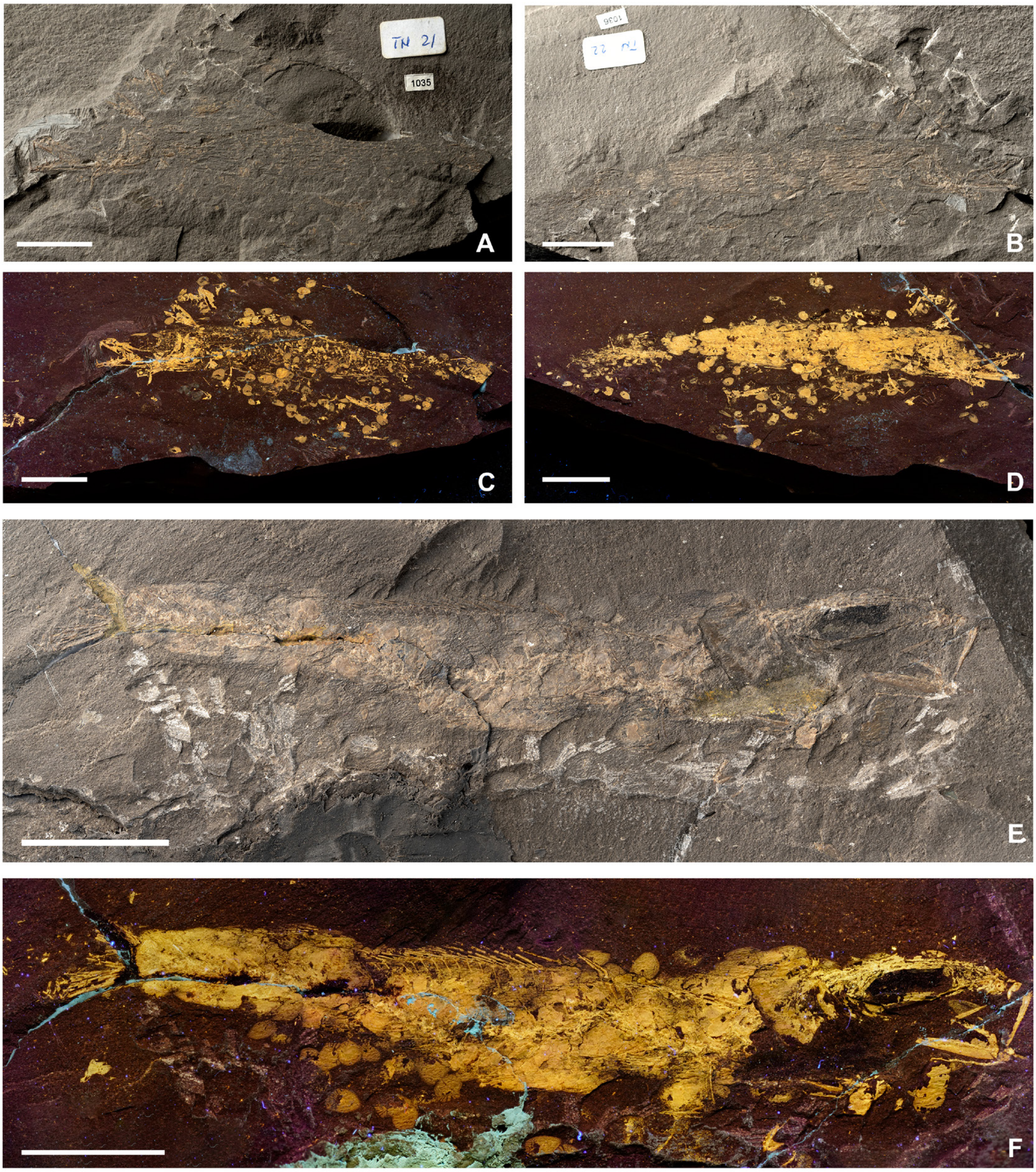


Fig. 26 - *Wudelenia diabolica* n. gen. et sp. Lateral view of the holotype, MUSE-PAL 1035–1036, in natural (A–B) and under UV light (C–D). Lateral view of the paratype, MUSE-PAL 7027, in natural (E) and under UV light (F). Scale bars 20 mm.

are well developed. The neural spines are straight and slender. The haemal spines are long and slender, emerging from the mid-length of the ventral margin of the centrum and curved posteriorly. Parapophyses seem to be absent. The ribs are long and thin, articulated to the lateral sides of the abdominal centra. Due to the poor preservation of the vertebral column, it is difficult to determine their exact number. There are a few poorly preserved, thin, and short epineurals, which are firmly attached to the base of the neural arches of the abdominal vertebrae.

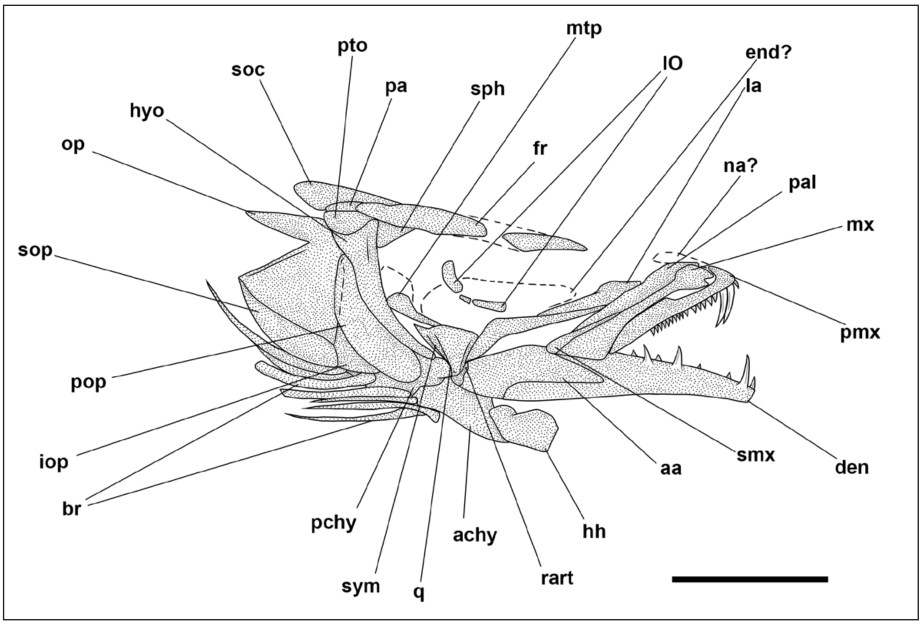


Fig. 27 - *Wudelenia diabolica* n. gen. et sp. Holotype, MUSE-PAL 1035-1036, interpretive reconstruction of the skull. Scale bar 10 mm.

The caudal fin and skeleton are exposed only in MUSE-PAL 7027 (Fig. 26E–F), although poorly preserved. The caudal skeleton consists of five autogenous and closely spaced hypurals, plus an autogenous parhypural, three epurals and two uroneurals. There is a moderately deep notch between the second and third hypural plates (Fig. 28). The parhypural is autogenous and apparently lacks a parhypurapophysis. The haemal spines of the second and third preural centra are autogenous, slender, and thin. The preservation of the caudal-fin rays is inadequate, not allowing recognition of the forked caudal fin typical of the gempylids. It is possible to notice 17 principal rays (9+8), and there are at least six dorsal and six ventral procurrent rays (6, I, 9+8, I, 6).

There is no trace of the supraneurals. There are two dorsal fins, separated only by a very short gap. The first spinous dorsal fin contains 12 thin and slender spines (see MUSE-PAL 7027; Fig. 26E–F) similar in length, supported by 11 pterygiophores. The second dorsal fin has two small spines, followed by 31 distally branched rays. The first spine is short and tiny compared to the second one and to the following rays, of which the third and fourth represent the longest of the series. The second dorsal fin is supported by 33 delicate pterygiophores. Due to the inadequate preservation of the vertebral column is not possible to determine the pterygiophore formulae of the first and second dorsal fins. The anal fin is always poorly preserved in the available material. Eight or nine displaced rays are preserved in the holotype, while in the paratype there are no rays preserved, and only the first four pterygiophores can be recognized. The first anal-fin pterygiophore is the largest of the series, while the others are almost identical to their dorsal counterparts. There is no trace of finlets.

