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BONY FISHES (OSTEICHTHYES) FROM THE SINEMURIAN (JURASSIC) OSTENO KONSERVAT-LAGERSTÄTTE (COMO, NW ITALY)

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Keywords: Lombardy basin; Actinistia; Actinopterygii; *Ostenolepis marianii* gen. n.. et sp.; *Peripeltopleurus jurassicus* sp. n.; *Pholidolepis teruzzii* sp. n..

Abstract: Located in the Lombardy Basin of Northern Italy, the Osteno Konservat-Lagerstätte preserves an exceptionally diverse Lower Jurassic marine assemblage that, despite yielding extraordinary amounts of data over the past 60 years due to the remarkable preservation of its specimens, has long had its vertebrate component largely overlooked. This study presents a detailed morphological and taxonomic analysis of the bony fish fauna recovered from this unique deposit. Seven distinct taxa have been identified, four of which are shared with the renowned Lyme Regis Lagerstätte (Dorset, UK): *Holophagus* cf. *gulo*, *Dapedium* sp., *Furo* sp., and *Dorsetichthys bechei*, a unique stem teleost whose occurrence at Osteno further strengthens the possibility of faunal contact between English and northern Italian Sinemurian communities. Three novelties characterize the Osteno ichthyofauna: *Ostenolepis marianii* gen. n. sp. n., a small palaeoniscimorph with finely ornamented scales; *Peripeltopleurus jurassicus* sp. n., the last representative of the Peltopleuriformes, an order previously restricted to the Middle and Upper Triassic; and *Pholidolepis teruzzii* sp. n., a stem-teleost related to *Pholidolepis dorsentensis* from Lyme Regis, but lacking any scale covering. The discovery of these taxa significantly contributes to our understanding of Sinemurian ichthyofaunas while shedding new light on the paleoenvironmental dynamics along the northwestern margin of the Neotethys. Overall, this study underscores the critical importance of the Osteno site for reconstructing patterns of diversity and biogeographic connectivity during a pivotal interval in vertebrate evolution.

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Introduction

In the last two centuries many studies contributed to increase our knowledge of the structure and composition of the Liassic biotic communities of the Lombardy Basin, the westernmost and frankly marine unit of the Southern Alps area (e.g. Stoppani 1857; Parona 1894; Bonarelli 1894; Bettoni 1900; Sacchi-Vialli & Cantaluppi 1962; Cita 1965; Gaetani 1970; Tintori 1977; Cobianchi 1992; Jadoul et al. 2004; Dal Sasso et al. 2018).

Among the Liassic fossiliferous localities of the Lombardy Basin, the Osteno site is certainly the most relevant, representing an extraordinary but neglected Konservat-Lagerstätte that comprises

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an almost unknown bony fish assemblage. The relevance of this locality is outstanding but, despite the remarkable quality of the preservation of the fossils and their attractive appearance, they received only limited attention (Tang 2002). The fossiliferous deposits of the Osteno Konservat-Lagerstätte date back to the Sinemurian, approximately coeval to the Lyme Regis Lagerstätte (Dorset, U.K.), known since the late 17th century. These two localities are not only close at the stratigraphic level but also share many similarities at biotic level (Garassino 1994).

The fossiliferous outcrop is located in the vicinity of the town of Claino con Osteno (Como Province), along the northern shore of Lake Lugano (also known as Ceresio) (Fig. 1B). Two main quarries have yielded a number of specimens currently housed in the Museo di Storia Naturale di Milano (MSNM): "Porto Franco" (also recognized as Crotto del Doglio, Fig. 1C, D), located approximately 3 kilometres west of Claino con Osteno, and "Cava Quaglietto," which lies to the east of the town. The site was initially discovered in 1964 by Pio Mariani and subsequently documented by Pinna (1967) and other paleontologists of the Museo di Storia Naturale di Milano (MSNM) (e.g., Pinna 1968, 1969, 1972, Pinna et al. 1982). Controlled excavations (Fig. 1E) carried out in the "Porto Franco" quarry in the 1980s and 1990s led to discovery of numerous exquisitely preserved fossils (Arduini et al. 1980, 1982b; Arduini 1988; Bonci & Vannucci 1986; Garassino 1996). Field excavations were stopped in 2002, and the quarry subsequently become permanently abandoned (Fig. 1G).

The fossiliferous sediments of Osteno yield a variety of marine fossils, including bivalves, brachiopods, cephalopods (Pinna 1972, 1985), crustaceans and other arthropods (Pinna 1967, 1968, 1969, 1972; Pinna et al. 1982b; Arduini et al. 1980, 1984; Garassino 1996; Garassino & Donovan 2000, Garassino & Teruzzi 1990; Teruzzi 1990; Braig et al. 2023), nematodes (Arduini et al. 1983), polychaetes (Arduini et al. 1982a), xiphosurans (Lasmdell et al. 2021), acorn worms (Arduini et al. 1980), ophiuroids (Pinna 1985), and cartilaginous and bony fishes, associated with rare plant remains (Bonci & Vannucci 1986). Notably, the assemblage is overwhelmingly dominated by exquisitely preserved invertebrates, many of which exhibit distinct traces of soft tissues (see Garassino & Teruzzi 2015, and Lasmdell et al. 2021 for an overview of the assemblage).

Vertebrate remains represent less than 12% of the faunal assemblage (Pinna 1985), with more than hundred specimens of fish discovered. Only four taxa of cartilaginous fishes have been described, the neoselachian sharks *Ostenoselache stenosoma* and *Synechodus pinnai* and the holocephalans *Squaloraja* sp. plus and an unnamed myriacanthid (Duffin 1987, 1992, 1998; Duffin et al. 2023). The bony fish diversity is largely unknown, only superficially examined in a short popular publication (Duffin & Patterson 1993).

The goal of this paper is therefore to provide a detailed morphological and taxonomic analysis of the bony fish fauna of the Osteno Konservat-Lagerstätte, and to discuss its paleoenvironmental and biogeographic significance.

Geological setting

The Osteno Lagerstätte is located in the western part of the Lombardy Basin, in the Southern Alps domain. The Lombardy Basin developed on the Adria passive continental margin due to the extensional tectonic regime associated with the opening of the Penninic Ocean and of the Central Atlantic Ocean (Winterer & Bosellini 1981). This extension was responsible for the drowning of the lower Hettangian carbonate platforms and a change in the depositional style; the rift-related setting results in a horst and graben topography that led to the definition of structural highs, where condensed successions were deposited, and subsiding basins, characterized by thick syntectonic cherty limestone and marls (Jadoul et al. 1992, 2005; Bertotti et al. 1993).

In the area of Lake Lugano the Lugano fault, a major N-S, E-dipping normal fault, separates a structural high (the Arbostora or Lugano high) to the west from a basinal area (Monte Generoso Basin) to the east (Bernoulli 1964). Whereas the Arbostora high is characterized by a condensed Rhaetian to Sinemurian succession a few hundreds of meters thick, capped by the lower Sinemurian skeletal calcarenite of the Saltrio beds (Jadoul et al. 2005), the Monte Generoso Basin stores about 3000 m of Hettangian to upper Pliensbachian basinal cherty limestone and marls of the Moltrasio Limestone ("Lombardische Kieselkalk" in Bernoulli 1964). The succession is capped by upper Pliensbachian red nodular limestone of the Domaro Limestone

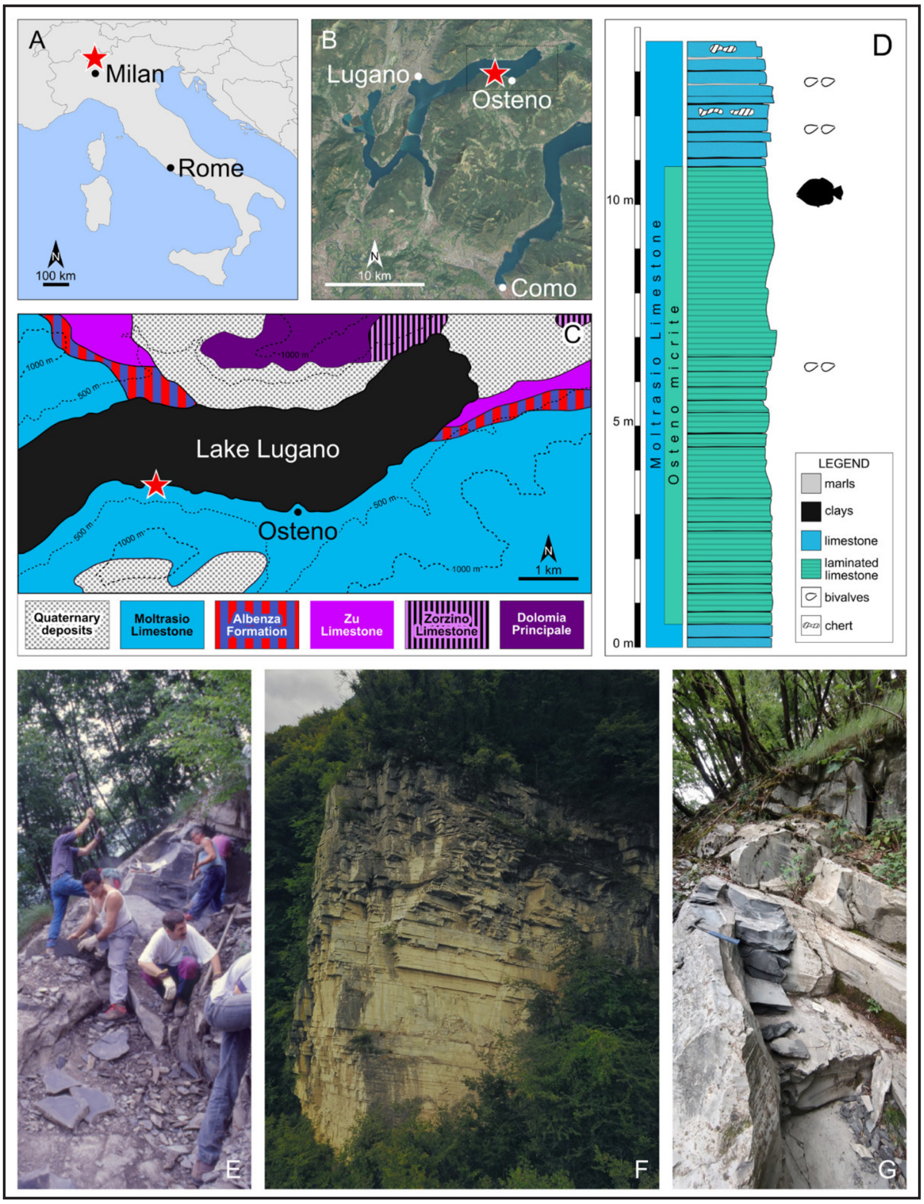

Fig. 1 - Location and geological map of the Osteno Lagerstätte, Como Province, Northwestern Italy, indicated with a star. (A-B) Location of the Osteno Lagerstätte in Italy. (C) Geological map of the easternmost region of Lugano Lake (modified from Montrasio et al. 1990, after Jadoul & Galli 2008). (D) Stratigraphic section of the Porto Franco outcrop. (E) Excavations at the Porto Franco site (circa 1990, modified from Garassino & Teruzzi 2015). (F) Porto Franco outcrop from the Lugano Lake. (G) Current conditions of the Porto Franco site.

(Schirolli 2007). These two units are grouped in the Medolo Group (Schirolli 2007).

The Moltrasio Limestone within the Generoso Basin consists of a monotonous succession of well bedded dark-grey fine limestones with marly interbeds and frequent black cherts nodules and layers (Bernoulli et al. 2018); it is generally poorly fossiliferous, although some belemnites, ammonites, and brachiopods have been found, suggesting an age comprised between the Hettangian (201 million years ago) and the early Pliensbachian (Carixian, 190 million years ago).

The fossiliferous sediments of the site of Osteno are included in the Moltrasio Limestone (Fig. 1C) and correspond to a 10 m-thick stratigraphic interval of laminated micritic limestones exposed in two quarries in the surroundings of the town of Osteno (Fig. 1D). This interval was informally referred to as "Osteno Formation" or "Osteno micrite" by Pinna (1985). The three-dimensional shape and extension of this interval of fossiliferous limestone are unknown.

The micritic limestone in the fossiliferous bed is rich in calcitized monoaxone siliceous sponge spicules and radiolarians, as well as oxidized pyrite grains and organic matter (Pinna 1985; Garassino & Teruzzi 2015). The interval yielded only a few calcitic fossils of brachiopods and ophiuroids, scarce aragonitic molluscs preserved as moulds, abundant fossils of invertebrates with exceptional preservation, fishes and plant remains. Fossils are often heavily compressed; the fossiliferous bed of the Osteno

Lagerstätte can be referred to the upper part of the lower Sinemurian *Arietites bucklandi* ammonite Zone (198.30 Ma) based on the presence of the ammonite *Coroniceras bisulcatum* (Bruguière 1789), thereby implying a minimum age of 198.30 Ma (Hesselbo et al. 2020).

Materials and Methods

Specimens were documented using a Sony α6000 camera equipped with a 7artisans 60mm f2.8 Macro II lens. Images were captured under naturally diffused LED lighting, which allowed for the acquisition of multiple high-resolution photographs for each specimen. Although ultraviolet (UV) photography was attempted, the minimal fluorescence yielded uninformative results. When necessary, specimens were treated with a demineralized water impregnation to enhance the contrast between the specimen and the surrounding matrix, thereby emphasizing key morphological details. Measurements were obtained to the nearest 0.1 mm using a dial calliper, and the standard length (SL) was consistently used throughout the study.

For consistency with previous research, the traditional nomenclature for skull roof bones was maintained. The identification and terminology of the cephalic sensory canals adhere to Northcutt (1989), while the nomenclatures for fin rays and fulcra follow Arratia (2008, 2009), and that for scales conforms to Schultze (1966, 1996, 2015). In addition, the terminology for the caudal skeleton and the vertebral count is based on the work of Nybelin (1963), Arratia & Schultze (1992), and Schultze & Arratia (2013). The anatomical nomenclature and taxonomic classification of Palaeoniscimorpha are derived from Schultze et al. (2021). All the specimens are housed in the paleontological collections of the Museo di Storia Naturale di Milano (MSNM).

A phylogenetic analysis was performed in order to detect the phylogenetic position of a new taxon, represented by the specimen MSNM V659. The character matrix was compiled in MESQUITE v.3.03 (Maddison & Maddison 2008), and the phylogenetic analysis was performed in TNT 1.6 (Goloboff & Morales 2023) using traditional search method, 1000 replicates, 100 random seeds, tree bisection and reconnection (TBR) and ten trees saved per replication with collapsing trees after search. All characters are unordered and given equal weight. MSNM V659 is scored for 24 characters. Characters are denoted by "ch." preceding the character number followed by the character state in brackets (e.g.: ch.1[0]). See Shen & Arratia (2021) for the definition of the characters, the matrix used is available in appendix (Table S1). Complete strict consensus (Fig. S1) and 50% Majority rule (Fig. S2) trees are available in appendix.

Abbreviations: abc, abdominal centra; amptg, anal medial pterygiophore; ang, angular; ant, antorbital; ap, anterior process; apptg, anal proximal pterygiophore; as, anal stay; asbo, accessory suborbital; bf, basal fulcra; bf-r, base fin-ray; br, branchiostegal ray; bsp, basipterygium; cac, caudal centra; cha, caudal haemal arch; chs, caudal haemal spine; cl, cleithrum; clv, clavicle; cor, coracoid; de, dentary; dmptg, dorsal medial pterygiophore; dpcl, dorsal postcleithrum; dpf-r, dorsal principal fin-ray; dpptg, dorsal proximal pterygiophore; ds, dorsal stay; dsp, dermosphenotic; dyc, displospondylous centrum; ep, epural; epp, epineural process; f-f, fringing fulcra; fr, frontal; h, hypural; hpu, haemal spine of preural centra; ifo, infraorbital; ioc, infraorbital sensory canal; it-st, intertemporo-supratemporal; l., left; lac,lachrymal; lls, lateral line scale; ln, leptolepid notch; mx, maxilla; na, nasal; nc, nothocordal calcification; npu, neural arch of pre ural centra; ns, neural spine; oc, otic sensory canal; op, opercle; orn, ornamentation; pa, parietal; paxp, pelvic axillary process; pexp, pectoral axillary process; pexpf-r, pectoral fin-ray; pmx, premaxilla; poc, preopercular sensory canal; pop, preopercle; pp, posterior process; psp, parasphenoid; q, quadrate; r., right; ro, rostral; ruf-r, reduced uppermost hypaxial finray; sc, scale; scl, supracleithrum; scr, sclerotic ring; smx, supramaxilla; sn, supraneural; so, supraorbital; sob, suborbital; soc, supraorbital sensory canal; uc, ural centrum; ud, urodermal; una, ural neural arch; vpcl, ventral postcleithrum.

Systematic Paleontology

Superclass **OSTEICHTHYES** Huxley, 1880
Class **SARCOPTERYGII** Romer, 1955
Subclass ACTINISTIA Cope, 1871
Order **Coelacanthiformes** Berg, 1937
Suborder **Latimeroidei** Schultze, 1993
Family Latimeriidae Berg, 1940
Subfamily Latimeriinae Ferrante & Cavin, 2023
Holophagus Egerton, 1861

Holophagus cf. ***gulo*** (Egerton, 1861)

Figs. 2, 3

1985 "cf. *Holophagus*" Egerton, 1861 - Pinna, p .175.
1993 "cf. *Holophagus gulo*" (Egerton, 1861) - Duffin & Patterson, p. 20, 29, fig. 15 (MSNM V587).
2015 "cf. *Holophagus gulo*" (Egerton, 1861) - Garassino & Teruzzi, p.43, 57, fig. 68 (MSNM V600).
2021 "cf. *Holophagus gulo*" (Egerton, 1861) - Lamsdell et al., p. 4.

Material: MSNM V530, isolated scale, in part and counterpart (MSNM V601); MSNM V543 (Fig. 3A, B), isolated urohyal;

MSNM V561, isolated scale; MSNM V586, isolated scale; MSNM V587, isolated scale (Fig. 2); MSNM V588, isolated scale; MSNM V589, isolated scale; MSNM V591, isolated scale; MSNM V592, isolated scale; MSNM V593, isolated scale; MSNM V597, isolated scale; MSNM V598, isolated scale, in part and counterpart (MSNM V610); MSNM V599, isolated scale; MSNM V600, isolated scale, in part and counterpart (MSNM V667); MSNM V602, isolated scale; MSNM V607, isolated scale; MSNM V666; MSNM V668, two associated scales.

Description. The majority of the available specimens is represented by well-preserved isolated scales, two of which are associated in MSNM V668. The largest available scale (MSNM V600/V667) has a length of 18.9 mm and a depth of 13.8 mm, while the smallest one (MSNM V593) has a length of 8.5 mm and a depth of 7.5 mm.

The scales are oblong, almost subcircular in outline, with a slightly pointed posterior (caudal) margin and rounded anterior (rostral) margin. Overall, the scales are slightly longer than high. They exhibit an ornamented pattern on the posterior field. The posterior field has a rhomboid shape and occupies less than one-third of the surface of the scales, exhibiting a densely ornamented pattern. The anterior and both the lateral fields are covered by thin and feebly developed parallel ridges (ca. 0.02 mm wide) radiating longitudinally from the anterior margin of the posterior field. These longitudinal ridges extend on the posterior field where they are covered by thick and closely spaced enamel ornamentations (width up to 0.2 mm). In some specimens, the thin ridges produce a fringed pattern along the lateral margins of the scale (e.g., MSNM V587 – Fig. 2).

A single isolated partially complete urohyal (MSNM V543, Fig. 3A, B) is also available. As in other coelacanths (Fig. 3C), it is dorsoventrally flattened, exhibiting a characteristic morphology, with a narrow anterior region and an expanded and ostensibly bifid posterior end. The posterior expanded region shows a median depressed area that separates the two contralateral (bifurcated) distal ends.

Remarks. The morphology of the scales described herein is consistent to that of the coelacanth species *Holophagus gulo* to which they are tentatively referred (see also Duffin & Patterson 1993).

According to Forey (1998), the scales of coelacanths exhibit a peculiar morphology, with circular to subcircular outline with extensively ornamented posterior field, which occupies less than one-third of the scale surface. Morphological features of coelacanth scales are commonly recognized as taxonomically relevant (e.g., Forey 1998; Holder et al. 1999; Wendruff & Wilson 2012). The morphology of the urohyal appears to be unknown in *Holophagus gulo*. However, due to the relatively common occurrence of scales referred to this species, we consider the possibility to tentatively refer this isolated bone of the visceral skeleton to this coelacanth species.

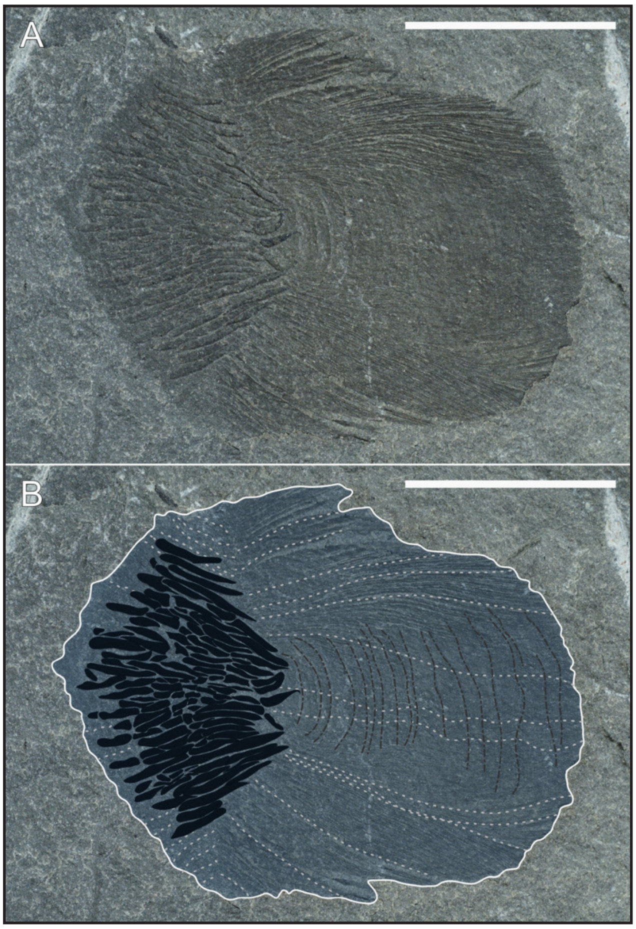

Fig. 2 - *Holophagus* cf. *gulo* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V587. (A) isolated scale in lateral view, anterior facing right. (B) Anatomical characters drawn over picture A. Light blue polygon with white outline, scale area; white dotted lines, ridges; grey dotted lines, concentric crests; blue polygons, posterior field enamel ridges. Scale bars 5 mm.

Holophagus gulo is a genus of latimerid coelacanth restricted to the Lower Lias (Sinemurian, *Caenisites turneri* Zone to *Asteroceras obtusum* Zone. Charmouth Mudstone Formation, Black Ven Mudstone Member; Forey et al. 2010) of Dorset, UK (Woodward 1891; Gardiner 1960; Forey 1998; Ferrante & Cavin 2025). According to Forey (1998) the scales of *H. gulo* exhibit an ornament of very fine and closely spaced elongated ridges (see also Egerton 1861). *H. gulo* is one of the only two coelacanthiforms known for the Sinemurian (Forey

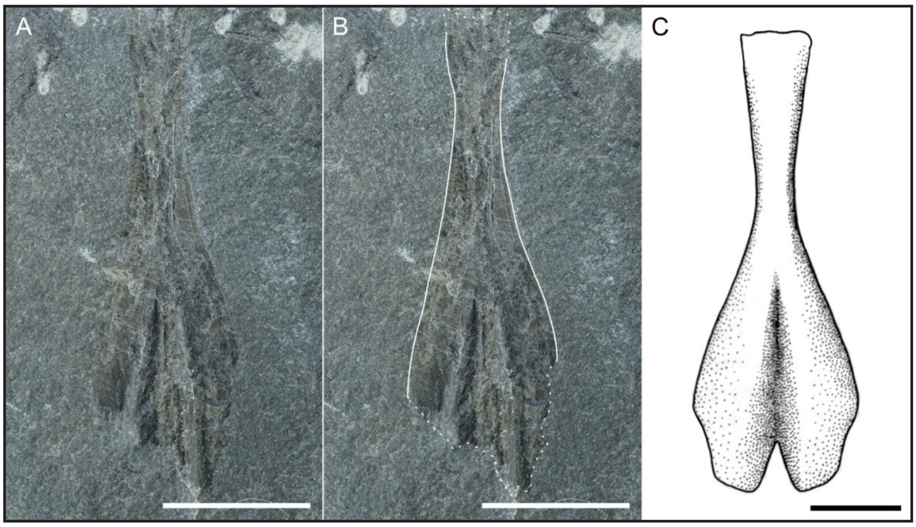

Fig. 3 - *Holophagus* cf. *gulo* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. (A) MSNM V543, isolated urohyal in ventral view, anterior facing up. (B) Outline of the urohyal traced over picture A. (C) *Macropoma lewesiensis* Mantell 1822: restoration of the urohyal in ventral view, anterior facing up (modified from Forey 1998). Scale bars in A and B 5 mm, scale bar in C 10 mm.

1998), the other being *Diplurus,* which shows a different ornamentation of the posterior field, with elongate and parallel prominent enamel ridges (see Forey 1998).

Class **ACTINOPTERYGII** Cope, 1887
Superorder **Palaeoniscimorpha** Lund, Poplin et McCarthy, 1995
Ostenolepis gen. n.

Diagnosis: *Ostenolepis* is distinguished from all other palaeoniscimorphs by the following combination of features: body fusiform with elongated skull; frontals elongated, with a straight suture; squared parietals representing one third of the frontals; elongate intertemporo-supratemporal bone reaching the nasal, passing above the dermosphenotic; about 29 pectoral-fin rays, 38 pelvic-fin rays, at least 22 dorsal-fin rays and around 25 anal-fin rays; pelvic-fin rays bearing posterior spines, usually one, on the distal margin; four large and elongate diagonal dorsal caudal fulcra extending anteriad to the caudal peduncle in front of the dorsal margin of the caudal fin; at least three elongate ventral basal caudal fulcra; at least 50 lateral-line scales nearly twice the size of the surrounding scales, with a shield-like morphology and a pit line on the exposed field; seven or eight scale rows between the lateral-line scale row and the dorsal-fin base, and seven or eight scale rows between the lateral line scale row and the pelvic-fin base; ganoid scales with a unique ornamentation pattern characterized by anterior grooves and posterior spines.

Type species: *Ostenolepis marianii* sp. n., by monotypy and designation herein.

Etymology: The generic name refers to the site where the specimens were recovered (Claino con Osteno, Como Province, Italy), incorporating the suffix "lepis" (from Ancient Greek, meaning "scale") to emphasize the distinctive ganoid scalation of this new taxon.

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Ostenolepis marianii sp. n.
Figs. 4-9

1984 "cf. *Cosmolepis*" Egerton, 1855 - Schaeffer & Patterson, p. 72.
1984 "cf. *Pteroniscus*" Berg, 1949 - Schaeffer & Patterson, p. 72.
1985 "cf. *Cosmolepis*" Egerton, 1855 - Pinna, p. 175.
1985 "cf. *Pteroniscus*" Berg, 1949 - Pinna, p. 175.
1993 "cf. *Cosmolepis ornatus"* Egerton, 1855 - Duffin & Patterson, p. 20, 31, fig. p. 31.
1993 "Coccolepididae*"* Berg, 1949 - Duffin & Patterson, p. 20, 30, fig.16 (MSNM V617).
1998 "cf. *Cosmolepis*" Egerton, 1855 - Duffin, p. 5.
1998 "cf. *Pteroniscus*" Berg, 1949 - Duffin, p. 5.
2015 "cf. *Cosmolepis ornatus"* Egerton, 1855 - Garassino & Teruzzi, p. 45, fig. 69 (MSNM V621 - wrong specimen).
2015 "Coccolepididae*"* Berg, 1949 - Garassino & Teruzzi, p. 45.
2021 "cf. *Cosmolepis*" Egerton, 1855 - Jaselli & Duffin, p. 165.
2021 "cf. *Pteroniscus*" Berg, 1949 - Jaselli & Duffin, p. 165.

Diagnosis: as for the genus.

Etymology: The specific epithet honours Pio Mariani, who discovered the Osteno site in 1964.

Holotype: MSNM V617, an almost complete, articulated skeleton lacking the antero-dorsal region of the trunk, as well as the anterior portion of the dorsal fin, and most of the paired fins (the right pectoral is present, but highly compressed). The skull is compressed dorso-ventrally, obscuring the anatomy of most of its opercular and ventral portions (Fig. 4, 6).

Paratypes: MSNM V538, largely incomplete specimen comprising associated and isolated scales covering, and two isolated and fragmented skeletal elements (Fig. 5C, 8); MSNM V554, an incomplete, articulated skeleton representing the mid-section of the trunk, exposed in ventral view, showing the paired fins (Fig. 5D); MSNM V652, an incomplete and heavily twisted, articulated skeleton represented by the posterior half of the body, its scale cover, and portions of the pelvic and anal fins, in part and counterpart (Fig. 5A-B, 7).

Measurements: see Table 1

Description. Small sized fish, with a total length of 89.9 mm, a standard length of 65.6 mm, and an estimated body depth of 19 mm (measurements based on the holotype); the ratio between total length and body depth is 6.8, describing a fusiform body shape (Schultze et al. 2021). Based on the body proportions of the holotype, an estimated total length of ca. 130 mm can be hypoth-

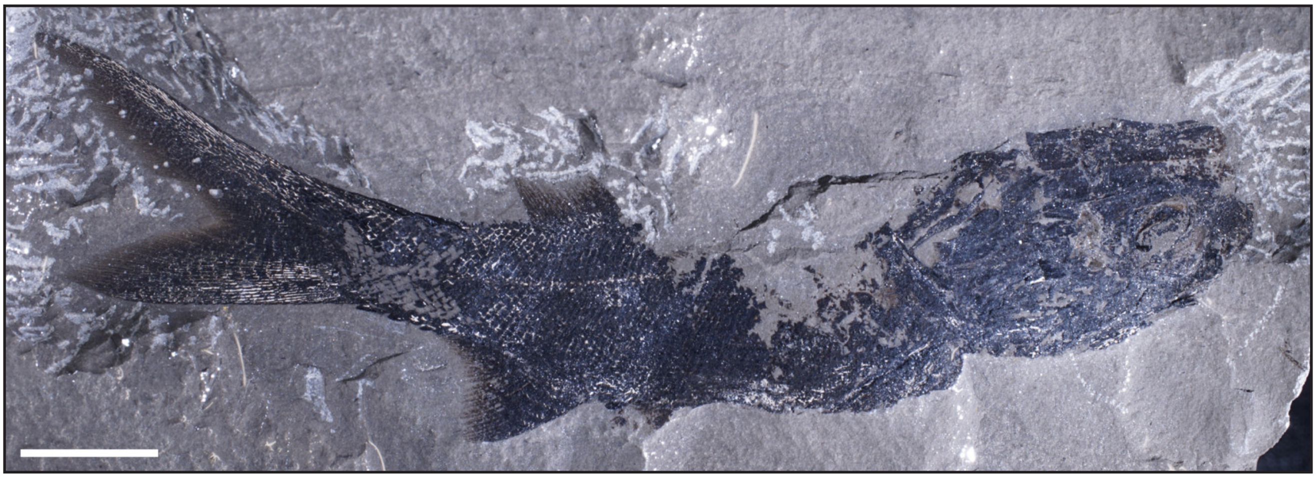


Fig. 4 - *Ostenolepis marianii* gen. n. sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Holotype, MSNM V617, in right lateral view. Scale bar 10 mm.

esized for MSNM V652. The head is contained about three times in the SL; it is characterized by a terminal mouth, a moderately long postorbital gape, a maxilla with an enlarged postorbital plate, and well-developed parietals and intertemporo-supratemporals. The paired fins are well developed, with remarkably broad pelvic fins. The anal fin has a relatively elongate base and a triangular shape. The pterygial formula (Westoll 1944) cannot be assessed due to the inadequate preservation of the available specimens. The caudal fin is greatly developed, heterocercal, with a dorsal lobe covered by rhombic ganoid scales, much developed than those of the ventral lobe. Scales are highly ornamented with anterior grooves and posterior spines.

The head region can be observed exclusively in the holotype (Fig. 6), where it is moderately well-preserved. The cranial bones often lack their superficial layers, making the identification and description of the various elements highly problematic.

The morphology of the bones of the snout region is difficult to interpret because the margins of the bones scarcely defined. However, it seems that a relatively small and laterally placed nasal (1.8 mm per 1.9 mm), and a median and relatively large (3.4 mm in height and 3.0 mm in width) rostral, almost triangular in outline, are recognizable. The nasal seems to carry a small posterior notch, probably representing part of the posterior nostril. The rostral carries a larger notch, probably representing part of the anterior nostril. The nasal articulates medially with the frontal and posteriorly possibly with the intertemporo-supratemporal and the dermosphenotic. The outer surface of both the nasal and rostral shows a peculiar ornamentation formed by delicate concentric ridges.

The paired frontals are elongate and by far represent the largest bones of the skull roof (13.5 mm). The suture line connecting the two contralateral frontals is straight. Both the frontals are narrowed anteriorly (ca. 2.5 mm) and expanded posteriorly (ca. 3.0 mm); the anterior margin of the frontals is gently curved, approximately semicircular, while the posterior margin is straight, forming well-defined right

	Standard length	Total length	Head length	Pectoral-fin base length	Longest pectoral-fin ray	Pelvic-fin base length	Longest pelvic-fin ray	Anal-fin base length	Longest anal-fin ray	Anal-fin height	Longest caudal-fin ray
MSNM V617	65.6	89.9	21.6	9.6	?	?	?	7.9	9.6	6.9	22.1
MSNM V554	?	?	?	10.6	20.8	12.4	16.3	?	?	?	?
MSNM V652	?	?	?	?	?	12.0	16.4	?	?	?	30.8

Tab. 1 - Measurements (in mm) of the specimens referred to *Ostenolepis marianii* gen. n. sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy.

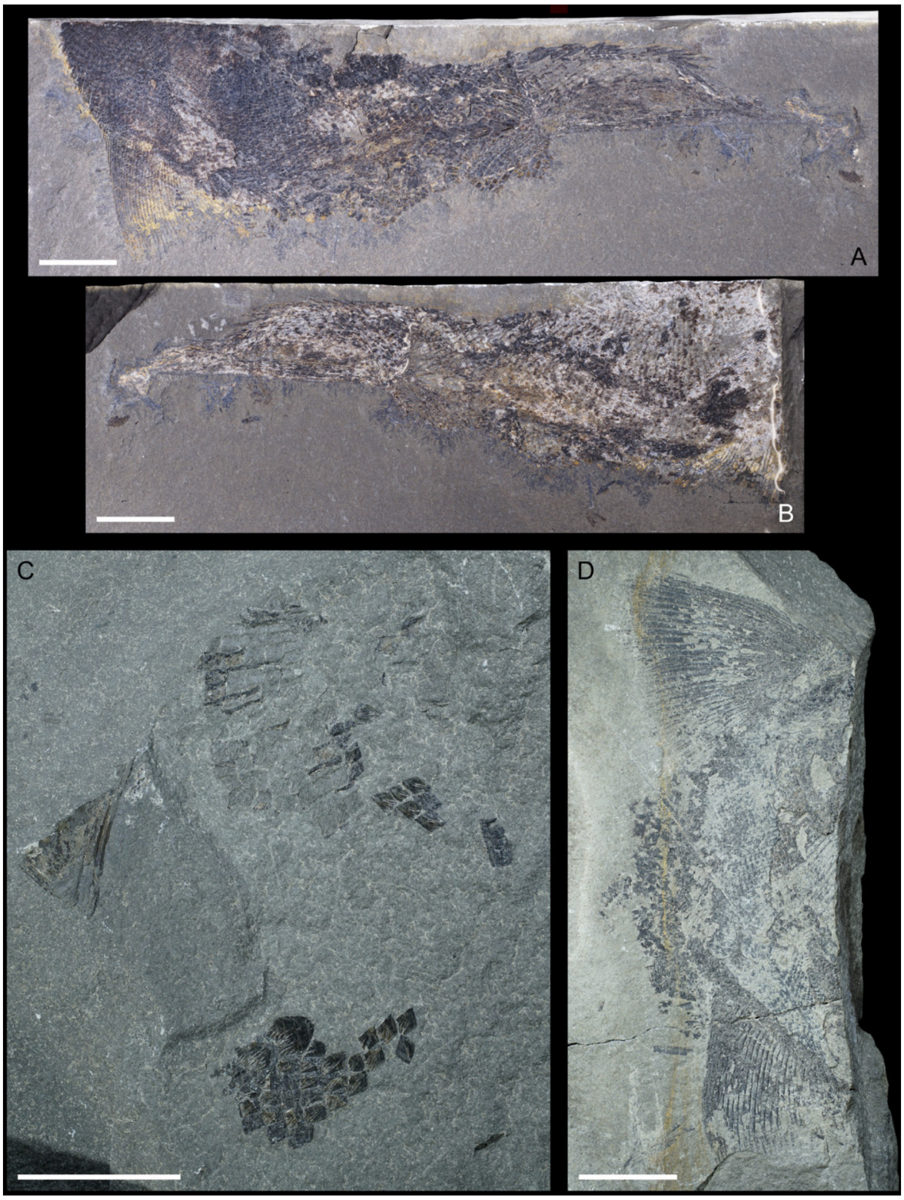


Fig. 5 - *Ostenolepis marianii* gen. n. sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Paratypes. (A) MSNM V652B, in ventral view, anterior facing left. (B) MSNM V652A, in ventral view, anterior facing right. (C) MSNM V538. (D) MSNM V554, in ventral view, anterior facing up. Scale bars 10 mm.

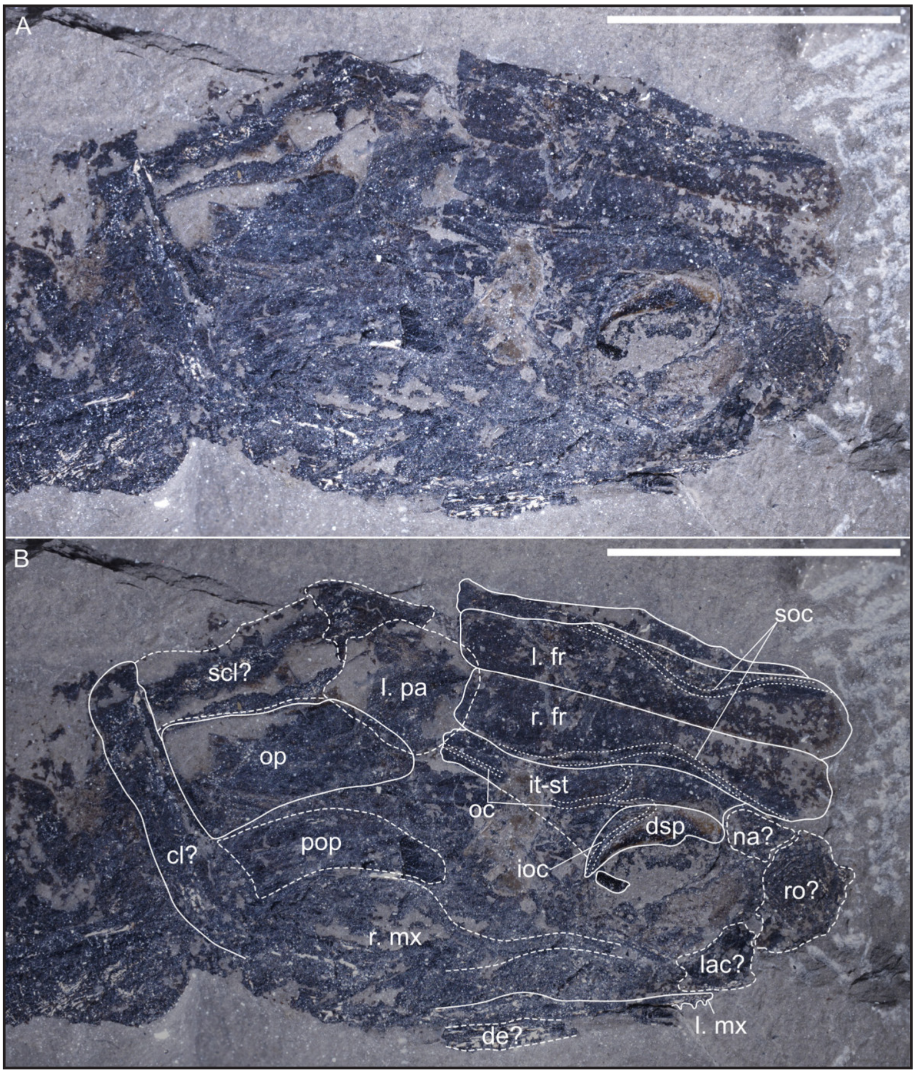
angles. The central portion of each frontal is slightly constricted above the orbit (ca. 2.0 mm). The left parietal can be recognized, being subquadrangular in outline (with a length of about 3 mm per side) and with a gently curved lateral margin. The supraorbital sensory canals can be traced thanks to the numerous pores piercing the surface of the bones; they run along the lateral margins of the frontals and the parietals, they also extend anteriorly into the nasals.

The frontals, and probably also the parietals, articulate laterally with the elongate (ca. 10.9 mm in length) intertemporo-supratemporal. The intertemporo-supratemporal tapers anteriorly, showing an anterior width of 0.9 mm and a posterior one of 2.4 mm. The intertemporo-supratemporal shows traces of the otic sensory canal, which runs longitudinally on this bone, and a small branch of the same canal that moves medially towards the parietal.

Anterolaterally to the intertemporo-supratemporal, it is possible to recognize what we interpret as a dermosphenotic, clearly distinguishable thanks to its ganoine cover. This bone is almost crescent-shaped and likely formed most of the upper wall of the orbit; it bears the postorbital section of the infraorbital sensory canal, which runs parallel to the posterior margin of the bone, passing anteromedially in the intertemporo-supratemporal.

Inside the orbit, there are four faint bone fragments that might represent the ossicles of the sclerotic ring.

Fig. 6 - *Ostenolepis marianii* gen. n. sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Holotype, MSNM V617. (A) head skeleton in dorso-lateral view. (B) Anatomical characters drawn over picture A. Scale bars 10 mm.



A single, poorly preserved and relatively large (ca. 3.5 mm in length) bone with irregular outline and placed along the antero-ventral border of the orbit is interpreted herein as a fragment of a lachrymal.

Some bones placed ventral to the intertemporo-supratemporal, and posterior to the dermosphenotic might represent fragments of the infraorbitals.

The remaining portion of the cheek area and the entire opercular series are poorly preserved, with eroded outer surface and margins of the bones. The preopercle is partially recognizable in the holotype and seems to articulate with the maxilla along its entire ventral margin.

The opercle is placed dorsally to the preopercle, being sub-rectangular in outline, almost two times higher than long. Growth lines are visible on the opercle and the subopercle. In MSNM V538 there is what appears to be a portion of a large (5.8 mm per 10.7 mm) element of the opercular series ornamented with four parallel ridges (Fig. 5B).

The broadly enlarged posterior plate of the maxilla is placed ventral to the preopercle; its margins are not clearly identifiable, although the region in which the posterior plate and the narrow anterior branch of the maxilla are connected is well distinguishable. The anterior branch of the maxilla is developed rostrally and curves gently upwards anteriorly ventrally to the orbit region; the ventral margin of the maxilla is not clearly recognizable.

There are only four preserved marginal maxillary teeth similar in size and shape, associated with the anteriormost portion of the maxilla. These are about 0.2 mm long, conical with pointed distal tip, and a smooth outer surface and the apex covered by an acrodin cap. The lower jaw is extremely fragmented.

The caudal fin is epicercal and inequilobate, with the upper lobe longer, but not deeper, than the ventral lobe. There are at least 50 epichordal rays which are shorter than the hypochordal ones. The hypochordal rays consist of nine procurrent and 20 principal rays. The ventral margin of the hypochordal caudal lobe is associated with fringing fulcra. All the principal caudal-fin rays seem to be evenly segmented from their bases, bifurcating distally. No accessory flap is visible. The distal ends of the dorsal and ventral lobes meet approximately at the midline, forming a deep cleft with a shallow acute angle (ca. 30°).

The dorsal fin, only partially preserved in the holotype, lies between the pelvic and anal fins, and contains not less than 22 rays. The dorsal-fin outline cannot be described due to the absence of its anterior portion; however, its rays are approximately half the length of the pelvic and anal-fin rays.

The anal fin is triangular in outline and originates behind the posterior end of the dorsal fin. It contains about 29 rays of which nine are procurrent and about 20 are principal and distally bifurcated. The anterior margin of the first anal-fin ray is associated with fringing fulcra. At least three basal fulcra border the base of the anal fin.

The pectoral girdle, like the entire posterior portion of the cranium, is poorly preserved. The best-preserved element, located dorsal to the opercle, is sub-rectangular in shape, almost twice as deep as long, and is interpreted herein as a supracleithrum. This bone shows ornamentation in the form of small ganoine tubercules. Posterior to the opercular series and supracleithrum, it is possible to recognize a relatively large cleithrum. The pectoral fins originate in the hypaxial portion of the flanks. The pectoral fins are large, triangular in outline and remarkably deep (see measurements, Tab. 1). There are at least 29 pectoral-fin rays, as shown in MSNM V554. The first rays are not preserved, but at least two procurrent rays are present. The first 20 rays are enlarged, reaching up to 1 mm in width, bearing a ridge in the anterior half. The posterior nine pectoral-fin rays are narrower, ca. 0.5 mm. The anterior margin of the pectoral-fin is associated with fringing fulcra.

The pelvic fins (Fig. 7A) lie abdominally on the body and originate approximately at the trunk mid length. Their bases are similar in length to that of the anal fin. The pelvic fins are smaller than the pectoral one, showing a triangular shape, twice longer than deep. There are about 38 rays in the pelvic fin, of which the first ten are procurrent rays (the first 4 are short, unsegmented, stout and spinous), while the others are unbranched principal rays. Each ray is enlarged, reaching 1 mm in width. The anterior margin of the first pelvic-fin ray is associated with fringing fulcra. MSNM V554 shows posteriorly oriented minute spines emerging along the posterior margin of some segments of the rays (Fig. 7B).

The number of scales along the lateral line is unknown, due to the lack of the portion of the trunk directly behind the pectoral girdle. However, it is possible to observe at least 45 lateral-line scales, although the series cannot be traced in the caudal peduncle. There are seven or eight scale rows below the base of the dorsal fin and above the lateral line and seven or eight scale rows below the lateral line and above the anal-fin base.

The rhomboid ganoid scales are arranged in longitudinal and vertical rows, the latter oriented antero-dorsad to postero-ventrad, each scale articulated vertically via a peg and socket articulation, with very low and broad-based pegs.

Scale size and shape vary greatly along the entire trunk. However, due to incompleteness of the specimens or their inadequate preservation, most of the anterior scales cannot be described (regions A, B and E of Esin 1990).

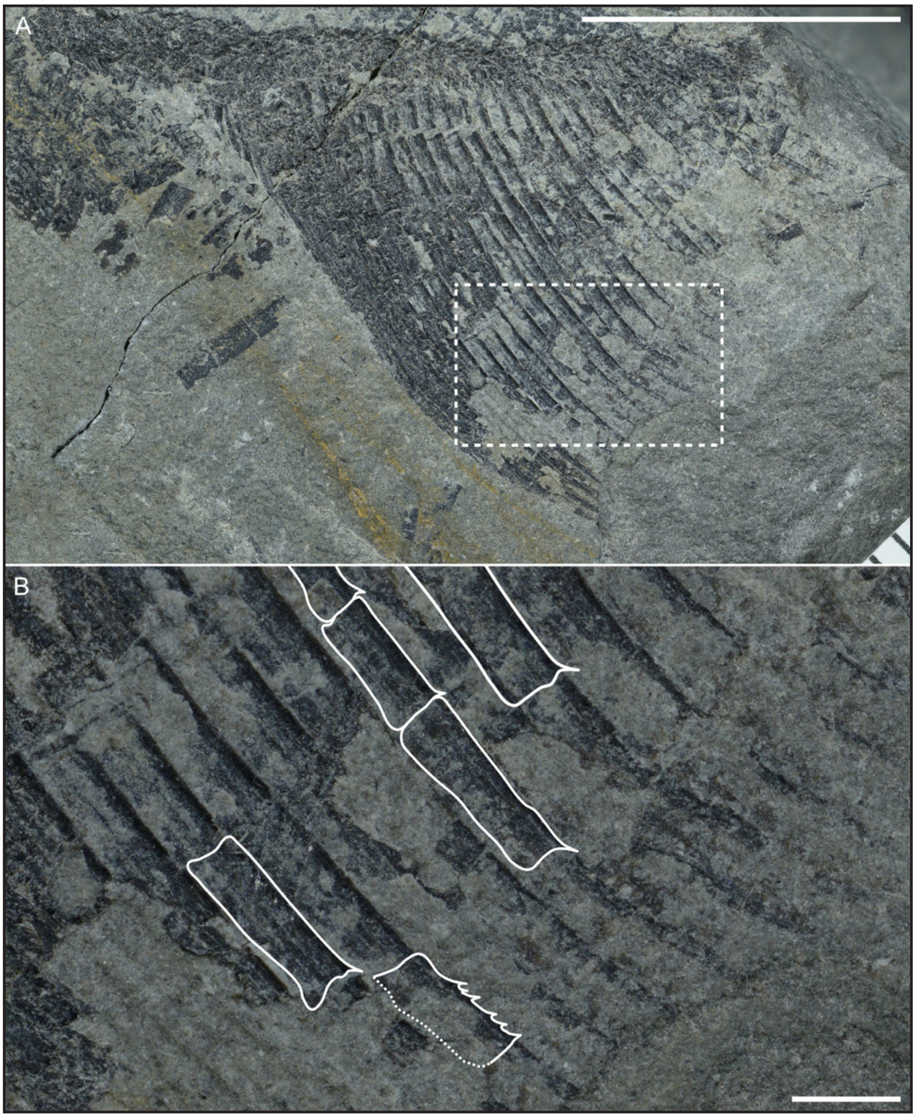
Generally, the scales are rhombic and of moderate size (mostly not exceeding 2 mm in both length and height) with a thick ganoine cover. All these scales show a peculiar ornamentation; the anterior portion of the scale is ornamented with two or more grooves that run parallel (rarely branching and bifurcating) rostro-caudally. The posterior, and sometimes the ventral, margin of each scale bears two to six thin and sharp, protruding ganoine spines (Fig. 8).

The scales of the ventral region, between the paired fins, are distinctly smaller, rectangular in shape, with a less ornamented outer surface.

The scales just above the bases of the pelvic and anal fins, and below the base of the dorsal fin, are small and difficult to distinguish from each other, exhibiting an irregular arrangement.

The lateral-line scales differ greatly from the other scales. These scales are deeper, roughly two times the depth of the adjacent scales, and shield-like, with a more developed anterior ornamentation, thus with a greater number of grooves, and

Fig. 7 - *Ostenolepis marianii* gen. n. sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Paratype, MSNM V554. (A) Left pelvic fin in medial view. (B) Detail of the distal fin rays with outline of the spined segments. Scale bar in A 10 mm, scale bar in B 1 mm.



posterior spines concentrated along the longitudinal axis. They also bear a single opening of the lateral line canal in the exposed field. Scales of this region tend to be slightly deeper than broad (Fig. 8).

The scales of the region F (Esin 1990), just above the paired fins, are characterized by a smaller size and a more prominent ornamentation representing a clearly recognizable feature.

The scale ornamentation and the serration of the posterior margins are absent around the region of the hinge line, which is quite sharp. The scales behind the hinge line, up to the tip of the tail, clearly differ from the others in being smaller, elongate, narrow and devoid of ornamentation. The course of the lateral line in the upper caudal lobe is not recognizable.

Four large elongate diagonal dorsal caudal fulcra are present in front of the caudal fin. They are followed by a series of more than 24 dorsal caudal fulcra, diminishing in size until the tip of the caudal lobe. At least three ventral fulcra border the ventral base of the caudal fin.