The posttemporal is poorly preserved and difficult to recognize. The supracleithrum has an elongate and broad ovoid shape, slightly tapering dorsally and quite expanded posteriorly. The cleithrum is crescent-shaped. The coracoid is large and tapered anteriorly. Both postcleithra and the scapula are poorly preserved and hard to describe properly. The pectoral-fin radials are difficult to detect. The pectoral fin inserts in the lower third of the body flanks and contains 18 unbranched rays (see MUSE-PAL 1036; Fig. 26B, D). The pelvic girdle is placed under

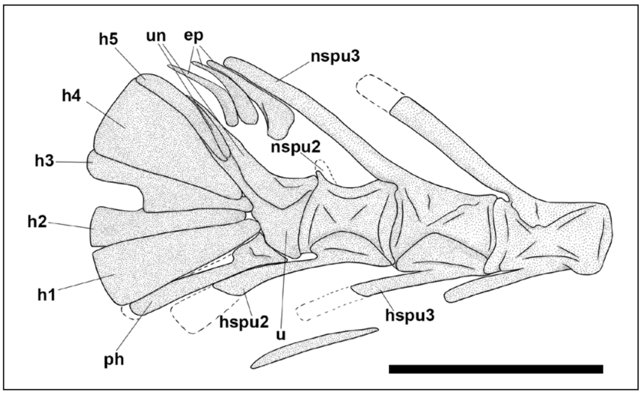


Fig. 28 - *Wudelenia diabolica* n. gen. et sp. Paratype, MUSE-PAL 7027, interpretive reconstruction of the caudal skeleton. Scale bar 10 mm.

	MUSE-PAL 5473
SL (mm)	78.2
TL (mm)	96.44
HL	32.6
PD1	39.7
PA	63.2
PP	35.2
PV	37.6
DFL1	18.8
AFL	22.4
PFL	9.5
VFL	11.4
PRO	13.8
O	8.4
POO	10.8
PRO (%HL)	42
O (%HL)	25.9
POO (%HL)	32.9
DRL	16.5
AFR	12.9
BD	30.5
CPL	13.8
CPH	14.1

Tab. 13 - Measurements of *Krampusichthys tridentinus* n. gen. et. sp. Values are as percentage of SL.

the pectoral girdle. The basipterygium has an anterior central process that extends to the level of the cleithrum and a poorly preserved posterior process. The pelvic fin consists of one spine and five rays, similar in length to the pectoral fin.

Both the available specimens exhibit a dense squamation of large, rounded ctenoid scales, characterized by several small spiniform ctenii and up to ten radii. The lateral line and the lateral-line scale are poorly preserved and difficult to recognize.

Discussion. The main differences between the three genera of gempylids from Solteri (*Krampusichthys tridentinus* n. gen. et sp., *Laurinichthys boschelei* n. gen. et sp., and *Wudelenia diabolica* n. gen. et sp.) concern the physiognomy of the body, morphometric and meristic traits. *K. tridentinus* n. gen. et sp. is characterized by a deeper body when compared to the other two taxa, which present a more fusiform outline (BD: 30.5% of SL and CPH: 14.1% of SL in *K. tridentinus* n. gen. et sp. vs BD: 14.1% of SL and CPH: 5.6% of SL in *W. diabolica* n. gen. et sp.; Tab. 13–14). A few differences can be noticed in the cranium: *L. boschelei* n. gen. et sp. shows a rather high and developed supraoccipital crest compared to the other two low-crested taxa. Furthermore, the three genera can also be distinguished for their dentition: *K. tridentinus* n. gen. et sp. bears up to 29 premaxillary teeth plus one or two fangs and seven conical teeth in the dentary with three large fangs; *L. boschelei* n. gen. et sp. has 20 premaxillary teeth with a single fang on the tip of the upper jaw while the lower jaw bears at least nine conical teeth and a single fang on the tip; *W. diabolica* n. gen. et sp. bears up to 16 premaxillary teeth and two large fangs while on the dentary it has five conical teeth plus three fangs (see Tab. 11). Another difference between *K. tridentinus* n. gen. et sp. and *W. diabolica* n. gen. et sp. relates to the vertebral column: with 32 (14+18) and 40 (16+24) vertebrae, respectively (Tab. 11). The main meristic differences can be found in the first dorsal fin, which in *L. boschelei* n. gen. et sp. is remarkably longer than in the other two taxa (18 spines vs 9–13 in *K. tridentinus* n. gen. et sp. and 12 in *W. diabolica* n. gen. et sp.; Tab. 11). While the second dorsal fin of *W. diabolica* n. gen. et sp. contains two spines followed by 31 rays, compared to that of *K. tridentinus* n. gen. et sp., which bears one or two spines followed by 18 to 26 rays (Tab. 11). Moreover, the pectoral fin of *L. boschelei* n. gen. et sp. has fewer rays compared to the other two taxa (14 vs 15–19 in *K. tridentinus* n. gen. et sp. and 18 in *W. diabolica* n. gen. et sp.; Tab. 11). Lastly, *K. tridentinus* n. gen. et sp. and *W. diabolica* n. gen. et sp. share moderately large ctenoid scales, compared to the small and deciduous cycloid scales of *L. boschelei* n. gen. et sp.

	MUSE-PAL 1035-1036
SL (mm)	116.74
TL (mm)	136.4
HL	28.7
PD1	?
PA	?
PP	30.3
PV	36.3
DFL1	?
AFL	?
PFL	5.4
VFL	?
PRO	8.2
O	7.7
POO	14.2
PRO (%HL)	28.7
O (%HL)	26.9
POO (%HL)	49.5
DRL	?
AFR	?
BD	14.1
CPL	?
CPH	5.6

Tab. 14 - Measurements of *Wudelenia diabolica* n. gen. et. sp. Values are as percentage of SL.

Percomorphacea *incertae sedis*

Erebusia n. gen.

Type species (by monotypy): *Erebusia tenebrae* n. gen. et sp.

Etymology: Named after “*Έρεβος*” (Latin Erebus), the personification of darkness in Greek mythology. The term “*Erebus*” also indicates the Underworld.

Diagnosis: A percomorph characterized by the following combination of features: body moderately high with deep caudal peduncle; large and compact head with large circular orbit, its diameter corresponding to half of the head length; supraoccipital crest low; upper jaw dentition consisting of few retrorse conical teeth; lower jaw dentition consisting of a single fang on the anterior tip of the dentary and few conical and pointed teeth; 32 vertebrae (13+19); five autogenous hypurals; 17 caudal fin rays (9+8); single and continuous dorsal fin consisting of 12 spines and 24 rays; anal fin containing two spines and at least 17 rays; pectoral fin containing 15 rays; pelvic fin containing one spine plus five rays; body covered with small cycloid scales (see Tab. 15).

Erebusia tenebrae n. gen. et sp.

Figs. 29–32

Holotype (by monotypy): MUSE-PAL-SB 2463, a nearly complete articulated skeleton, 51.2 mm SL.

Etymology: From the Latin word *"tenebra"*, meaning "darkness", in reference to the deep-water setting of the Solteri site, where this taxon lived.

Diagnosis: As for the genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. *Erebusia tenebrae* n. gen. et sp. is a small-sized percomorph with a moderately deep body and a large head characterized by a huge circular orbit and a blunt snout (Figs. 29–31). The maximum body depth is located after the head region and remains constant up to the anal-fin insertion. The caudal peduncle is rather deep, reaching almost half of the maximum body depth. The mouth is terminal and large, bearing a large fang on the anteriormost tip of the dentary. There is a single and continuous, long-based dorsal fin, and the anal-fin base is almost half the length of the dorsal-fin base.

The neurocranium is rather deep and compact, with a remarkably large orbit (O: 41.5% of HL; Tab. 16). The ethmoid region is rather short and poorly preserved. The mesethmoid is quadrangular and small. The lateral ethmoid is mostly preserved as an impression only, exhibiting a narrow columnar shape, and forming the anterior wall of the orbit. The vomer appears to be rather small and triangular. The frontals are the largest bones of the skull roof and show a curved outline that follows the profile of the orbit (Figs. 30–31). The parietals are almost rectangular. The supraoccipital bears a relatively low median crest. The pterotic has an irregular shape. The sphenotic is triangular, slightly protruding outwards, forming part of the dorso-posterior edge of the orbit. The epioccipital, prootic, and pterosphenoid are not recognizable due to inadequate preservation. It is difficult to understand whether the basisphenoid was present or not in origin. The straight and slender parasphenoid is preserved as a feeble impression only.

The bones of the infraorbital series are poorly preserved and difficult to recognize.