Remarks. The material described herein has been cursorily examined and tentatively identified a couple of times in the past four decades. Pinna (1985) reported the occurrence of a single palaeoniscimorph specimen pertaining to the genus *Pteroniscus* Berg, 1949, but he did not provide any inventory number, picture, or description of it; he also indicated the presence of rare specimens of *Cosmolepis* Egerton, 1853, even in this case, without any specific information. Duffin and Patterson (1993) recognized two taxa within the Osteno palaeoniscimorph remains. Based on their short descriptions, it is possible to hypothesize that MSNM V538 (as figured in Duffin & Patterson 1993; pp. 31) and MSNM V652 were compared, based on scale morphology, with the British Jurassic species *Cosmolepis ornatus*. The other two

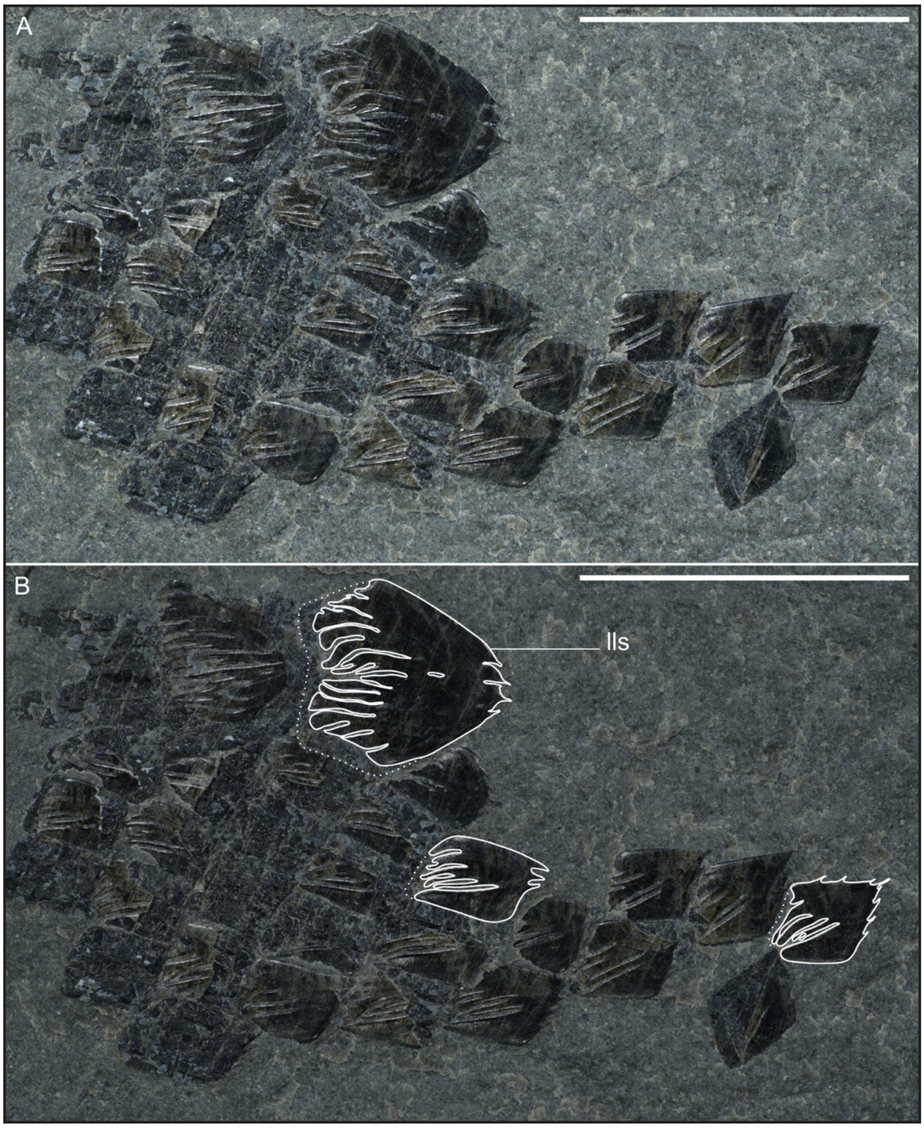


Fig. 8 - *Ostenolepis marianii* gen. n. sp. n.from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Paratype, MSNM V538. Anterior facing left. (A) Articulated mid-trunk scales (B) Drawing of a lateral line scale and two trunk scales on A. Scale bars 5 mm.

specimens, MSNM V617 and MSNM V554, were regarded as pertaining to a separate taxon based on their thinner and unornamented scales with serrated posterior margins, as well as to their overall body physiognomy, which are in some ways similar to those of the members of the family Coccolepididae, especially *Coccolepis liassica* Woodward, 1890, *Pteroniscus*, and *Indaginilepis* Schultze, 1970, evidencing some differences in the morphology and ornamentation of the scales.

The detailed morphological analysis of the fossils reported herein reveals that there is no substantial evidence that can justify the recognition of two separate palaeoniscimorph taxa. A closer examination of the scales, which is useful in discriminating specimens from the same locality following the method proposed by Schultze (1966), especially of the holotype, as well as of the anatomy of the paired fins clearly suggests that these four specimens can be unambiguously referred to the same taxon.

As far as the affinities of the palaeoniscimorphs from Osteno is concerned, the attribution to the Jurassic-Cretaceous Coccolepididae, can be excluded due to the lack of small and regularly spaced tubercles that ornate the dermal bones of the skull roof, lack of spines and/or tubercles on scales and fin rays, and lack of a massive supracleithrum larger than the cleithrum (see, e.g., López-Arbarello et al. 2013; López-Arbarello & Ebert 2021). However, it is interesting to note a certain degree of similarity in the skeletal preservation with many coccolepidids that are usually characterized by a poorly preserved head, most likely related to a convergent reduced degree of ossification (see, e.g., Cooper et al. 2024).

The assignment to other Jurassic palaeoniscimorph lineages can be easily ruled out as well as. For example, the Centrolepididae exhibits a complex dermal ornamentation formed by a thick

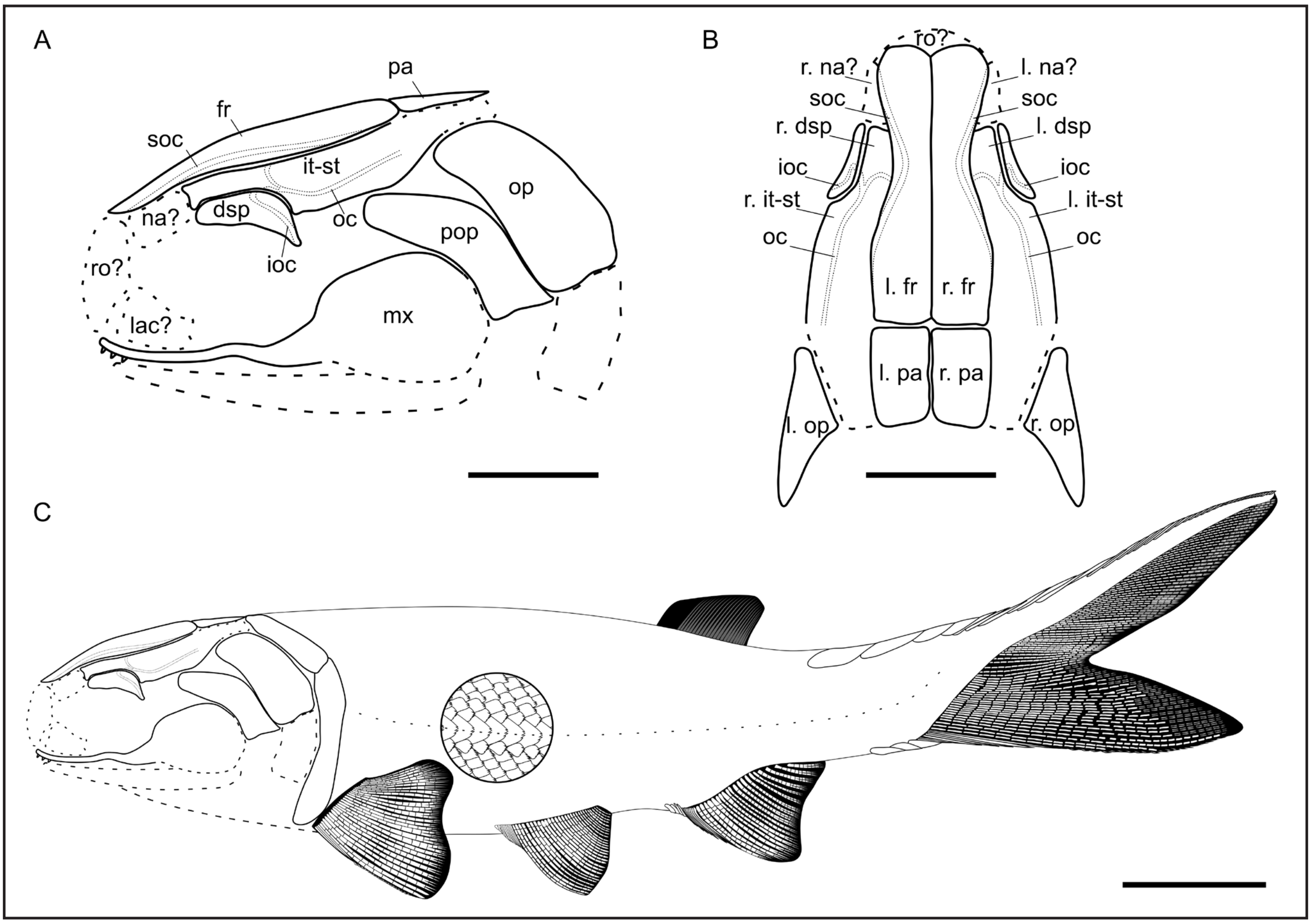


Fig. 9 - Interpretative reconstruction of *Ostenolepis marianii* gen. n. sp. n.from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Reconstruction based on the holotype, MSNM V617; skeletal elements in dashed lines inferred from *Pteroniscus turkestanensis* (Gorizdro-Kulczycka, 1926). (A) Skull skeleton in left lateral view. (B) Skull skeleton in dorsal view. (C) Full body reconstruction in left lateral view. Scale bars in A and B 5 mm, in C 10 mm.

enameloid layer – (Gardiner 1960), the Platysiagidae have a large and expanded preopercle, and a peculiar dermal ornamentation (Gardiner 1960), and the Ptycholepidae are characterized by unique ridged ganoine ornamentation, and a dentition formed by minute and closely spaced teeth (Woodward 1891; Gardiner 1960).

The affinity with *Coccolepis liassica* from the Lower Jurassic of southern England (see López-Arbarello et al. 2013), is not supported due to a specific set of anatomical features that have not been observed in the fossils described herein, especially the ornamentation of the skull roof, with tubercles and ridges, and the presence of cycloid scales with an anterior margin with concentric lines and a posterior margin with perpendicular rows of tubercles or ridges. Furthermore, *C. liassica* has basal fulcra exclusively in front of the dorsal fin and the dorsal lobe of the caudal fin, while the fossils described herein show basal fulcra also in front of the ventral lobe of the caudal fin.

Duffin & Patterson (1993) evidenced a similarity in the squamation pattern between the palaeoniscimorphs from Osteno and *Cosmolepis ornatus* Egerton 1858 from the Lower Jurassic of southern England. However, the longitudinal ornamentation of the scales of *C. ornatus* results from the presence of ganoine ridges emerging from the surface, and not from grooves like in the Osteno fossils; in addition, posterior spines have not been reported in *C. ornatus* (Egerton 1853; Woodward 1890; Gardiner 1967). The relative size of the paired fins is also different, with *C. ornatus* showing pectoral fins smaller than the pelvic ones, and the dorsal fin placed anterior to the anal fin origin. Finally, the intertemporo-supratemporal and the dermosphenotic are preceded anteriorly by two rows of supraorbitals in *C. ornatus*, thereby evidencing a completely different cranial architecture with respect to the fossils from Osteno.

Indaginilepis rhombifera from the Lower Cretaceous of northern Germany, seems to show similar cranial features and in body proportions and overall physiognomy. However, even in this case, there is clear morphological evidence that allows to exclude any possible attribution to this taxon, including the dorsal-fin insertion placed well anterior to that of the anal fin and the posterior placement of the anal fin leading to a remarkable reduction of the caudal peduncle , the complete lack of fringing fulcra, and the presence of serrated scales, without superficial ornamentation (Schultze 1970).

The palaeoniscimorph that shows the highest degree of similarity with the fossils from Osteno is *Pteroniscus turkestanensis* (Gorizdro-Kulczycka, 1926) from the Middle-Upper Jurassic freshwater deposits of the Karatau Range, Kazakhstan (Berg 1949). Despite being characterized by a considerably larger size (up to 25 cm in total length), *P. turkestanensis*, shows a similar cranial morphology with developed frontals separated from each other by a straight medial suture, small parietals, and elongated intertemporo-supratemporals; median and pelvic fins are similar in relative size and shape, and in having fringing fulcra associated with the anteriormost fin ray. The most striking similarity between *Ostenolepis marianii* and *P. turkestanensis* is the presence of the finely serrated posterior margins on the segments of the fin rays (Skrzycka 2014, p.8, fig. 8G); a similar condition, however, has been reported also in *Cteniolepidotrichia turfanensis* from the Cretaceous of China (Poplin & Su 1992) and in the Carboniferous "*Elonichthys" ypsilepis* from North America (e.g., Hay 1900; Bardack 1979).

The scales of *P. turkestanensis* are very similar to those of the fossils from Osteno described herein in showing longitudinal ornamentation in the anterior portion and spines along the posterior margin (Skrzycka 2014, fig. 8H, pp. 8); however, it should be emphasized that the longitudinal ornamentation in *P. turkestanensis* seems to be represented by emerging ridges and not by furrows; in addition, the lateral-line scales of *P. turkestanensis* do not show a specific morphology like that described above.

The differences between the fossils from Osteno and *P. turkestanensis*, however, are evident both in the structure of the skull, and in the proportion of the body. The presence intertemporo-supratemporal that articulates anterolaterally with the dermosphenotic, separating it from the frontal, and probably with the nasal anteriorly, is different from the condition typical of *P. turkestanensis* in which both the intertemporo-supratemporal and the dermosphenotic articulate with the frontal, and only the dermosphenotic articulates the nasal. The dorsal fin of the fossils from Osteno is placed more posteriorly along the trunk, terminating well posteriorly to the anal-fin insertion; conversely, the dorsal fin of in *P. turkestanensis* terminates at about the level of the anal-fin insertion. As a final note, in this comparative discussion it is also interesting to take into account the different paleobiotopes occupied by the fully marine fishes from Osteno and the lacustrine *P. turkestanensis*.

Overall, the palaeoniscimorph *Ostenolepis marianii* (Fig. 9) shows a generalized basal actinopterygian morphology, evidenced by a set of primitive characters, including a single median rostral, a crescent-shaped dermosphenotic (possibly contacting or situated close to the nasal), a large and anteriorly placed orbit, long jaws, a well-developed postorbital gape, a maxilla with an enlarged postorbital plate, basal fulcra present, fringing fulcra present, dorsal and ventral caudal fulcra, an epicercal tail with a prominent scaly dorsal lobe and rhomboid ganoid scales with peg and socket articulation. However, it also shows certain derived cranial features, such as a single intertemporo-supratemporal, and frontals much longer than the parietals (see Schultze et al. 2021). Although it is not possible to provide a substantial support for a family-level assignment of *Ostenolepis marianii*, the similarities with *P. turkestanensis* might be indicative of a possible relationship between these two taxa. However, the incompleteness of the available material does not allow a detailed comparative analysis between these two taxa for which much complete and better-preserved specimens would be desirable.

Subclass NEOPTERYGII Regan, 1923
Order **Dapediiformes** Thies & Waschkewitz, 2016
Family Dapediidae Lehman, 1966
Genus *Dapedium* Leach, 1822

***Dapedium* sp.**

Fig. 10

1984 "cf. *Dapedium*" Leach, 1822 - Schaeffer & Patterson, p. 73.
1985 "cf. *Dapedium*" Leach, 1822 - Pinna, p. 175.
1993 "*Dapedium*" Leach, 1822 - Duffin & Patterson, p. 20, 34, fig. 22 (MSNM V630).

	Length	Height	Caudal peduncle depth	Longest caudal-fin ray	Maximum caudal-fin width	Estimated standard length
MSNM V620-MSNM V630	55.4	69.1	29.6	46.1	68.0	~200

Tab. 2 - Measurements (in mm) of the specimens referred to *Dapedium* sp. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy.

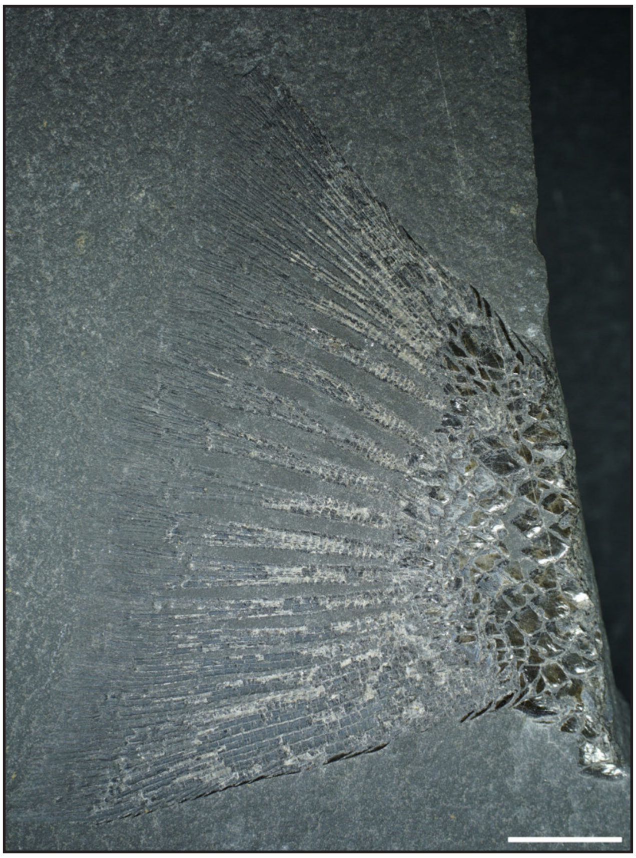


Fig. 10 - *Dapedium* sp. from the Sinemurian Osteno Lagerstätte from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V630, in right lateral view. Scale bar 10 mm.

1998 "*Dapedium* sp." Leach, 1822 - Duffin, p. 5.
2015 "*Dapedium* sp." Leach, 1822 - Garassino & Teruzzi, p. 46, fig. 71 (MSNM V630).
2021 "*Dapedium*" Leach, 1822 - Jaselli & Duffin, p. 165.

Material: MSNM V620 - MSNM V630, a largely incomplete articulated skeleton solely represented by the caudal fin and part of the caudal peduncle, in part and counterpart (Fig. 10).

Measurements: see Table 2.

Description. The endoskeletal caudal-fin support is not exposed due to the dense scale cover, thereby preventing any observation of the relationship between endoskeletal elements and caudal-fin rays.

The scales are thick and rhomboid in outline, with no peculiar ornamentations visible, and bearing serrations along their caudal margin (Fig. 10).

The ganoid scale coating continues towards the upper lobe of the caudal fin forming an upper scaled lobe that is relatively elongated distally, the same feature is not present on the ventral lobe.

The caudal fin consists of 25 rays, of which 23 are principal (sensu Schultze & Arratia 1989). A single dorsal and a single ventral procurrent rays are present. All the caudal-fin rays are multifurcated.

The dorsal and ventral edges of the outer caudal-fin rays are fringed with fulcra, with at least 26 fulcral scales present along the dorsal edge, and up to 29 fulcra along the ventral edge.

Remarks. This specimen was tentatively referred to the genus *Dapedium by* Duffin & Patterson (1993) due to the number and distribution of the caudal-fin rays and the sigmoid margin of the caudal peduncle, very similar to that of the *Dapedium* material from Lyme Regis, Dorset (UK).

As a matter of fact, the taxonomic relevance of these characters has not been confirmed since the diagnosis of *Dapedium* is almost exclusively based on cranial features and squamation patterns (Maxwell & Lòpez-Arbarello 2018).

The genus *Dapedium* was geographically restricted to Europe (Maxwell & Lòpez-Arbarello 2018), with a stratigraphic distribution that ranges from the late Norian (Late Triassic) (Tintori 1983) to the earliest Middle Jurassic (Earliest Aalenian; Maxwell & Lòpez-Arbarello 2018). The genus *Dapedium* currently includes 15 nominal species (Maxwell & Lòpez-Arbarello 2018), in large part described during the XIXth century based on incomplete material. For this reason, a broad scale taxonomic revision would be desirable in order to define the validity of the species included in the genus. Six of these species (*D. politum* -type species-, *D. colei*, *D. punctatum*, *D. granulatum*, *D. magnevillei*, and *D. radiatum*) are reported from the Lyme Regis locality (Forey et al. 2010).

The external morphology of MSNM V620-630 is comparable to the morphology of the caudal fin of *Dapedium* due to the presence of a dorsal lobe, the presence of fulcra at both fin margins, and the presence of thick caudal-fin rays, well separated from each other (Wenz 1967).

Thies & Waschkewitz (2016) regarded the number of caudal-fin rays as a potentially valuable taxonomic feature of the Toarcian *Dapedium pholitodum* from the Posidonia Shales. Wenz (1967), commenting on Woodward (1895), highlighted that *D. politum* bears 25 caudal-fin rays. As reported above, the incomplete specimen described herein also exhibits 25 caudal-fin rays.

The presence or absence of ornamentation on the trunk scale covering of *Dapedium* is a morphological character used to discriminate different species within the genus (Maxwell & Lòpez-Arbarello 2018). However, this is not applicable to MSNM V620-630, as the ornamentation is never present on the scales of the caudal peduncle (except in *D. magnevillei*). The Osteno specimen however shares the presence of serrations on the posterior margin of the scales of the caudal peduncle, character shared with the species *D. politum* (Maxwell & Lòpez-Arbarello 2018).

The dorsal development of the caudal peduncle into a scaled lobe, a primitive feature also found in some Ginglymodi (Patterson 1973), suggests the persistence of a partial external heterocercal caudal fin (Wenz 1967). Although this sigmoid profile of the posterior margin of the caudal peduncle does not represent a diagnostic character neither recognised nor explored in literature so far, it is interesting to note that it is consistent within the genus *Dapedium*.

Given the incompleteness of the single available specimen, and the lack of diagnostic features needed for a more precise identification, we assign this specimen to an undetermined species of the genus *Dapedium*.

Superdivision **Holostei** Müller, 1845
Division Halecomorphi Cope, 1872
Order **Ophiopsiformes** Ebert, 2018
Family Furidae Jordan, 1923

Genus *Furo* Gistel, 1848

Remarks. As pointed out by Ebert (2019), the diagnosis of the genus *Furo* is under discussion, and it can be provisionally defined by combination of several features. The halecomorph genus *Furo* was formerly known as *Eugnathus* Agassiz 1843 and subsequently renamed by Gistel (1848) since the genus name *Eugnathus* was previously used for an insect.

Furo sp.

Figs. 11-12

1984 "*Furo* (=*Eugnathus*)" Gistel, 1848 - Schaeffer & Patterson, p. 74.
1985 "*Furo*" Gistel, 1848 - Pinna, p. 175.
1993 "*Furo*" Gistel, 1848 - Duffin & Patterson, p. 20, 33, fig. 20 (MSNM V623).
1998 *Furo* sp. Gistel, 1848 - Duffin, p. 5.
2015 *Furo* sp. Gistel, 1848 - Garassino & Teruzzi, p. 47.
2021 "*Furo*" Gistel, 1848 - Jaselli & Duffin, p. 165.

Material: MSNM V623, an incomplete articulated skeleton represented by the head and anterior-most portion of the trunk, including a portion of the dorsal fin (Fig. 11A, 12); MSNM V634, an incomplete partially articulated skeleton represented by the head and anterior part of the trunk, including the pectoral fin (Fig. 11B); MSNM V642, a largely incomplete articulated skeleton represented by a pectoral fin and part of the adjacent scale covering, in part and counterpart (Fig 11C).

Description. The body is elongate (Fig. 11) with a narrow and rostrally tapered head, terminal mouth, strong dentition and ganoid scales with pectinated posterior margin, long paired fin and triangular dorsal fin; SL and other measurements cannot be determined due to the incompleteness of the available material. The preservation of the skull elements is not fully adequate, with the outer surface often deeply eroded, thereby preventing the recognition of the bone margins.

Rostral and nasals are not preserved in the available material, but the skull roof is exposed in both the MSNM V634 and MSNM V623 (Fig. 12). The skull roof is narrow, being at least three times as long as wide. Two contralateral paired and rostrocaudally elongate frontals are clearly recognizable, representing the largest bones of the skull roof; the suture between the two antimeres is straight for most of its length, becoming convolute caudally, near the articulation with the parietals; the posterior portion of both the frontals is ornamented with ganoine tubercules, visible in MSNM V623. Traces of the supraorbital canal are recognizable in MSNM V623; it runs through the frontals, passing above the dorsal border of the eye socket and then curving ventrally. The sclerotic ring ossifications cannot be recognized. at least two well developed supraorbitals are visible, of which the anterior one is stout, representing the better-preserved skeletal element in both the specimens with a preserved head. A narrow anterior infraorbital is visible, being longer than deep, and rostrally tapered; it articulates with the frontal and the maxilla, although its rostral and caudal portions are not clear due to inadequate

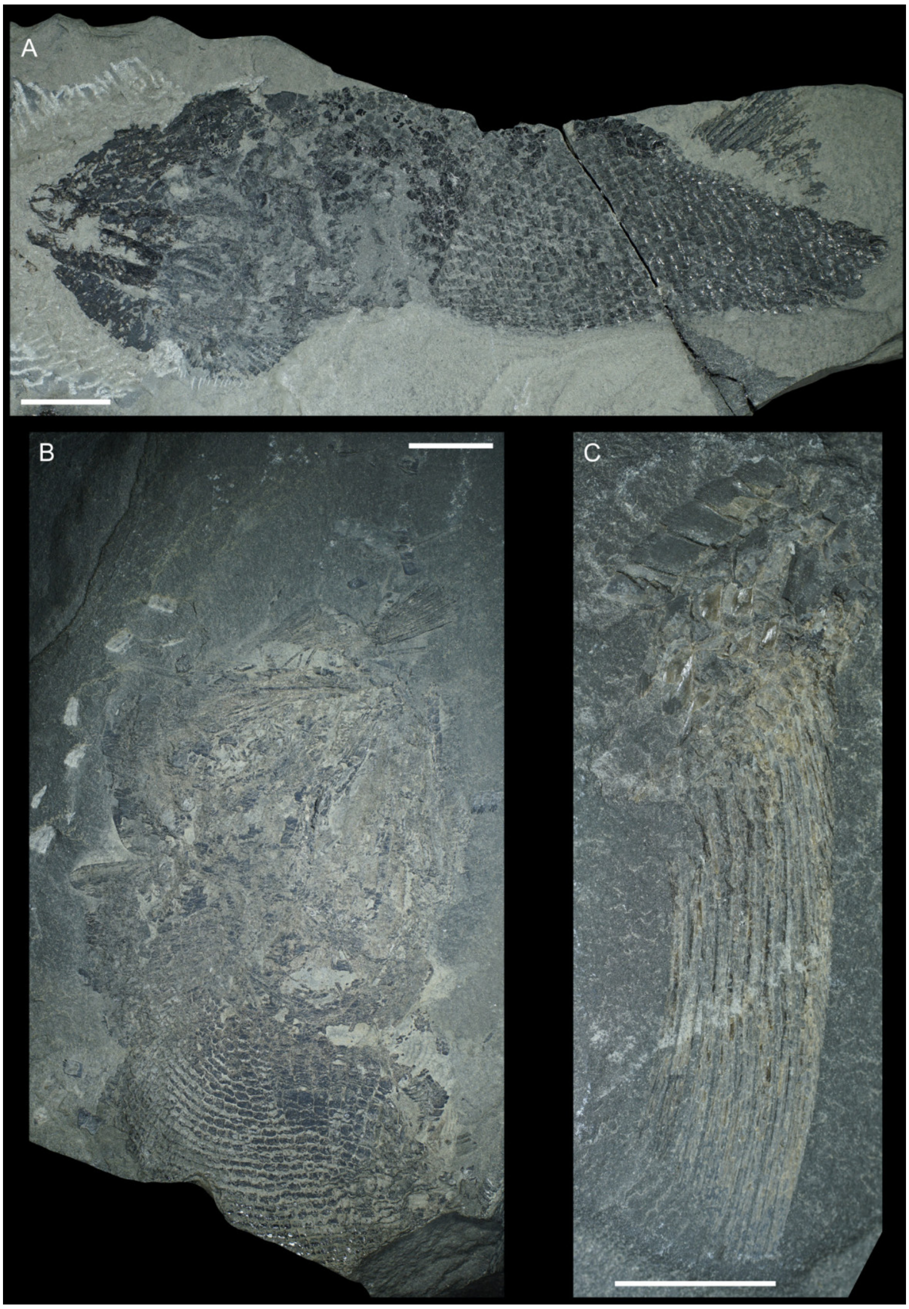


Fig. 11 - *Furo* sp. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. (A) MSNM V623, in left lateral view. (B) MSNM V634. (C) MSNM V642. Scale bars 10 mm.

preservation. A second infraorbital is feebly recognizable and seems to be larger than the anterior one. The cheek and the opercular regions of the head skeleton are not preserved, as well as the posterior portion of the skull roof.