The mouth is rather large and terminal, with the upper and lower jaws exhibiting the same length. The premaxilla is partially complete, lacking its anterior portion, which is preserved as an impression only; the ascending process appears to be narrow and distally pointed; it is not possible to determine whether the articular and postmaxillary processes were present or not in origin. The premaxilla has five small conical teeth with retrorse tips that are preserved, possibly representing only a part of the original complement (Fig. 31). The maxilla is remarkably elongate and slender. The lower jaw is slightly shorter than the upper jaw, and it is displaced from its original position. The large dentary is partially preserved and shows an almost triangular outline and has a poorly preserved coronoid process; there is a single large fang in the anterior-most tip of the bone, followed by four smaller conical pointed teeth, the rest of the original dentition is not preserved (Fig. 31). The anguloarticular and retroarticular are poorly preserved.

	MUSE-PAL -SB 2463
Dorsal-fin rays	XII, 24
Anal-fin rays	II, 17+
Pectoral-fin rays	15
Pelvic-fin rays	I+5
Caudal-fin rays (principal)	17 (9+8)
Caudal-fin rays (procurrent)	5+7-8
Vertebrae	32 (13+19)
Branchiostegial rays	4+

Tab. 15 - Summary of the meristic traits of *Erebusia tenebrae* n. gen. et. sp.

	MUSE-PAL -SB 2463
SL (mm)	51.2
TL (mm)	58.3
HL (mm)	14.2
PRO (%HL)	33.4
O (%HL)	41.5
POO (%HL)	19.9

Tab. 16 - Measurements of *Erebusia tenebrae* n. gen. et. sp. Values are as percentage of HL.

Most of the suspensorium is poorly preserved or scarcely exposed. The quadrate is almost triangular. The hyomandibula has a slim and curved ventral shaft and two articular heads. The ectopterygoid is slender and strongly arched. The endo- and metapterygoid are feebly recognizable, based on a delicate impression only. The palatine is toothless and slightly expanded anteriorly.

The opercular series is also poorly preserved. The preopercle exhibits an elongate and curved shape, with an anteroventrally expanded ventral arm. The opercle is almost rectangular, slightly expanded ventrally. The interopercle and subopercle are not preserved.

Of the hyoid apparatus, the anterior ceratohyal is partially preserved with only its posterior portion left, and the posterior ceratohyal is similarly repre-

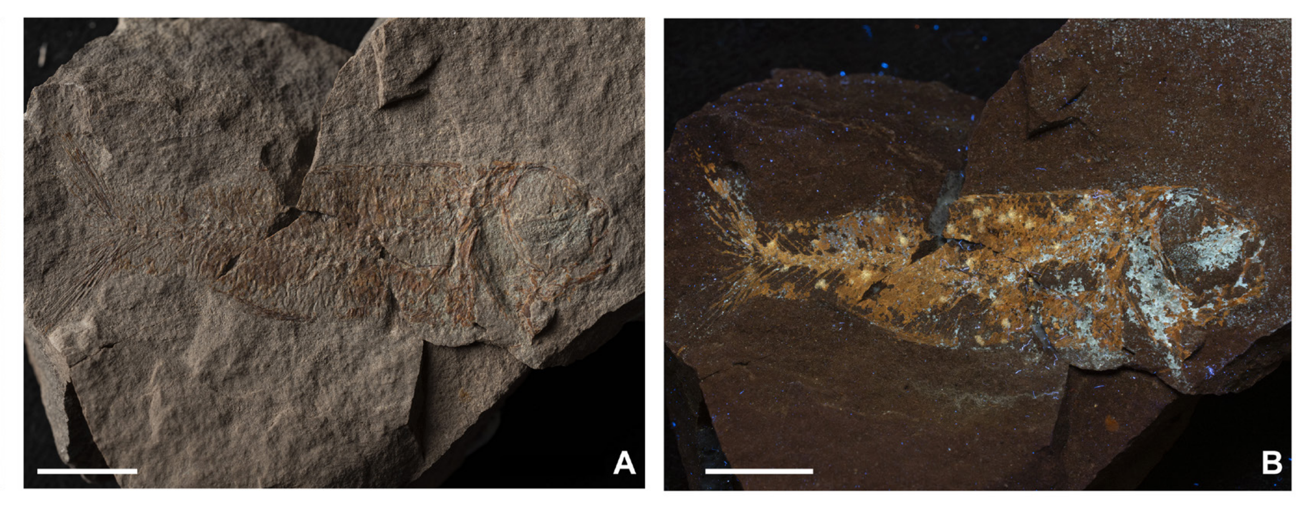


Fig. 29 - *Erebusia tenebrae* n. gen. et sp. Lateral view of the holotype, MUSE-PAL-SB 2463, in natural (A) and under UV light (B). Scale bar 10 mm.

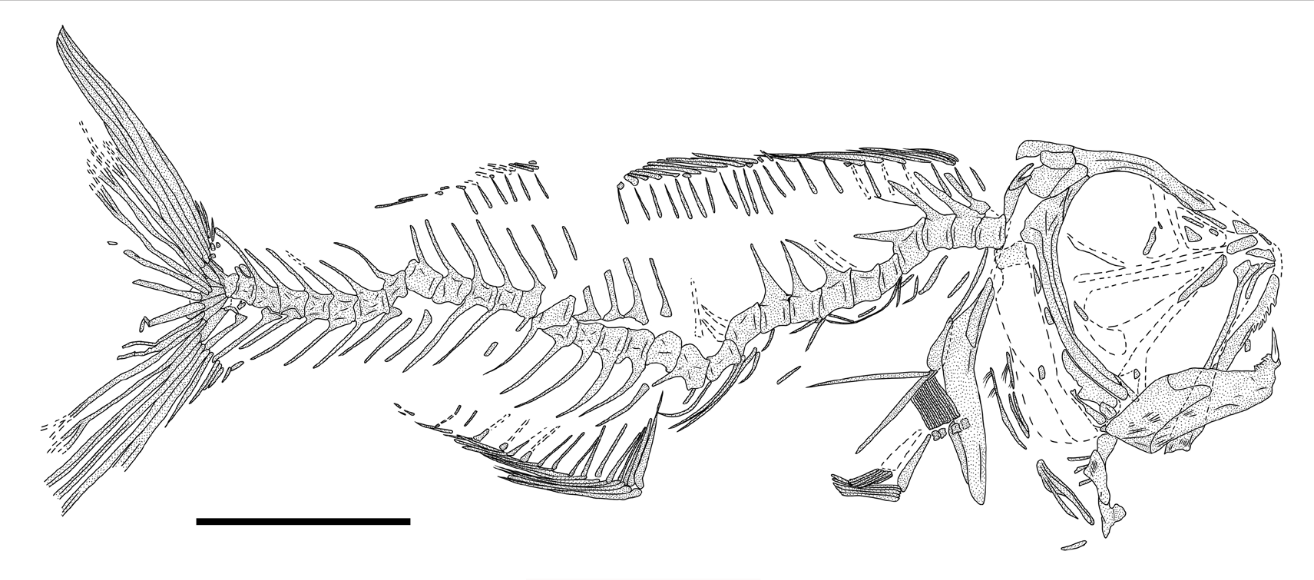


Fig. 30 - *Erebusia tenebrae* n. gen. et sp. Holotype, MUSE-PAL-SB 2463, interpretive reconstruction. Scale bar 10 mm.

sented by a few fragments. There are at least four slender and saber-like branchiostegal rays. Incomplete ceratobranchials are partially exposed in the opercular region.

The vertebral column is twisted, S-shaped in the middle portion of the body and contains 32 (13+19) vertebrae (Fig. 30). The centra are almost rectangular, being only slightly longer than high, except for the last caudal centra that are very compressed and squared. The neural spines are slender and straight, emerging from the mid-posterior portion of each centrum. The haemal spines are slender, gently curved, and emerge from the mid-posterior portion of the centrum. The neural prezygapopheses are notably expanded. The ribs are thin and flexible, articulated to the lateral sides of the abdominal vertebrae. There are some extensively fragmented epineurals.