What seems to be the preserved portion of a premaxilla can be observed rostrally to the dentary; it is a rectangular bony fragment, elongated rostrocaudally. The maxilla is not completely preserved, lacking its anteriormost and posteriormost portions; it is slender and gradually expanded distally; in MSNM V623, the maxilla bears six stout, conical and smooth teeth along its straight ventral border.

A feebly recognizable relatively narrow supramaxilla is present in MSNM V623 along the posterodorsal border of the maxilla.

The dentary is long, straight, and slender, becoming gradually deeper in its posterior region. In MSNM V623, at least two stout and conical teeth can be observed along its linear dorsal border; the dentary teeth seem to be slightly larger than the maxillary ones. A large gular is exposed in MSNM V623, being rostrally narrower and caudally expanded. Posteriorly to the gular there are at least twelve branchiostegal rays; the length of the branchiostegal rays increases from the first to the pos-

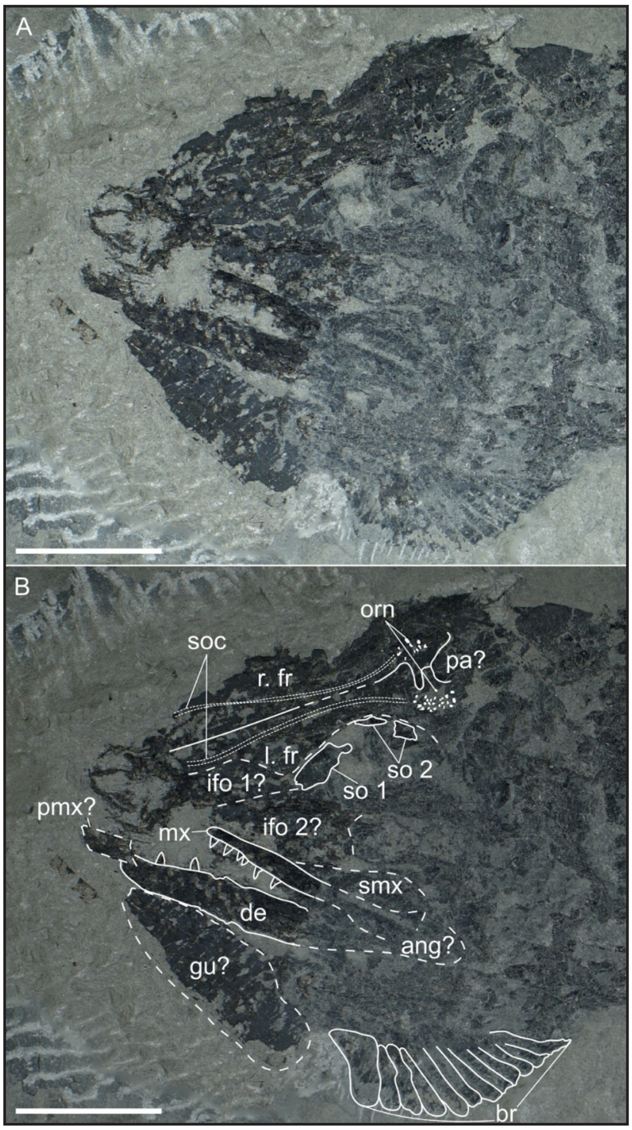


Fig. 12 - *Furo* sp. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V623. (A) Head skeleton in left lateral view. (B) Anatomical characters drawn over picture A. Scale bars 10 mm.

terior-most, with the last ray being 1.5 times longer than the first one, it being 4.2 mm in length; in addition, the width of the branchiostegal rays decreases rostro-caudally, with the last ray being 0.5 times as wide as the first one, it being 2.2 mm in width.

The dorsal fin is partially exposed in MSNM V623 and inserts after the 24th scale row and contains at least 14 rays whose proximal and distal portions are inadequately preserved.

An elongate and short based (roughly 10 mm in length) pectoral fin (the first and longest ray being 3.44 cm) can be observed in MSNM V642. This pectoral fin contains at least twelve rays, that branch at least two times in the distal half of the fin. Two basal fulcra precede the first ray; the anterior margin of the first ray bears not less than thirty tiny fringing fulcra.

The scales are rhombic and covered by ganoine. In the anterior-most area of the trunk, the exposed portion of the scales is higher than longer, as clearly recognizable in MSNM V634. The scales are smooth, and they bear a pectinated ornamentation on the posterior margin. Isolated scales exhibit a peg-and-socket articulation, with a well-developed peg. The ventral scales are not recognizable in the available specimens. Due to the incompleteness of the available specimens, the total number of scale rows remains elusive.

Remarks. A complete and detailed description of *Furo* is still not available, but it is generally reported as an elongated ganoine-scaled halecomorph fish characterized by a pointed snout and a terminal mouth, long pectoral fins, symmetrical caudal fin, fringing fulcra on all fins (small on the pectoral fins), and head length approximately equal to the body depth (Forey et al. 2010). A more precise set of morphological characters was summarized by Lane & Ebert (2012) and Ebert (2019), including two suborbitals, no sclerotic ring ossification, large teeth on the jaws, caudal-fin externally symmetrical, short dorsal fin with 13–16 dorsal-fin rays, dorsal fin insertion at the same level as the pelvic fin insertion (23rd-30th scale row from postcleithra to insertion), 23–27 principal caudal-fin rays, and scales of the stomach area and those located anterior to the caudal fin insertion longer than deep. *Furo* is characterised by smooth ganoid scales with a pectinated posterior margin ornamentation, quite different from that of the similar *Heterolepidotus*, which shows a serrated ornamentation (Forey et al. 2010). The attribution of the specimens described herein from the Sinemurian of Osteno to an indeterminate species of the genus *Furo* is therefore based on the overall configuration and morphological structure of the head and skull, especially the presence of two supraorbitals, of elongate jaws and of strong teeth, and morphology of fins and scales (e.g., Lane & Ebert 2012; Ebert 2019).

The genus *Furo* is currently regarded as restricted to Sinemurian of the United Kingdom (Blue Lias Formation and Charmouth Mudstone Formation, Black Ven Mudstone Member; Forey et al. 2010), with two species, *F. orthostomus* (Agassiz 1843; type species) and *F. philpotiae (*Agassiz 1839)

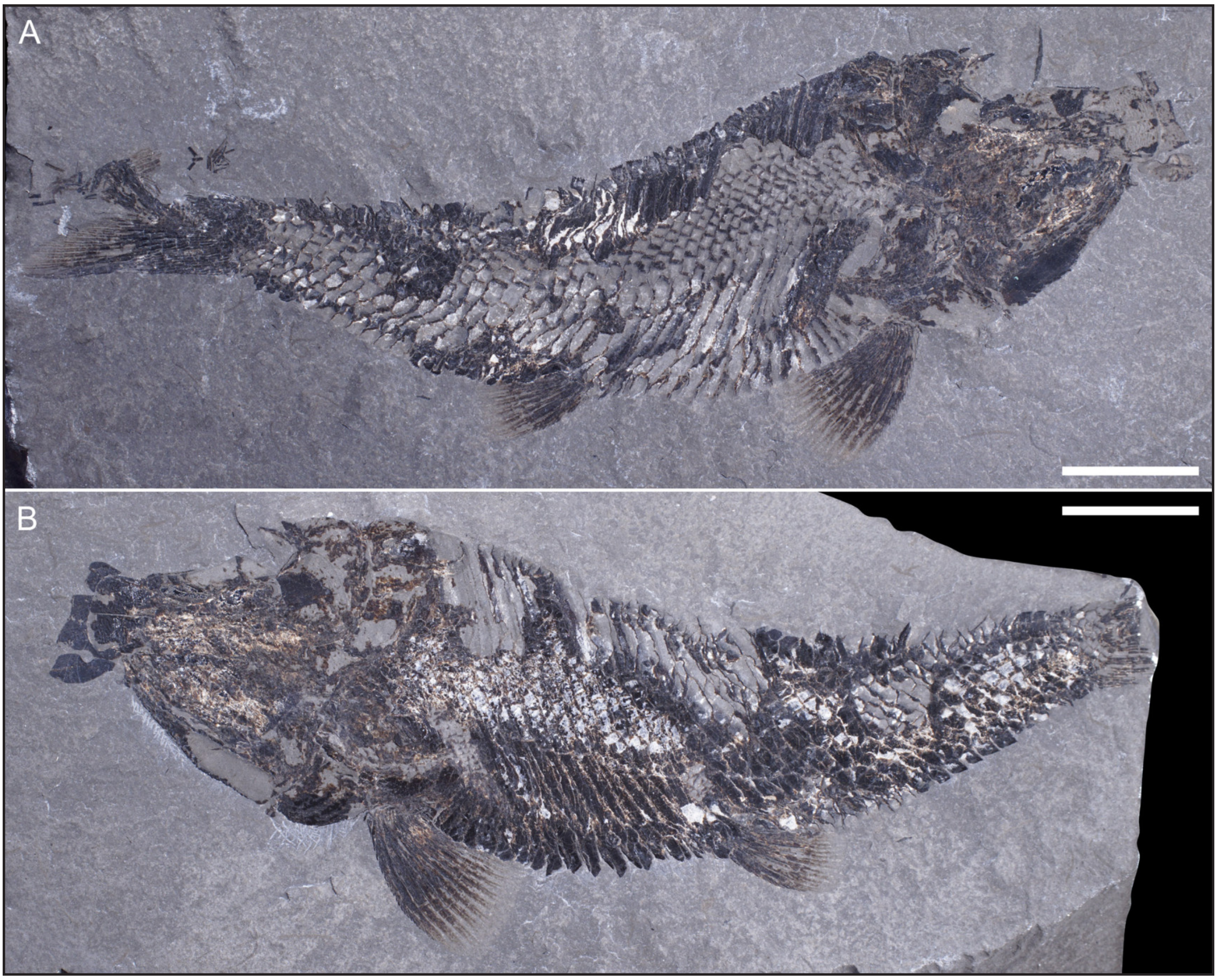


Fig. 13 - *Peripeltopleurus jurassicus* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Holotype, MSNM V659. (A) MSNM V659A, part. (B) MSNM V659b, counterpart. Scale bars 10 mm

(see Ebert 2019; López-Arbarello & Ebert 2024). The characters useful for the separation of these two species are related to the overall size, number of scale rows at the level of the pelvic fin, and number of dorsal- and caudal-fin rays. In addition, these two species can be separated based on the width of the skull roof (Forey et al. 2010), which is narrower in *F. orthostomus* (about three times as long as its maximum width), whereas *F. philpotiae* has a more laterally expanded skull roof (about twice as long as its maximum width).

Subclass NEOPTERYGII Regan, 1923
Order **Peltopleuriformes** Gardiner, 1967
Superfamily Thoracopteroidea Shen & Arratia, 2021
Family Wushaichthyidae Shen & Arratia, 2021

Peripeltopleurus Bürgin, 1992

Diagnosis: see Bürgin, 1992
Type species: *Peripeltopleurus vexillipinnis* Bürgin, 1992

Peripeltopleurus jurassicus sp. n.

Figs. 13 – 15

1984 "*Placopleurus*" Brough, 1939 - Schaeffer & Patterson, p. 73.
1985 "*Placopleurus*" Brough, 1939 - Pinna, p. 175.
1993 "cf. *Peripeltopleurus*" Bürgin, 1992 - Duffin & Patterson, p. 20, 32,33, fig. 18 (MSNM V659).
1998 "cf. *Peripeltopleurus*" Bürgin, 1992 - Duffin, p. 5.
2015 "cf. *Peripeltopleurus*" Bürgin, 1992 - Garassino & Teruzzi, p. 46.
2021 "*Peripeltopleurus*" Bürgin, 1992 - Jaselli & Duffin, p. 165.

Diagnosis: Large and deeply fusiform *Peripeltopleurus* with a broad skull roof; frontals heavily ornamented with ganoine bumps and short transversal crests that appear to be developed also in the posterior region of the skull roof; broad snout, due to the presence

	Standard length	Total length	Head length	Body depth	Longest pectoral-fin ray	Pectoral-fin width	Longest pelvic-fin ray	Pelvic-fin width	Longest caudal-fin ray
MSNM V659	77.5	89.1	~30	~17	16.0	10.0	11.0	6.0	20.0

Tab. 3 - Measurements (in mm) of the holotype (MSNM V659) of *Peripeltopleurus jurassicus* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy.

of an expanded rostral and lacking a ventral protrusion; remarkably developed ventral lobe of the caudal fin.

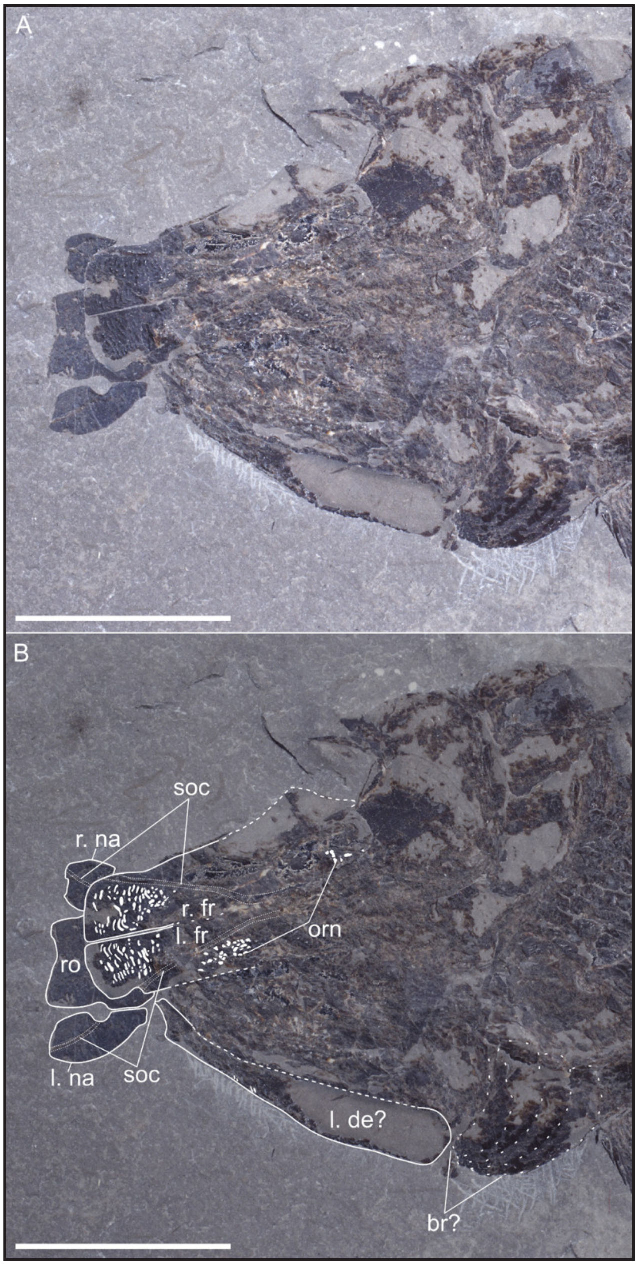


Fig. 14 - *Peripeltopleurus jurassicus* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Holotype, MSNM V659B. (A) Head skeleton in dorsal view. (B) Anatomical characters drawn over picture A. Scale bars 10 mm.

Etymology: The specific epithet highlights the peculiarity of this taxon, it being the first described peltopleuriform recovered after the Triassic-Jurassic boundary.

Holotype: MSNM V659: Partially complete articulated skeleton, lacking the dorsal and anal fins, dorso-ventrally exposed, in part and counterpart (Fig. 13, 14).

Measurements: see Table 3.

Description. The single available specimen is small-sized (estimated standard length of 77.5 mm, total length of 89.1 mm) and shows a fusiform body (Fig. 13). The head occupies one fourth of the standard length; the body depth cannot be determined due to the dorso-ventral preservation. The surface of the skull roof is covered with small tubercules and ridges of ganoine. The paired fins are large. The pectoral fin almost doubles the pelvic fin in size, representing one seventh of the total body length. A single row of lateral trunk scales is greatly deepened dorso-ventrally.

The rostral is broad anteriorly, showing a subrectangular outline, becoming expanded posteriorly with two lateral extensions that make it as wide as the paired frontals that articulate with it. The rostral also articulates laterally with the nasals (Fig. 14). A distinct notch for the anterior nostril can be observed along the lateral margins.

Two nasals are recognizable, of which the left one is completely exposed, while the right one is partially covered by the adjacent frontal. The left nasal is elongate and drop shaped, becoming narrow posteriorly. The medial margin of each nasal, articulates for most of its length with the rostral and bears a distinct notch for the anterior nostril at its midlength. The lateral margin of each nasal is convex. No posterior nostril notch is visible. The supraorbital canal is recognizable in both the nasals, being represented by a concave canal running from the rostro-lateral edge to the nostril notch. The ornamentation of the snout region cannot be recognized due to inadequate preservation.

Only the anterior portion of the paired frontals is well-preserved and clearly recognizable. The

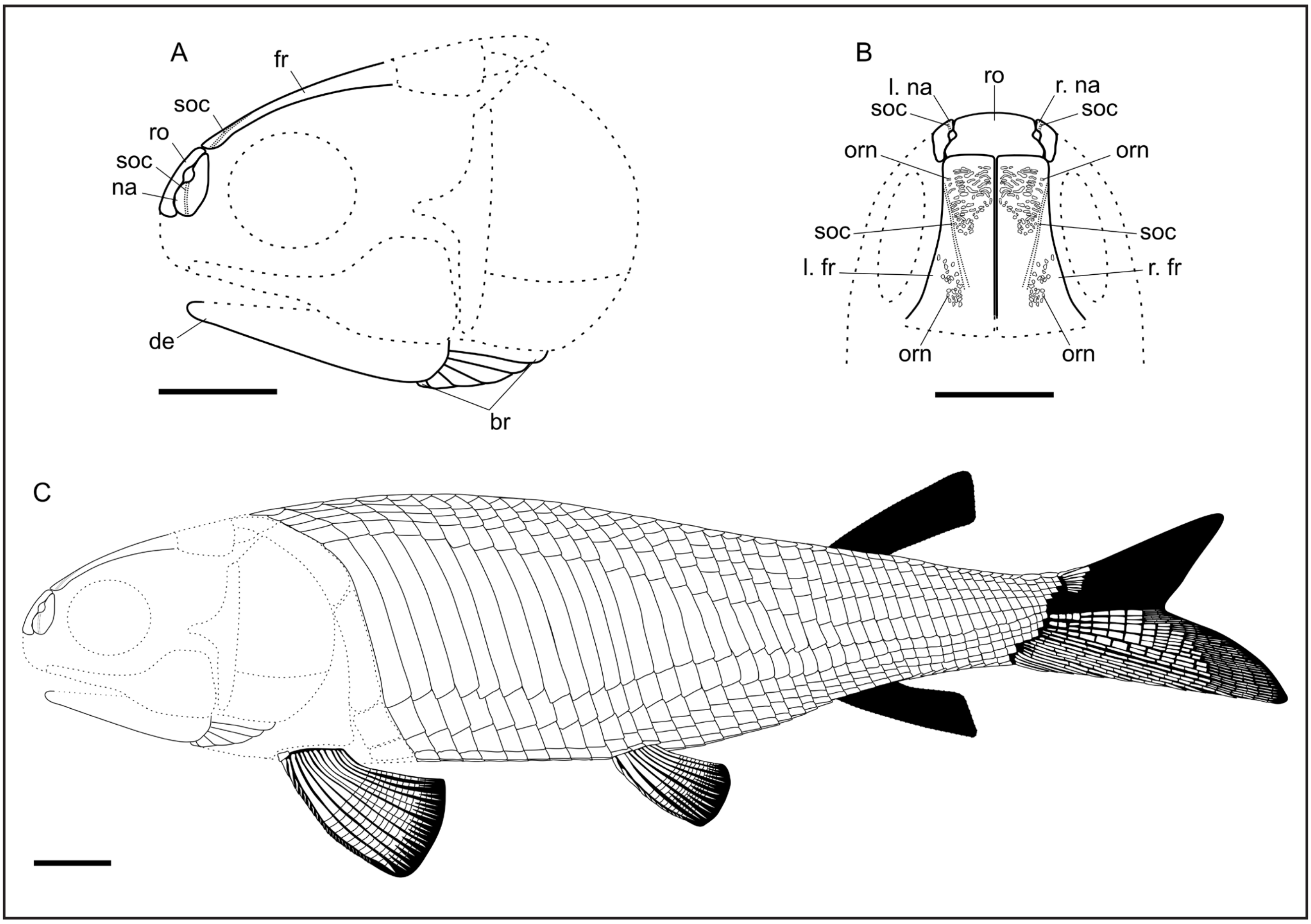


Fig. 15 - Interpretative reconstruction of *Peripeltopleurus jurassicus* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Reconstruction based on the holotype, MSNM V659; skeletal elements in dashed lines inferred from *P. vexillipinnis* and *P. hypsisomus* (Bürgin 1992). (A) Skull skeleton in left lateral view. (B) Skull skeleton in dorsal view. (C) Full body reconstruction in left lateral view. Scale bars 10 mm.

medial articulation between the two frontals is straight, and both the elements anteriorly articulate anteriorly with the rostral. Each frontal is quadrangular, elongate and posteriorly expanded, with straight anterior margin and gently curved lateral margins. The supraorbital sensory canal is recognizable in the anterior half of the frontal starting from its antero-lateral corner and extending backward towards the dorsal midline; it extends anteriorly into the nasal. The posterior portion of the skull roof is poorly preserved, making difficult to recognize the outline of the skeletal elements.

The frontals are heavily ornamented with ganoine bumps and short, mostly transversal, crests; this ornamentation is visible also in some other posterior regions of the skull roof, although it is impossible to identify to which element it is related due to the inadequate preservation of this portion of the skull roof; the lateral portion of the frontals is ornamented with large, rounded and well-spaced ganoine tubercules.

What is interpreted herein as the dentary is preserved in both part and counterpart; the anteriormost portion is preserved in lateral view in MSNM V659B and the posteriormost portion is preserved in medial view in MSNM V659A. The dentary appears to be elongate and wedge-shaped, narrowed anteriorly and expanded posteriorly, with a length of 13.5 mm. Longitudinal ganoine ridges can be recognize ventrally along the outer surface of the dentary, in MSNM V659B.

Only a small portion of the ventral part of the head skeleton is recognizable, being represented by at least three possible broad branchiostegal rays placed posteriorly to the dentary and anteriorly to the pectoral fin.

The caudal fin is represented by the proximal portion of the fin and the hypaxial lobe. The caudal peduncle is moderately large, being also characterized by a slight protrusion of the scale covering to the epaxial lobe. The caudal fin likely was deeply forked in origin; the hypaxial lobe seems to be slightly broader and longer than the epaxial one, suggesting a possible hypocercal outline. The caudal-fin rays are segmented and multifurcated distally; the overall number of caudal-fin rays cannot be properly determined due to inadequate preservation, and the hypaxial lobe seems to be contain at least 16 rays (four procurrent rays plus 12 principal rays). Fringing and basal fulcra are not present. Of the epaxial lobe, despite its incompleteness, at least two poorly preserved basal fulcra and eight rays seem to be present. Two well-developed scutes precede the basal fulcra. The scale cover prevents the observation of the endoskeleton of the caudal fin.

The dorsal and anal fins and their endoskeletal supports are not preserved.

The morphology of the pectoral girdle is only scarcely recognizable, solely represented by the ventral portion of the cleithrum. The rest of the girdle is in large part hidden by the thick scale cover. The left pectoral fin is recognizable, being rather long and enlarged presenting 11 flattened, broad, and elongated fin rays which are segmented and distally bifurcated. Three basal fulcra are attached to the base of the anteriormost pectoral-fin ray and are followed by 22 fringing fulcra that are associated with the leading edge of the ray.

The pelvic girdle cannot be observed due to the scale covering. The left pelvic fin is well developed, almost half the size of the pectoral fin; it originates at the level of the 16th to 18th vertical scale rows. The fin has a single anterior basal fulcrum, followed by eight flattened, broad, elongated, segmented and distally bifurcated fin rays. The leading edge is associated with ten fringing fulcra.

Thick ganoid scales of lepisosteid type cover the entire body. These are generally rhomboid in outline with no peculiar ornamentation, and they cover the whole trunk and caudal peduncle. The squamation consists of several scale rows, whose precise number (between 35 and 40 vertical rows) is difficult to determine. The anterior part of the body flanks, are covered by a horizontal series of at least 23 greatly deepened scales; the deepest scales are the anterior 12, with a maximum depth/width ratio of 8:1; by the 13th row backward the depth of these scales decreases abruptly, until the 22nd to 23rd vertical row, where their shape and size are identical to those of the adjacent scales. The horizontal row ventral to the deepened scale row also consists of slightly deepened scales. Some scales, placed along the body margins of the specimen, are feebly ornamented with serrations, especially along their posterior margin; these ornamented scales are concentrated postero-ventrally to the left pelvic fin and dorsally to the row of deepened scales, along most of the length of the body, excluding the caudal peduncle. The scales of the caudal peduncle are rhomboid with regular size and shape. Scales on the hinge line are relatively smaller and bear no ornamentation.

Remarks. Pinna (1985) reported the occurrence of a single specimen belonging to the genus *Placopleurus* Brough, 1939, in the Osteno assemblage, without any mention to its catalogue number or the reasons for such a taxonomic assignment. Most likely, the specimen referred to *Placopleurus* is MSNM V659, and this attribution was related to the presence of the deepened trunk scales, typical of this genus. However, the assignment to *Placopleurus* is certainly erroneous, due to the size of MSNM V659 (*Placopleurus* does not exceed 55 mm in standard length) and the lack of a specific series of morphological characters including very small pelvic fins, large basal fulcra on the dorsal lobe of the caudal fin, and absence of a vertical slit in the posterior part of the deepened lateral trunk scales and of at least two vertical thin ridges along the anterior margin of each scale (Tintori et al. 2016).

Duffin & Patterson (1993) referred the specimen described herein to the family Peltopleuridae, and tentatively assigned it to the genus *Peripeltopleurus* Bürgin, 1992, due to the presence of deepened trunk scales and the relative size of the pectoral fins that are consistent with those of the genus created by Bürgin (1992) from the Middle Triassic of Northern Italy and Switzerland.

However, these morphological features make it difficult to unambiguously support the placement of MSNM V659 to the genus *Peripeltopleurus* or even to the order Peltopleuriformes. Some of the most salient peltopleuriform apomorphies are related to skeletal structures not preserved in MSNM V659, including the cheek area (Xu & Ma 2016; Xu et al. 2018), pectoral girdle (Xu et al. 2018) and medial fins (Gardiner 1967; Bürgin 1990, 1992; Lombardo 1999; Tintori et al. 2012; Xu et al. 2015; Xu & Ma 2016).

The recognizable characters, such as those referred to the snout, extent of the paired fins, development of the trunk squamation, and possible hypocercal tail, do not offer substantial evidence to formulate a conclusive systematic definition. For these reasons, a phylogenetic analysis (se "Discussion" section below) has been carried out to conclusively demonstrate the systematic relationships of this fossil.