The caudal skeleton consists of five autogenous hypurals, an autogenous parhypural, a single uroneural, and an undetermined number of epurals (Fig. 32). The haemal spines of the second and third preural vertebrae are autogenous. The neural spine of the second preural vertebra is reduced to a short crest. The caudal fin is deeply forked and bears 17 (9+8) distally branched principal rays plus at least five

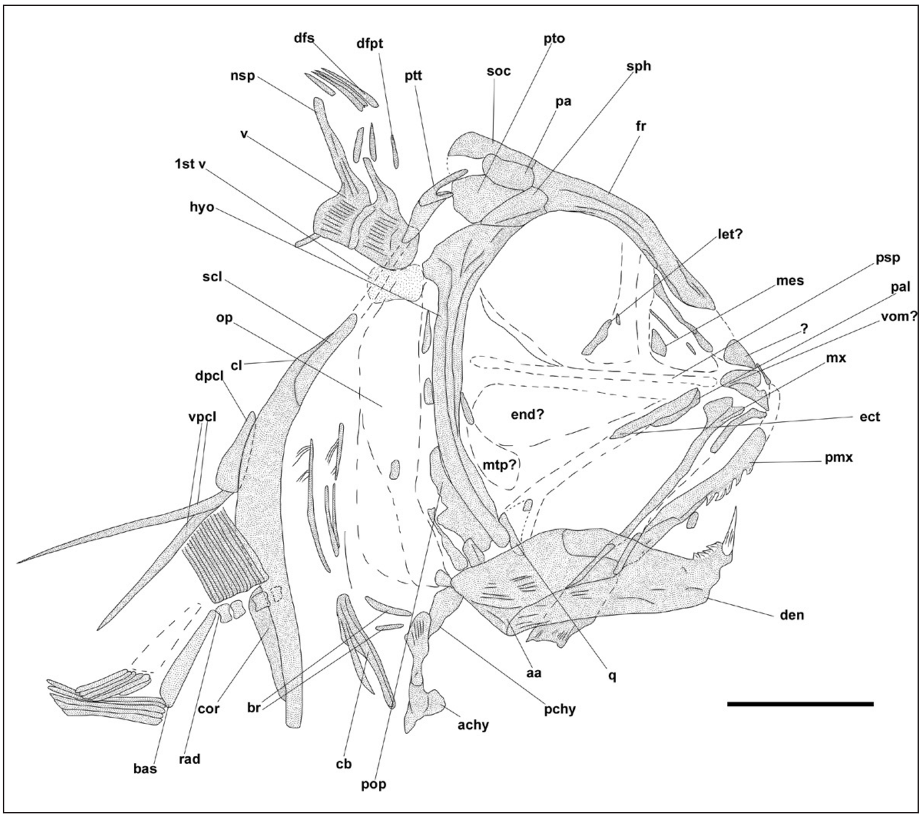


Fig. 31 - *Erebusia tenebrae* n. gen. et sp. Holotype, MUSE-PAL-SB 2463, interpretive reconstruction of the cranium. Scale bar 5 mm.

dorsal and seven or eight ventral procurrent rays (5, I, 8+7, I, 7–8).

There is no trace of supraneurals, likely due to inadequate preservation. A single continuous dorsal fin runs from the second vertebra backward to the 23rd centrum. The dorsal fin contains at least 12 thin and slender spines plus 24 rays; some rays are missing in the middle portion of the body (Fig. 30). The first pterygiophore seems to be inserted in the second interneural space (the first vertebra is poorly preserved and displaced from its original position), but the rest of the dorsal-fin formula cannot be determined due to inadequate preservation (Figs. 30–31). The anal fin inserts around the mid-length of the body, and comprises two spines and at least 17 rays, supported by not less than 17 pterygiophores.

The posttemporal is deeply bifurcate anteriorly. The supracleithrum is straight and narrow. The cleithrum is large and slightly curved (Fig. 31). The coracoid is triangular, while the scapula is poorly preserved. The dorsal postcleithrum is narrow and tube-like, while the ventral postcleithrum is elongate, extremely thin, with a pointed distal end. There are four pectoral-fin radials. The pectoral fin inserts low on the body and contains 15 unbranched and short rays. The pelvic girdle inserts just below the pectoral girdle. The basipterygium has an elongate anterior process. The pelvic fin consists of one spine plus five rays.

The body is covered by a dense cover of small cycloid scales. The lateral-line scales are not preserved.

Discussion. *Erebusia tenebrae* n. gen. et sp. can be referred to the Percomorphacea by lacking the second ural centrum, as well as by having five hypurals, pelvic fins with five rays, free pelvic-fin radials absent, and 17 principal caudal rays. This new genus, interpreted as incertae sedis within the Percomorphacea, does not exhibit diagnostic morphological features that might allow for a specific placement at the family level. Despite the presence of a single quite distinctive fang on the tip of the dentary, *E. tenebrae* n. gen. et sp. cannot be ascribed to the gempylids due to the presence of a single dorsal fin, a large and compact body, a different morphology of the bones of the opercular series and a shorter ethmoid region (Russo 1983; Gago 1998). It cannot be assigned to the stromateiforms by having a fang in the lower jaw, less than 24 rays in the anal fin and less than 18 rays in the pectoral fin (Pastana et al. 2022).

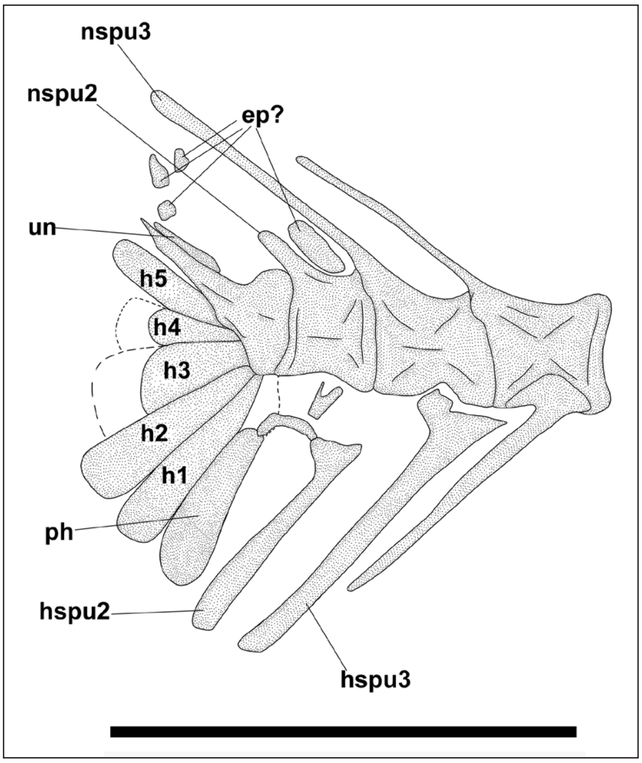


Fig. 32 - *Erebusia tenebrae* n. gen. et sp. Holotype, MUSE-PAL-SB 2463, interpretive reconstruction of the caudal skeleton. Scale bar 5 mm.

Genus *Ammutichthys* n. gen.

Type species (by monotypy): *Ammutichthys loricatus* n. gen. et sp.

Etymology: From the Ancient Egyptian monstrous goddess Ammut (or "Ammit", the "devourer of the dead") and the Greek word *"ἰχθύς"* meaning "fish".

Diagnosis: A percomorph characterized by a unique combination of the following features: head large and wide, representing more than one third of SL (HL: 38.5% of SL; Tab. 17); lower jaw dentition characterized by seven to eight large pointed conical teeth; preopercle with strongly serrated posterior and ventral margins; large opercle with three spines emerging from the posterior margin; 25 vertebrae; extremely large pectoral fins (PFL: 33.9% of SL; Tab. 17), reaching the mid-length of the body and containing 20 branched rays; pelvic fins with one spine plus eight rays; body densely covered by large plate-like scales.

Ammutichthys loricatus n. gen. et sp.

Figs. 33–36

1994 Lophiidae – Roccaforte et al., p. 374.

Holotype (by monotypy): MUSE-PAL 1030-1031, a nearly complete articulated skeleton, 101.2 mm SL.

Etymology: From the Latin word *"loricatus"*, meaning "armored", in reference to the dense scale cover characteristic of this species.

Diagnosis: As for genus.

Type locality and horizon: Solteri (Trento). Organic-rich calcareous marl horizon belonging to the Chiusole Formation (Ypresian, lower Eocene).

Description. The holotype and only known specimen of *Ammutichthys loricatus* n. gen. et sp. is dorsoventrally flattened. The head is large (HL: 38.5% of SL; see Tab. 17; Fig. 33), and the body appears to be rather compact. The orbits are large and almost circular.

The neurocranium is broad and antero-posteriorly compact (Figs. 33–34). The anteriormost portion of the head and the ethmoid region are poorly preserved. The mesethmoid and lateral ethmoid are poorly preserved. The vomer is stout and pointed anteriorly. The frontals are the largest bones of the skull roof, being laterally compressed anteriorly and expanded in the post-orbital portion; they articulate posteriorly with the supraoccipital and the parietals and posterolaterally with the sphenotic. The parietals are small and ovoid in shape, separated from each other by the supraoccipital. The supraoccipital is large and robust. The pterotic has an irregular shape, while the sphenotic is small and triangular. The epioccipitals are short and robust, with a quadrangular shape and gently rounded edges. The basisphenoid and pterosphenoid are not exposed. The parasphenoid is long and rod-like, partially visible behind the frontals.

The nasals and the bones of the infraorbital series are not recognizable.

The mouth is large and terminal. Both the upper and lower jaws are incomplete and at least partially displaced from their original position (Figs. 33–35). The premaxilla has a curved profile and bears 14 small conical teeth. The maxilla has an expanded posterior end. There is a splint-like supramaxilla. The dentary is rather thick, bearing eight long and pointed conical teeth (Figs. 34–35). The anguloarticular is large and trapezoid in shape. The retroarticular is a small and minute triangular element in the posteroventral corner of the mandible.

The quadrate is triangular, with a gently curved posterior profile. The symplectic is small and slightly curved. The hyomandibula has a narrow and elongate ventral shaft and two short and stout dorsal articular heads. The metapterygoid is trapezoid in outline and has a slightly curved posterior margin that articulates with the hyomandibula (Fig. 34). The ectopterygoid is narrow and characterized by a straight horizontal arm. The endopterygoid is

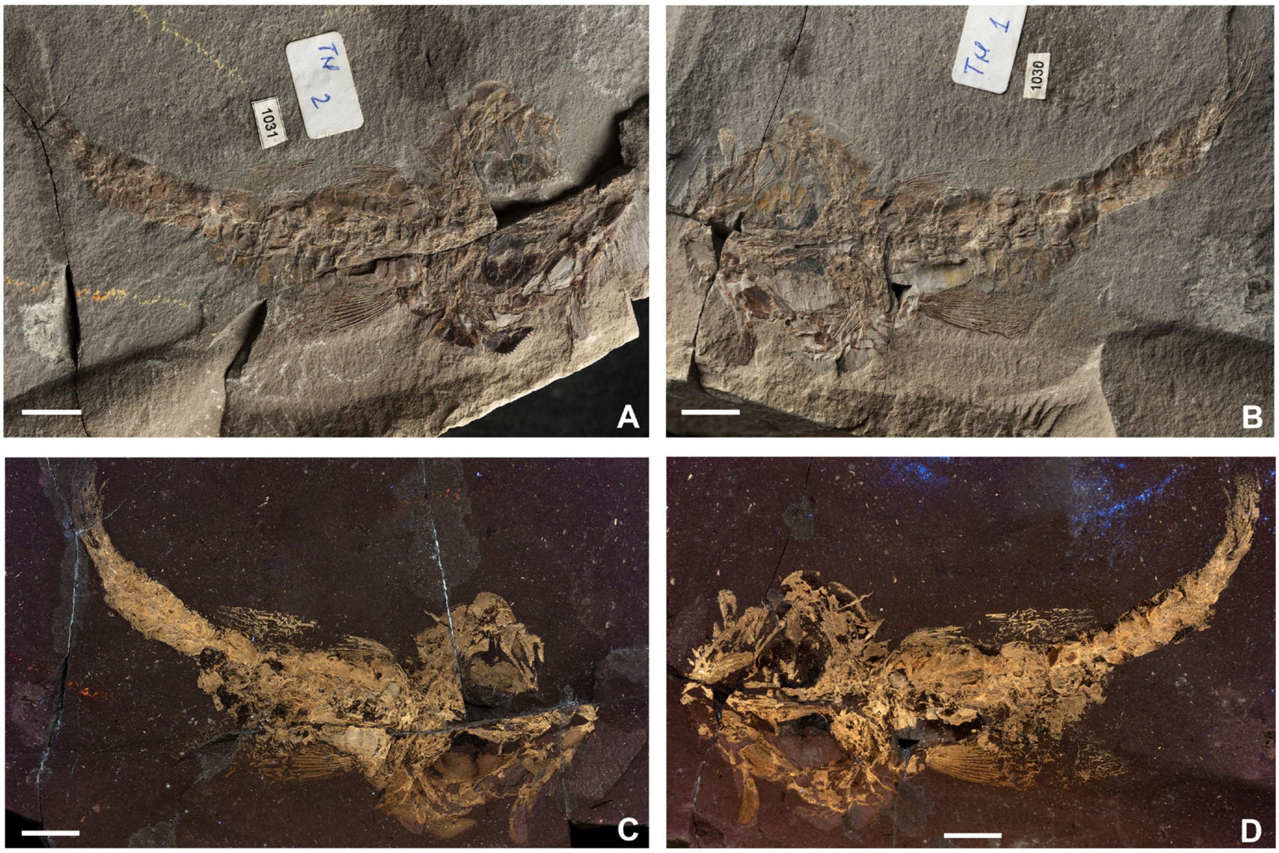


Fig. 33 - *Ammutichthys loricatus* n. gen. et sp. Dorsal view of the holotype, MUSE 1030-1031 in natural (A–B) and under UV light (C–D). Scale bars 10 mm.

very large, flat, and expanded posteriorly. The palatine is poorly preserved.

The preopercle is crescent-shaped and has extensively serrated ventral and posterior margins, bearing about 24 small spines (Figs. 33–34). The opercle is postero-dorsally expanded: it exhibits a straight anterior margin, a finely serrated ventral margin, and a rounded and curved posterior margin bearing a moderate notch and three thick and elongate spines. The subopercle is poorly preserved and appears to be triangular with a rounded profile and feebly serrated ventral and anterior margins. The interopercle is poorly preserved.

	MUSE-PAL 1030-1031
SL (mm)	101.2
TL (mm)	124.1
HL	38.5
PD1	49.2
PA	?
PP	38.4
PV	38.8
PFL	33.9
VFL	14.2
PRO	16.2
O	9
POO	8.7

Tab. 17 - Measurements of *Ammutichthys loricatus* n. gen. et. sp. Values are as percentage of SL.

The hyoid apparatus and branchial skeleton are not preserved in the sole available specimen, except for a few incomplete ceratobranchials.

The vertebral column is almost entirely preserved, although in large part hidden by the thick scales. The vertebral column contains 25 vertebrae, for which it is difficult to determine the exact number of abdominal and caudal elements. The centra are thick and rectangular in outline, slightly longer than high, except for the first one that is shorter and antero-posteriorly compact. Due to the dorsoventral flattening and the thick scales that cover parts of the vertebral column, it is difficult to observe the morphology of the neural and haemal spines. Ribs and intermuscular bones are inadequately preserved and difficult to describe.

The caudal skeleton is also poorly preserved. 14 principal rays (7+7) plus four to five dorsal and four ventral procurrent rays are preserved in the caudal fin.