Infraclass TELEOSTEI Müller, 1845, sensu Arratia 1999
Order **Dorsetichthyiformes** Nelson, Grande & Wilson, 2016
Family Dorsetichthyidae Nelson, Grande & Wilson, 2016
Genus *Dorsetichthys* Arratia, 2013

Dorsetichthys bechei (Agassiz, 1837)

Figs. 16-20

1984 "*Pholidophorus*" (Agassiz, 1837) - Schaeffer & Patterson, p. 73.
1985 "*Pholidophorus*" (Agassiz, 1837) - Pinna, p. 175.
1993 *Pholidophorus bechei* (Agassiz, 1837) - Duffin & Patterson, p. 20, 35-37, fig. 24, 25 (MSNM V409 - MSNM V594).
1998 *Pholidophorus* cf. *bechei* (Agassiz, 1837) - Duffin, p. 5.
2015 *Pholidophorus bechei* (Agassiz, 1837) - Garassino & Teruzzi, p. 47, fig. 73, 74, 75 (MSNM V664 – MSNM V629 – MSNM V556)

Emended diagnosis (emended from Patterson 1968; Arratia 2013 and Atterby et al. 2024): Elongated teleost of about 200 mm total length; bones and scales covered with a thin layer of ganoine; frontals acutely sharp anteriorly and sutured with rostral by a narrow contact; partially fused skull roof plate; braincase elements fuse so that there are no sutures, thin lateral strut extending across the subtemporal fossa of the braincase; five infraorbital bones between the antorbital and dermosphenotic, one or two suborbital bones, two or three supraorbital bones; supraorbital and otic canals with branched tubules; maxilla heavily ornamented with longitudinal ridges of ganoine; preopercle expanded anteroventrally and with a deeply notched posterior margin; preopercular sensory canal with about 20 long tubules opening on the ventral and posteroventral borders of the preopercle; chordacentral type of vertebrae; diplospondyly in the caudal region; epipleural intermuscular bones absent; posttemporal broad, with no distinct dorsal process to articulate with cranium; notochord uncalcified behind the first ural centrum; first and second ural neural arches unmodified; four epurals; last four or five posterior ural neural arches modified as uroneurals; tendon-bone 'urodermals' absent; hemi-heterocercal caudal fin with twenty-two to twenty-four principal caudal-fin rays; the uppermost hypaxial fin-ray reduced: ganoid scales of lepisosteoid type, with smooth surface and posterior margin; elongated pelvic axillary process.

Type species: *Pholidophorus bechei* (Agassiz, 1837)

Material: MSNM V409-MSNM V638: nearly complete articulated skeleton, in part and counterpart (Fig. 16). MSNM V547-575: patch of articulated scales. MSNM V558: two isolated head skeletons, one of which with associated pectoral girdle and fin (Fig. 17, 18). MSNM V572: poorly preserved head skeleton with associated pectoral girdle and fin. MSNM V573: isolated caudal fin and caudal peduncle. MSNM V595: incomplete head skeleton with preserved opercular and infraorbital series. MSNM V604: patch of articulated scales. MSNM V629: nearly complete articulated skeleton. MSNM V633: incomplete articulated skeleton comprising the posterior region of the head and the anterior-most portion of the trunk (Fig. 19). MSNM V650: isolated head skeleton, in part and counterpart. MSNM V654: patch of articulated scales. MSNM V658: largely incomplete articulated skeleton comprising the head and the anterior-most portion of the trunk. MSNM V662: partially complete articulated skeleton comprising the pectoral girdle, most of the trunk and a portion of the caudal fin. MSNM V664: nearly complete articulated skeleton, in part and counterpart.

Measurements: see Table 4.

Description. Moderately small species, with the largest available specimen of the assemblage described herein, MSNM V409-MSNM V638 (Fig. 16), reaching a total length of 167.7 mm and a SL of 146.9 mm. The head is almost triangular in outline (up to 43 mm in length), representing a third of SL, being slightly greater than the maximum depth of the body (38 mm) measured in the predorsal region. The bones of the skull are covered with a thin layer of ganoin and are finely ornamented, with the ornamentation being more pronounced in larger specimens. The caudal peduncle is narrower than the trunk. The pectoral fins are located immediately posterior to the skull, ventrally and closer to the ventral midline of the body. The dorsal and pelvic fins originate at the midlength of the trunk, the anal fin is posterior to the base of the dorsal fin. All the fins are comparatively small, with well-developed rays, and fringing fulcra are associated with the leading

	Standard length (mm)	Total length (mm)	Head length	Head depth	Pre-orbital length	Orbital diameter	Body depth	Pre-dorsal length	Pre-anal length	Pre-pelvic length	Longest pectoral-fin ray	Longest pelvic-fin ray	Longest dorsal-fin ray	Longest anal-fin ray	Longest caudal-fin ray
MSNM V409-V638	146.9	167.7	24.1	18.4	05.1	6.1	25.4	52.2	?	58.9	?	?	?	?	19.8
MSNM V664	120.8	139.1	23.4	?	?	?	?	?	?	?	?	?	?	?	15.5
MSNM V658	106.8	119.1	27.2	19.0	?	8.9	20.8	?	?	?	?	?	?	?	17.8

Tab. 4 - Measurements (as % SL) of the specimens referred to *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy.

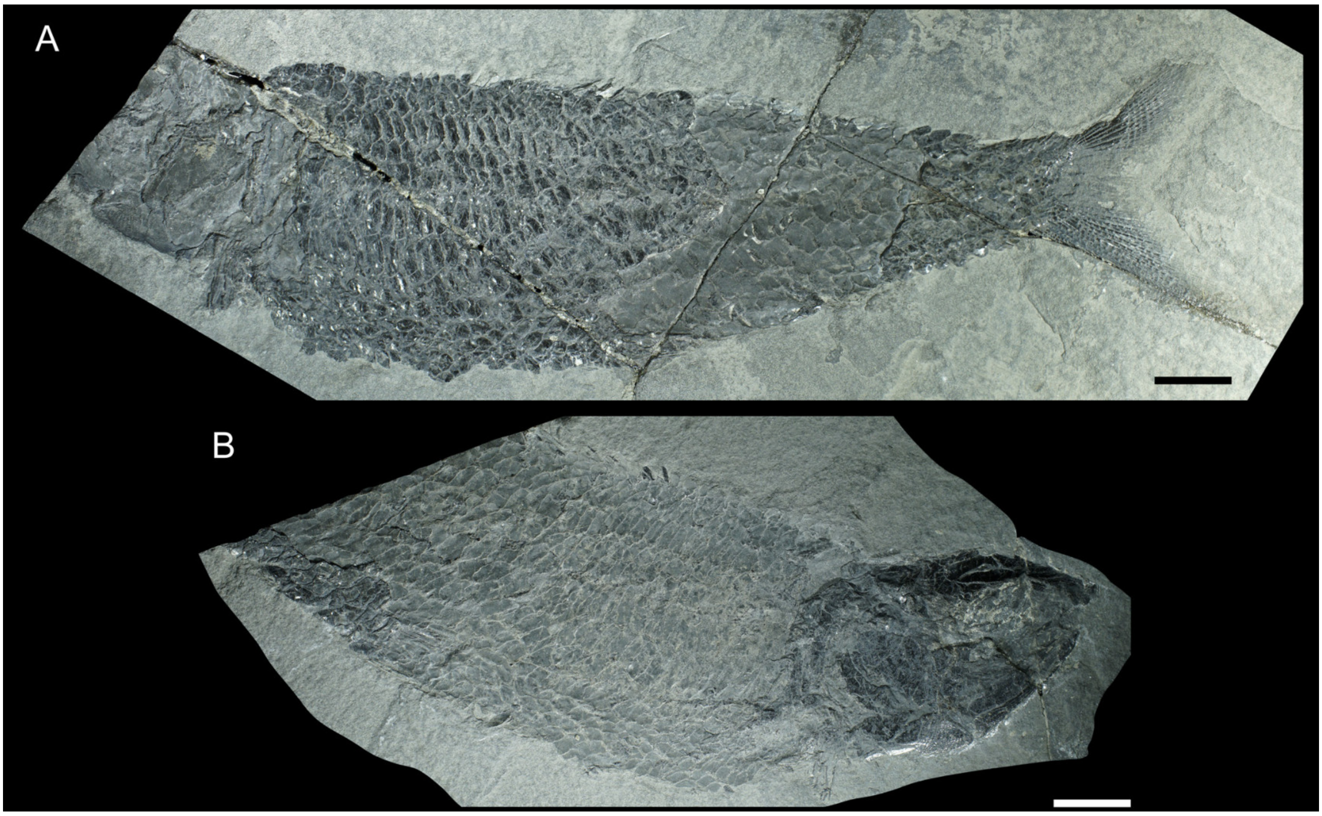


Fig. 16 - *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte. (A) MSNM V409, part. (B) MSNM V638, counterpart. Scale bars 10 mm.

margin of the fins. The caudal fin is hemi-heterocercal, with numerous epaxial and hypaxial fringing fulcra. The ganoid scales are of lepisosteoid type, with unornamented surface and smooth posterior margin, and cover the entire body, preventing the description of the internal skeletal structure.

The anterior portion of the cranial roof is never completely preserved in the available specimens. Only in MSNM V638, a medial and impaired element is visible, and interpreted herein as the rostral; only its ventral and posterior margins are preserved; it appears to be thick and articulates posteriorly with the nasals and the frontals.

The nasal is partially exposed in MSNM V409 and MSNM V664, where it is an elongate and subrectangular element with unclear anterior and posterior margins; each nasal is ornamented with ridges and ganoine tubercles and articulates medially with the frontal, anteriorly with the rostral and posteriorly with the anterior supraorbital. In MSNM V638 it is possible to observe a circular opening completely surrounded by ossified tissue in the ventrolateral portion of the nasal, possibly representing the posterior nostril.

The frontals are the largest bones of the skull roof, almost triangular in outline. The anterior portion of the frontals is well preserved in MSNM V650, MSNM V638 and MSNM V664, in which it possible to observe their very narrow and stout anterior ends that separate the two contralateral nasals. Posteriorly the frontals are considerably expanded, reaching their maximum lateral extension in the postorbital region; the posteriormost portion of the frontals is never well-preserved and their posterior margins difficult to recognize. The whole outer surface of the frontals is covered by ganoine with marked ornamentation, forming radiating ridges of tuberculations in the anterior half of the bone. The suture between the two frontals is generally straight in the anterior area, while the posterior part is poorly preserved but seems to be characterised by irregular sinuosity. The frontals are furrowed by the supraorbital sensory canal, but its complete path is difficult to observe due to inadequate preservation; in MSNM V558, there are traces of the supraorbital sensory canal that runs longitudinally in the pre-orbital region, curving ventrally at midlength of the orbit, and dorsally before the posterior end of

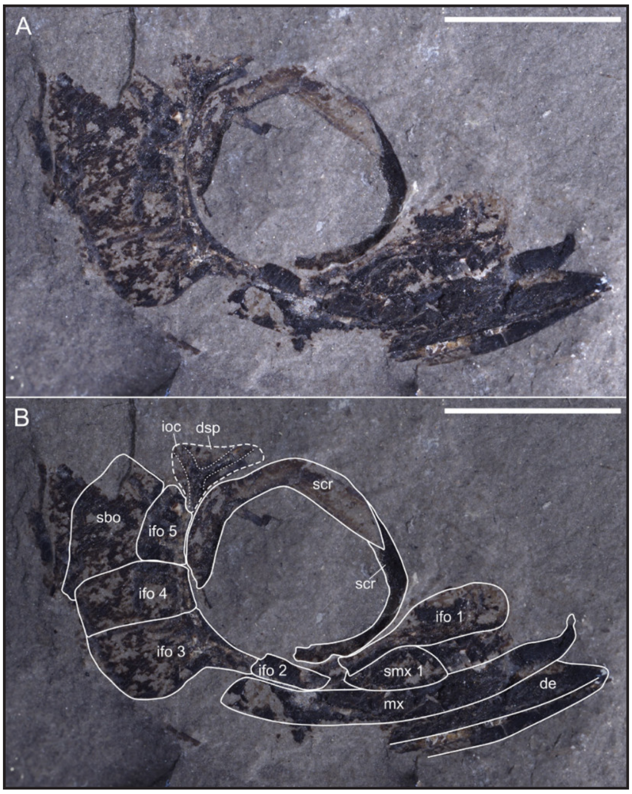


Fig. 17 - *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V588 (A) Head skeleton in right lateral view. (B) Anatomical characters drawn over picture A. Scale bars 5 mm.

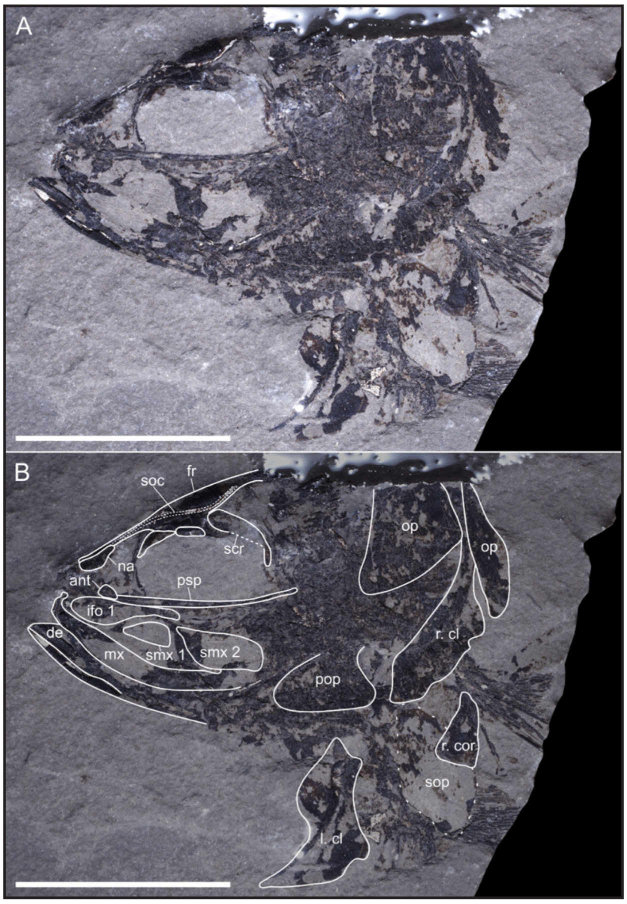


Fig. 18 - *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V588 (A) Head skeleton in left lateral view. (B) Anatomical characters drawn over picture A. Scale bars 10 mm.

the orbit. The elongate and slender parasphenoid is partially exposed in the orbital region.

At least two supraorbitals are present. The first supraorbital tapers anteriorly and articulates with the nasal anteriorly, and with the frontal medially. The second supraorbital is just behind to the first one being much elongate and articulating medially with the frontal. In MSNM V664 an additional supraorbital element is partially recognizable and possibly represents a third supraorbital. All the supraorbitals are heavily ornamented with tuberculations and ganoine ridges.

The elements of the infraorbital series are recognizable in MSNM V558 (Fig. 17), that also shows a small, squared antorbital. The first infraorbital is elongate and more expanded in the anterior region, with smooth margins. The second infraorbital is the smallest element of the series, being elongate and rectangular in outline. The third infraorbital is the largest element of the series being well exposed in the posteroventral corner of the orbit. It is posteriorly enlarged into a sub-rectangular shape characterized by a concave anterodorsal margin and an anterior protrusion for the articulation with the second infraorbital. The fourth and fifth infraorbitals are preserved only in MSNM V588; these are subquadrangular elements of similar size that overlap a posteriorly placed large suborbital subrectangular in outline. At the postero-dorsal margin of the orbit, dorsal to the fifth infraorbital; it is recognizable a triangular dermosphenotic presenting the bifurcation of the infraorbital canal (Fig. 17).

The sclerotic ring is visible in MSNM V558 in which it is formed by two poorly preserved ossicles.

The premaxilla is not clearly recognizable in the available material, whereas the gently curved and elongate maxilla is commonly well-preserved in the examined specimens, especially its narrowed and proximally pointed anterior portion. The outer surface of the maxilla is ornamented with longitudinal parallel ridges, which are much evident in larger specimens.

Two thin supramaxillae cover most of the dorsal margin of the maxilla (Fig. 18). The anterior supramaxilla is small and almost triangular in shape. The posterior supramaxilla is large two times as the anterior one and has triangular shape due to its pointed posterior end. Both the supramaxillae are ornamented with ganoine tubercules and striations.

The lower jaw is clearly exposed in the majority of the available specimens, even if partially obscured by the maxillary. Overall, the lower jaw is gently curved. The dentary forms most of the lower jaw and shows a prominent ridge on its lateral surface that separate the upper dental from the ventral splenial parts (e.g., Nybelin 1966, Atterby et al. 2024); the outer surface of the splenial part is feebly ornamented with delicate striae and rugosities, while that of the dental part is smooth. The dorsal margin and the posterior portions of the lower jaw are not adequately preserved in the examined specimens.

The bones of the palatoquadrate and suspensorium are obscured by those of the circumorbital series and, therefore, cannot be described.

The bones of the opercular series are located posterior to the distal portion of the skull roof and are covered by a relatively thick and smooth ganoine layer. The preopercle is usually recognizable in the available material. The vertical arm gradually expands ventrally at the convergence with the horizontal arm; the postero-ventral corned is rounded and just above to it, the posterior margin of the preopercle is notched while the ventral margin is linear. The preopercular sensory canal follows the curved anterior margin of the bone; posterior to the canal, there are more than ten slightly curved tubules, often due to a thickening of the ganoine cover, which seem to contact the posterior margin, being densely arranged only in the horizontal arm. The opercle is triangular, with a slightly curved dorsal margin. The subopercle is deeper than the opercle and placed immediately ventral to it. Only the posterior portion of the interopercle is visible, located posterior to the postero-ventral corner of the preopercle; its postero-ventral margin is gently rounded.

The caudal fin is hemi-heterocercal and clearly visible in MSNM V409 and MSNM V658A. Overall, it consists of 22 principal -fin rays, with the outermost ray in each lobe unbranched and ten segmented rays in each lobe. The seven upper principal rays are deeply cleft basally and they possess a slender unsegmented proximal portion. The first lower principal -ray is preceded by six unbranched but segmented rays, the first of which is associated with fringing fulcra. In MSNM V658A there is the impression of a very small, single-segmented ray that may represent the uppermost epaxial ray, as well as of six segmented basal fulcra that are associated with the outer margin of this ray, and pass distally to fringing fulcra; in MSNM V629, anterior to the dorsal basal fulcra, there are two unpaired structures, a shield-shaped median scale and, anteriorly to it, an elongate scale with a long tapering anterior process.

The dorsal fin is partially articulated in MSNM V629, formed by 11 or 12 rays, the first of which is associated with well-developed fringing fulcra.

The anal fin is always inadequately preserved.

The pectoral girdle is preserved in MSNM V558, MSNM V572, MSNM V658B, and MSNM V664. Although its connection with the posterior elements of the skull roof is not visible, a subrectangular element, deeper than long can be recognized dorsal to cleithrum and possibly represents the supracleithrum. The extrascapular cannot be recognized in any of the examined specimens. The cleithrum is crescent-shaped, with a vertical arm longer than the horizontal one. The postero-ventral region of the cleithrum is broadly expanded, ending into a ventrally directed pointed tip. The expanded anteromedial region is commonly covered by the bones of the opercular series; no serrated appendages are visible along the anterior surface of this bone. MSNM V658 probably presents, preceding the antero-ventral tip of the cleithrum, an elongated clavicula. There are two postcleithra, of which the dorsal one is much larger than the ventral one, even wider than the vertical arm of the cleithrum. The ventral postcleithrum is triangular in shape, and similar in size to the surrounding scales from which it is often difficult to distinguish. The pectoral fin inserts ventrally to the ventral postcleithrum and is always scarcely preserved; however, based on what is recognizable in MSNM V572 and MSNM V633, there are eleven enlarged plus eight thinner distally segmented rays, the first of which is associated with fringing fulcra.

The pelvic fins are poorly preserved in all the available specimens, recognizable as impression only of eight unsegmented rays in MSNM V633. In MSNM V409-V638, MSNM V629, and MSNM V633 there is a peculiar elongate, triangular and distally tapering ganoid scale, located above the pelvic fin and interpreted herein as the pelvic axillary process (Fig. 19).

The scale cover comprises about 40 anterodorsal-posteroventral rows of rhombic ganoid scales of

Fig. 19 - *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. MSNM V633. Detail of the pelvic region. Scale bar 10 mm.

lepisosteid type, although the count can be problematic due to the often-imperfect preservation of the trunk. Three rows of scales with a greater depth are located in the central area of the trunk, posterior to the postcleithrum and up to about midlength of the trunk. All the scales show no traces of ornamentation on the outer surface and have a smooth posterior margin.

Remarks. Duffin & Patterson (1993), reported the presence of 15 specimens attributable to *D. bechei* from the Osteno site, but no description or list of those specimens has been provided.

Our examination of the material from the Osteno site indicates the presence of 14 specimens of *Dorsetichthys bechei*.

Dorsetichthys is a monotypic genus of stem-teleost known from the Lower Jurassic of the United Kingdom (Lyme Regis, Dorset), that includes the species *D. bechei* (Arratia 2013). This species was previously assigned to the genus *Pholidophorus* (Agassiz 1844; Woodward 1895; Nybelin 1966; Patterson 1968).

D. bechei (Fig. 20) is distinguished from other stem-Teleostei by a series of characters listed by Arratia (2013), including: size of about 200 mm in total length; skull bones and scales covered with a thin layer of ganoine; frontals acutely sharp anteriorly; maxilla heavily ornamented with longitudinal ridges of ganoine; preopercle expanded anteroventrally and with a deeply notched posterior margin; preopercular sensory canal with twenty tubules opening on the ventral and posteroventral borders of the preopercle; hemi-heterocercal caudal fin and ganoid scales of lepisosteoid type, with unornamented surface and smooth posterior margin.

These characters have been observed in the specimens from Osteno described herein. Moreover, they also show additional features, not present in the diagnosis of the taxon provided by Arratia (2013), but described in previous descriptive studies focused on British material of *D. bechei*, including the ornamentation of the skull (Woodward 1895; Nybelin 1966), the arrangement of the scale cover (Woodward 1895; Nybelin 1966), and the structure and configuration of the paired (Woodward 1895; Nybelin 1966), and caudal fins (Patterson 1968).

In addition, it is worth to mention that the Osteno specimens allow to describe the anatomy of the cleithrum of *D. bechei*, usually inadequately preserved in the available material. Additionally, we also report the occurrence of the pelvic axillary process, previously not observed by Arratia (2013) and only recently regarded to as present by Hart et al. (2020) in a single specimen attributed to *D. bechei*.

Family incertae sedis
Pholidolepis Nybelin, 1966

Emended diagnosis (from Nybelin, 1966 and Patterson, 1968): Small sized teleost similar to *Dorsetichthys bechei* but differing in the following features: cranial bones covered with a very thin layer of ganoin; second supramaxilla with a pronounced process emerging from its antero-dorsal corner; posteroventral margin of the preopercle notched; preopercular sensory canal running near its anterior margin; uncostricted notochord, vertebrae formed by calcified hemicentra, often fused; caudal region characterized by diplospondyly; notochord uncalcified beyond the second ural centrum; neural arch of the second ural vertebra modified; four epurals; twenty to twenty-one principal caudal rays; uppermost hypaxial fin-ray reduced; four urodermals; caudal scutes small; urodermals and caudal scutes without ganoin; fulcra absent on all fins except along the dorsal and sometimes the ventral margin of the caudal fin.

Type species: *Pholidolepis dorsetensis* Nybelin, 1966

Distribution: Lower Jurassic, Sinemurian, United Kingdom (Lyme Regis, Dorset).

Pholidolepis teruzzii sp. n.
Figs. 21-31

Diagnosis: Small sized *Pholidolepis*, reaching about 110 mm in total length; body elongate, maximum body depth about one-fifth of SL; head length less than one quarter of SL; preopercular sensory canal with more than ten tubules; bifid abdominal neural arches; first four caudal haemal arches and spines suture not ossified; rod-like supraneurals; body naked.

Etymology: The specific epithet honours Giorgio Teruzzi, Curator of Invertebrate Paleontology at the MSNM and director of the excavations at the Porto Franco site, for his outstanding scientific contributions, including pivotal work on the fossils from Osteno.

Holotype: MSNM V564-V621: almost complete, articulated skeleton, in part and counterpart (Fig. 21, 30).

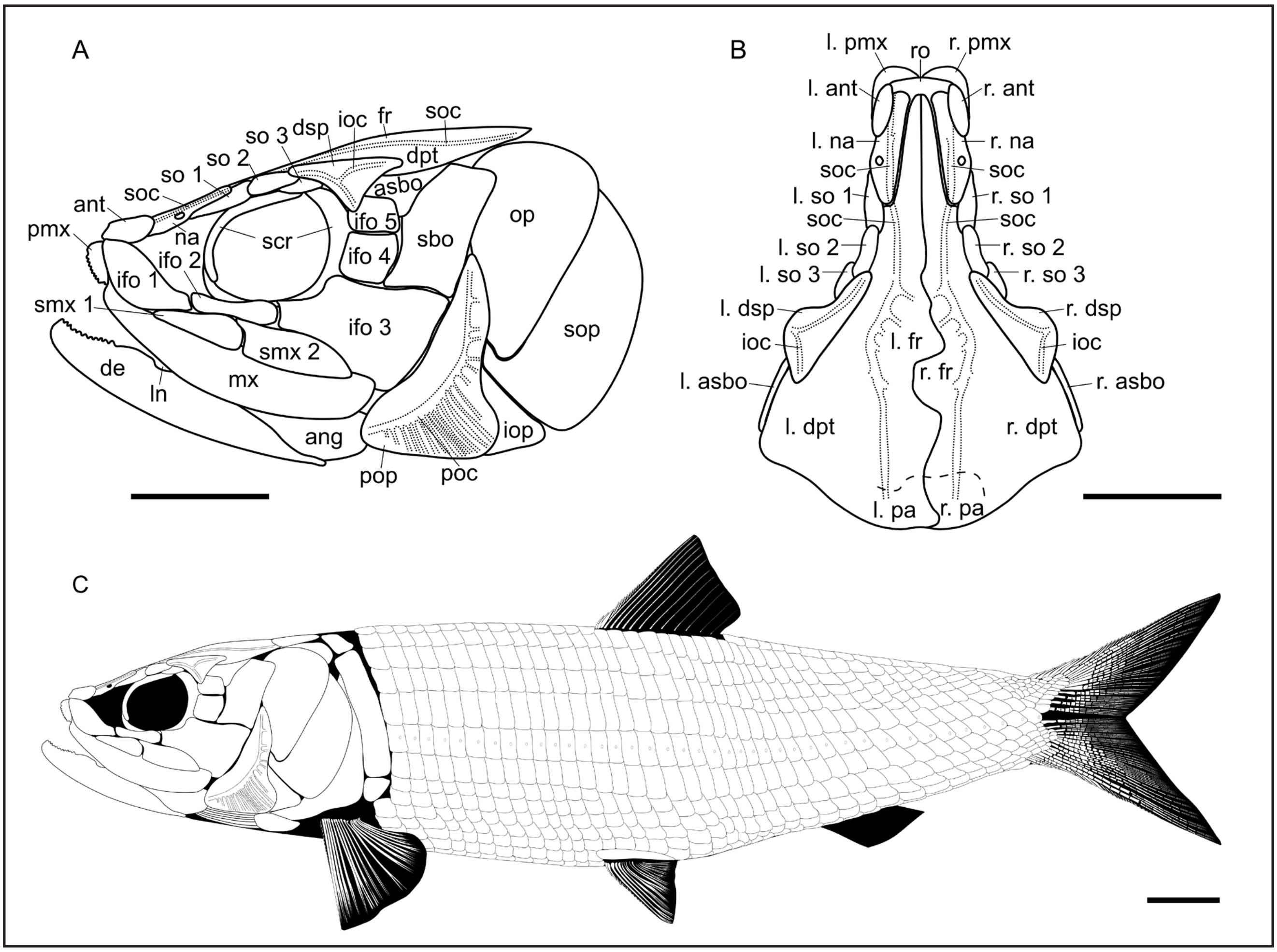


Fig. 20 - Interpretative reconstruction of *Dorsetichthys bechei* from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Reconstruction mainly based on MSNM V409 and MSNM V638 (part and counterpart), skull anatomy follows Atterby et al. (2024) and Nybelin (1966). (A) Skull skeleton in left lateral view. (B) Skull skeleton in dorsal view. (C) Full body reconstruction in left lateral view. Scale bars 10 mm.