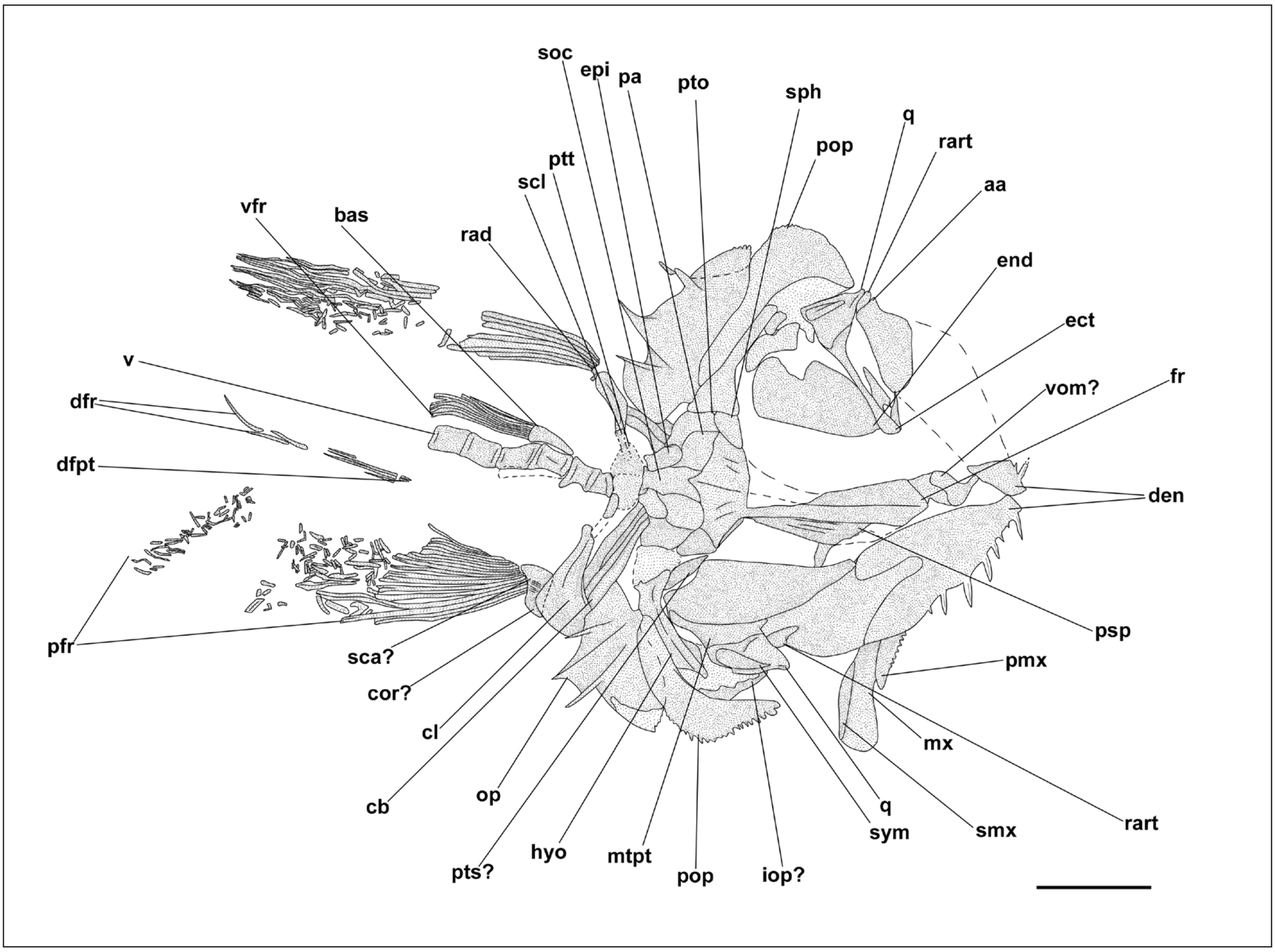


Fig. 34 - *Ammutichthys loricatus* n. gen. et sp. Holotype MUSE 1031, interpretive drawing of the cranium and paired fins. Scale bar 10 mm.

The other median fins are inadequately preserved. Of the dorsal fin, six or seven thin and elongate spines can be observed (Fig. 34).

The morphology and structure of the pectoral girdle are difficult to interpret due to inadequate preservation. The posttemporal and supracleithrum are partially preserved as an impression only. The cleithrum is broadly curved. The coracoid and scapula are fragmented, and there is no evidence of the postcleithra. Only a single pectoral-fin radial is visible (Fig. 34). The pectoral fins are extremely large (PFL: 33.9% of SL; see Tab. 17), extending backward to the posterior half of the body; they comprise 20 distally branched rays. The pelvic girdle is located slightly posterior to the pectoral girdle. The basipterygium extends for the length of two vertebrae. The pelvic fins are quite elongate and include one spine plus eight rays (see MUSE-PAL 1030; Figs. 33B, D, 36).

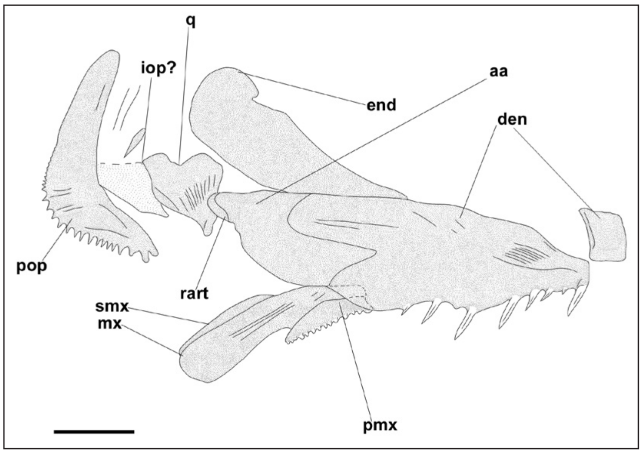


Fig. 35 - *Ammutichthys loricatus* n. gen. et sp. Holotype, MUSE 1031, interpretive drawing of the jaws. Scale bar 5 mm.

The whole body is covered by large, dense, and thick cycloid scales, characterized by seven to eight radii (see MUSE-PAL 1031; Fig. 33A, C). The lateral line and the lateral-line scales are not preserved.

Discussion. *Ammutichthys loricatus* n. gen. et sp. is regarded herein as a percomorph due to the presence of a preopercle with serrated margins, dorsal-fin spines, fewer than 17 principal caudal-fin rays, and absence of free pelvic-fin radials. This new taxon, however, shows some features that are uncommonly found in percomorph fishes, such as the pelvic fins containing one spine plus eight rays, known, for example, in the syngnathoid *Solenostomus* Lacepède, 1803 and in some cyprinodontoids and pleuronectiforms (Wiley & Johnson 2010). If we consider the other percomorph taxa found in Solteri, despite the lower and upper jaws being very similar to those of certain trichiuroids (especially gempylids), any alignment of *A. loricatus* n. gen. et sp. with Trichiuroidea can be ruled out since it has less than 32 vertebrae (25; Tab. 18) and large pectoral fins extending backward beyond the mid-length of the body. *A. loricatus* n. gen. et sp. cannot be referred to the stromateiforms due to the presence of fang-like teeth. This specimen was previously mentioned by Roccaforte et al. (1994), who erroneously interpreted it as an indeterminate monkfish of the family Lophiidae (order Lophiiformes). However, *A. loricatus* n. gen. et sp. differs from representatives of the order by lacking a highly modified first dorsal fin, with the first three spines forming a luring apparatus, and greatly elongate pectoral-fin radials (pseudobrachium), typical of lophiiforms (e.g., Pietsch & Carnevale 2011; Carnevale & Pietsch 2012).

Teleostei indet.

Fig. 37

Description. Almost a fourth of the findings from Solteri cannot be confidently assigned to a specific taxon and are therefore referred to as indeterminate teleosts due to their fragmentary nature and poor preservation. The majority of these are represented by small, isolated bones, even if there are some large specimens (e.g., MUSE-PAL 8159-8160; Fig. 37).

DISCUSSION

The overall composition of the ichthyofauna of Solteri reflects a pelagic ecosystem that is largely dominated by stomiiforms (59% of the available specimens), primarily by the family Gonostomatidae (Fig. 38). Other typical pelagic groups, such as the myctophiforms, are less abundant, representing ca. 6% of the available specimens. This is in stark contrast with the preliminary observations by Venzo et al. (1986), who stated that most of the findings at Solteri are myctophids, followed by clupeids, plus a beryciform and a fragment of a syngnathiform. Among the percomorphs, the most common taxa are the gempylids (about 6%), followed by a few centrolophids (almost 1%) and other indeterminate percomorphs (ca. 3% of the available specimens). A peculiar aspect of the taxonomic composition of the Solteri ichthyofauna is the complete absence of chondrichthyan remains.

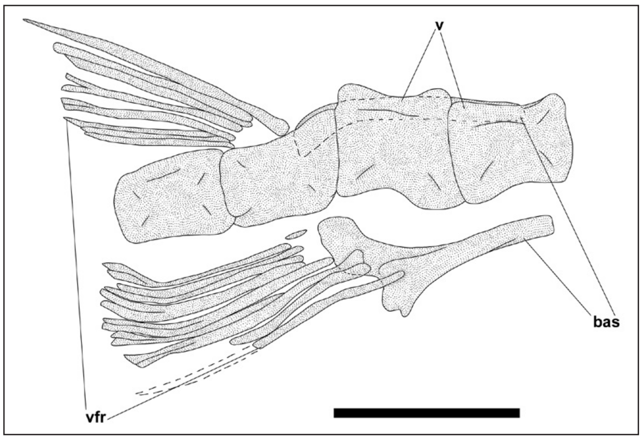


Fig. 36 - *Ammutichthys loricatus* n. gen. et sp. Holotype, MUSE 1031, interpretive drawing of the pelvic girdle. Scale bar 5 mm.