Paratypes: MSNM V529: isolated caudal fin and caudal peduncle. MSNM V540: incomplete articulated skeleton comprising the posterior half of the trunk and the caudal fin. MSNM V533: isolated caudal fin and caudal peduncle. MSNM V556: isolated head skeleton with associated pectoral girdle and fin. MSNM V559: isolated head skeleton with associated pectoral girdle and fin. MSNM V562: isolated caudal fin and caudal peduncle. MSNM V563: disarticulated and largely incomplete skeleton. MSNM V565: isolated caudal fin and caudal peduncle. MSNM V567: isolated head skeleton. MSNM V568: isolated and incomplete head skeleton (Fig. 23 A, B). MSNM V570: incomplete articulated skeleton comprising the anterior half of the trunk and the head. MSNM V579: isolated and incomplete head skeleton, in part and counterpart. MSNM V594: isolated and incomplete head skeleton (Fig. 23 C, D). MSNM V596: isolated caudal fin and caudal peduncle. MSNM V613: almost complete articulated skeleton (Fig. 22). MSNM V625: incomplete articulated skeleton comprising most of the trunk, the unpaired fins, the pelvic girdle and the caudal fin (Fig. 25). MSNM V641: complete, articulated skeleton. MSNM V645: isolated caudal fin and caudal peduncle, in part and counterpart. MSNM V646: incomplete articulated skeleton comprising the posterior half of the trunk, median fins, pelvic girdle and caudal fin (Figs. 24, 27, 28). MSNM V648: isolated caudal fin and caudal peduncle, in part and counterpart (Fig. 26). MSNM V656: isolated pectoral girdle and fin, in part and counterpart (Fig. 29).

Other material: MSNM V581: articulated caudal fin lacking the caudal peduncle, in part and counterpart. MSNM V649: poorly preserved caudal fin, in part and counterpart.

Measurements: see Table 5.

Description. The body is elongate, with a total length reaching around 110 mm, and SL being slightly less than 100 mm. The head is almost triangular in outline, representing at least one fifth of the SL, comparable to the maximum depth of the body measured in the predorsal region. The caudal peduncle is narrower than the trunk (Fig. 21). The head and pelvic girdle bones are covered with a thin layer of ganoin, and some bones of the head are ornamented with ganoin striations and tubercles. The pectoral fins insert close to ventral margin of the body, while the pelvic fins are placed approxi-

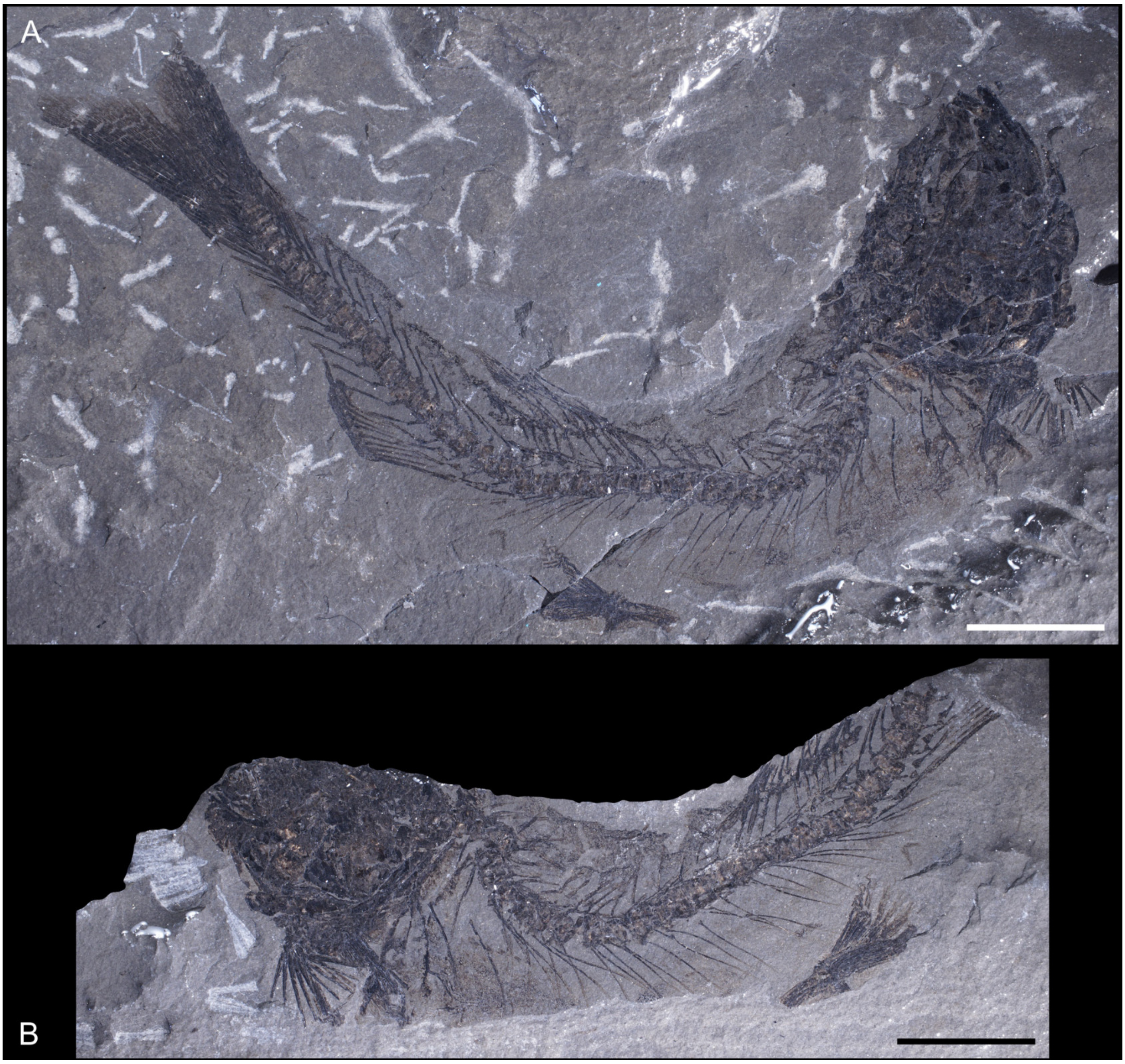


Fig. 21 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Holotype, in right lateral view. (A) MSNM V621. (B) MSNM V564. Scale bars 10 mm.

mately at mid-length of the trunk. The dorsal fin is opposite to the pelvic fins and the anal fin is placed midway between the pelvic and caudal fins. Both the median and paired fins are of moderate size, and the rays are rather delicate. Fringing fulcra are exclusively present on both lobes of the caudal fin. The caudal fin is homocercal and forked. The body appears to be naked. Two thin dark stripes, rostro-caudally oriented, run dorsally and ventrally along the body, likely representing part of the original pigmentation.

	Standard length (mm)	Total length (mm)	Head length	Head depth	Pre-orbital length	Orbital diameter	Body depth	Pre-dorsal length	Pre-anal length	Pre-pelvic length	Longest pectoral-fin ray	Longest pelvic-fin ray	Longest dorsal-fin ray	Longest anal-fin ray	Longest caudal-fin ray	Dorsal base length	Pelvic base length	Anal base length
MSNM V564-V621	81.3	93.4	22.8	18.8	6.1	8.7	21.4	48.3	83.0	60.3	8.5	7.7	8.7	?	17.5	10.8	6.9	7.9
MSNM V641	84.0	95.4	23.8	16.7	4.8	6.2	16.0	47.8	78.1	59.2	7.1	8.8	9.4	8.5	20.8	10.1	6.8	7.5

Tab. 5 - Measurements (as %SL) of the specimens referred to *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy.

Due to inadequate preservation, it is not possible to give a description of the elements of the braincase. In the available specimens, however, an elongated, narrow parasphenoid is often visible in the lower portion of the orbit; a median ridge, which includes the parabasal canal, is often recognizable on the parasphenoid; in MSNM V568 (Fig. 23) and especially in MSNM V567, the posterior portion of the parasphenoid can be recognized, although its description is prevented by the limited degree of preservation.

The skull roof is poorly preserved in any of the available specimens.

The rostral is partially recognizable in MSNM V613 (Fig. 22); it appears to be sub-rectangular in outline, twice as wide as long; its outer margins are not clearly preserved and it appears to be crossed longitudinally by the ethmoidal commissure.

The nasals are elongate and large, separated from each other by the rostral portion of the two frontals. The anterior margin of the nasals is never well preserved, but MSNM V613 (Fig. 22) suggests that the nasal articulates with the rostral and the antorbital anteriorly. MSNM V556 shows the right nasal protruding rostrally at least as much as the frontals. No notch for the posterior nostril can be observed.

The frontals, as clearly visible in the holotype as well as in MSNM V556, MSNM V567, MSNM V594 (Fig. 23C, D), MSNM V559, but especially in MSNM V568 (Fig. 23A, B) and MSNM V563, are the largest bones of the skull roof. The two paired frontals are separated from each by a suture, which is often difficult to trace; the rostral portion of the suture is straight and shows a clear sinuosity in the supraorbital area. Each frontal tapers anteriorly and expands postorbitally. The anterior margin of the frontal is gently curved, while its lateral margin is slightly concave in the area just above the orbit.

The supraorbital sensory canal of the frontal is clearly exposed in MSNM V563 and MSNM V568, whereas in MSNM V556 it is possible to appreciate how the canal crosses the nasal from their antero-ventral to the postero-medial margin and then enters the frontals; the canal bends postero-laterally at the level of the orbit and then runs rostro-caudally following the lateral profile of the skull roof; three short tubules, mesially protruding, are clearly visible in the area where the canal bends laterally as best seen in MSNM V568 (Fig. 23A, B).The frontals are ornamented with ganoin tubercles (see MSNM V594 - Fig. 23C, D).

The parietals are feebly recognizable in MSNM V568 (Fig. 23A, B), in which they appear almost quadrangular, less wide than the frontals. The dermopterotic is never well preserved in the available material. In MSNM V556 an extrascapular seems to be recognizable, apparently characterized by a distinctly rounded posterior margin.

A small, triangular antorbital can be recognized in MSNM V613; it articulates with the nasal dorsally, the rostral antero-dorsally, and the first infraorbital ventrally.

The infraorbital series is well exposed in MSNM V594 and partially preserved in MSNM V567 and MSNM V613 where only the posterior portion is recognizable. The first infraorbital is rather large, elongate, and anteriorly expanded. The second infraorbital is smaller, rod-like element, forming along the midventral border of the orbit, just above the anterior process of the second supramaxilla. The third infraorbital is the largest element of the series, extending from the postero-ventral corner of the orbit to the anterior margin of the preopercle; it is quadrangular in outline, higher than long, with a tubular anterior portion that articulates with the second infraorbital. The fourth and fifth infraorbitals form the posterior border of the orbit. The dermosphenotic is placed at the postero-dorsal margin of the orbit, posterior to the supraorbital and dorsal to the fifth infraorbital; it is recognizable in MSNM V594 due to the presence of the bifurcation of the infraorbital canal and it appears to be a triangular in outline.

The fourth and fifth infraorbitals articulates posteriorly with a large suborbital, which articulates ventrally also with the third infraorbital, and posteriorly with the opercle. In MSNM V594, what appears to be an accessory suborbital is faintly visible posteriorly to the fifth infraorbital and ventrally to the dermosphenotic.

Two fragmentary supraorbitals can be recognized in MSNM V594, articulated dorsally with the frontal. The first supraorbital is short and triangular, slightly tapered anteriorly, while the second supraorbital is twice the length of the first one and notably tapered posteriorly.

The right premaxilla is exposed in MSNM V613; this element has a triangular shape, but its margins are not well defined; it is placed antero-ventrally to the anterior branch of the maxilla and it bears at least five small conical teeth along its ventral margin.

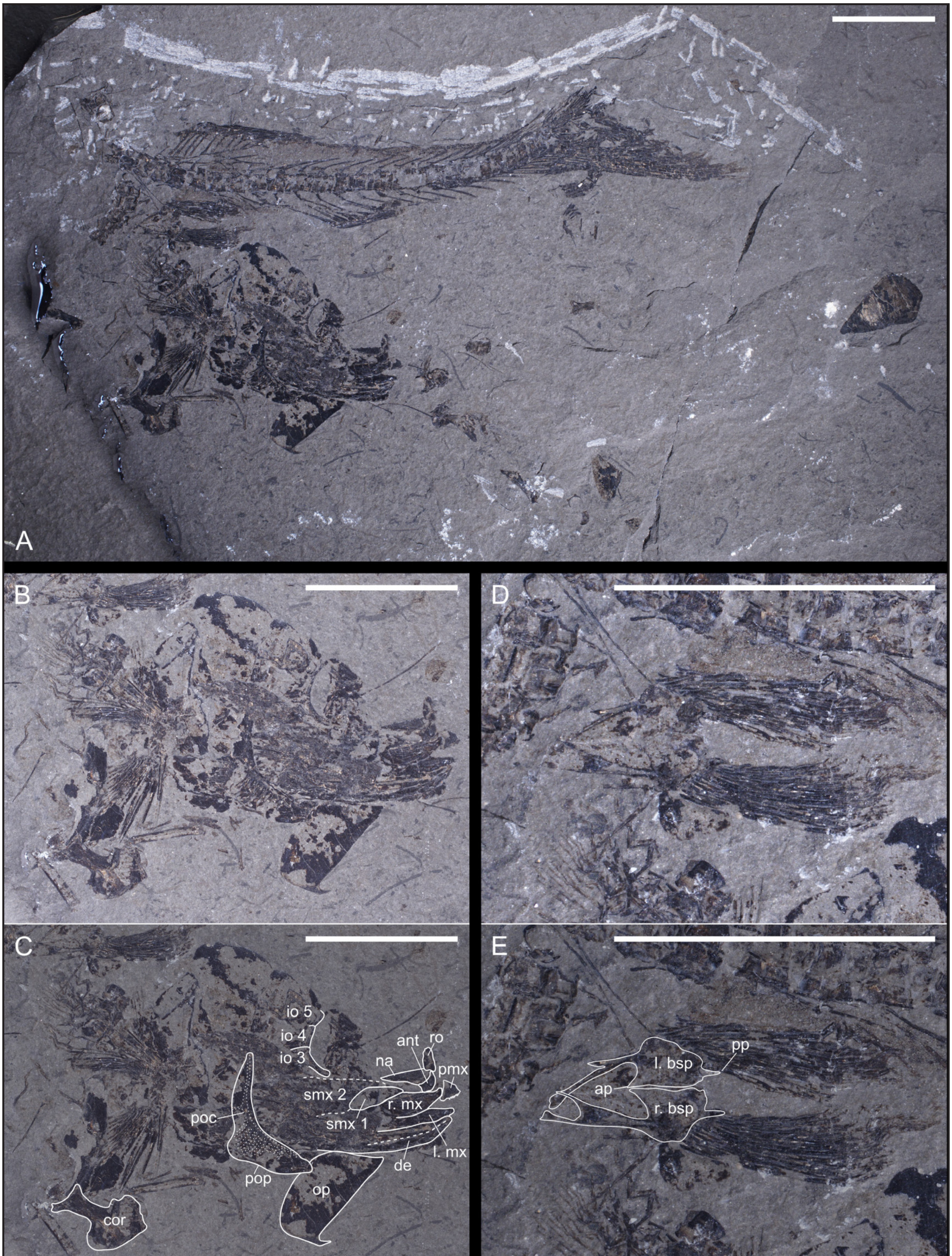


Fig. 22 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V613. (A) Full specimen. (B) Close up of the head skeleton. (C) Anatomical characters drawn over picture B. (D) Close up of the pelvic girdle. (E) Anatomical characters drawn over picture D. Scale bars 10 mm.

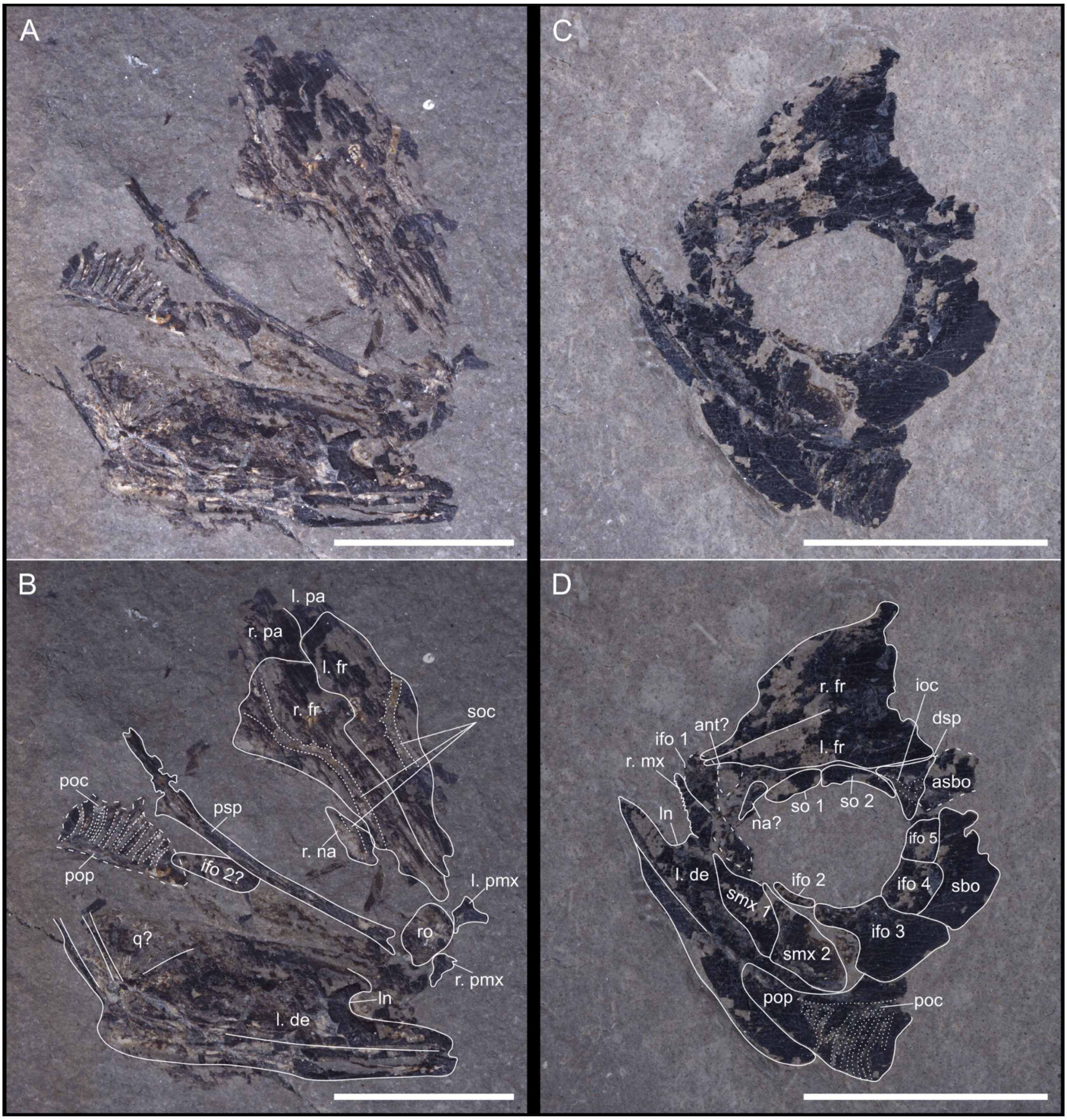


Fig. 23 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. (A) Paratype, MSNM V568. (B) Anatomical characters drawn over picture A. (C) Paratype, MSNM V594. (D) Anatomical characters drawn over picture E. Scale bars 10 mm.

The holotype, MSNM V556 and MSNM V568 also show what appear to be poorly preserved premaxillary teeth.

The maxilla is not completely preserved in any of the examined specimens. It is curved, with the outer surface characterized by weakly developed oblique striations, as can be seen in MSNM V579, MSNM V594 and MSNM V613. Numerous tiny teeth can be observed along the ventral border of the maxilla, as visible in MSNM V594 (Fig. 26 C-D).

The supramaxillae are visible in MSNM V579, MSNM V594 (Fig. 23C, D), and MSNM V613 where these almost entirely cover the dorsal margin of the maxilla. The anterior supramaxilla is elongated, whereas the larger second supramaxilla exhibits a well-developed antero-dorsal process that extends anteriorly over the dorsal margin of the anterior supramaxilla.

The lower jaw is never fully exposed, being usually covered by the maxilla. Its anterior region is partially recognizable in MSNM V568 and in MSNM V594 (Fig. 23) in which its antero-dorsal margin, anterior to the coronoid process, forms a downward notch, equivalent to the 'leptolepid notch' (e.g., Nybelin 1966; Arratia 2013; Atterby et al. 2024). The ridge separating the dorsal part of the dentary and the relatively low ventral splenial part is clearly visible.

The bones of the suspensorium are obscured by those of the circumorbital series and, therefore, cannot be properly described. In MSNM V568 it is possible to observe the margins of a triangular bone at the level of the posterior region of the lower jaw, which might represent the quadrate (Fig, 23A, B). The preopercle is rather large and characterized by well-developed vertical and horizontal arms. A deep notch can be observed ventrally along the posterior margin. The preopercular sensory canal runs very close to the anterior margin of the preopercle. At least 11 narrow and curved tubules, can be recognized in the horizontal arm of the preopercle in MSNM V568 (Fig. 23A, B) and MSNM V613 (Fig. 22B, C). The opercle and subopercle are well exposed in MSNM V613 (Fig. 22). The opercle is almost triangular in outline, with a gently curved dorsal margin, and straight anterior and posterior margins.

The suboperculum is larger than the opercle, showing a rounded postero-ventral margin, and a straight and obliquely-oriented anterior margin; the anterior margin culminates into a strong and recurved antero-dorsal process.

The interopercle is not properly exposed in the examined material and therefore its morphology remains unclear.

The notochord is unconstricted. Vertebrae are formed by calcified hemicentra, a dorsal and a ventral one - often fused, that form a ring surrounding the space occupied by the notochord, this tissue clearly differ from the endochondral bone of the neural and haemal arches and spines for the darker colour, dense, fibrous texture and vertical striations. The neural and haemal arches articulate with the ring calcifications dorso-laterally and ventro-laterally, not laterally, respectively. The centra are slightly deeper than long, and all centra lack pre- and postzygapophyses. Short parapophyses articulate with the antero-lateral portion of the abdominal centra, near their ventral margin, where the ribs articulate.

The number of centra is highly variable and, due to inadequate preservation of the anteriormost region of the vertebral column, it is not possible to provide a reliable evaluation. However, there are about 44 centra in the holotype and in MSNM V613, and about 45 in MSNM V541. The centra are divided into about 25 abdominal and 20 caudal, so that the caudal region is shorter than the abdominal one. The caudal region is characterized by 10 diplospondylous vertebrae, as best seen in MSNM V646. The last complete centrum is the first preural one in certain specimens, but it is normally the first ural. Behind this point the notochord is uncalcified (Fig. 24).

The neural and haemal arches of the abdominal centra are autogenous; neural spines are not fused in the abdominal portion of the vertebral column, being bifid as clearly visible in MSNM V625 (Fig. 25). This condition cannot be observed in the anteriormost abdominal neural arches due to the poor preservation of the available specimens. No specimens show bifid neural or haemal spines in the caudal region. The neural arches are posteriorly directed. The centra of the abdominal region show epineural processes that emerge from the posterolateral margin of the neural arches. The epineural processes of the neural arches extend throughout the abdominal region, up to the level of the posterior dorsal-fin pterygiophore. The epineural processes are long, extending laterally for the length of about two centra, being thinner than the haemal arches Supraneural bones are present but poorly preserved in the holotype and in MSNM V625, they seems to be vertical, rod like elements often bearing an expanded dorsal end. Their total number is unknown due to their poor conservation of the anteriormost region of the trunk in the available material, but they end before the first dorsal pterygiophore (Fig. 25).

The neural spines of the abdominal region are slightly longer than the epineural processes. The neural and haemal spines of the caudal region are narrow and are obliquely oriented, gradually increasing their inclination caudally. The haemal spines are short, never extending between the anal-fin pterygiophores. The caudal vertebrae exhibit an expanded proximal portion of the haemal spine. This expansion occurs in the area where the haemal arches and the corresponding haemal spine suture. In the available specimens, the first four caudal vertebrae haemal

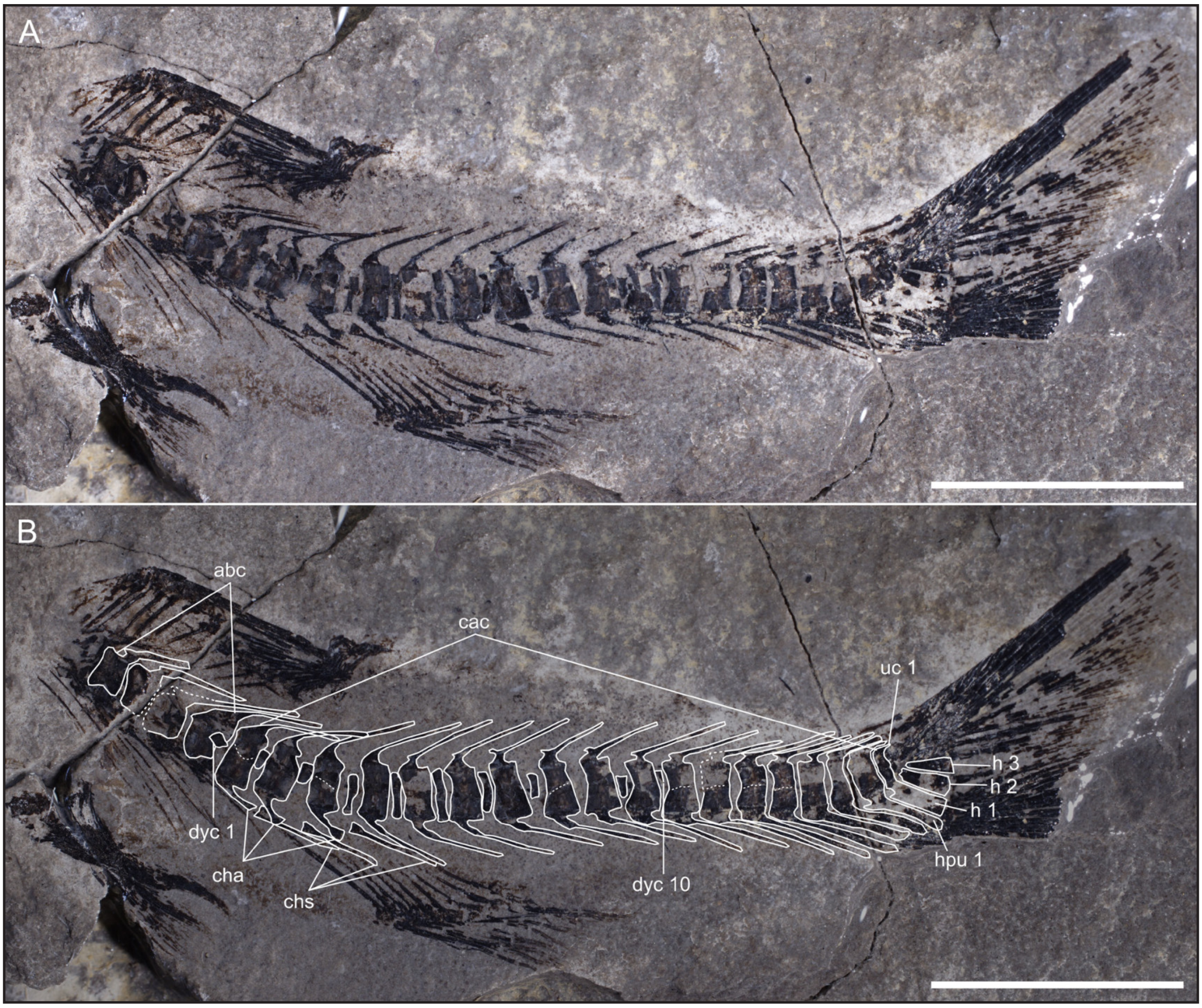


Fig. 24 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V646A (A) Full specimen in left lateral view. (B) Anatomical characters drawn over picture A. Scale bars 10 mm.

arches and their respective haemal spines are clearly separated: the separation occurs in the expanded region, resulting in an enlarged distal portion of the haemal arches and an enlarge proximal portion of the haemal spine, both forming a club-like shape. This suggests the presence of a non-ossified, possibly cartilaginous, suture between the haemal arches and the haemal spines in this area of the vertebral column (Fig. 24).

The total number of ribs cannot be properly evaluated due to the inadequate preservation of the specimens, although at least 20 rib pairs can be recognized in the holotype. The ribs are well ossified, tapered distally and almost reach the ventral margin of the body.

The caudal fin is deeply forked, with slightly asymmetric lobes. The neural spines of the first three pre-ural vertebrae gradually decrease in length so that their distal ends are located at the same level, near the neural spine of the first ural vertebra. The neural arc of the second ural centrum is elongated and narrow, covering part of the upper margin of the third uroneural. The first hypural is clearly recognizable by a horizontal groove and an antero-ventrally directed peg-like process located at the proximal portion of the bone (Nybelin 1966). The entire hypural series is recognizable in MSNM V645 and MSNM V648 and shows 11 elements that gradually decrease in size posteriorly in the series. The first four preural haemal spines are enlarged and support caudal-fin rays. Four rod-like epurals, can be observed in MSNM V64 and in MSNM V648. Four urodermals are visible in MSNM V648. The caudal fin usually contains 20 (I,9+9,I) principal

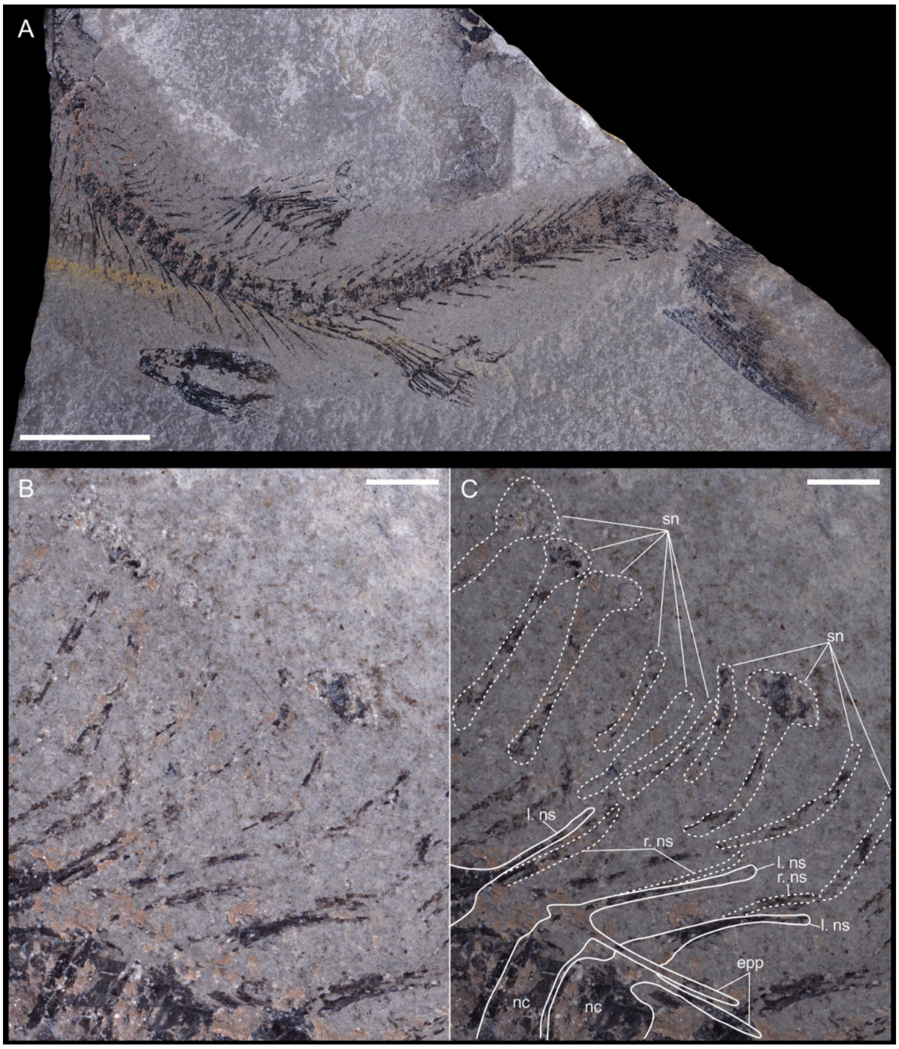


Fig. 25 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V625 (A) Full specimen in left lateral view. (B) Close up of the antero-dorsal portion of the trunk. (C) Anatomical characters drawn over picture B. Scale bars 10 mm in A, 1 mm in B and C.

rays, although 21 (I,9+10,I) rays can be observed in MSNM V645. The total number of fringing fulcra clothing the leading margins of the upper and lower principal rays is high but remains unknown due to inadequate preservation. In rare cases the seven uppermost hypaxial rays can be deeply cleft basally, crossing the upper hypurals and ending on the third hypural. The proximal ends of the innermost caudal-fin rays are expanded: the base of the innermost ray of the upper lobe of the fin, which articulates with the third hypural, is much larger than the other fin ray bases (Fig. 26).

The dorsal fin originates at the midlenght of the trunk, and it is well exposed in MSNM V570, MSNM V613, and especially in MSNM V615, MSNM V641 and MSNM V646 (Fig. 28). The dorsal-fin rays are usually disarticulated and for this reason their total cannot be determined; however, considering that 11 dorsal proximal pterygiophores are commonly preserved, it is reasonable to conclude that the dorsal fin has more than 11 rays in origin. The dorsal-fin rays are segmented and branched distally. The first proximal dorsal-fin pterygiophore bears an antero-ventral process with a flat bony flange that seems to have a bifurcated anterior margin. The six anteriormost proximal pterygiophores are similar in length, whereas the posterior elements of the series gradually decrease slightly in size. Median pterygiophores are badly preserved, but they seem to be rectangular elements dorsal to the proximal pterygiophores. A short and posteriorly tapered dorsal stay is present at the posterior end of the dorsal-fin base.

The anal fin is partially preserved in MSNM V556. Due to the disarticulation and displacement of part of the fins, total number of anal-fin rays cannot be determined; however, considering that nine anal-fin pterygiophores are preserved, it is reasonable to hypothesize that the fin contained more than nine rays. The anal fin rays are segmented from

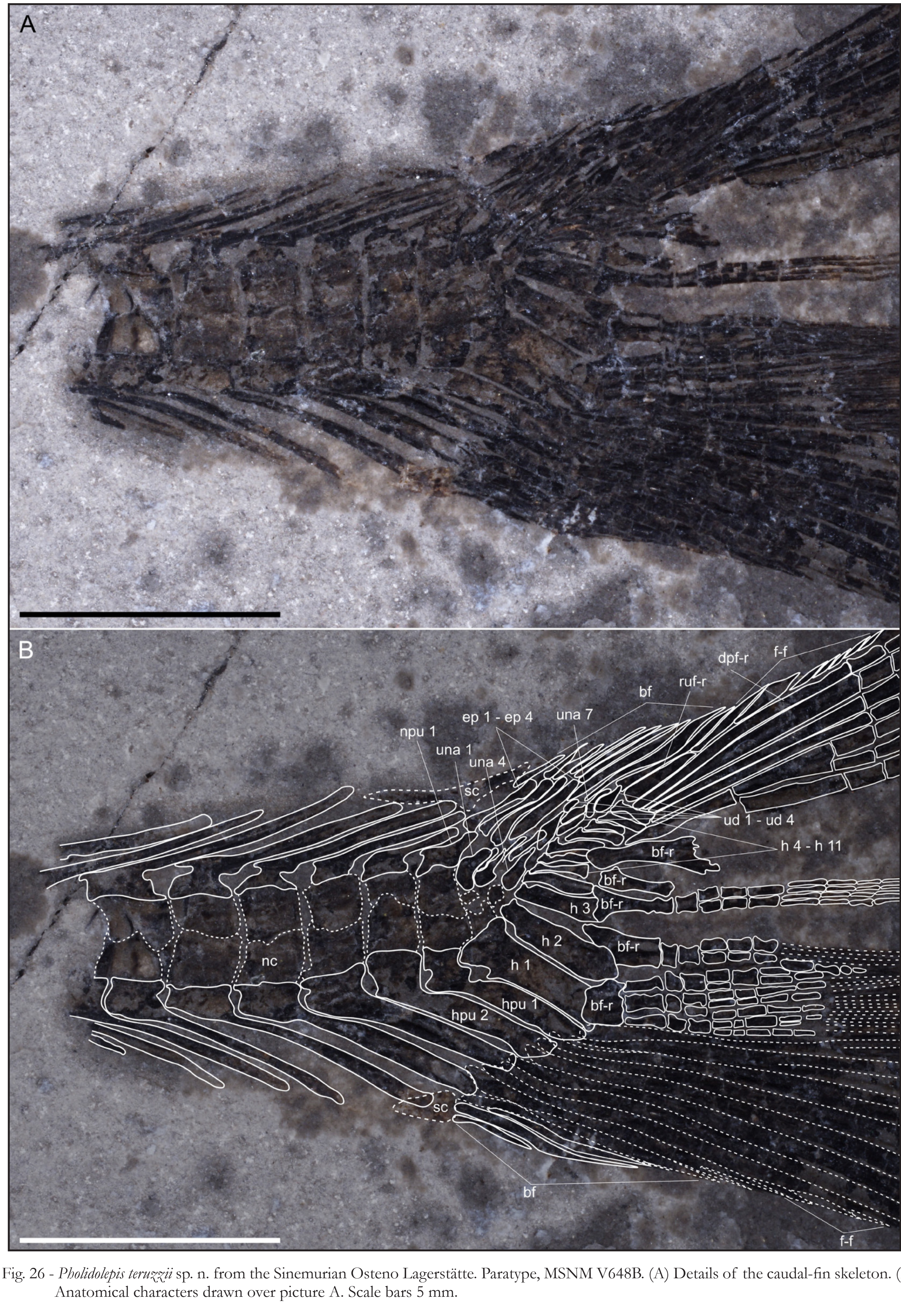


Fig. 26 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V648B. (A) Details of the caudal-fin skeleton. (B) Anatomical characters drawn over picture A. Scale bars 5 mm.

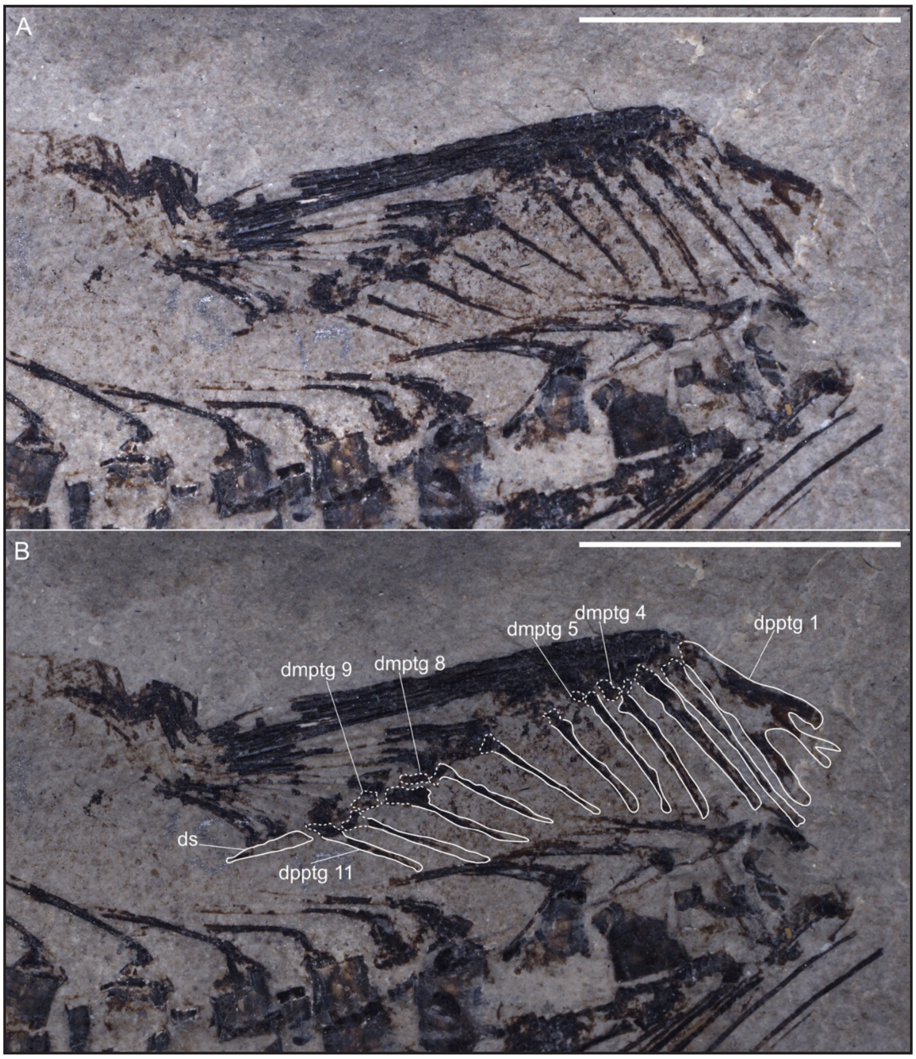


Fig. 27 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V646B. (A) Detail of the dorsal fin skeleton. (B) Anatomical characters drawn over picture A. Scale bars 5 mm.

their mid-length and distally branched. The anteriormost proximal pterygiophore is longer than the others. Median pterygiophores are not well preserved, they are elongated element placed ventrocaudally to the proximal pterygiophores. An anal stay can be observed at the posterior end of the anal-fin base.

In the pectoral girdle, perfectly preserved in MSNM V656 (Fig. 29), a small squarish supracleithrum is the dorsal most element of the series. The cleithrum is the largest bone of the pectoral girdle; it is thick and crescent shaped, with a narrow vertical arm and an expanded ventral region and a straight anteroventral border. The serrated appendages (see Arratia 2013) appear to be absent. There are two postcleithra. The dorsal postcleithrum is the largest one and is located posterior to the vertical arm of the cleithrum. A curved junction is present between the dorsal postcleithrum and the small and quadrangular ventral postcleithrum. Antero-ventrally to the cleithrum there is drop-shaped clavicle, which has a rounded anterior margin. The coracoid is partially exposed in MSNM V613 (Fig. 22); it is flattened, with a narrow anterior branch and a broad posterior region. In MSNM V656 at least four rod-like radials can be recognized. The pectoral fins insert very low along the flanks, close to the ventral margin of the body. The pectoral fin consists of 19 segmented and distally branched fin rays. The first ray is remarkably thick; probably due to the fusion of at least one long and narrow basal fulcrum (Arratia 2013), the first pectoral-fin ray also shows an expanded proximal region probably characterized by a basal articular cavity. The presence of an elongated pectoral axillary process is visible in MSNM V656.

The pelvic girdle is placed at the midlenght of the trunk being clearly exposed in MSNM V570, MSNM V613 (Fig. 22), and MSNM V625. The basipterygium is notably expanded posteriorly, showing the median and lateral processes fused for more

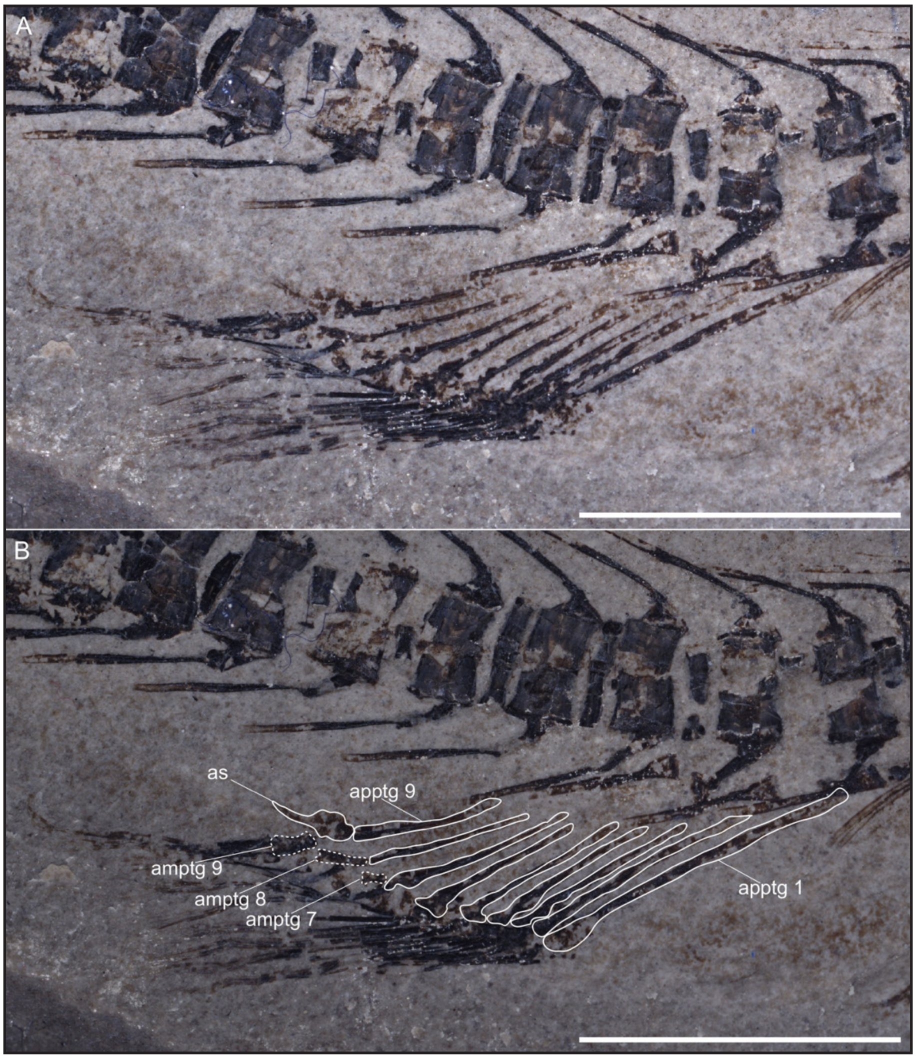


Fig. 28 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V646B. (A) Detail of the anal fin skeleton. (B) Anatomical characters drawn over picture A. Scale bars 5 mm.

than half of their length; the lateral lamina does not extend laterally beyond the lateral process of the basipterygium. The pelvic fin consists of 16 segmented and distally branched rays, becoming moderately shorter medially.

In front of the basal fulcra on the upper margin of the caudal fin there is a thick and elongated median scale, lacking the ganoin cover. A similar scale is placed in front of the lower caudal lobe (Fig. 26). No other scales have been observed in the material referred to the genus *Pholidolepis* from Osteno, suggesting that these specimens had a naked body.

Two thin longitudinal stripes run dorsally and ventrally along the trunk, starting from the head up to the tail, showing dark coloration, likely representing part of the original pigmentation; these can be observed in the holotype (Fig. 30) and in MSNM V540, MSNM V565, MSNM V570, MSNM V625 and MSNM V646.

Remarks. Although Duffin & Patterson (1993) reported the presence of 27 specimens likely pertaining to the genus *Pholidolepis* from Osteno, our examination revealed the presence of only 24 specimens.

Pholidolepis is a stem-teleost genus primarily known from the Lower Jurassic of the United Kingdom (Lyme Regis, Dorset), which includes the species *P. dorsetensis* (Nybelin 1966), and, according to Nybelin (1974), also the Triassic *Leptolepis africana* (Gardiner 1960). *Pholidolepis* is distinguished from other stem-teleosts by a series of characters listed and discussed by Nybelin (1966) and Patterson (1968). Many of these characters are shared by the specimens described from Osteno described herein, including: small size, skull bones covered with a thin layer of ganoin and scarcely ornamented; two well-developed supramaxillae, second supramaxilla with marked process emerging from its

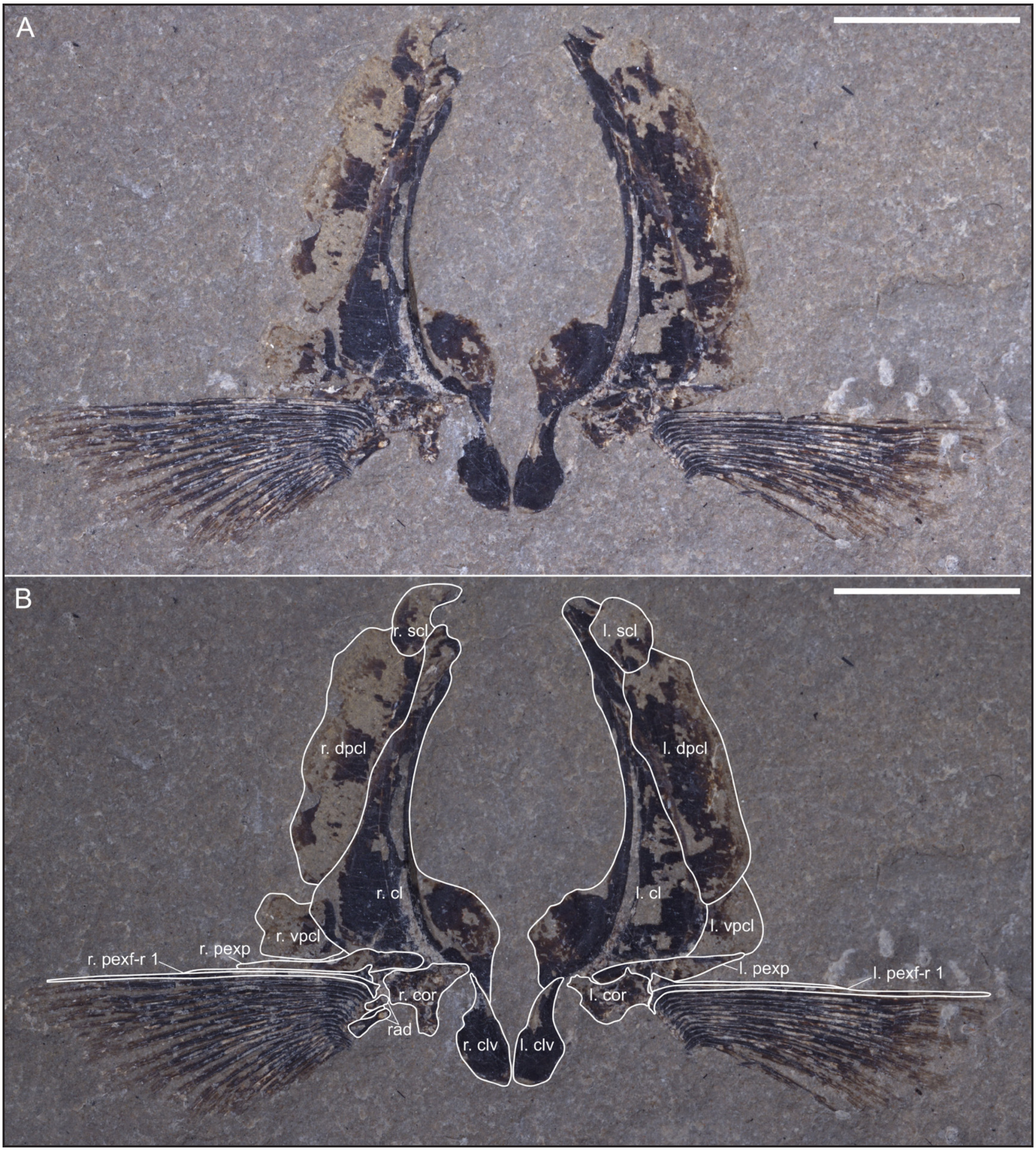


Fig. 29 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Paratype, MSNM V656a. (A) Pectoral girdle skeleton. (B) Anatomical characters drawn over picture A. Scale bars 5 mm.

antero-dorsal corner; preopercle with preopercular sensory canal running near the anterior margin of the bone and bearing numerous tubules; fulcra only along dorsal and ventral margin of caudal fin; notochord uncalcified beyond the second ural centrum; and structure and composition of the caudal fin skeleton. The Lyme Regis material, as pointed out by Nybelin (1966), is poorly preserved, not allowing a complete description of the anatomical structure of *Pholidolepis dorsetensis*. The specimens

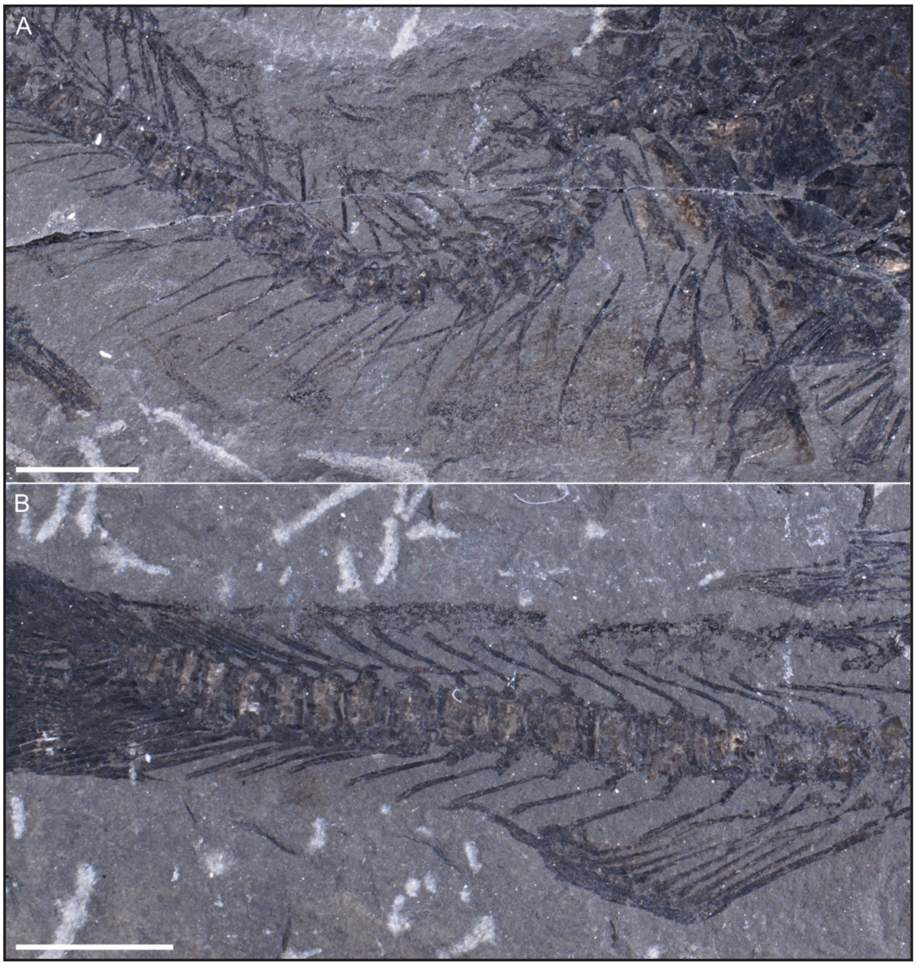


Fig. 30 - *Pholidolepis teruzzii* sp. n. from the Sinemurian Osteno Lagerstätte. Holotype, MSNM V621. (A) Close up of the anteriormost portion of the trunk showing trace of colour. (B) Close up of the posteriormost portion of the trunk showing trace of colour. Scale bars 5 mm.

from Osteno, on the other hand, allow a more accurate description of a large part of the skull, and the poorly known axial skeleton and fins.