TAPHONOMIC REMARKS

No field information on the excavations carried out in 1979 at the Angelini Quarry at Solteri is available. Nevertheless, it is still possible to discuss some taphonomic aspects of the fossil-bearing layers of this site. The preservation of the specimens ranges from poor (Fig. 3C), with a high degree of disarticulation, to excellent, presenting a high degree of completeness of the fully articulated skeletal remains (Fig. 7A–B). The preservation can even be exceptional, with specimens showing soft tissues preserved as a thin, black organic film, defining the body outline, photophores, eyeballs, and sometimes even part of the viscera (Figs. 4A–B, 7A). The bones are generally articulated, but there are a few examples of complete disarticulation of the skeleton. It is not uncommon to find isolated heads or tails with some vertebrae attached, possibly hinting at a detachment

	MUSE-PAL 1030-1031
1st Dorsal-fin rays	3+
2nd Dorsal-fin rays	?
Anal-fin rays	?
Pectoral-fin rays	20
Pelvic-fin rays	I+8
Caudal-fin rays (principal)	14 (7+7)
Caudal-fin rays (procurrent)	4/5+4
Vertebrae	25
Branchiostegial rays	?

Tab. 18 - Summary of the meristic traits of *Ammutichthys loricatus* n. gen. et. sp.

of these body portions due to extreme bending of the vertebral column when the soft tissues were still in place (Fig. 11E; see Chellouche et al. 2012). Overall, it is possible to estimate that almost a quarter of the available specimens are so poorly preserved that any attempt of detailed taxonomic placement is prevented (and are therefore ascribed to "Teleostei indet.", see Fig. 38). In contrast, about 20.5% of the specimens can be identified at the species level, with the best-preserved specimens being small-sized fishes, usually under 10 cm SL (e.g., MUSE-PAL 2079; Fig. 7A–B); large individuals are rare and usually represented by highly disarticulated and/or damaged skeletal elements or fragments (e.g., MUSE-PAL 8159-8160; Fig. 37).

One of the most striking and puzzling aspects of the preservation of the fishes of Solteri is the alteration of their vertebral column: despite almost half of the fishes (47%) show unaltered backbones, the remaining ones exhibit various degrees and types of deformation (Figs. 3C, 11D-F, 13F, H, 26E–F). Concave or convex conditions of the backbone are almost missing in the Solteri fishes, while almost 45% of the specimens show a considerably deformed axial skeleton, riddled with continuous twists and undulations (Fig. 11D, F).

Strong deformations of the backbone can appear as "S-shaped" deformations, often caused by sea-bottom currents (see Chellouche et al. 2012; Marramà et al. 2016) or by post-mortem contortions (see Bieńkowska-Wasiluk 2010). However, rather than "S-shaped", the vertebral column of the Solteri fishes appears to be more undulate and irregular, without any alteration of the external body outline, which appears to be almost intact (e.g., MUSE-PAL 1045, MUSE-PAL 5549; Fig.11D, F). Interestingly, this kind of deformation of the vertebral column seems to be taxon-specific and primarily affects the elongate and narrow bodies of the abundant gonostomatids (see Weiler 1929; Bieńkowska-Wasiluk 2004, 2010). These alterations are hardly caused by the action of sea-bottom currents, since the body outline and the external appearance of the fish are unaltered, and usually the skeletons are not disarticulated or scattered. These post-mortem deformations could be caused by necrolitic processes occurring as the carcasses were decomposing. A possible explanation could be related to the decay of collagen-rich tissues that strengthen the axial skeleton, therefore causing extreme flexion of the weakened vertebral column without affecting the overall external body of the fish. The backbone of gonostomatids is rather delicate and, hence, could be more prone to higher degrees of flexion and distortion following the decay of the soft tissues (see Jerzmańska 1960). This undulate bending occurs also in narrow-bodied percomorphs (e.g., Gempylidae), exhibiting wavy and irregular deformations, always coupled with an intact body outline (see Figs. 21C, E–F, 26E–F). Similar deformations of the vertebral column in slender and narrow-bodied fishes (e.g., Argentinidae and Gonostomatidae) were also recorded in Oligocene sites from Poland (Menilitic-Krosno Series, Jaso shale). However, in these cases, the irregular deformation of the backbone is associated with severe deformation of the body outline, contrary to the Solteri fishes (see Bieńkowska-Wasiluk 2010, fig. 29 C–C'; Jerzmańska 1960, pl. V, fig. 2). In that case, the specimens were deformed when they reached the bottom, where the action of currents acted on carcasses affected by dehydration and soft tissues decay (see Bieńkowska-Wasiluk 2010).

Other examples of undulate deformations of the axial skeletons, in this case from shallower water environments, were recorded in a gobiid fish from the Oligocene of Perarolo (Rupelian, Italy; Marramà et al. 2022) and in *Saurichthys* Agassiz, 1834 from the Ladinian of Monte S. Giorgio (Switzerland-Italy; Beardmore & Furrer 2016, 2019). In the case of *Saurichthys*, the specimens show strong curvatures of the axial skeleton, although they differ from the fishes from Solteri since, in some cases, the backbone breaks out from the body wall. This kind of deformation of the vertebral column has been interpreted as related to post-mortem processes, like weak currents, which affected the carcasses standing on the bottom for long periods (Beardmore & Furrer 2016).

Typical tetany features (flabelled fin rays, dorsally concave backbone) are not so frequent in our material, except for a few specimens showing

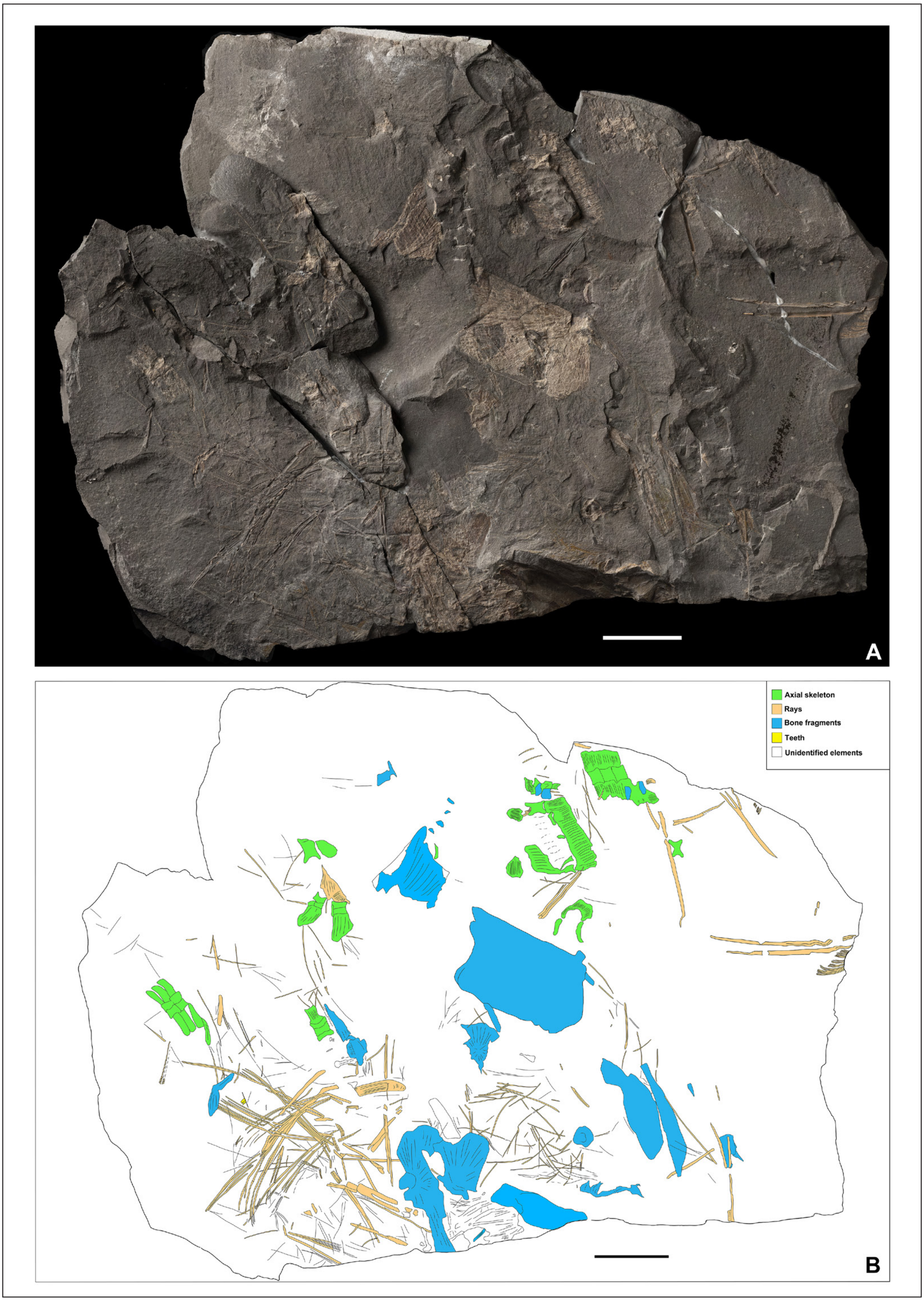


Fig. 37 - Teleostei indet. MUSE-PAL 8159, (A) and interpretive drawing highlighting the main components on the slab (B). Scale bars 50 mm.

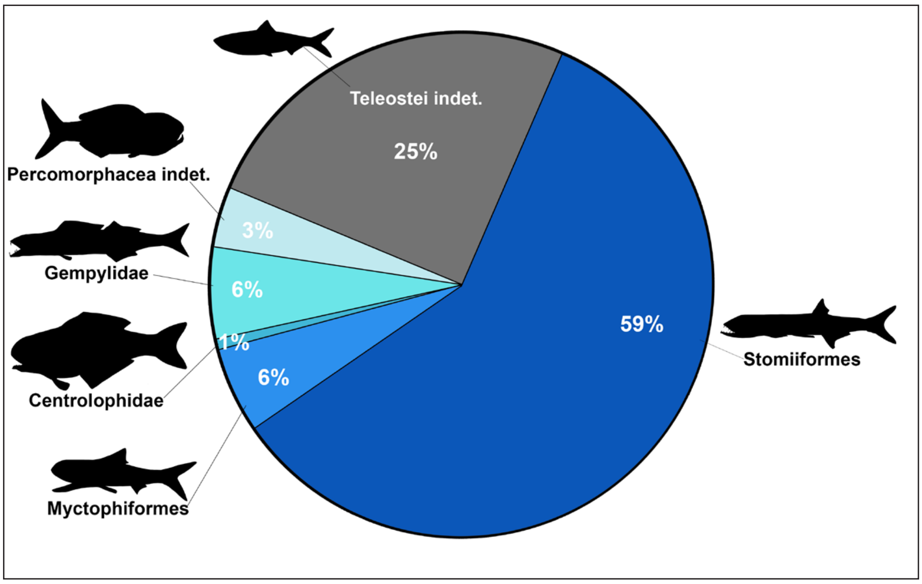


Fig. 38 - Taxonomic composition of the ichthyofauna of Solteri. Indeterminate teleost silhouette from www.phylopic.org.

widely gaping jaws, commonly regarded as an indicator of muscular tetany, possibly resulting from a variety of factors (temperature shock, high salinity, respiratory stress; e.g., Weiler 1929; Carnevale et al. 2022).

Overall, the preservation of the fishes from Solteri is more similar to the specimens from the coeval bathyal site of Monte Solane (Giusberti et al. 2014; Calzoni et al. in prep.), in which several specimens show moderate or poor preservation, with remarkable degrees of deformation and disarticulation, and some showing a similar pattern of undulate alteration of the vertebral column associated with unaltered body outlines (Giusberti et al. 2014).

PALEOECOLOGICAL REMARKS

The dominance of pelagic groups like stomiiforms and myctophiforms may indicate that the Solteri fish assemblage possibly inhabited the mesopelagic zone. The present distribution of the fish families recognized in the Solteri assemblage is primarily focused on the mesopelagic domain (200-1000 m), where gonostomatids can be extremely abundant (see Reading & Horton 2023). The extant gonostomatid species are mesopelagic and bathypelagic and usually inhabit depths ranging from 200 m to 2000 m, reaching about 3000 m in some cases (Weitzman 1997; Miya & Nishida 2000; Harold 2002). The Phosichthyidae are also mesopelagic and bathypelagic fishes that commonly live in depths from 250 to 600 m, although some species of the genus *Vinciguerria* can reach depths of about 2000 m (Weitzman 1997; Harold 2002; Grădianu et al. 2020). The lanternfishes of the family Myctophidae are today some of the most distinctive inhabitants of the mesopelagic zone, with a few species being bathy- or benthopelagic (Paxton & Hulley 2002); they commonly live in depth ranges reaching up to 1000 m, with some species living even further below, down to depths of 2000 m (Craddock & Hartel 2005). During the earliest part of the Paleogene, at least until the late Eocene, the Myctophidae inhabited the upper mesopelagic zone, mostly over the outer shelf and the upper slope (Schwarzhans & Carnevale 2021). These fishes then gradually colonized the lower mesopelagic zone and the deeper oceanic waters from the late Eocene, with a prominent presence in the mesopelagic domain from the Oligocene (Schwarzhans & Carnevale 2021). The extant representatives of the family Gempylidae are typical mesopelagic predators showing a bathymetric range from 200 to 500 m (Nakamura & Parin 1993), whereas extant species of the family Centrolophidae are commonly epipelagic or mesopelagic, and some species are found below 500 m up to depths of more than 1400 m (McDowall 2001; Last et al. 2013). Therefore, based on the composition of the fish assemblage, it is reasonable to conclude that the fossil-bearing layers of Solteri accumulated at upper bathyal depths, at around 250-400 meters, in the upper part of the mesopelagic zone.

EVOLUTIONARY IMPLICATIONS OF THE SOLTERI ICHTHYOFAUNA FOR THE MESOPELAGIC FOSSIL RECORD

The Solteri fish assemblage provides new insights that can help to better define the evolutionary paleoecology of certain groups of teleosts poorly represented in the lower Paleogene skeletal record (e.g., stomiiforms, myctophiforms, stromateiforms). For this reason, the Solteri ichthyofauna provides new information that expands our knowledge on the geographical and chronostratigraphic distribution of these groups.

Among the stomiiforms, the Gonostomatidae are mostly represented in the Oligocene deposits of eastern Europe (see Danil'chenko 1960; Jerzmańska 1974; Prokofiev 2005; Gregorová 2011; Přikryl 2013; Grădianu et al. 2017; Bieńkowska-Wasiluk 2021), but the earliest known species of the family based on skeletal remains is *Primaevistomias weitzmani* from the middle Eocene deposits of the Caucasus (Bartonian of Gorny Luch, Russia; Prokofiev & Bannikov 2002). The Ypresian Gonostomatidae from Solteri (*Scopeloides violator* n. sp. and *S. bellator* n. sp.) are therefore some of the oldest known species of this family, together with the material reported from the possibly coeval site of Monte Solane (Giusberti et al. 2014).

As far as the Phosichthyidae are concerned, these are also mostly represented in the Oligocene deposits of eastern Europe (see Danil'chenko 1960; Prokofiev 2002a; Grădianu et al. 2020) and from the Miocene deposits of the north Pacific (see, e.g., Ohe 1993; Yabumoto & Uyeno 1994; Nam et al. 2019; Nazarkin 2021). The earliest representative of the family known to date is *Sytchevskia distincta* from the Lutetian of Georgia (Prokofiev 2002a). The Phosichthyid from Solteri, *Solterichthys macrognathus* n. gen et sp., is therefore the oldest member of the family, extending back the stratigraphic range of phosichthyids to the Ypresian.

The earliest myctophiforms, if we exclude some problematic taxa from the Upper Cretaceous of Japan (Uyeno & Matsui 1993), are represented by the genera *Eomyctophum* and *Oligophus*, from the Eocene and Oligocene of eastern Europe (Schwarzhans & Carnevale 2021). *Eomyctophum mainardii* n. sp. from Solteri is therefore one of the oldest unquestionable representatives of the family, also expanding the geographic distribution of the genus *Eomyctophum* to southern Europe.

Among the Centrolophidae, the earliest known member of the family is *Butyrumichthys henricii*, from the lower Ypresian Fur Formation (Denmark; Schrøder et al. 2023). *Eogorgon bizzarinii* n. gen. et sp., along with *Zorzinia postalensis* from Bolca (Bannikov 2000), is one of the most ancient putative representatives of the family.

Gempylids have been reported from several Eocene localities, with their earliest member, *Argestichthys vysotzkyi*, from the basal Eocene strata of the Danata Formation (Turkmenistan; Prokofiev 2002b), and other representatives from Europe and New Zealand (e.g., *Progempylus edwardsi* from the Ypresian of England; Beckett et al. 2018; *Eothyrsites holosquamatus* Chapman, 1935 from the Bartonian of New Zealand; Rust & Robinson 2023). The three gempylid species from Solteri, *Krampusichthys tridentinus* n. gen. et sp., *Laurinichthys boschelei* n. gen. et sp., and *Wudelenia diabolica* n. gen. et sp., further expand our knowledge of the gempylid diversity in the early Paleogene.

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