The morphology of the specimens described herein allows to confirm the similarity with *Dorsetichthys bechei* (Nybelin 1966, 1974; Arratia 2013; Atterby et al. 2024), providing further support to the possible phylogenetic affinity between *Pholidolepis* and, which were discussed by Nybelin (1966, 1974).

Based on a supposed difference in the number of fin rays, Duffin & Patterson (1993) suggested that the Osteno *Pholidolepis* specimens possibly represent a new species. Our observations on the Osteno specimens, however, do not confirm the observations by Duffin & Patterson (1993) as far as the number of fin rays is concerned, since their number in the pectoral (18) and pelvic (15) fins is very close to that of *P. dorsetensis*, which has 19 or 20 pectoral-fin rays and 15 pelvic-fin rays. The number of median-fin rays cannot be compared due to the inadequate preservation of these structures in the Osteno specimens; however, it is possible to compare the number of proximal pterygiophores with *P. teruzzii* sp. n. showing 12 dorsal proximal pterygiophores and nine anal proximal pterygiophores, versus 11 and nine in *P. dorsetensis* (Nybelin 1966), respectively. The incompleteness of the English material does not allow for a more precise comparative analysis, as it does not allow the observation of the morphology of the dorsal- and anal-fin pterygiophores nor the possible presence of the dorsal and anal stays, which are instead present in *P. teruzzii* sp. n. Another clear difference between the two Liassic species of *Pholidolepis* is related to the number of diplospondylous centra, which are 11 in *P. dorsetensis*, and invariably ten in *P. teruzzii* sp. n.

The absence of a scale covering on the trunk of the specimens from Osteno is much relevant for taxonomic purposes; since the only recognizable scales in *P. teruzzii* sp. n. are those described in the caudal fin area, while *P. dorsetensis*, is characterized by a complete cover of cycloid scales with delicate concentric striations (Nybelin 1966, 1974; Patterson 1968).

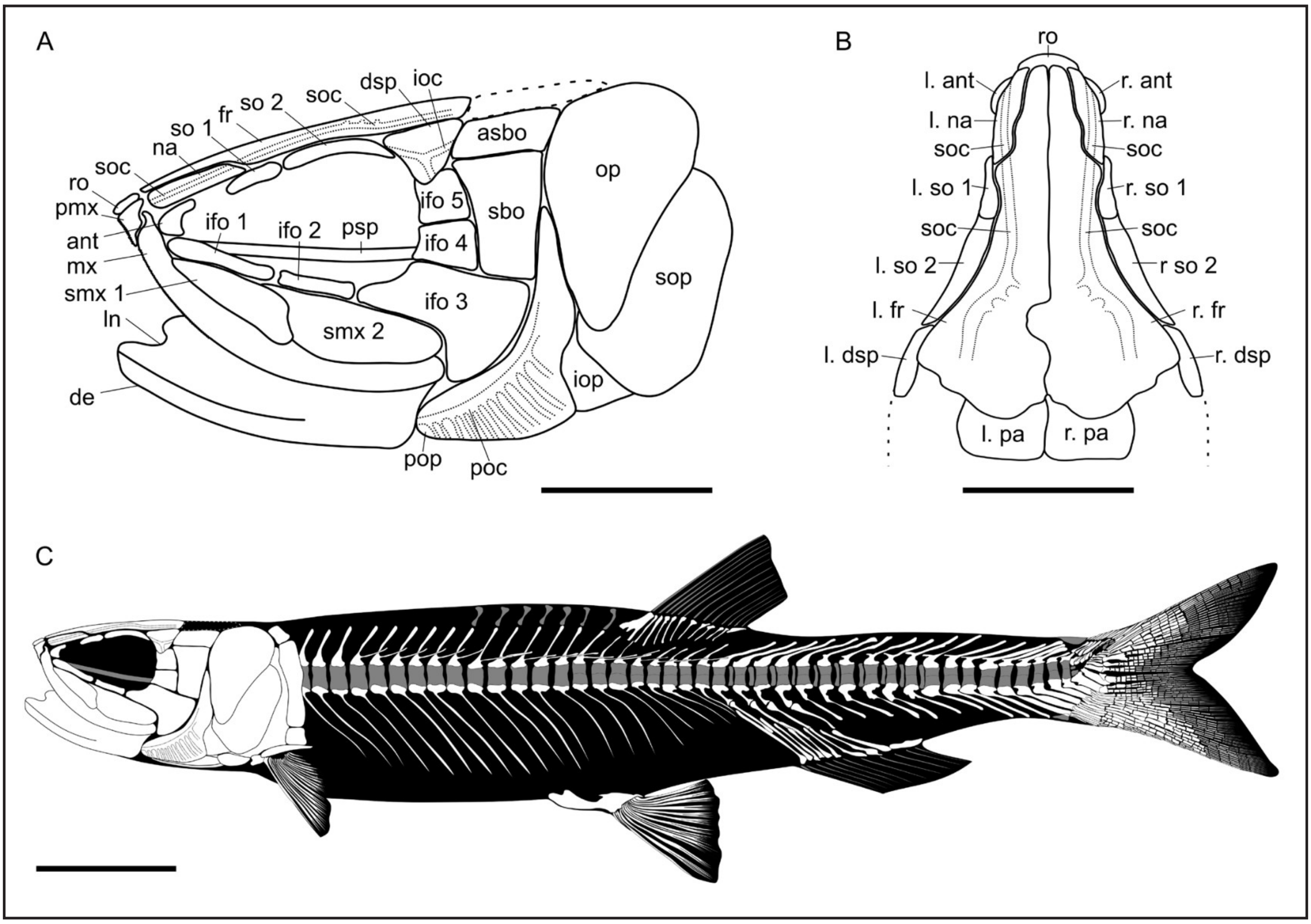


Fig. 31 - Interpretative reconstruction of the whole skeleton of *Pholidolepis teruzzii* sp. n., from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Reconstruction based on the holotype, MSNM V564-V621. (A) Skull skeleton in left lateral view. (B) Skull skeleton in dorsal view. (C) Full body reconstruction in left lateral view. Scale bars 5 mm for A and B, 10 mm for C.

The differences observed between the specimens from Lyme Regis and those from Osteno provide substantial evidence to recognize the existence of two separate Sinemurian species within the genus *Pholidolepis*, one of which being characterized by the complete absence of cycloid scales along the entire trunk (Fig. 31). The preservation of some specimens of *P. teruzzii* sp. n. also allows to observe what appear to be the traces of the original pigmentation in the form of longitudinal stripes throughout the trunk. The presence of these stripes suggests a disruptive coloration pattern. Considering the small size and the relatively high number of specimens in the Osteno assemblage, it is reasonable to hypothesize that it was a schooling fish, thereby implying that the horizontal stripes and their associated confusion effect functioned as a deterrent against predators (Price et al. 2008), which were possibly represented by *Dapedium*, *Furo* and *Holophagus*.

Discussion

Phylogenetic relationships of *Peripeltolpeurus jurassicus* sp. n. (MSNM V659)

In order to explore the phylogenetic relationships of this specimen, we codified the recognizable features of MSNM V659 into the morphological dataset assembled by Shen & Arratia (2021). This dataset, which builds upon the earlier dataset by Xu (2020), represents a comprehensive phylogenetic analysis with extensive sampling of neopterygian clades and has been built to enhance the scoring of characters within the peltopleuriforms.

Being our analysis solely focused on understanding the affinities of the specimen under study within the Neopterygii (see, e.g., Lee 2013), the matrix developed by Shen & Arratia (2021) was not modified, except for the inclusion of MSNM V659 (see Table S1, in appendix, for the complete matrix), and the analyses was conducted with similar parameters.

The topology of the strict consensus is shown in Fig. 32B, and it is based on 33 equally parsimonious trees. The tree length is 364. The strict consensus topology indicates that MSNM V659 should be assigned to the Peltopleuriformes along with *Wushaichthys*, *Peripeltopleurus*, the thoracopterids, and the species of the polyphyletic genus *Peltopleurus*. In particular, MSNM V659 is placed in an unresolved polytomy that includes the representatives of the family Wushaichthyidae (*Wushaichthys* and *Peripeltopleurus*) and the monophyletic Thoracopteridae. In the 50% Majority rule consensus tree (Fig. 32C) - consistency index (CI) of 0.442, and retention index (RI) of 0.768 - the position of MSNM V659 is better defined, as the specimen is placed in a polytomous relationship with the two other species of the genus *Peripeltopleurus*, sharing with them the origin of the dorsal fin, it being nearly opposite to the origin of the anal fin and well posterior to the origins of the pelvic fins (ch.107[0]), with this genus being the sister group to the genus *Wushaichthys*, whose monophyly is supported by the presence of broad posttemporals, nearly as wide as the extrascapular (ch.100[0]) and by the presence of a two rows of lateral line scales (ch.137[1]). No autapomorphies were recovered for MSNM V659.

The genus *Peripeltopleurus* consists of three species from the Middle Triassic of Monte San Giorgio (Italy - Switzerland), of which only two are included in the matrix of Shen & Arratia (2021); *P. vexillipinnis* (type species) and *P. hypsisomus*, whereas the third species, *P. besanensis*, is excluded due to its incompleteness.

A direct comparison of MSNM V659 with the three known species of *Peripeltopleurus* reveals some evident morphological differences. The snout of MSNM V659 is much broader, due to the presence of a much expanded rostral, while the ventral protrusion that commonly occur in the Triassic species is not present in MSNM V659. While the overall size of the skull roof cannot be assessed, the ornamentation and the extension of the supraorbital canal of the frontals appear to be much more developed posteriorly than in the known species of *Peripeltopleurus*. The external appearance of the caudal fin of MSNM V659 shows similarities with that of *P. hypsisomus* (see Bürgin 1992), although its dorso-ventral asymmetry appears to be even more developed in MSNM V659.

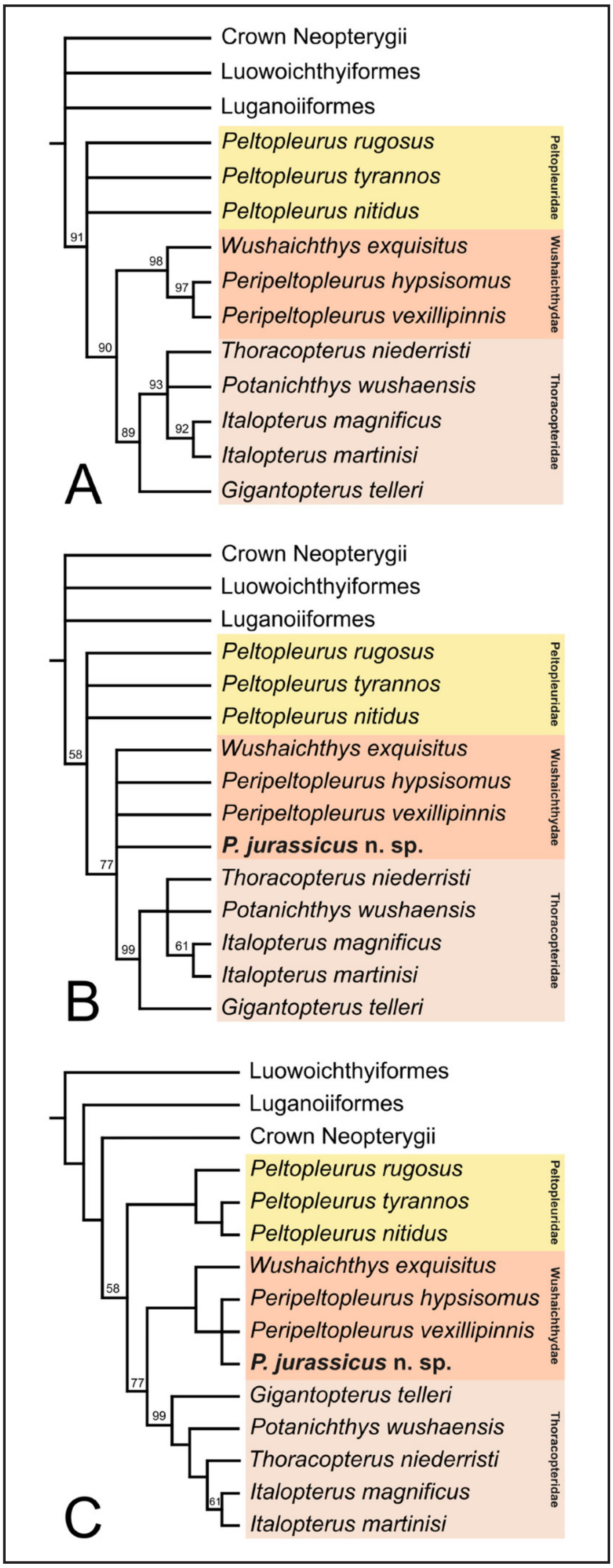


Fig. 32 - Hypothesis of phylogenetic relationships of *Peripeltopleurus jurassicus* sp. n. from the Sinemurian Osteno Lagerstätte, Como Province, Northwestern Italy. Zoom-in view on the order Peltopleuriformes. (A) Tree topology recovered by Shen & Arratia (2021). (B) Strict consensus tree. (C) 50% Majority rule tree. Numbers on nodes are bootstrap values above 50%. Colour coding based on Shen & Arratia (2021). Characters supporting nodes from Shen & Arratia (2021).

Since the clear and stated morphological differences with the Triassic species of the genus *Peripeltopleurus* and the undoubtedly Jurassic age of the discussed specimen, we propose MSNM V659 as a holotype and the only specimen of *Peripeltopleurus jurassicus* sp. n. (Fig. 15). The recognition of a new species of the genus *Peripeltopleurus*, and more generally of the order Peltopleuriformes, in the Sinemurian is extremely interesting since this group has a stratigraphic distribution so far limited to the Middle-Upper Triassic (Anisian – Norian; Xu & Ma 2016) of Europe and China. This specimen, therefore, for the first time provides unambiguous evidence of the persistence of the Peltopleuriformes after the Triassic-Jurassic boundary within at least the western portion of the already known distribution area.

Paleoenvironmental remarks

The detailed analysis of the bony fishes from the Osteno Lagerstätte provides new data about the composition of the vertebrate assemblage of this Lower Jurassic site. In addition to the previously known cartilaginous fishes *Synechodus pinnai* (Duffin 1987), *Ostenoselache stenosoma* Duffin 1998, *Squaloraja* sp. (Duffin et al. 2023), and an unnamed myriacanthid (Duffin 1992), seven osteichthyan taxa have been recognized (see Table 6), thereby resulting in an overall vertebrate diversity of 11 taxa.

The faunal assemblage from Osteno provides compelling evidence for a diverse Lower Jurassic bony fish community. The taxa recovered include both well-known elements and three new taxa.

The Osteno assemblage exhibits a moderate diversity, especially when compared with the abundant and diverse European marine Jurassic faunas (Schaeffer & Patterson 1984). Several factors may explain the seemingly low diversity at Osteno.

First, the site has been explored for only a few years (Garassino & Teruzzi 2015) whereas many deposits (e.g., Lyme Regis, Forey et al. 2010) have been continuously collected for nearly 200 years. Moreover, the difficulty of accessing the known outcrops and the hazardous nature of the excavation operations—which have also led to tragic outcomes—have further limited the discovery of additional specimens. Finally, the non-laminated nature of the fossil-bearing sediments makes the excavation process complex; the discovery of the specimens is always fortuitous.

Tab. 6 - Summary of osteichthyan taxa and the number of specimens known for each taxon of the Osteno Lagerstätte.

Taxon	n.
Holophagus cf. *gulo*	19
Ostenolepis marianii n. gen. et sp.	4
Dapedium sp.	1
Furo sp.	3
Peripeltopleurus jurassicus n. sp.	1
Dorsetichthys bechei	14
Pholidolepis teruzzii n. sp.	24

Nonetheless, despite the apparent reduced diversity, these specimens provide valuable data regarding the structure of the fish communities that inhabited the northwestern margin of the Neotethys during the Lower Jurassic. Vertebrate remains from this interval—particularly from the Sinemurian—are in fact often known only from isolated findings (e.g., Maisch et al. 2008; Young et al. 2024; Pratas & Sousa et al. 2025).

Prior to the discovery of the Osteno Lagerstätte, knowledge of Sinemurian fish faunas almost exclusively derived from the Lyme Regis site in southern England—a locality known since the 19th century (see Forey et al. 2010 for a summary), where more than 40 fish species have been recognized. The Osteno Lagerstätte is thus of crucial relevance for adding data to Sinemurian marine ichthyofaunas.

For a detailed comparative analysis of the faunas of the Osteno Lagerstätte and Lyme Regis, it is necessary to consider the age of the aforementioned assemblages. Osteno, as stated before, dates back to the lower Sinemurian, *Arietites bucklandi* ammonite Zone (199.46–198.30 Ma; Hesselbo et al. 2020). Conversely, the age of the Lyme Regis site is more complex to define. The Lyme Regis site is part of the "Jurassic Coast" of Dorset and comprises the Blue Lias Formation (Hettangian–Lower Sinemurian) and the Charmouth Mudstone Formation (Sinemurian-Pliensbachian) (Page 2010 and references therein). Given the scarcity of stratigraphic data available for the fish specimens (Forey et al. 2010), we decided to include in the faunal comparison (Table 7) all the bony fish genera from Lyme Regis whose temporal range is restricted to the Sinemurian, thus those coming from the Blue Lias Formation and from the Black Ven Mudstone Member (Lower-Upper Sinemurian) of the Charmouth Mudstone Formation (Page 2010).

The similarities between the two fish assemblages are high despite the lower taxonomic diversity recognized at Osteno. Five genera are present in

	Lyme Regis	Osteno Lagerstätte
Class Sarcopterygii		
Family Latimeriidae		
Holophagus	X	X
Class Actinopterygii		
Superorder Palaeoniscimorpha		
Cosmolepis	X	
Ostenolepis		X
Family Coccolepididae		
"Coccolepis"	X	
Family Saurychthyidae		
Saurorhynchus	X	
Family Chondrosteidae		
Chondrosteus	X	
Subclass Neopterygii		
Heterolepidotus	X	
Osteorachis	X	
Family Caturidae		
Caturus	X	
Family Centrolepidae		
Centrolepis	X	
Family Dapediidae		
Dapedium	X	X
Family Furidae		
Furo	X	X
Family Platysiagidae		
Platysiagum	X	
Family Ptycholepidae		
Ptycholepis	X	
Family Wushaichthyidae		
Peripeltopleurus		X
Infraclass Teleostei		
Pholidolepis	X	X
Pholidophoroides	X	
Pholidophoropsis	X	
Proleptolepis	X	
Family Dorsetichthyidae		
Dorsetichthys	X	X

Tab. 7 - Summary of the bony fishes genera from Lyme Regis and Osteno Lagerstätte. In blue the shared genera, in orange the exclusive ones from the Osteno Lagerstätte

both the sites (*Holophagus*, *Dapedium*, *Furo*, *Dorsetichthys* and *Pholidolepis*). The affinity becomes even more pronounced when chondrichthyans are considered, since the genera *Synechodus* and *Squaloraja* have been recorded from both Osteno (Duffin 1987; Duffin & Patterson 1993; Duffin et al. 2023) and Lyme Regis (Forey et al. 2010).

The compositional similarity of the fish fauna of Osteno with that of Lyme Regis, might be the result of a possible geographic connectivity between these two sites. During the Sinemurian, both the Osteno and Lyme Regis areas were situated on the northwestern margin of the Neotethys (Fig. 33), which was characterized by a mosaic of shallow marine basins and emerged landmasses (e.g., Stampfli et al. 2001). Apparently, during the Sinemurian there was no direct latitudinal connections across Europe, as suggested by the ammonoid assemblages showing a sharp separation between a large Northwest European Province and a southern Mediterranean Province (Page 2003). However, the composition of the fish assemblages clearly indicate that the two sites experienced biotic exchanges. In particular, the occurrence of *Dorsetichthys bechei* in both the sites represents unquestionable evidence of the persistent connection between the two areas.

There are few paleoecological insights that the identification of the ichthyofauna can provide regarding the Osteno paleobiotope. The presence of vertebrates on the seafloor—excluding those naturally benthic—is attributed to the vertical transport of the carcasses into an environment with limited or no oxygen availability (Pinna 1985). The moderate to low-quality preservation of the available fish specimens suggests that they were subject to prolonged transport through the water column (Schäfer 1972), a duration likely longer than that experienced by the benthic invertebrate taxa (Pinna 1985). The seafloor of the Osteno paleobiotope was characterized by partially dysaerobic conditions alternated with anoxic episodes due to eutrophy (Pinna 1985), both possibly linked to the complete absence of bottom currents. This explains the exceptional preservation of soft tissues in numerous invertebrate taxa.

Some specimens of *Pholidolepis teruzzii* sp. n. (MSNM V570, MSNM V613 – Fig. 22) exhibit a peculiar orientation; their head, partially disarticulated, lies laterally to the body but in the opposite

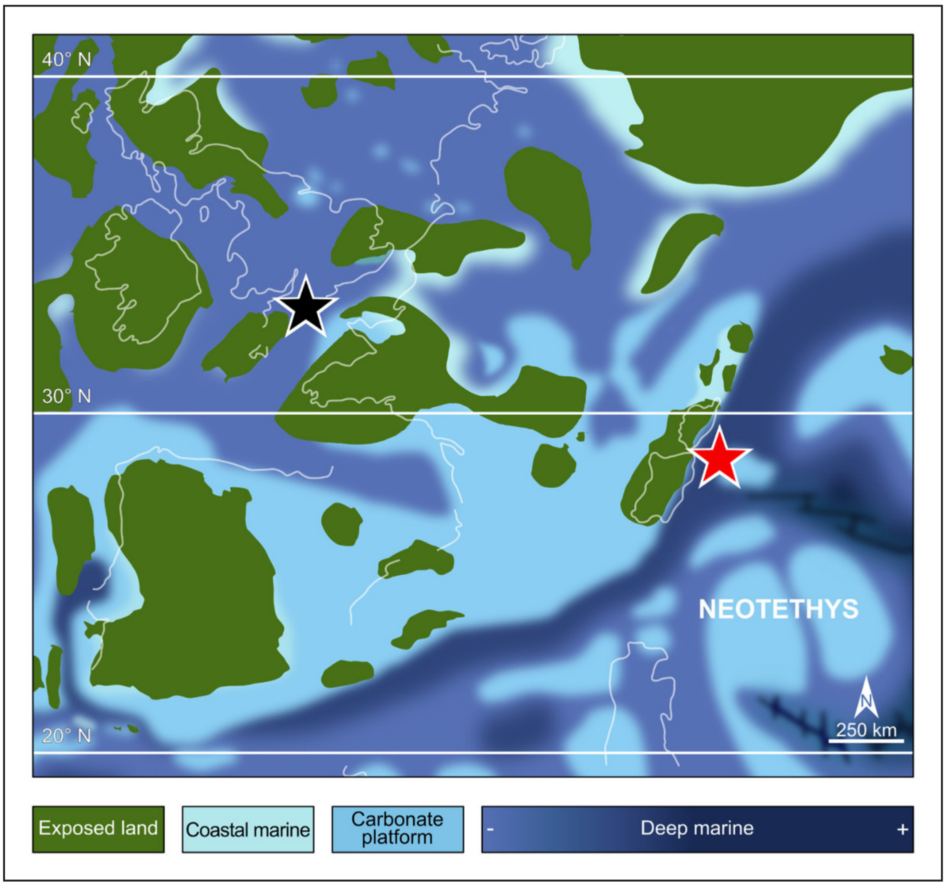


Fig. 33 - Paleogeographic reconstruction of the northwestern margin of the Neotethys during the late Sinemurian with the location of the Osteno Lagerstätte (red star) and Lyme Regis (black star) (modified from Thierry et al. 2000).

direction and the distal-most fin ray segments are disarticulated and scattered posterior to the fin itself. This arrangement (unimodal antero-posterior dispersal) indicates the presence of occasional bottom currents (Tintori 1992), a condition never hypothesized for the Osteno fossiliferous deposits. The absence of surfaces with multiple specimens exhibiting iso-orientation prevents definitive confirmation of the presence of bottom currents. However, their possible presence implies mixing of some water layers, introducing oxygen to the bottom thus creating a dysaerobic environment favourable for epibenthic organisms, as previously hypothesized by Pinna (1985).

There is no direct evidence of trophic interactions among the bony fishes of Osteno, aside from the already known presence of possible regurgitates and coprolites containing skeletal remains, primarily of chondrichthyans (Pinna 1985; Duffin 1998). However, some specimens of *Dorsetichthys bechei* (MSNM V558 - Figs.18, 19; MSNM V650) and *Pholidolepis teruzzii* sp. n. (MSNM V556, MSNM V594 - Fig. 23C, D) consist of almost complete articulated skulls and caudal fins, with no traces of the remaining body parts. This closely corresponds to the definition of pabulites (Klug et al. 2021); these specimens could represent leftovers of the meals of the predators where the prey was either decapitated or had its caudal fin removed in a predation event.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access.

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